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REVISIONS OF THE GENERA OF MALLOPHAGA.  
I. THE *RALLICOLA*-COMPLEX.

BY

THERESA CLAY,  
British Museum (Natural History).

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From *Theresa Clay*  
Entomological Dept.,  
British Museum (Natural History),  
Cromwell Road,  
S. Kensington, London, S.W.7.

*Please return*

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By

ThERESA CLAY,  
*British Museum (Natural History).*

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(With Plate 1 and 57 figures in the text.)

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INTRODUCTION.

There are a number of species belonging to the superfamily Ischnocera in which the females have one to three stout setae borne on a ventral tubercle each side of segment IX of the abdomen. Seven genera or subgenera have been erected to include the known species as follows:—

Genus	Type species	Host distribution*
<i>Rallicola</i> Johnston & Harrison, 1911.	<i>R.</i> " <i>attenuatus</i> (Nitzsch)". = <i>R. ortygometrae</i> (Schrank). (Figs. 1-4.)	Rallidae. (GRUIFORMES.)
<i>Parricola</i> Harrison, 1915	<i>P. sulcata</i> (Piaget). (Figs. 5-8.)	Jacanidae. (CHARADRIIFORMES.)
<i>Aptericola</i> Harrison, 1915.	<i>A. gadowi</i> Harrison. (Figs. 9-11, 45.)	APTERYGIIFORMES.
<i>Wilsoniella</i> Eichler, 1940.	<i>W. absitus</i> (Kellogg). (See Guimarães, 1940, 307, figs. 17-24.)	Opisthocomidae. (GALLIFORMES.)
<i>Furnaricola</i> Carriker, 1944.	<i>F. acutifrons</i> Carriker. (Figs. 12-13.)	Furnarioidea. (PASSERIFORMES.)
<i>Corvicola</i> Carriker, 1949.	<i>C. insulanus</i> Carriker.	Corvidae. (PASSERIFORMES.)
<i>Epipicus</i> Carriker, 1949.	<i>E. scapanoides</i> Carriker.	Picidae. (PICIFORMES.)

Apart from species parasitizing the above hosts, specimens have been seen from the following hosts and host groups:—

*Aramus*, *Psophia*, *Rhynochetos* (GRUIFORMES).

*Centropus* species (CUCULIFORMES).

*Macgregoria pulchra* (PASSERIFORMES).

*Eurylaimus ochromelas* (PASSERIFORMES). These are the types of *Rallicola unguiculatus* (Piaget) 1880 collected from a skin; it is possible that *Eurylaimus* is not the true host.

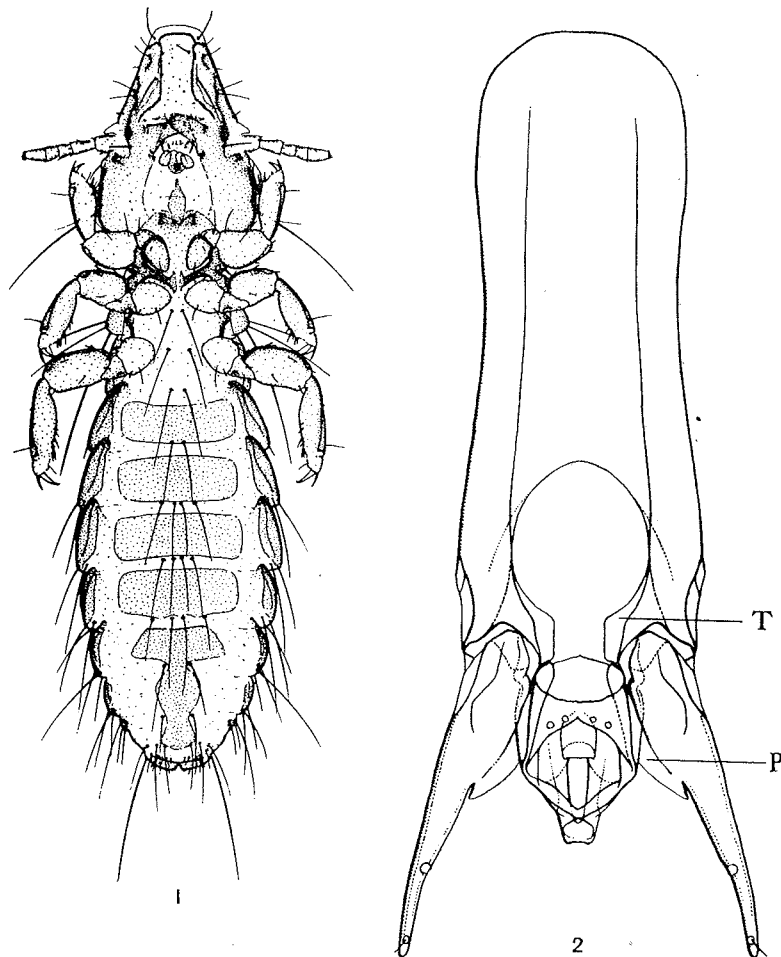
The single species in *Wilsoniella* differs from all the other species in the form of the marginal carina which is interrupted laterally each side, the absence of

\* Classification of hosts according to Wetmore, 1940.

the post-spiracular setae on segment VII, and in the position of the setae-bearing tubercles. *Wilsoniella* can be considered as a distinct genus and will not be further discussed. The other species have the following characters in common:

*Head\**.—Marginal carina always interrupted medially, that is, there is never a complete carina round the anterior margin of head; marginal carinae never interrupted laterally (with the possible exception of *Furnaricola cephalosa*, but only figure seen); dorsal preantennal suture, when present, originates at

Figures 1 and 2.



*Rallicola ortygometrae* (Schrank).

1. Male. 2. Male genitalia.

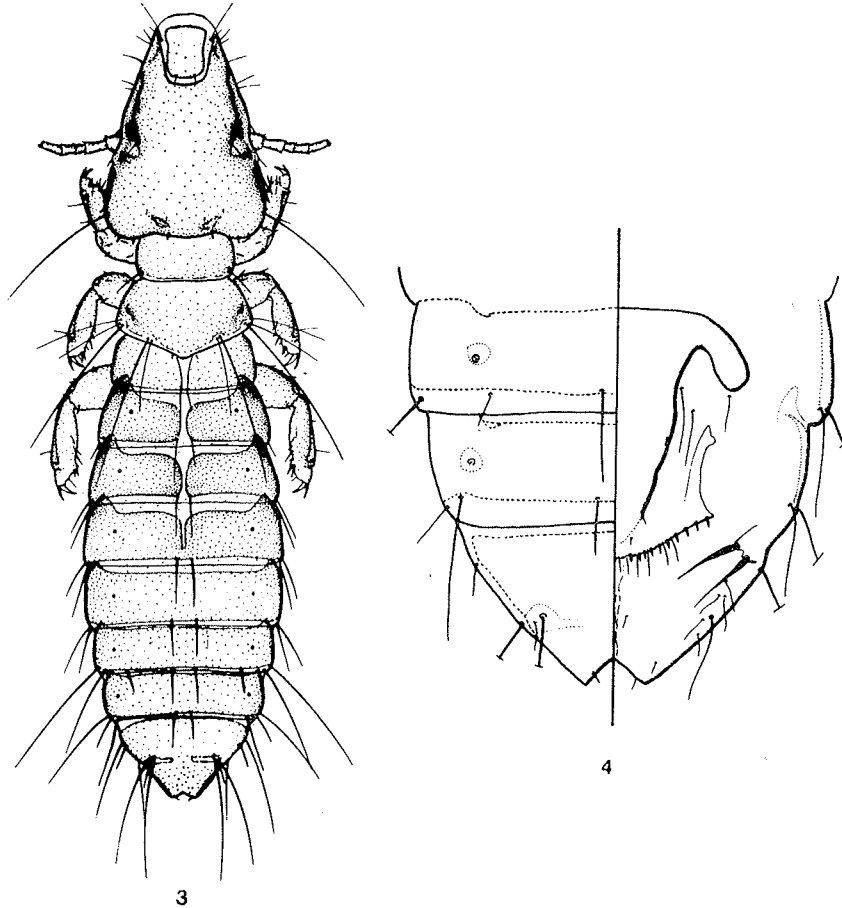
distal end of marginal carinae; dorsal anterior plate usually present with rounded, flattened or pointed posterior margin, never prolonged into a thickened posterior point. Ventral carina always interrupted medianly, and carried forward and fused to distal end of marginal carina each side; pulvinus with lobes attached to the flattened parallel edges of the ventral carinae. Gular plate developed. First marginal temporal seta may or may not be on lens; never

\* For terminology of head see Clay, 1951.

more than one elongated marginal temporal seta (the 4th) each side (as in *Brielia* and *Sturmidocetus*; the *Degeeriella*-complex, *Penenirmus* and *Philopterus* always have at least two elongated marginal temporal setae each side).

*Abdomen\**.—In the male, segments IX–X are fused and never separated from XI by a definite suture, although in at least one species (that from *Porphyrio madagascariensis*, fig. 23) tergal plates IX–X are separated from

Figures 3 and 4.



*Rallicola ortygometrae* (Schrank).  
3. Female. 4. Terminal segments of female abdomen.

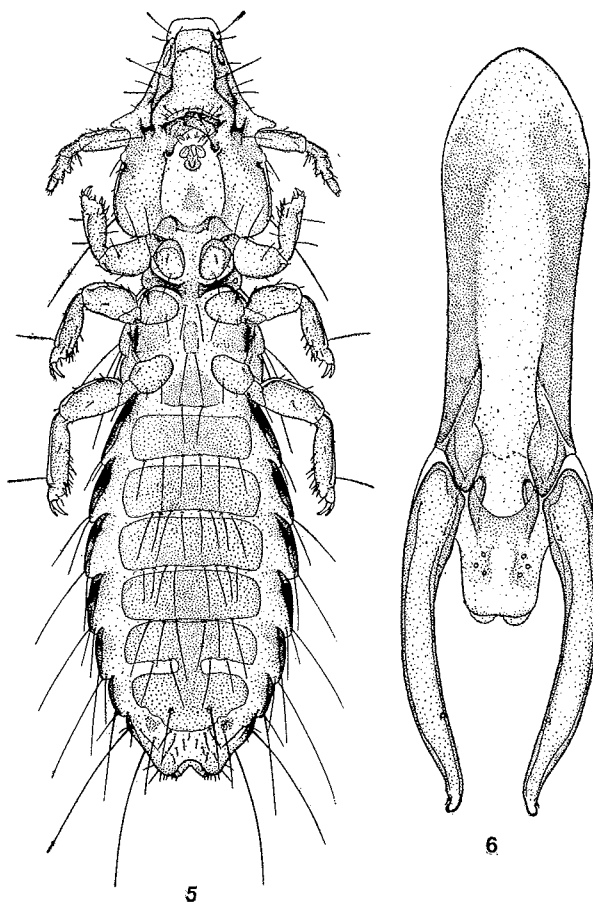
tergal plate XI. Tergal plates IX–X always continuous across the segment and not greatly narrowed medianly as in *Brielia* (fig. 22). Male genital opening terminal or dorso- or ventro-terminal, rarely on the dorsal surface. If the opening is dorsal then the distance between marginal setae of X and edge of opening always considerably greater than between latter and terminal margin of abdomen (cf. figs. 21 and 22). In the female the fused segments IX–X are never fully separated by a suture from XI and the tergal plates IX–XI are always continuous across the segment. Female with edge of vulva set with fine setae and small spine-like setae and with tubercle on ventro-lateral edge of

\* For the purposes of this paper the apparent first segment of the abdomen is referred to as abdominal segment II and the apparent eighth as the fused abdominal segments IX–X.

segment IX bearing one to three long, stout setae. Post-spiracular setae usually present on segments VII and VIII only.

The above characters distinguish this group of species from all other known Ischnocera. Apart from these there are other characters which show variation throughout the group and it is the object of this paper to discuss the variation and to decide whether it can be used as a basis for generic differentiation. It is natural that the species of Mallophaga from host groups containing a small number of closely related species should form a compact and homogeneous group.

Figures 5 and 6.



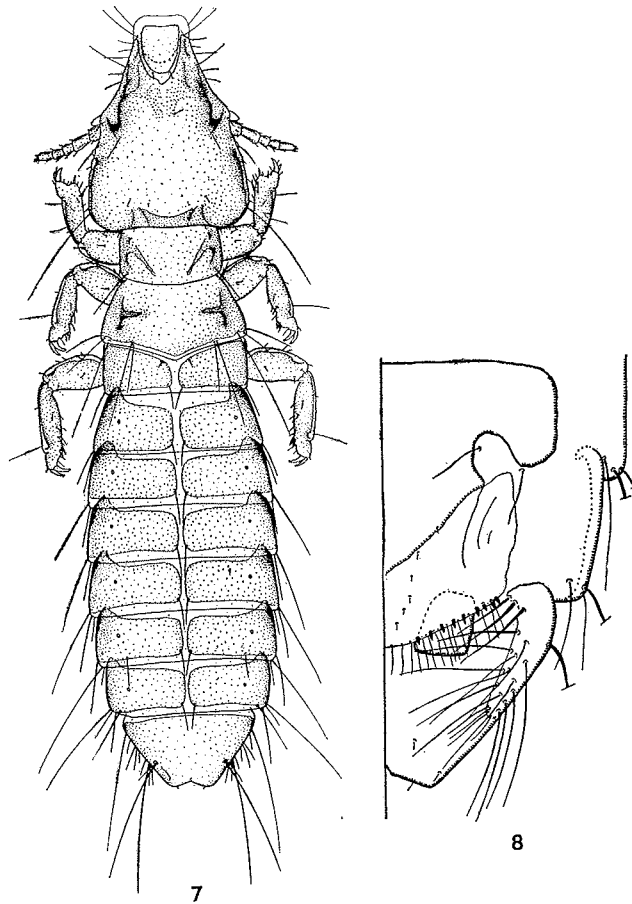
*Rallicola sulcatus* (Piaget).  
5. Male. 6. Male genitalia.

Fortunately, in the case of the *Rallicola*-complex, it is possible to consider the variation in the species parasitizing a family of hosts—the Rallidae—containing a large number of somewhat diverse members. This host family (according to Peters, 1934) contains 132 species belonging to 52 genera; specimens of *Rallicola* have been examined from forty-seven of these species belonging to twenty-five genera. Thus, an analysis of the characters found in this group of species parasitic on related hosts will give some idea of the range of variation within one of the genera of the *Rallicola*-complex, namely *Rallicola*, sens. str.

VARIATION IN THE *RALLICOLA* SPECIES PARASITIZING THE RALLIDAE

*Head.*—The characters of the dorsal preantennal region vary considerably in this group: the dorsal preantennal suture may be absent (fig. 14), or visible only at the lateral edges and not forming a complete suture across the head (fig. 15), or it may be well defined, cutting off a distinct dorsal anterior plate (fig. 16). Thus, there is a series showing increased specialization of the head rather similar to that in *Brüelia* (see Clay, 1951, 186), but in *Rallicola* there is

Figures 7 and 8.



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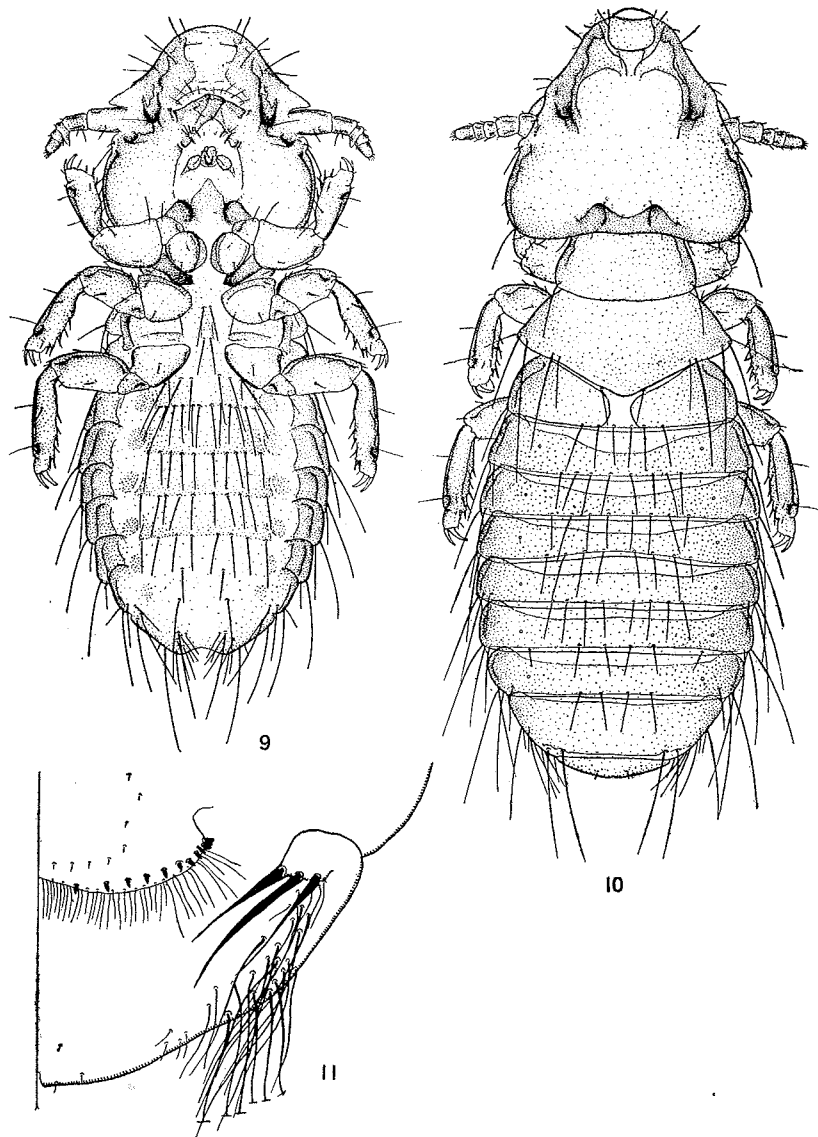
*Rallicola sulcatus* (Piaget).

7. Female. 8. Terminal segments of female abdomen.

never a lateral break in the marginal carinae (as in some species of *Brüelia*) and the dorsal preantennal suture, when present, always arises at the distal end of the laterally unbroken marginal carinae. The hyaline margin may be absent (fig. 15), small (fig. 14), or broadly extended (fig. 16); it may arise at the distal end of the marginal carinae (fig. 14) or some way posteriorly on the lateral margin (fig. 31) and is often continued some considerable distance posteriorly as a thin covering (fig. 16). The dorsal anterior plate may be well defined (fig. 16) or not defined (fig. 14). In the species from *Gymnocrex plumbeiventris* the anterior part of the anterior plate is striated; in some species which are

otherwise well pigmented the anterior plate is only slightly so. The anterior dorsal setae may be on the posterior margin of the anterior plate (fig. 16) or within the dorsal suture (*R. flavescens*). The characters of the ventral carinae are basically similar throughout the group, but the position of the point of

Figures 9-11.



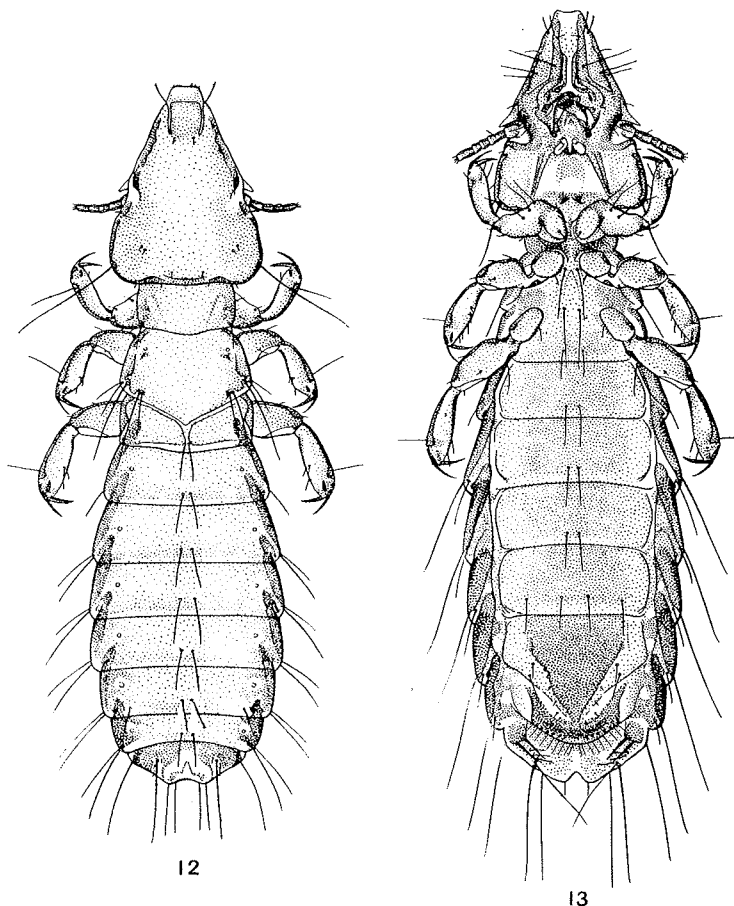
*Rallicola gadowi* Harrison.

9. Male. 10. Female. 11. Genital region of female.

fusion between the ventral and marginal carinae varies: it may be at the level of the origin of the dorsal preantennal suture (fig. 16) or some way anterior to this (fig. 31). In many species there is a small more heavily pigmented area between the ventral and marginal carinae near their distal points of fusion

(fig. 16, S); in others it is not apparent. There may be a slight indication of dorsal carinae (*R. cuspidatus*), and also various thickenings arising from the marginal carinae in the preantennal region. Temporal carinae may be present (species from *Sarothura lineata* (fig. 31)), but are usually absent.

Figures 12 and 13.



*Rallicola subsimilis* (Carriker).

12. Male. 13. Female.

The two anterior tergal setae usually present on abdominal segment II cannot be seen in either of the two available specimens (in poor condition) of this species.

It should be unnecessary to discuss the sexual dimorphism of the antennae except that it is still used by some authors as a generic character. The species parasitizing the Rallidae show all grades of sexual dimorphism of the antennae: it may be absent (figs. 1, 17), the male may have segment I slightly enlarged (*R. bisetosus*), or considerably enlarged with the distal post-axial angle of segment III slightly (fig. 18) or markedly prolonged (fig. 19); segment I may have a stout seta borne on a hyaline (fig. 19) or a sclerotized, distally bilobed process (fig. 20).

*Thorax*.—This shows no special features and is similar throughout the group.

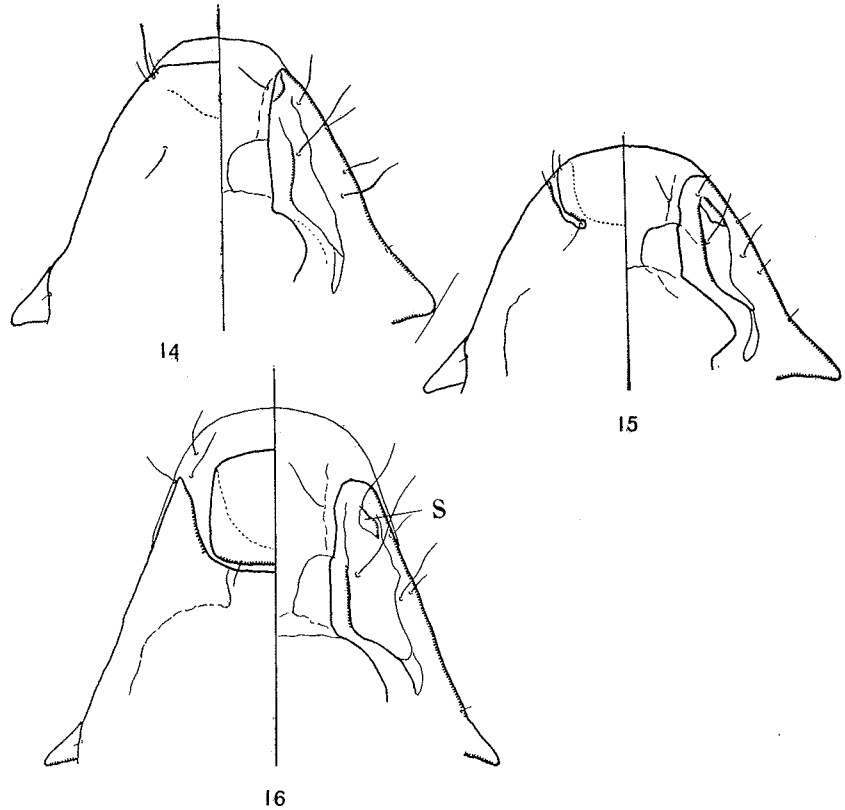
*Abdomen*.—*Tegites*: In both sexes these plates show variation. In the male, tergite II seems to be always at least partially divided medianly. In *R. lugens*



the remaining tergites form continuous plates across the segments, in other species, II, III, or IV may be interrupted medianly. The fused tergal plates of IX-X may be partially or completely (fig. 23) divided from that of XI.

In the female tergites II and III seem to be always medianly interrupted; the remaining tergites may be in the form of continuous plates (*R. lugens*), or II-V may be completely or partially (*R. ortygometae*) interrupted, or II-VII (*R. fulicae*) or II-VIII (one of the species from *Porphyrion madagascariensis*) may be interrupted medianly. The fused tergal plates of IX-X may be fused with that of XI (species from *Sarothura lineata*) or partially divided (species from *Limnocorax flavirostris*). The posterior margin of the last segment may be flattened or bifid.

Figures 14-16.



Heads of *Rallicola* spp.

14. *Rallicola lugens* (Giebel). 15. *R. minutus* (Nitzsch). 16. Species from *Rallus elegans levipes* Bangs.

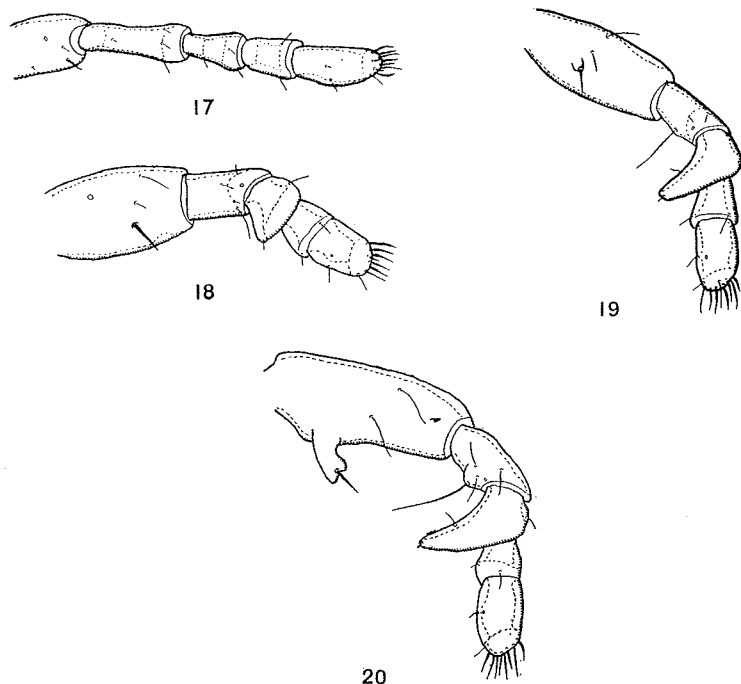
*Sternites*.—In the male the sternal thickening is in the form of median plates, with those of the posterior segments fused to form an irregular-shaped genital plate (fig. 1); in some species this plate is not apparent.

In the female the sternal thickening of some species is in the form of median plates which are lobed laterally; in others the lobe is detached and the sternal thickening in the form of a median plate with a small rounded lateral plate each side (species from *Megacrex*), in others the median plate is apparently absent and segments II-VI show only the small lateral plate (*R. minutus*).

*Female Genital Region*.—In its characteristic form the genital plate has two lateral lobes anteriorly (fig. 35), but in some species the lobes are separated from

the plate and appear as irregular-shaped sclerites each side. The stout setae borne on lateral tubercles, which are characteristic of the genus, vary in number from two to three each side; in some species the number cannot be used as a specific character as it varies from specimen to specimen and from side to side of the specimen.

Figures 17-20.

Male antennae of *Rallicola* spp.

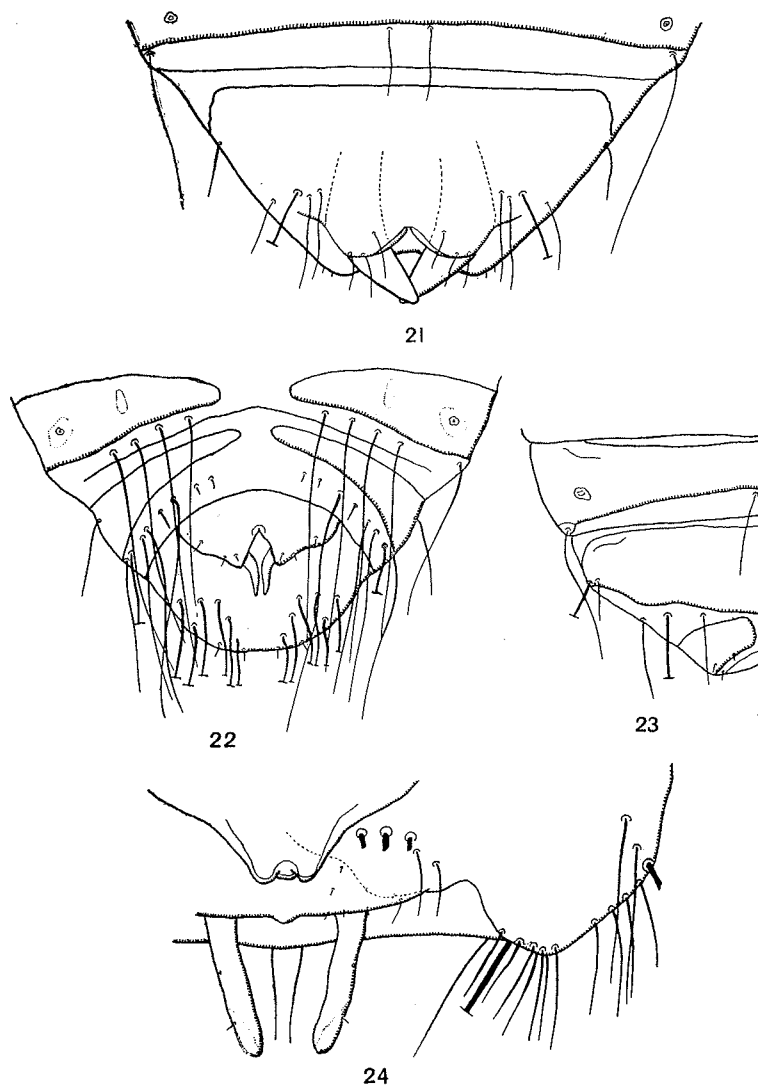
17. *R. ortygometae* (Schrank). 18. *R. fulicae* (Denny). 19. *R. sarothurae* sp. n.  
20. *R. lugens* (Giebel).

*Terminal Segments of the Male Abdomen.*—There is some variation in the position and form of the anal and genital openings in this group of species. The most primitive position in the Ischnocera for the anal opening seems to be terminal or ventro-terminal with the three associated setae (the anal setae) terminal and ventral, whilst the opening of the genital chamber is ventral. In some genera, however, the genital and anal openings are dorsal on what is probably segment XI, immediately posterior to the posterior margin of what is probably the fused ninth and tenth segments; the three anal setae are dorsal and can always be seen associated with the openings (as in *Brüelia*, fig. 22). Some genera always have the opening of the genital chamber definitely ventral and others definitely dorsal, but there are a number of genera, of which *Rallicola* is one, in which the species may have the opening terminal, dorso- or ventro-terminal or even dorsal; the condition apparently depending on the relative development of the dorsal and ventral abdominal sclerites with which the openings are associated. In *Rallicola* the usual position of the anus is dorso-terminal with the anal setae dorsal and the opening of the genital chamber terminal (fig. 33), but in some species (fig. 21) the openings are dorsal and approach the condition found in *Brüelia* (fig. 22). Again, in some species (fig. 24)\*, the tergum (? epiproct) is prolonged so that one or more of the anal setae are internal.

\* In the reproduction of fig. 24 the anal setae have been lost; they should lie on the dotted line.

The end of the male abdomen may be modified in various ways: in the species from *Amaurornis akool* the dorsal margin of the last segment has a median point; in those from *Gallinula chloropus*, *Limnocorax flavirostris*, *Rallina tricolor* and *Sarothura lineata* (fig. 33) the ventral margin of the last

Figures 21-24.



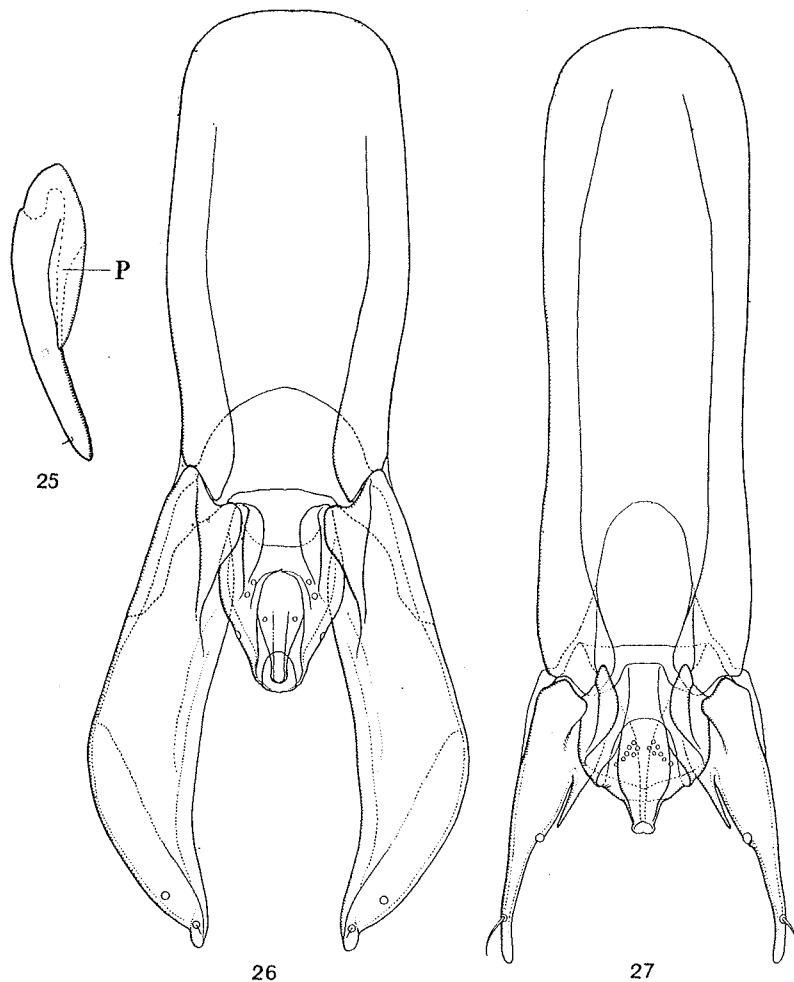
Terminal segments of abdomen.

21. *Rallicola cuspidatus* (Scopoli), dorsal. 22. *Brüelia* species from *Corvus corax* Linn., dorsal. 23. *Rallicola* sp. from *Porphyrio madagascariensis* (Latham), dorsal. 24. *R. andinus* Carriker, ventral.

segment has a small median point and in that from *Porzana tabuensis* it is longer and heavily pigmented. In the species from *Fulica americana* (fig. 54), *Gymnocorax plumbeiventris* and *Tribonyx mortieri* segment VIII (or IX) has a well-developed ventral median lobe; in other species (that from *Gallinula*, for instance) there may be only a small median point.

*The Male Genitalia.*—Although these structures are mainly similar throughout the group there is considerable variation in details. In many species there is a sclerotized part of the basal plate inside the normal lateral sclerotization which articulates with the head of the paramere (fig. 2, T). This thickening is part of the outer sclerotized bar, but may appear free to a greater or less

Figures 25-27.



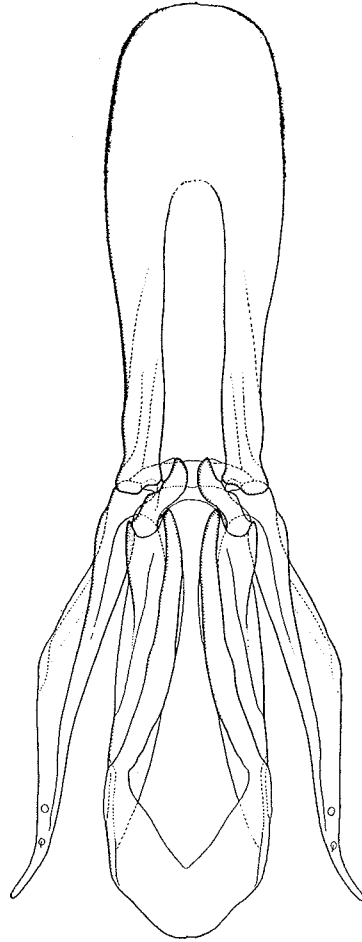
Male genitalia of *Rallicola* spp.

25. *R. fulicae* (Denny), paramere only. 26. *R. cuspidatus* (Scopoli). 27. *R. minutus* (Nitzsch).

extent forming the so-called "tubercle" (Carriker, 1944, 85); in some species it appears merely as the bifid end of the outer sclerotized bar. The parameres are always elongated, but vary in shape (figs. 25-28). Arising from the head of each paramere there may be a process, either well sclerotized and easily seen (fig. 25, P) or hyaline and liable to distortion in mounted specimens (fig. 2, P; figs. 43, 45, 47). It may be small (*R. ortygometae*, fig. 2) and does seem to be absent in some species; in *R. fulicae* (fig. 25) these processes are large and appear as two structures each side of the mesosome, reaching over half the length of the parameres.

The mesosome is usually shorter than the parameres and may have a well-sclerotized penis (fig. 2), but in some species (*R. mystax*, fig. 28) it is greatly elongated and prolonged beyond the end of the parameres. In the species from *Himantornis* the mesosome is asymmetrical and the penis is elongated and curled back on itself (fig. 36).

Figure 28.



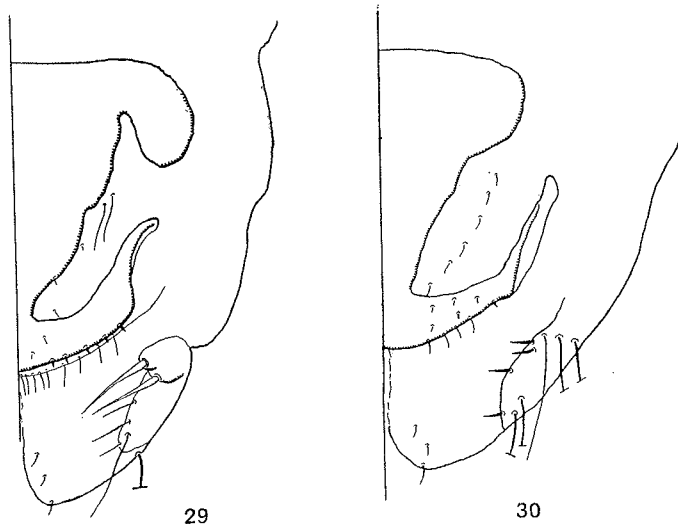
*Rallicola mystax* (Giebel), male genitalia

Thus, in a group of species from one family of hosts are found all the characters listed by Carriker (1944, 85) for the separation of *Rallicola*, *Parricola* and *Furnaricola*, namely, the presence or absence of sexual dimorphism of the antennae; the median separation or not of the tergites; presence or absence of "tubercles" in the male genitalia; and the length of the parameres. *Parricola* is said (*ibid.*) to lack the tubercle on which the female spine-like setae are borne and to have divided sternites in both sexes; these characters have not been found in the species examined from six members of the Jacanidae. In the original descriptions of *Corvicola* and *Epipicus* no attempt was made to give any characters distinguishing these supposed genera from *Rallicola*, *Parricola* and *Furnaricola*.

SPECIES OF THE *RALLICOLA*-COMPLEX FROM OTHER HOST GROUPS.

Having discussed the variation within a group of species from related hosts, those from less closely related or unrelated hosts can now be considered.

Figures 29 and 30.



Female genital regions.

29. *Rallicola subsimilis* (Carriker). 30. *Bruelia* sp. from *Corvus corax* Linn.

## GRUIFORMES.

The Rallidae is the only family in the Ralloidea, the latter usually considered as a superfamily within the order Gruiformes. This order contains a number of rather diverse suborders of which the following (in addition to the Ralloidea) are parasitized by species of the *Rallicola*-complex: the Rhynocheti and the families Aramidae and Psophiidae usually included in the superfamily Gruoidea of the suborder Grues.

**RHYNOCHETI.** This contains a single species, *Rhynochetos jubatus*, which is parasitized by a typical *Rallicola* belonging to the group found on the Rallidae.

**ARAMIDAE.** This again contains a single species, *Aramus scolopaceus*, which is parasitized by a distinctive species of *Rallicola* (*R. funebris*). It has the dorsal anterior plate modified centrally (fig. 40), the mesosome of the male genitalia elongated (fig. 39) and the female genital plate greatly reduced. Tergal plates II-VIII are divided medianly in both sexes and the female has a ventral sclerite each side of abdominal segments IX-X; similar sclerites are found also in some of the species from the Jacanidae.

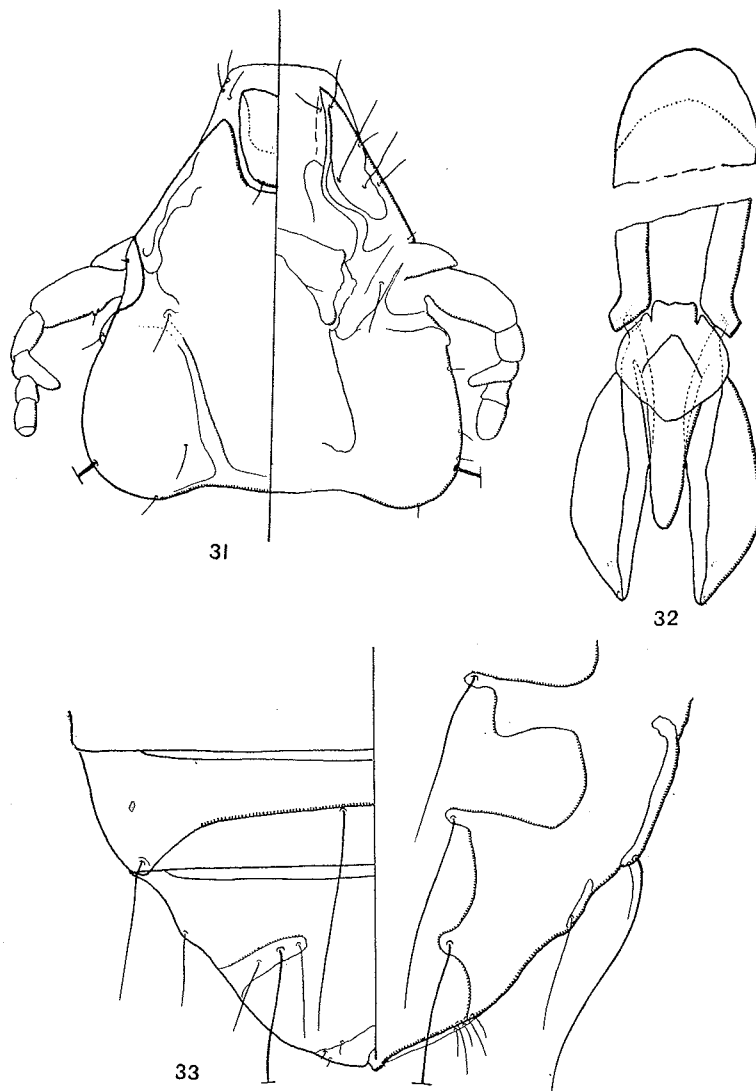
**PSOPHIIDAE.** This family contains one genus parasitized by the most distinctive species (*R. foedus*) of the *Rallicola*-complex. Its characteristic appearance is mainly due to the elongated abdomen with entire tergal plates and absence of well-marked pleurites (Pl. I, figs. 1-2). The head has a narrow hyaline margin, no definite anterior dorsal plate nor anterior dorsal suture; in these characters it resembles somewhat the species found on *Porphyrio porphyrio*. The female genital plate lacks the lateral lobes or the discrete lateral sclerites found in species from other members of the Gruiformes.

## CHARADRIIFORMES.

**JACANIDAE.** This is the only family of the Jacanoidea, usually placed as a superfamily of the suborder Charadrii of the Charadriiformes; some authors

consider that the affinities of this superfamily lie with the Gruiformes (see Clay, 1950). The species from the Jacanidae were separated by Harrison as a subgenus, *Parricola* (figs. 5-8). Specimens have been examined from the six genera of the Jacanidae and these show characters and a similar range of

Figures 31-33.



*Rallicola sarothurae* sp. n., male.

31. Head (for details of antenna see fig. 19). 32. Genitalia. 33. Terminal segments of abdomen.

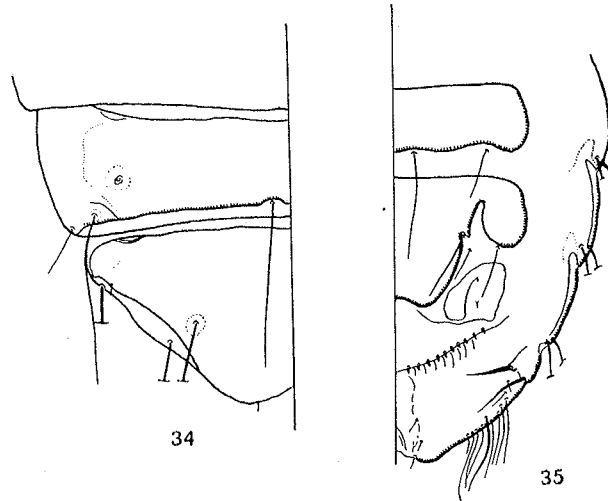
variation as in the species from the Rallidae. The species from *Hydrophasianus* and *Actophilornis* have small ventral sclerites on abdominal segments IX-X in the female as in species from *Aramus*. In the male genitalia the " tubercle " may (species from *Jacana*) or may not (species from *Irideparra*) be delineated ; the paramere may be narrow (species from *Jacana*) or broadened (species from *Actophilornis*) ; the form of the mesosome is variable. There are, therefore,

no characters which make it possible to separate the species parasitizing the Jacanidae from those found on the Rallidae either generically or subgenerically, in fact, the species on *Jacana spinosa* (*R. exiguifrons*) is apparently nearer to that on *Crex crex* than is the species from *Porphyrio porphyrio*.

#### APTERYGIFORMES.

The single genus *Apteryx* is parasitized by species which Harrison (1915) separated from *Rallicola* as a subgenus *Aptericola* (figs. 9-11). These species form a distinctive group mainly due to their stouter habitus and the well-developed dorsal carinae of the head. This last character may be directly correlated with the broader head (see Clay, 1951, 190); the *Rallicola* species from *Macgregoria pulchra* (Passeres), with a similar stout habitus, also has dorsal carinae although these are less well developed than those of the species from *Apteryx*.

Figures 34 and 35.



*Rallicola sarothuræ* sp. n., female abdomen.  
34. Dorsal. 35. Ventral.

#### PASSERIFORMES.

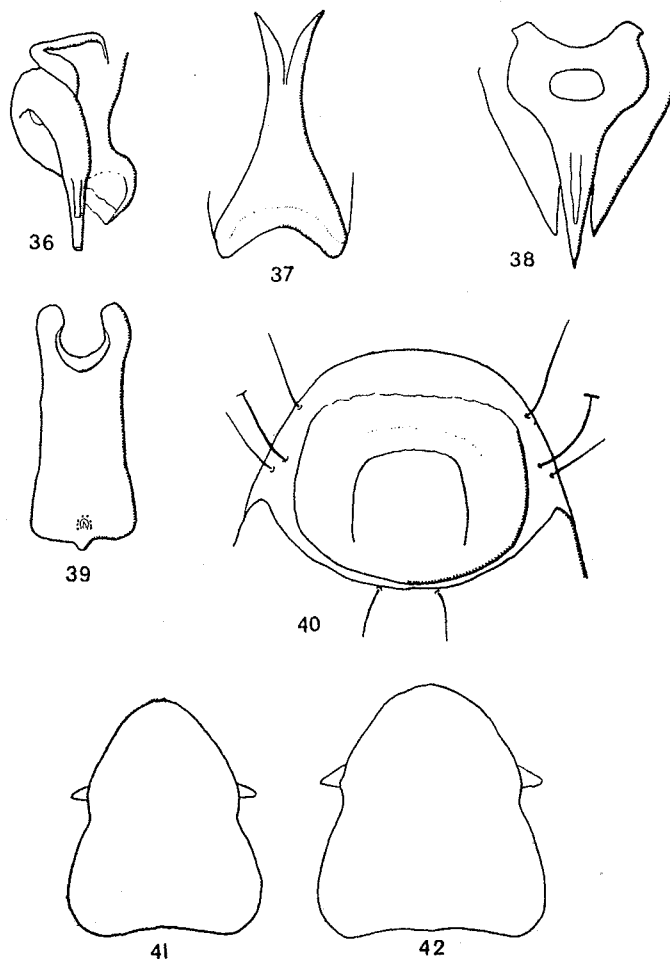
A number of species have been described from the superfamily Furnaroidea and separated as a distinct genus, *Furnaricola* (Carriker, 1944). The characters of the head of these species are somewhat diverse, but fall within the *Rallicola* range of variation (with the possible exception of *F. cephalosa*, figure only seen). There also seem to be no characters of the abdomen which make it possible to separate the *Furnaricola* group of species from *Rallicola*: in some species (*F. acutifrons*) the sclerotization of the female genital plate is continuous with that round the edge of the vulva, giving an anchor-shaped mark like that characteristic of *Brüelia* species (figs. 29-30), but other species have the form of the female genital plate typical of *Rallicola*. The male genitalia show some variation: *F. laticephalata* and *F. heterocephala* have the process from the head of the paramere as in some species of *Rallicola* from the Rallidae. The group of species from the Furnaroidea, therefore, show considerable variation amongst themselves and have no constant characters on which a generic separation could be made.

*Corvicola* Carriker was erected for a single species, *insulana* taken from *Corvus kubaryi*. However, *insulana* appears to be identical with specimens found on *Porphyrio poliocephalus melanotus* and close to a second species,



*Rallicola lugens* (Giebel) from the same host; it cannot, therefore, be separated generically from *Rallicola*. According to Carriker (1949, 4) the type series of *insulana* comprises fourteen males and thirteen females taken from four different individuals of *Corvus kubaryi* collected by Rollin H. Baker on Guam Island (Marianas); Mr. Rollin H. Baker (*in litt.*) shows that there is no reason

Figures 36-42.



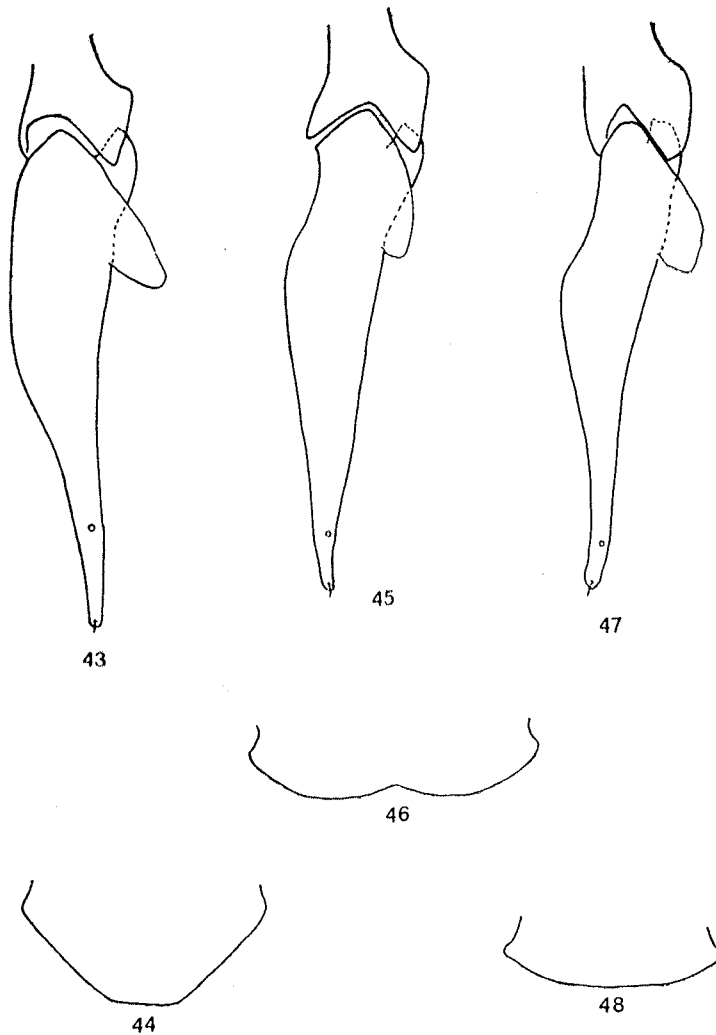
Figs. 36-39. Parts of mesosome of male genitalia of *Rallicola* spp.  
36. *R. flavescens* (Piaget). 37. *R. unguiculatus* (Piaget), 1880. 38. *R. foedus* (Nitzsch).  
39. *R. funebris* (Nitzsch).

Figs. 40-42. Heads of *Rallicola* spp.  
40. *R. funebris* (Nitzsch), anterior plate. 41. *R. lugens* (Giebel), outline. 42. *R. insulanus*  
(Carriker), outline.

to doubt the authenticity of the host record. It seems reasonably certain, therefore, that this species of *Rallicola* has become established on *Corvus kubaryi*. According to Mayr (1945, 298) *Corvus kubaryi* is restricted to Guam and Rota in the Marianas, while *Porphyrio poliocephalus* is found, in this region, only in the Palau group, the subspecies being *pelewensis*. Neither of the closely related species of *Rallicola* occurring on *Porphyrio poliocephalus* has

been seen from this subspecies, but it is unlikely that they differ from those of *P. p. melanotus*. It seems likely that at some time the distribution of *Corvus kubaryi* and *Porphyrio poliocephalus* overlapped and that the *Corvus* acquired the *Rallicola* species, possibly by feeding on the dead bodies of the rail. The

Figures 43-48.



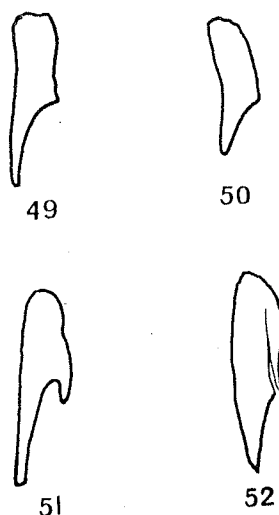
- Rallicola gracilentus* nom. nov.  
 43. Paramere. 44. Vulva.  
*Rallicola gadowi* Harrison.  
 45. Paramere. 46. Vulva.  
*Rallicola novaezealandiae* Harrison.  
 47. Paramere. 48. Vulva.

other explanation is that the specimens of the *Rallicola* were temporary stragglers on the *Corvus* from one of the species of Rallidae occurring on Guam. According to Mayr (1945) the following are found on Guam: *Rallus ovstoni*, *Poliolimnas cinereus* and *Gallinula chloropus*. From none of these genera have

species of *Rallicola* resembling those on *Porphyrio* been seen, and it is most unlikely that they would have a second species the same as that on *Porphyrio poliocephalus*. This case is an example of the dangers of erecting new genera based on the phylogenetic position of the host and not on the morphological characters of the parasite.

A further species from one of the Passeriformes (*Macgregoria pulchra*, family Paradisaeidae) has been seen. As these specimens were taken from a skin there must be some doubt about the host record, but twenty-one specimens of males, females and nymphs were collected and the species in general habitus and male genitalia is unlike any seen from the Rallidae. It shows, however, no characters on which it can be separated generically from *Rallicola*. The dorsal and temporal carinae are slightly developed and the male has a strongly

Figures 49-52.



Parameres of *Rallicola* species (after Carriker, 1944)

49. *R. acutifrons* (Carriker). 50. *R. parvigenitalis* (Carriker). 51. *R. titicacae* (Carriker).  
52. *R. heterocephalus* (Carriker).

sclerotized ventral prolongation of segment VIII, reaching beyond the end of the abdomen; the mesosome is unlike any seen in other members of the group, but these structures tend to be variable (cf. species from *Gallinula*, fig. 27, and *Porzana*, fig. 28). A single male taken from a skin of *Urocissa flavirostris* (Corvidae), and quite likely a straggler, has a similar stout habitus, but no sclerotized ventral prolongation of segment VIII; the genitalia, relatively much larger than in any other species, has the mesosome quite different, but the process on the inner edge of the paramere is well developed as in some of the species from the Furnaroidea and Rallidae.

#### PICIFORMES.

*Epipicus* Carriker was erected for a single species taken from a woodpecker; although this is a distinctive species there seems to be no characters as given in the description and figures which warrants its separation from *Rallicola*.

#### CUCULIFORMES.

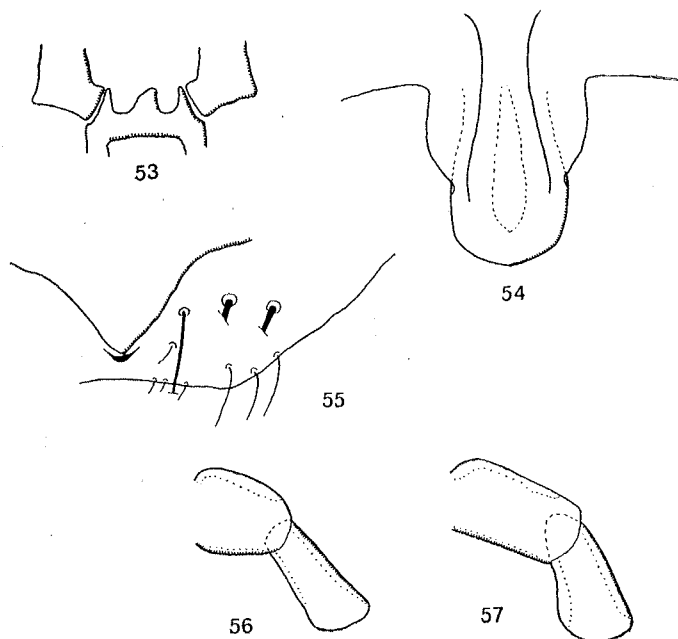
A species of *Rallicola* has been taken from *Centropus sinensis* (fifty-two specimens from three localities), from *C. rufipennis* (three specimens from a skin)

and from *C. bengalensis* (one specimen from a skin). The characters of this species fall within the range of variation found in *Rallicola* from the Rallidae. Possibly conspecific with the species from *Centropus* is *Rallicola unguiculatus* (Piaget) alleged to have come from *Eurylaimus ochromelas*, but as many of Piaget's specimens have been found to be stragglers the host record must be considered as quite unreliable. Also close to the species from *Centropus*, probably only subspecifically distinct, are five specimens taken from a skin of *Gallinax cinerea*, Canton, a host record which also needs confirmation.

THE PHYLOGENETIC ORIGIN OF *RALLICOLA*.

The facts discussed above show that on morphological grounds all these species should be included in one genus. With the exception of *Aptericola* (possibly a good subgenus) and *Epipicus* (containing only one species) all the genera which have been described contain species which would be generically unplaceable if their hosts were unknown. Before deciding to relegate the genera listed on the first page (with the exception of *Wilsoniella*) as synonyms of *Rallicola* it is necessary to consider whether the species from some of the host

Figures 53-57.



53. *R. subsimilis* (Carriker), proximal part of mesosome. 54. *R. advenus* (Kellogg), lobe-like process on sternite VIII (or ? IX) of male. 55. *R. exiguifrons* (Carriker), last abdominal sternite of male. 56. *R. ortygometrae* (Schrank), 1st two male antennal segments. 57. *R. clayae* Tandan, 1st two male antennal segments.

groups may have a different phylogenetic origin or are more closely related to other genera than to the rest of the *Rallicola*-complex. The following are possible explanations of the present distribution of *Rallicola*:

*Relationship between the host groups.* This would mean that the host orders on which *Rallicola* occurs are more closely related to one another than to any other orders. This is of course not supported by any other evidence and cannot be put forward as a serious explanation. However, some of these host groups

may have a comparatively recent common ancestor which was parasitized by *Rallicola*. The Apterygiformes are considered to be related to the Rallidae by some authors, and Harrison (1915, 100) suggested that the presence of *Rallicola* on both host groups denoted such a relationship. Further, some ornithologists place the Jacanoidea in the Gruiformes near the Rallidae. Thus, it is possible that *Rallicola* was present on an ancestral stock which gave rise to the Apterygiformes, Rallidae, Jacanidae, Aramididae, Psophiidae and Rhynchotidae. Its occurrence on other host groups could be explained by one of the theories discussed below.

*Discontinuous distribution.* This would mean that a *Rallicola* ancestor similar to the present-day species was parasitic on the ancestral stock which gave rise to modern birds before the divergence of the Apterygiformes, and that *Rallicola* has become extinct on those groups on which it is now absent. This theory would have to postulate that there had been little change in the species of the genus in spite of the time involved and the diversity of environments. *Rallicola* species found on the Gruiformes, which if this theory were true would be more closely related to one another than those on the Passeriformes, do in fact show considerable diversity. Hence, it would be expected that the species found on the different host orders would have diverged to a greater extent.

However, if this theory is the correct interpretation of the present distribution of the species, there is no phylogenetic reason for not placing them in a single genus.

*Parallel evolution.* This would mean that a primitive ancestral stock parasitic on a common ancestor continued to evolve on parallel lines after the parasites were separated on the different host groups. *Wilsoniella* on *Opisthocomus* might have belonged to the same stock but evolved on rather different lines. The present distribution could be explained by the extinction of the genus on other host orders descended from the same ancestor. This theory is open to the same criticism as the last, namely, that during the time and the diversity of environments involved such a close degree of parallel evolution is difficult to accept. However, if this theory is correct the species can again be contained in a single genus.

*Parallel evolution and divergence on the different host orders.* The ancestral *Rallicola* stock might have retained primitive characters until the separation of the present-day host groups. On some orders the primitive stock might have split into two lines, one retaining the general characters of the ancestor and evolving on lines parallel with those on the other host groups, the other perhaps losing some of the characters of the primitive stock and evolving on different lines. This idea is suggested by a certain similarity between some of the species of *Furnaricola* and *Brüelia*, both parasitic on the Passeriformes. In the female the abdomen is similar, including the diagnostic genital region. A comparison of figs. 29 and 30 shows that the *Brüelia* species differs only in the absence of the lateral tubercle-borne stout setae. The head in nymphs of some of *Rallicola* species is similar to that of nymphs of many *Brüelia* species and of the more primitive type of *Brüelia* adult. It could be presumed that a primitive type of Ischnocera with a circumfasciate head, male genital opening terminal, and the female genital region of the *Rallicola*-type branched into two lines on the Passeriformes. One of these lost the stout tubercle-borne setae of the female and the male opening became dorsal, thus developing into the genus *Brüelia*, the species of which may have the head modified to a greater or less extent (see Clay, 1951). The other branch changed little except for the median interruption of the marginal carina, a character which was also developed independently in the *Rallicola* stock on the other host orders. If this was the case, then *Furnaricola*, the species on *Macgregoria pulchra* and *Brüelia*, would be more closely related to each other than *Furnaricola* is to *Rallicola*, and it would be phylogenetically incorrect to amalgamate the two latter genera. Similar problems have been discussed elsewhere (Clay, 1949, 294; 1951, 174) where

it has been suggested that in the present incomplete state of knowledge of the group, genera should be based on morphological criteria only. It seems possible, however, that *Brüelia* and *Rallicola* have been derived from a common ancestor.

*Convergence.* This would postulate unrelated stocks developing the *Rallicola*-type of head carinae and sutures, the genital region of the female abdomen, and male genitalia on the same general lines in the different environments found on the diverse host groups on which these species occur. This seems unlikely and need not be further considered. It is possible, however, that the presence of the tubercle-borne setae in the female *Wilsoniella* may be a case of convergence and does not denote any phylogenetical relationship.

*Secondary infestations.* The genus may have evolved on a ralline ancestor, it being most widely spread on the family Rallidae, or possibly on an ancestral stock which gave rise to the Apterygiformes, Rallidae and some of the related families included in the Gruiformes; its sporadic occurrence on other orders being due to secondary infestations. This would explain the similarity of the species on the different host groups and the fact that *Rallicola* has been recorded from three (possibly four) families of the Passeriformes, one genus of the Cuculi and one family (Jacanidae) of the Charadriiformes, although this last case may be explained by relationship between the Jacanidae and Rallidae. The occurrence of a ralline-infesting species (*R. insulana*) established on a member of the Passeres, *Corvus kubaryi*, suggests that this is a recent case of secondary infestation and that the species of *Rallicola* may not be strongly host-specific. This theory, suggesting that the present distribution of *Rallicola* has been brought about partly by relationship between the hosts and partly by secondary infestations, seems to explain the facts most simply and means that there is no phylogenetic objection to placing all the species in one genus. This is also the most convenient classification.

A NEW SPECIES OF *RALLICOLA*.

*Rallicola sarothuræ* sp. n.

This species is distinguished from other described species by the anterior prolongation of the ventral carinae beyond the dorsal sclerotization of the marginal carinae and by the male genitalia. It is difficult to say where the affinities of this species lie, but *sarothuræ* seems to be nearest to *R. cuspidatus*, from which it can be distinguished by the shape of the head and male genitalia.

*Male.*—Head as shown in figs. 19 and 31. Thorax similar to that of *R. ortygometræ* (fig. 1). Abdomen with only tergite II definitely divided; sternites in the form of single median plates. Posterior segments as shown in fig. 33. Genitalia with broad parameres and somewhat elongate mesosome (fig. 32).

*Female.*—Head and thorax similar to that of male, without modified antennae. Abdomen with only tergite II definitely divided medianly. Sternites in the form of median plates slightly lobed laterally. Posterior segments as shown in figs. 34–35.

Measurements (in mm.) of types (in canada balsam)

	Male		Female	
	Length	Breadth	Length	Breadth
Head	0.45	0.40	0.47	0.43
Prothorax		0.25		0.25
Pterothorax		0.35		0.37
Abdomen	0.83	0.47	1.00	0.58
Total	1.48		1.70	
Genitalia	0.37			

*Abdominal chaetotaxy* (male and female).—Dorsal, II : 2 anterior (elongated) and 2 posterior ; III–VI : 4 ; VII : 1 post-spiracular each side and 2–4 central ; VIII–XI : see figs. 33–34. Ventral, II–VI : 4 ; VII–XI : see figs. 33, 35.

Holotype (male) and allotype (female) slide 6530 in the Meinertzhagen collection, British Museum (Natural History) from *Sarothura antoni* Madarasz & Neumann from Kenya. Paratypes : 8 ♀♀, 9 ♀♀ from the same host species, Kenya.

#### KEY TO THE SPECIES OF *RALLICOLA*.

A key to the species is given below although there are still many undescribed from the Rallidae alone ; for this reason additional characters are given in brackets after some of the species to distinguish them from known but undescribed species. The key is based almost entirely on the males as the characters on which the females are separated, such as the form of the tergal and sternal plates, are not always given in descriptions and where the material is inadequate are difficult to make out correctly\*. In some cases two forms are not separated in the key ; this means that either they are closely related subspecies, or that the original description or the available material is inadequate for separation. An asterisk denotes that no specimens of a species have been seen. The following species are omitted from the key for the reasons given :—

- R. acuminatus* (Piaget) = *R. sulcatus* (Piaget).  
*R. attenuatus* (Burmeister) = *R. ortygometae* (Schrank).  
*R. bipustulatus* (Piaget). There are no specimens in the Piaget collection, the host is wrong and the description and figure inadequate for recognition.  
*R. bisetosus* (Piaget). A specimen from *Rallina tricolor* will be selected as lectotype.  
*R. bresslaui* Pessôa & Guimarães = *R. funebris* (Nitzsch).  
*R. californicus* (Kellogg & Chapman). No specimens seen from the type hosts ; figure and description inadequate for recognition.  
*R. chanchotambo* (Carriker). Known only from the female.  
*R. dubius* (Piaget) = *R. gracilis* (Piaget).  
*R. fallax* (Piaget) = *R. lugens* (Giebel).  
*R. gracilis* (Piaget). Female only.  
*R. intermedius* (Giebel) = *R. mystax* (Giebel).  
*R. microcephalus* Uchida, 1948. No figure and unrecognizable from description. No holotype nor type host designated, but as the only male was taken from *Gallinula chloropus indica*, this specimen will presumably subsequently be designated as lectotype.  
*R. minhaensis* (Kellogg & Chapman). Generic position doubtful, but may prove to be a *Rallicola*.  
*R. minutotrabeulatus* (Osborn) = *R. advenus* (Kellogg).  
*R. parvulus* (Piaget) = *R. minutus* (Nitzsch).  
*R. porzanae* (Piaget). Female only seen.  
*R. subfallax* (Piaget) = *R. lugens* (Giebel).  
*R. unguiculatus* (Piaget), 1890 nec *R. unguiculatus* (Piaget), 1880. This species is represented in the Piaget collection by a single male, the true host of which is unknown. It is, however, apparently conspecific with the male specimen which will be designated as the lectotype of *Oncophorus major* Piaget, 1888. *O. major* Piaget, 1888 is invalidated by *O. major* Piaget, 1885, and as the former is a good species it is here re-named.  
*Rallicola piageti* nom. nov. for *Oncophorus major* Piaget, 1888.  
As *Rallicola gracilis* Harrison, 1915 is pre-occupied by *R. gracilis* (Piaget), 1871 it is here re-named :  
*Rallicola gracilentus* nom. nov. for *Rallicola gracilis* Harrison.

A complete list to 1950 of species, authors, references and type hosts is given in Hopkins & Clay, 1952, 318.

#### KEY.

- |  |                                     |
|--|-------------------------------------|
| 1. Penis elongated and recurved (fig. 36) .....                                | <i>flavescens</i> .                 |
| — Penis not as above .....   | 2.                                  |
| 2. Mesosome funnel-shaped (fig. 37) .....                                      | <i>unguiculatus</i> (Piaget), 1880. |
| — Mesosome not funnel-shaped ; reaching beyond the ends of the parameres ..... | 3.                                  |

\* It is possible that the size of the two anterior tergal setae on abdominal segment II (whether minute or elongated) might be useful characters in both sexes for a key, but these are seldom shown in figures.

See Emerson, 1955 (865); 1957 (972)  
 Timmermann, 1957 (986)

- Mesosome not funnel-shaped and not reaching beyond the ends of the parameres . . . . . 4.
- 3. Tergite III with more than 10 setae ; shape of mesosome characteristic (fig. 38) . . . . . *foedus* (1) †. (Pl. 1, figs. 1-2.)
- Tergite III with less than 4 setae ; shape of mesosome characteristic (fig. 28) . . . . . *mystax* (2).  
*zumpti*.
- 4. Segment I of ♂ antenna with stout seta on well-developed terminally bilobed process (fig. 20) . . . . . 5.
- Segment I of ♂ antenna without process or process not terminally bilobed (figs. 17-19) . . . . . 7.
- 5. Tergal plates II-VIII divided in mid-line in both sexes, dorsal anterior plate (fig. 40) and mesosome (fig. 39) characteristic . . . . . *funnebris* (3).
- Without above combination of characters. (Terminal margins of abdomen without median processes.) . . . . . 6.
- 6. Preantennal margin broadly rounded anteriorly (fig. 42) . . . . . *insulanus*.
- Preantennal margin pointed anteriorly (fig. 41) . . . . . *lugens*. (Fig. 20.)
- 7. Ocular seta elongated, 1st marginal temporal seta on lens, dorsal carinae well developed, 1st segment of ♂ antenna without process, more than 6 central dorsal setae on abdominal segment III. Mesosome narrowing distally. (♂ without ventral prolongation of abdominal segment VIII.) . . . . . 8.
- Without above combination of characters . . . . . 10.
- 8. Normally 2 stout setae each side of ♀ genital region, shape of vulva and paramere characteristic (figs. 43-44) . . . . . *gracilentus* nom. nov.
- Normally 3 stout setae each side of ♀ genital region, shape of vulva and parameres not as above (figs. 45-48) . . . . . 9.
- 9. Vulva with median emargination (fig. 46), shape of paramere characteristic (fig. 45) . . . . . *gadovi*. (Figs. 9-11.)
- Vulva without median emargination (fig. 48), shape of paramere characteristic (fig. 47) . . . . . *novaezealandiae*.
- 10 Abdominal segment III with more than 10 dorsal setae. (Mesosome broadening distally.) . . . . . *scapanoides*\*.
- Abdominal segment III with less than 6 dorsal setae . . . . . 11.
- 11. Proximal part of mesosome with central process in addition to lateral processes (fig. 53) . . . . . 12.
- Proximal part of mesosome with lateral processes only (fig. 32) . . . . . 13.
- 12. Paramere narrows abruptly about midway (fig. 49) . . . . . *acutifrons*\*.
- Paramere narrows abruptly near distal end (fig. 50) . . . . . *subsimilis*. (Figs. 12-13, 29, 53.)  
*parvigenitalis*\*.
- 13. No definite hyaline margin to head (fig. 15) . . . . . 14.
- Definite hyaline margin to head (fig. 16) . . . . . 16.
- 14. Distal post-axial angle of 3rd segment of ♂ antenna prolonged as definite process (fig. 18). (1st segment without well-developed unilobed seta-bearing process.) . . . . . 15.
- Distal post-axial angle of 3rd segment of ♂ antenna not prolonged as above . . . . . *minutus*. (Fig. 27.)
- 15. ♂ sternite VIII (or ? IX) with lobe-like process reaching to or beyond end of abdomen (fig. 54) . . . . . *adventus*.
- Without such process . . . . . *fulicae*. (Figs. 18, 25.)
- 16. ♂ sternite VIII (or ? IX) with bilobed process, terminal segments of abdomen diagnostic (fig. 24) . . . . . *andinus*.
- Without above characters . . . . . 17.
- 17. Paramere narrow, outer edge convex (fig. 6). (Paramere tip rounded, not flattened, and seta subapical. 1st segment of ♂ antenna longer than 2nd, distal post-axial angle of 3rd prolonged ; last ♂ abdominal sternite without lobe-like process.) . . . . . *sulcatus*. (Figs. 5-8.) *Paramere intermed. africana*
- Paramere broad, outer edge convex (fig. 26) . . . . . 18.
- Paramere with straight outer edge, inner with median lobe (fig. 51) . . . . . *titicacae*\*.

† Number in brackets after a name refers to notes on p. 586.



- Paramere with straight outer edge, no inner median lobe, inner edge narrowing abruptly (fig. 52) . . . . . 19.
- Paramere not as above . . . . . 21.
18. Ventral posterior margin of last ♂ abdominal segment without median point (fig. 21). (Mesosome characteristic, fig. 26.) . . . . . *cuspidatus* (4).
- Ventral posterior margin of last ♂ abdominal segment with median point (fig. 33). (Last ♂ abdominal sternite without lobe-like process.) . . . . . [(Figs. 19, 31-35.)  
*sarothourae* sp. n.
19. Head of paramere with process . . . . . 20.
- Head of paramere without process (according to original fig.) . . . . . *cephalotus*\*.
20. Ventral carinae of head projecting beyond sclerotized part of marginal carinae . . . . . *laticephalus*\*.
- Ventral carinae not as above. (Paramere, fig. 52.) . . . . . *heterocephalus*\*†.
21. 1st segment of ♂ antenna always definitely longer than 2nd; distal post-axial angle of 3rd distinctly prolonged (5). (Ventral posterior margin of last ♂ abdominal segment straight, last ♂ abdominal sternite without posterior lobe-like process; paramere tip rounded not flattened and seta sub-apical.) . . . . . *piageti* nom. nov.
- 1st segment of ♂ antenna equal to, or less or slightly longer than 2nd; distal post-axial angle of 3rd not distinctly prolonged (fig. 17) . . . . . 22. (*guami*\*) (6).
22. Ventral posterior margin of last ♂ abdominal segment with thickened median point . . . . . *bisetosus*.
- Without such point . . . . . 23.
23. ♂ with tergal plate IV divided in the midline; last sternal plate of abdomen pointed with discrete semi-circular sclerotization distal to point (fig. 55) . . . . . *exiguifrons*.
- Without above combination of characters . . . . . 24. (*affinis*) (7).
24. Segment I of ♂ antenna proportionally shorter (in relation to II) (fig. 56). (♀ abdominal tergites II-V divided or partly divided medianly) . . . . . *ortygometrae*. (Figs. 1-4, 17.)
- Segment I of ♂ antenna proportionally longer (in relation to II) (fig. 57). (♀ abdominal tergites II-VII divided medianly.) . . . . . *clayae*.

## NOTES TO KEY.

(1) A figure of *R. foedus* in the Nitzsch manuscript shows that this is the correct interpretation of the species.

Similarity

(2) The close relationship between *R. zumpti* (Kéler) from *Atlantisia rogersi* and *R. mystax* (Giebel) from *Porzana porzana*, together with the fact that they are unlike any other known species, suggests a close relationship between the hosts.

(3) A figure of *R. funebris* in the Nitzsch manuscript shows that this is the correct interpretation of the species.

(4) See Clay & Hopkins, 1951, 25 for a redescription of this species.

(5) One undescribed species has the first segment definitely longer than the second, but the third has no distinct prolongation.

(6) No specimens of *R. guami* Carriker have been seen and the description and figures are not sufficiently detailed to enable this species to be taken further in the key.

(7) The single ♂ type of *affinis* is in too poor condition to take it further in the key†.

† Through the kindness of Mr. M. A. Carriker it has been possible to examine paratypes of this species which show that it also has the head character as given under *laticephalus*; the two species cannot therefore be distinguished by this character.

‡ Since going to press the British Museum (Natural History) has acquired a further part of the Piaget collection which is almost certainly the unmounted residue of the specimens on which Piaget based his original descriptions. This contains specimens of *affinis* and it is now possible to show the differences between this species and *clayae* and *ortygometrae*. *R. ortygometrae*:—2-3 setae on sternite V; *affinis* and *clayae*:—5-6 such setae. *R. affinis*:—♂, tergal plates II-III completely divided. ♀, II-VI completely divided. *R. clayae*:—♂, tergal plates II only completely divided; ♀, II-VII.

## ACKNOWLEDGMENTS.

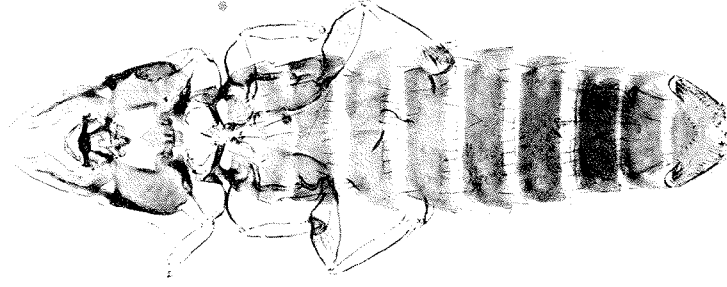
I am indebted to the Trustees of the British Museum for permission to publish figs 2, 26 to 28 drawn by Mr. A. J. E. Terzi and to publish fig. 26 which appeared in the *Bulletin of the British Museum (Nat. Hist.)*, *Entomology*, **2**, 26, f.34, and to Colonel R. Meinertzhagen for figs. 1, 3, 5, 6, 7, 9, 10, 12, 13 drawn by Mr. R. S. Pitcher. I am also indebted to Dr. S. Symmons and Mr. G. H. E. Hopkins for advice on various points.

## SUMMARY.

The various genera included in the *Rallicola*-complex are listed. The variation within a group of related species parasitizing one host family (the Rallidae) is discussed, and the characters and range of variation in the species from other host groups are compared. The phylogenetic origin and possible explanation for the present distribution of the *Rallicola*-complex are considered. In conclusion it is suggested that all the groups under discussion should be contained in the single genus *Rallicola*. A new species of *Rallicola* is described and two species re-named. A key to the known species of *Rallicola* is given.

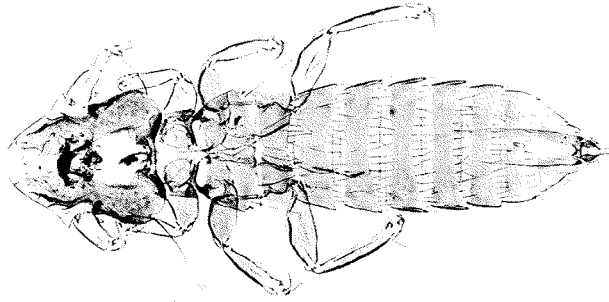
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Female  $\times$  40

*Rallicola foedus* (Nitzsch)



Male  $\times$  40