MALLOPHAGA AND THE PHYLOGENY OF THEIR HOSTS

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Introduction.

In a previous paper (Hopkins, 1942) I discussed the general principles of the use of mallophagous parasites in deducing the ancestry of their bird-hosts, going into somewhat more detail than I would have thought necessary had I then known of the existence of Harrison's paper in this Journal (1916b) and the discussion on it (Harrison, 1916a). I also gave a few examples of the use of the method. Since I wrote, I have discovered a very important new principle which must be applied to attempts to deduce phylogeny from the parasites, and I feel it incumbent on me to bring this to the notice of ornithologists. I also take the opportunity to bring forward a couple of new instances of deduction of phylogeny and to modify two of my former deductions.

The Principle of "Secondary Absence".

No experienced student of the Mallophaga (or the sucking-lice, either) could fail to have noted certain curious apparent anomalies in the distribution of parasites on host-groups, and it was this point which apparently caused the greatest amount of reserve among those who discussed Harrison's lecture (Harrison, 1916a). Cummings, himself a student of the Mallophaga and not an ornithologist, brought up this point strongly, instancing the occurrence of Goniodes-like forms on Penguins (as well as on Galliformes, Tinamiformes and Columbiformes), and the occurrence of Laemobothrion on various not very closely-related groups. He was inclined to explain such instances as being due either to convergence or to the establishement of lice which were originally

stragglers. Both these phenomena undoubtedly occur in the Mallophaga (the latter, at least, extremely rarely), but I believe that there is a much simpler explanation for the vast majority of such cases as Cummings instanced, especially as the resemblances are often far too close to be accounted for by convergence.

The explanation is so obvious that it is amazing that (so far as I have been able to ascertain) no-one has suggested it before:- the absence of a genus of lice (or a modification of it) on a given group of birds very often means nothing more or less than that the genus was formerly present but has died out. I mentioned this as a possibility in my former paper (1942, pp.99, 105), but my more recent work enables me to put it forward as being beyond the bounds of conjecture.

Two examples, out of the many available, will serve to illustrate this point. Disregarding certain doubtful records, the genus Falcolipeurus occurs on the Secretary-Bird, on both New and Old World Vultures, and on at least one member of the Aquilinae; it is absent on the vast bulk of the Hawks, Kites, Buzzards and Falcons, although according to modern classifications these are infinitely closer to the Old World Vultures than the latter are to their New World understudies. On the other hand, the members of the Hawk-Falcon group are universally infested by the genus Degeeriella s.str., which is not closely related to Falcolipeurus, and which occurs with the latter on at least one Eagle but is absent on both groups of Vultures and apparently also on the Secretary-Bird. Surely the explanation is obvious ---- the ancestral Falconiformes were infested with both Falcolipeurus and Degeeriella; the former genus has died out on nearly all the group except the Vultures and the Secretary-Bird, while Degeeriella has become

extinct on almost all those birds which have kept Falcolipeurus. The explanation can even go a step further: the vultures and the Secretary-Bird are all large, while the rest of the Falconiformes are (for the most part) relatively small; it is only on very large members of "the remainder" that we get Falcolipeurus, though Degeeriella occurs on all of them. It seems highly probable that Falcolipeurus and Degeeriella are in competition, and that the former has proved more suited to life on the larger hosts and the latter to life on the smaller ones. It seems to me that, if modern ornithologists are correct in placing the two groups of Vultures so far apart and the Old World forms so close to the Hawks, the absence of Falcolipeurus on Hawks must of necessity be secondary. The establishment of stragglers from some other bird-order on both groups of Vultures is ruled out by the fact that Falcolipeurus is strictly confined to the Falconiformes, while convergence will not explain the facts because the generic resemblance between the species found on Old World Vultures, New World Vultures and the Secretary-Bird is far too exact to be accounted for thus.

In another instance the factor of secondary absence seems even more obviously to have been concerned. The highly characteristic genus Tetrophthalmus lives in the pouches of Pelicans and of a few species of Cormorant; it is not known from any Gannet, I have examined dozens of Darters (Anhinga) and failed to find it, and it almost certainly does not occur in the pouches of the two European species of Phalacrocorax (the Common Cormorant and the Shag); it is probably much too early to assert that it does not occur in the pouches of other groups of the Pelecaniformes. Summarising: Tetrophthalmus has a highly specialised habitat in the pouches of certain Pelecaniformes, it is a specialised

and highly characteristic genus, and it occurs in the pouches of Pelicans and some Cormorants, but not in those of other Cormorants. It is not possible for the resemblances between the species of the genus which are known from Cormorants and those from Pelicans to have been brought about by convergence, and straggling would be very nearly impossible unless a Cormorant were to thrust its head into the pouch of a Pelican. It seems to me completely certain that Tetrophthalmus infested the "missing link" between Cormorants and Pelicans and has died out on most, but not all, of the Cormorants. It is perhaps relevant to note that the Cormorants infested by Tetrophthalmus are not all from one region, the genus being known from Cormorants in Australasia and America.

What is the bearing of the principle of secondary absence on our attempts to deduce phylogeny ? It in no way detracts from the value of the parasites as evidence of the ancestry of their hosts, and should even improve our deductions by placing them on a sounder basis. But it means that we are not entitled to draw any deductions from the absence of a genus and that we must ensure that the genera we use as criteria are truly representative of one another. To use the example of the Falconiformes, the fact that both groups of Vultures are infested with Falcolipeurus while the ordinary Hawks have Degeeriella does not mean that the New and Old World Vultures are more closely related to one another than they are to the ordinary Hawks, because Falcolipeurus and Degeeriella do not represent one another, in the sense that they are not closely-allied derivatives from one stock. But if the Old and New World Vultures possessed in common a genus derived from Degeeriella but different from the genus found on Hawks, or if the Hawks were

infested with a segregate from Falcolipeurus which differed from the genus as found on Old and New World Vultures, then we would be safe in deducing that the two groups of Vultures were more closely allied to each other than to the Hawks.

The systematic Position of Scopus and the Bustards.

In my former paper (1942) I argued from the evidence of the parasites that Scopus is either a member of the Charadriiformes or that it represents a very early offshoot from the Charadriiform branch of a common stem from which both Charadriiformes and Ciconiiformes arose. I still consider this latter alternative probable, but would withdraw the suggestion that Scopus necessarily arose from the Charadriiform branch; there is insufficient evidence on this point, because two of the genera of Mallophaga concerned are not representative in the sense in which I have used the word above. In consequence, Scopus may equally well be an early offshoot from the Ciconiiform branch rather than the Charadriiform.

I also stated that the Bustards are not Gruiformes. I still think the evidence is against their belonging to this order, but the evidence is much weaker than I then thought to be the case, since Otidoecus and Otilipeurus are not represented by allied genera on the Cranes. I still say that the parasite-evidence suggests strongly that the Bustards do not belong to the Gruiformes and are a very ancient and primitive group, but not that it proves this.

The systematic position of the Tropic-birds.

The Phaethontidae or Tropic-birds seem almost invariably to be included by ornithologists in the Pelecaniformes, though some authors

seem to have misgivings on the point. On the evidence of their mallophaga, Harrison (1926, p. 378) & Thompson (1938, p. 459) have suggested that they are a good deal nearer to the Laridae. Since these authors' papers will not have been read by many ornithologists, and one piece of evidence escaped Thompson (Harrison does not give the evidence) it may not be out of place to re-examine the question.

The parasites of the Pelecaniformes are rather well-known, but the different families possess rather different sets of parasites, one or more genera being often absent. But their "Esthiopterum" (present on all groups) is a Pectinopygus; they never possess a Philopterus s.l. nor a "Nirmus"; their "Menopon" is Eidmanniella, and their representative of Colpocephalum is a Colpocephalum s.str., with or without the addition of a Tetrophthalmus. The Charadriiformes have a totally distinct set of parasites: their representative of Philopterus is Saemundssonia, which is peculiar to themselves; they are infested by at least one segregate from Nirmus (usually Quadraceps), and they have no "Esthiopterum"; their "Menopon" is Austromenopon, and their "Colpocephalum" is Actornithophilus.

Few collectors of Mallophaga have had the opportunity to collect material from Tropic-birds, but we know three of the genera infesting this group of birds; these are Saemundssonia, Austromenopon and Actornithophilus. Not only are all these genera typical of the Charadriiformes, but the species would not seem out of place if encountered on a Gull or a Tern. I have stated elsewhere (1942, p. 100) that I regard three correspondences of parasite-genera from different hosts as establishing a certainty that the hosts are related, but this must now be modified by stating that the genera must represent one another in the sense in which I have used this phrase

above. In the present instance we find that three genera known from the Tropic-birds are the same as genera found on the Charadriiformes, that none of them show any close resemblance to those found on Pelecaniformes, and that two of the pairs of genera under discussion (Eidmanniella and Austromenopon, Colpocephalum and Actornithophilus) represent one another on the two orders of birds. I regard this as almost conclusive proof that the Tropic-birds belong to the order Charadriiformes, and that their peculiar foot (which I believe to be the main character which has caused their inclusion in the Pelecaniformes) has been acquired independently. I am informed that oological evidence would support my belief. As regards their position within the order, the evidence is not sufficient for a decision, especially while we know no "Nirmus" from the group, but the available evidence derived from their parasites would not bar their being placed very near to the Laridae (Gulls and Terns).