MALLOPHAGA FROM *APTERYX*, AND THEIR SIGNIFICANCE; WITH A NOTE ON THE GENUS *RALLICOLA*.

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(*From the Quick Laboratory, University of Cambridge.*)

(With 6 Text-figures.)

I.

Through the courtesy of Dr Hans Gadow I have had the opportunity of examining a number of skins of five species of *Apteryx* in the collection of the Cambridge University Museum. From these I have collected at least three species of Mallophaga, which I find to belong to the genus *Rallicola*. These are described below, with some discussion of the genus to which they belong, and of the significance of the occurrence of that genus upon *Apteryx*, from which no Mallophaga have previously been recorded.

The name *Rallicola* was proposed by Johnston and myself (1911, p. 324) for that part of Piaget's genus *Oncophorus* (1885, p. 35) found upon Rallidae, etc., the name *Oncophorus* being invalid, as it had been used by Rudow (1870). A full discussion will be found in our paper (*loc. cit.*). Piaget's genus included forms found upon owls, hornbills, rails and jacanas. The parasites of the two former groups do not seem to have much in common with those of the two latter, nor with each other; and probably should be included in two distinct genera. Those of the two latter groups fall within the limits of our genus *Rallicola*, together with the species from *Apteryx* described below. This genus thus includes species from three host families, which form three compact groups easily separable from one another by constant

though quite unimportant differences in form. As a matter of convenience, therefore, I suggest a division into sub-genera, *Rallicola s. str.* confined to Rallidae; *Parricola* found on Parridae; and *Aptericola* on Apterygidae. These divisions may be diagnosed as follows:

Genus *Rallicola*, Johnston and Harrison.

Philopteridae of small to moderate size; of a general form varying between that of *Philopterus* and *Degeeriella*, more resembling the latter; without distinct clypeal suture; with slight to well-marked sexual dimorphism of the antennae; with a definite indication of two distinct articles in the tarsus; with the transverse bands of the abdomen continuous, or divided only by a narrow median line. The best characters are, however, found in the ♂ genitalia, which have a characteristic form, with straight (rarely curved) divergent parameres, having two small lobes at their bases, and a solid median portion, details of which will appear below in the description of the species; and in the genital plate and ventral pleural margins of the eighth segment of the ♀, which have a very characteristic chaetotaxy. The inner margin of the pleuron at its anterior end is produced into a process directed backwards and inwards, which carries three, more rarely two, stout spinous hairs; while the pleuron behind is densely covered with hairs arranged in two or three longitudinal rows. The genital plate is strongly convex, sometimes with a median emargination, and is closely fringed with one or more rows of shorter hairs, the more anterior of which are frequently reduced to small spines. These structures are unusual in the *Ischnocera*, and bear at least a superficial resemblance to those found in some *Amblycera*. The straight divergent parameres of the ♂, embracing a single sac-like median structure, are also reminiscent of the Amblyceran condition; and it would seem as if *Rallicola* were a somewhat primitive Ischnoceran genus.

Rallicola s. str. is confined to the Rallidae, and is found upon all genera from the large forms such as *Fulica*, *Porphyrio*, *Aramus*, and *Ocydromus* down to small species of *Rallus* and *Porzana*. It possesses the characters detailed above, and is usually of small size, of the general proportions of a slender *Philopterus*, with the ♂ much smaller than the ♀. The space between the hind border of the signature and the mandibles is uncoloured. Type, *R. attenuata*, Burmeister.

Sub-genus *Parricola*, nov.

Species from the Parridae have the same general facies as those from rails, but are distinctly more slender forms, with little difference in size between the sexes, the ♂ being only very slightly smaller than the ♀. The transverse abdominal bands of the ♂ are entire; of the ♀ divided by a narrow uncoloured line. Type, *Rallicola* (*Parricola*) *sulcata*, Piaget.

Sub-genus *Aptericola*, nov.

Distinguished from the two previous subdivisions by its more robust form. The space immediately behind the signature is closed, except for a narrow median interruption, by two coloured bands, leaving two roughly semicircular clear areas in front of the mandibles. The ♂ is somewhat smaller than the ♀. The transverse bands of the abdomen are entire in both sexes. Type, *Rallicola* (*Aptericola*) *gadowi*, Harrison.

The following key will serve to differentiate these sub-genera:

A.	Uncoloured area in front of mandibles in two semicircular patches, not reaching hind border of signature	*Aptericola.*
AA.	Uncoloured area of usual shape, and extending to signature	*B.*
B.	Slender forms, deeply coloured, sexes of equal size	*Parricola.*
BB.	Broader forms, not usually deeply coloured, ♂ markedly smaller than ♀	*Rallicola s. str.*

Rallicola (*Aptericola*) *gadowi*, n. sp.

As it is not likely that more than one, or at most two, further species will be found in this subdivision, I dispense with the long description which is usually the only safe course in dealing with Mallophaga, and merely emphasise the differences between the three species here described. This, with the help of the figures, will render the species easy of recognition.

The general form of the ♂ will be apparent from Fig. 1. It differs from the ♂ of *A. novae-zealandiae* next described in its more robust form, and in the flat clypeal front, with broadly rounded angles, as well as in the longer parameres and shorter median portion of the genital apparatus, which has a wider and shorter basal plate. The features of the chaetotaxy, which would appear to be characteristic for the subdivision, are the three pairs of hairs upon the metathoracic border, and the

short median rows on the abdominal tergites, with an absence of lateral hairs save one at each side of the sixth segment.

The ♀ has the same general form as the ♂, but is larger, as will be seen from the measurements given, has filiform antennae, and the usual difference in shape and chaetotaxy of the hind end of the abdomen (Fig. 2). The females of the three species are easily differentiated by means of the shape of the genital plate, which in this species bears a median emargination, while in *A. novae-zealandiae* it is evenly rounded, and in *A. gracilis* has the shape of a truncated triangle.

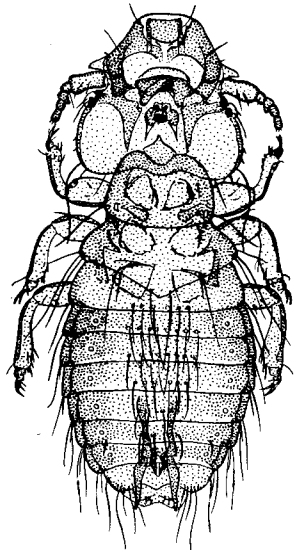

Fig. 1.

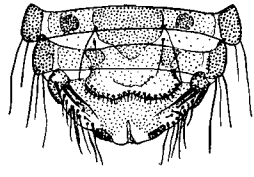

Fig. 2.

Measurements in millimetres.

	♂		♀	
	Length	Breadth	Length	Breadth
Head	0·59	0·62	0·64	0·67
Prothorax	0·17	0·40	0·18	0·44
Metathorax	0·27	0·57	0·27	0·64
Abdomen (from anterior angles)..	0·82	0·71	1·18	0·84
Total length and greatest breadth	1·76	0·71	2·15	0·84

Several ♂♂ and numerous ♀♀ from skins of *Apteryx australis* in the Cambridge University Museum. I also assign to this species a single ♀ from a skin of *Apteryx mantelli*, which is larger than the type, but shows no differences of specific value. The discovery of the ♂ may prove that this form is distinct.

Rallicola (*Aptericola*) *novae-zealandiae*, n. sp.

The ♂ of this species (Fig. 3) is, as already pointed out, more slender than the last, and has the clypeal front broadly rounded instead of truncate. The general coloration is considerably lighter. But the chief differences, or rather, those best adapted for distinguishing the species, are found in the genitalia. I figure those of the present species (Fig. 4). Unfortunately the ♂ of *A. gadowi* taken for dissection of these parts proved to have broken parameres, and as the males among my material were few, I did not care to sacrifice another. I have not, therefore,

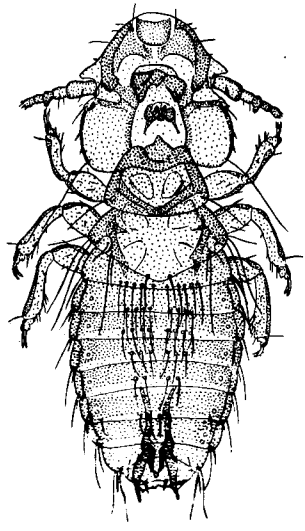

Fig. 3.

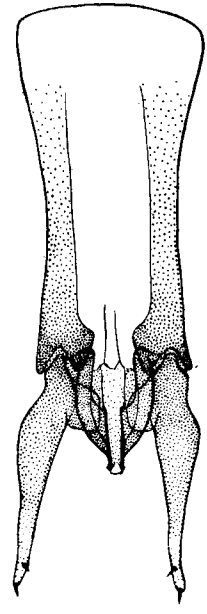

Fig. 4.

figured the genitalia of *A. gadowi*; but with the aid of the dissection, which has lost only the distal halves of the parameres, and of these halves, which happen to be extruded in the type mounted specimen, I am able to make safe comparisons. The genital apparatus consists of a basal plate, with parameres articulated distally, between which lies an undivided mesosome. At the base of each paramere, on the inner side, a short weakly-coloured lobe projects inwards under the mesosome. This lobe is certainly attached to the paramere, but has no appearance of being a normal process upon it, as it is so delicate in

comparison. It may represent a reduced endomere. The mesosome comes nearer in general form to that of *Docophoroides* than to any other with which I am acquainted. Its general shape will be seen from Fig. 4. A cylindrical chitinous tube, which is a direct continuation of the ejaculatory duct, runs through and slightly beyond it, constituting the penis, which opens dorsally by a triangular orifice. The genitalia of *A. gadowi* differ from those of *A. novae-zealandiae* in the following details. The basal plate is broader and shorter; the endomeral (?) lobe is distinctly smaller; the mesosome is shorter and slightly broader, with a more heavily chitinised penis; and the tip of the paramere is slightly spatulate instead of filiform, and bears two terminal bristles in place of the customary one.

The ♀ is larger than the ♂, with the usual differences in the hind end

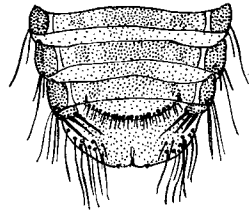

Fig. 5.

of the abdomen (Fig. 5). The genital plate is rounded, and the chitinous bands running forwards from its lateral insertions are not developed.

Measurements in millimetres.

	♂		♀	
	Length	Breadth	Length	Breadth
Head	0·59	0·57	0·59	0·61
Prothorax	0·17	0·39	0·18	0·39
Metathorax	0·26	0·55	0·26	0·58
Abdomen (from anterior angles)..	0·84	0·64	1·11	0·79
Total length and greatest breadth	1·68	0·64	2·18	0·79

Numerous ♂♂ and ♀♀ from skins of *Apteryx lawryi* in the Cambridge University Museum. One ♀ and several ⊙ ⊙ from skins of *Apteryx oweni*. One ♀ (straggler) from *Stringops habroptilus*.

Rallicola (*Aptericola*) *gracilis*, n. sp.

This well-marked species is described from a single ♀ taken from a skin of *Apteryx haasti* in the Cambridge University Museum.

Fig. 6 gives the general form. It differs from the females of the two previous species in the narrow and truncate hind end of the abdomen, in the shape of the genital plate, and in some details of the abdominal chaetotaxy. As these details will be obvious on a comparison of the

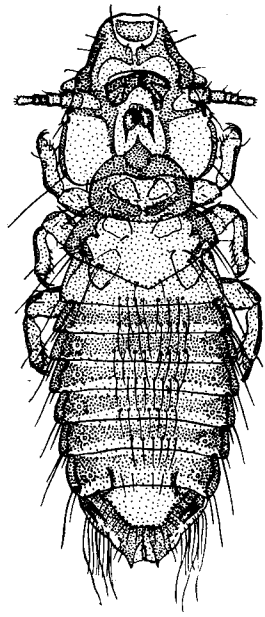

Fig. 6.

figures, there is no need for a detailed description. The present species is also smaller and more slender than those which precede it. The figure shows the dorsal aspect of the insect to the end of the sixth abdominal segment, the terminal portion being represented as if viewed ventrally.

Measurements in millimetres.

	♀	
	Length	Breadth
Head	0·60	0·60
Prothorax	0·17	0·42
Metathorax	0·26	0·49
Abdomen (from anterior angles) ..	1·09	0·74
Total length and greatest breadth	2·00	0·74

The types of these three species will be deposited in the Australian Museum, Sydney, New South Wales.

LIST OF HOSTS WITH PARASITES.

Apteryx australis	*Rallicola* (*Aptericola*)	*gadowi*	
,, *mantelli*	,,	,,	,,
,, *lawryi*	,,	,,	*novae-zealandiae*
,, *oweni*	,,	,,	,,
,, *haasti*	,,	,,	*gracilis*
Stringops habroptilus	,,	,,	*novae-zealandiae*

II.

In view of the conclusions which have been reached independently by Kellogg and myself (*vide* Harrison, 1914, and references to Kellogg's papers quoted therein; also Kellogg, 1914, pp. 259–60) that the relations of Mallophagan parasites are intimately bound up with the phyletic relationships of their hosts, a discussion of the significance of the occurrence upon *Apteryx* of the parasitic genus *Rallicola* is of considerable interest.

I do not think that there can be any reasonable doubt as to the species described above being true parasites of *Apteryx*. I have collected them from skins of five species, and, in the case of two of these species, from several individuals. The only other Mallophaga found upon these skins were a few immature *Menopon*, which were too young to afford any idea of their affinities. I have examined the good series of New Zealand birds contained in the Cambridge collection, and have not found these Mallophaga upon any other form, save a single individual on one out of six skins of *Stringops* examined. This accidental occurrence is easily understood, as *Stringops* and *Apteryx* are both nocturnal, and hide during the day in hollow stumps, etc. Occasional transference may take place when the two species are hiding together in one refuge, or even when one occupies a hollow that has recently been in possession of the other. The positive evidence is, therefore, fairly conclusive, and it is supported by the negative fact that no other Ischnoceran parasites were found upon the skins. No family of birds is without Ischnoceran Mallophaga, so that, as no other forms have been found which might be taken as the normal parasites, it is reasonable to conclude that the sub-genus *Aptericola* contains the normal Ischnoceran parasites of the Apterygidae.

There can be no possible question as to the correctness of my placing these parasites within the genus *Rallicola*. However much uncertainty may exist as to the value of the present classification of Mallophaga, there is no doubt that *Rallicola* is a good and distinct genus, well-defined, and clearly marked off from all other Ischnocera; and there is equally

no doubt that the sub-genus *Apterícola* is merely a group within the genus *Rallicola*, conveniently distinguished by its robust form. *Rallicola* is, as I have stated above, confined to rails, and found upon all sorts and sizes of rails over the length and breadth of the globe; and I have reasons, partly stated above, for considering it a somewhat primitive Ischnoceran genus, certainly more primitive than *Philopterus* and *Degeeriella*, which appear to have developed from the same branch of the original stock.

Only one other Mallophagan genus, *Pseudomenopon*, is found solely upon rails, and is generally distributed amongst them. This is, so far, monotypic, but will probably be found to contain a number of species when it is critically examined, as has been the case with other genera (e.g. *Docophoroides* and *Giebelia*). I have not succeeded in finding *Pseudomenopon* upon *Apteryx*. A few species of *Lipeurus*, *Philopterus*, *Degeeriella*, and one of *Laemobothrium* are also found upon rails, but these would seem to be comparatively late acquisitions, as they are not generally distributed, and have chiefly been found upon *Fulica*, *Gallinula*, and *Porphyrio*.

The robust form of the species of *Rallicola* from *Apteryx* may also possess some significance. In general, large Mallophaga are found upon large birds. This is not by any means always true. If it were, we should expect to find the largest Mallophagan species upon the ostrich, whereas it occurs upon a condor. Similarly *Ricinus*, which comprises fairly large species, is found chiefly upon small passerine birds. But, in general, when a genus is well distributed over a considerable number of nearly related hosts, the size of the parasite is roughly proportional to the size of the host. Thus species of *Lipeurus* found upon albatrosses are larger than those found upon the larger petrels; and these in their turn exceed in size those found upon the little storm petrels. The largest species of *Philopterus* are found upon ibis, storks, and vultures; of *Colpocephalum* on storks, cranes, hornbills, etc.; of *Goniodes* upon peafowl and tragopans; and many similar instances might be quoted. Arguing on general grounds, then, I should, had these species of *Apterícola* been submitted to me without any data as to the host, have given the opinion that they came from a group of large ralline birds. But no species of *Apteryx* is very large, and certain of them are smaller, bulk for bulk, than some of the larger rails, as, for instance, some species of *Ocydromus*, which carry *Rallicola* of the ordinary small type. A possible inference is that *Apteryx* is an offshoot of a larger-statured stock. Since it is generally agreed that the Apterygidae and

Dinornithidae are closely related, it is not so improbable as it may seem at first sight that *Aptericola* was the type of Ischnoceran Mallophaga found upon the Dinornithidae.

Finally I should like to discuss the Mallophagan parasites of the ostrich, rhea, and emu, to which, of living birds, *Apteryx* has hitherto been considered most closely related. I have already (1914, pp. 9–10) written something about the species found upon these three hosts. I have again looked into the matter carefully, and I am still of the opinion that these species, and their hosts with them, had common origin. In any case the Mallophaga of the larger ratite birds belong to a different family, and have no close relationship to the genus *Rallicola*. So the parasites of *Apteryx* differ radically from those of the remaining Ratitae, and are closely akin to those of the Rallidae.

I have tried, in the preceding five paragraphs, to put an unprejudiced statement of the case. The points I have wished to make in these paragraphs may be stated briefly as follows:

(i) *Aptericola* is a normal parasite of *Apteryx*.

(ii) *Aptericola* is certainly, at most, a sub-genus within the genus *Rallicola*.

(iii) *Rallicola* is a universal parasite of rails, and of nothing but rails, except for the Parridae and Apterygidae.

(iv) *Aptericola* possibly indicates the type of Ischnoceran parasite that existed upon the Dinornithidae.

(v) The Mallophaga of the remaining Ratitae have nothing in common with those of *Apteryx*.

The inference that I draw from these conclusions is that *Apteryx* (and possibly *Dinornis* also) is more closely akin to the Ralli than to any other living birds. Subsidiary deductions are that the Parridae are ralline rather than limicoline; and that the Ralli are probably distinct enough to justify ordinal rank.

Taking the latter first, though the position of the jacanas has been the subject of some discussion they are, in most recent classificatory schemes, definitely included amongst the Limicolae. This order has, however, the best limited groups of Mallophaga that we can point to. No person with any knowledge of the group could fail to determine at sight a parasite in any of the genera found upon limicolines, or, perhaps I had better say, upon the Charadriiform complex, as having come from a Charadriiform host. (With this group, by the way, the parasites of the Pterocles and Columbae show no close affinity.) The Mallophaga of the jacanas do not fall within these well-marked limits.

As to the position of the Ralli, they possess as their most widely distributed and characteristic parasites two well-marked genera, *Rallicola* and *Pseudomenopon*, one in each of the sub-orders of Mallophaga. *Rallicola* would seem to be a somewhat primitive genus, certainly more primitive than *Philopterus* and *Degeeriella*, the remaining genera of the same family; while the relation of *Pseudomenopon* to the other menoponid genera cannot, in the absence of any form showing an intermediate condition, be stated. The fact that *Pseudomenopon* does not occur on either Parridae or Apterygidae may indicate that it is of more recent development than *Rallicola*. An important negative fact is the non-occurrence of *Philopterus* upon rails. This genus, which is generally looked upon as the most specialised of the more specialised sub-order, is almost universally distributed among birds. The only important groups that are without it are the Galliform complex, comprising tinamous, fowls, pigeons, the hoatzin, and, on Mallophagan evidence, the penguins; and the Ratitae. Three or four species of *Philopterus* have certainly been described from some of the larger rails, but I have carefully searched a large number of species of ralline birds from all parts of the world without finding *Philopterus*; while all yielded *Rallicola*, and many *Pseudomenopon*. It is fairly obvious, then, that *Philopterus* can only have been acquired at a comparatively recent date by those species which possess it. Species of *Degeeriella*, *Lipeurus*, and *Laemobothrium* are also too few in number and too circumscribed in distribution to be included in other than the same category. The intrinsic parasites of the Ralli stand, then, in an isolated position with regard to the remaining Mallophaga. And all the evidence of Mallophagan distribution points to the conclusion that the condition of the parasites is intimately connected with the phylogenetic relationships of the hosts, and reflects these relationships to a greater or less extent. Consequently I cannot avoid the conclusion that the Ralli occupy an isolated position, which should entitle them to at least the same rank as the similarly isolated Galliform complex.

It may be as well, at this point, to clearly define my position in making such statements as to bird relationships as that conveyed in my last sentence. These statements are made frankly upon the evidence afforded by the parasites. They are, consequently, not comparable with the statements of a morphologist, based upon structural considerations; but are to be looked upon simply as suggestions, which I believe may be well founded, but which, until they receive morphological confirmation, must remain simply suggestions. I may state

them with an appearance of dogmatism, but I clearly understand that they are governed in every case by the above limitation. My excuse for making them is that the phyletic relations of birds have always presented a very difficult problem, and that none of the customary means has produced a satisfactory solution. So when I find that bird parasites, owing to their peculiar biological condition, seem to shed some light upon this problem, I think it worth while to put these indications on record. The morphologist can confirm or refute them at his leisure.

With this much explanation I proceed to the final question—Is *Apteryx* a rail? If not, how does it come to possess ralline parasites? The mature opinion of Prof. Kellogg, after twenty years' study of Mallophaga, is that "the host distribution of these wingless permanent ectoparasites is governed more by the genetic relationships of the hosts than by their geographic range, or by any other ecologic conditions" (1914, p. 259). That opinion is based on—"The fact, proved by abundant cases, that two host species of wholly distinct geographic range and with no possible opportunity for contact such as would permit of the migration of wingless parasites from one to the other, may have, nevertheless, one or more parasitic species common to them both, is associated almost always with the further fact that these common hosts are closely related genetically." Kellogg instances only the occurrence of the same parasitic species on two geographically segregated but phyletically connected hosts. In my paper (1914) published a month after Kellogg's, but which had gone to press more than a month before it, I carry the hypothesis further; and apply it to the case of closely related parasitic species upon closely related hosts. And though I cannot lay claim to the same wide knowledge of Mallophagan species that Prof. Kellogg possesses, I had nevertheless been studying the group for some five years, purely from this point of view. Only one other explanation of the distribution of Mallophaga can be put forward, namely that it is due to convergence. I have not overlooked this possibility, but I do not find any evidence of this cause myself, and I do not think that the most ardent advocate of convergence, were he to look carefully into the actual conditions of Mallophagan distribution, would claim these conditions as the result of convergence.

The only alternative is to believe that *Apteryx* and the rails are closely connected phyletically, unless one or other of the groups has acquired these particular parasites by some accidental transference. This supposition may be dismissed as far as the rails are concerned.

Rallicola occurs, as I have already pointed out, on all rails from *Ocydromus* to *Porzana*. Its occurrence is far too general for it to have been accidentally acquired. But with *Apteryx* the case is somewhat different. There are but six species of the genus, and I have described only three species of *Aptericola* taken from five of them. These are small numbers, and the suggestion of straggling at a comparatively recent date might be put forward. But *Aptericola* is, after all, a rail parasite, and could only have straggled from some ralline bird. New Zealand is rich in rails, and I have examined these with some interest, to see if any robust form such as *Aptericola* might be found upon them. I have collected Mallophaga from five species of *Ocydromus* from New Zealand itself; as well as from *O. sylvestris* of Lord Howe Island. A species of *Rallicola* has been described by Piaget from *O. lafresnayanus* of New Caledonia. I have also collected species of *Rallicola* from *Porphyrio*, *Hypotaenidia*, and *Porzana* from New Zealand. But in all these cases the parasite belongs to the small rail-infesting type; so it is not probable that *Apteryx* acquired its parasites from any existing rail. *Notornis* certainly remains unexamined, but there is no reason to suspect that its parasites would prove much different from those of *Porphyrio*. Moreover, the negative evidence, as I have stated above, of the absence of any other Ischnoceran parasite is in itself a very good reason for believing that *Aptericola* is and always has been the normal Ischnoceran parasite.

I conclude, then, that *Apteryx* is nearer akin to the Ralli than to any other living birds. The possibility of this relationship has already been foreshadowed by Fürbinger; and arguments for it have been set out at some length in Gadow's systematic volume in Bronn's *Thier-Reichs*, in both cases upon morphological grounds.

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