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The perils of using host relationships in parasite taxonomy: phylogeny of the *Degeeriella* complex

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Abstract

The taxonomy of lice (Insecta: Phthiraptera) is often heavily influenced by host taxonomy. The use of host information to define genera of avian lice in the widespread *Degeeriella* complex has been prevalent but has created problems. Several workers have suggested that genera defined on the basis of host association are not monophyletic. We used sequences of nuclear (elongation factor-1α) and mitochondrial (cytochrome oxidase I) genes to test the monophyly of several genera in the *Degeeriella* complex. Parsimony and likelihood analyses of these data indicated that many genera in the *Degeeriella* complex are not monophyletic, such that species occurring on the same host groups do not form monophyletic groups. Biological features of hosts (including predaceous habits, brood parasitism, and hole nesting) for species in the *Degeeriella* complex likely provide opportunities for switching of lice between host groups. In addition, dispersal of lice via phoresy on hippoboscid flies also likely provides opportunities for host switching in the *Degeeriella* complex. This study indicates that the overuse of host taxonomy in louse taxonomy can result in classifications that do not reflect phylogenetic history. © 2002 Elsevier Science (USA). All rights reserved.

1. Introduction

Taxonomic decisions for lice (Insecta: Phthiraptera) are often heavily influenced by host taxonomy. The generic names of many groups of lice, which are ectoparasites of birds and mammals, are often derived directly from host names (Hopkins and Clay, 1952). Many genera are confined to a single host group (e.g., *Cuculicola* on cuckoos, *Cotingacola* on cotingas), being circumscribed by both host occurrence and morphological differences. Some authors are even more extreme than the relatively conservative treatment of Hopkins and Clay (1952), recognizing large numbers of new genera of lice solely on the basis of their host occurrence (e.g., Zlotorzycka, 1964).

Other problems of potential circularity arise in the description of new species of lice. For example, many workers have fallen into the practice of using a new host record as a justification for erecting a new species, under the assumption that the same species of louse does not occur on multiple species of hosts. This practice has led to the description of new species on scant comparisons of morphological features with congenerics and often on the basis of single, poorly mounted specimens.

To some extent, reliance on host information in the description of phthirapteran diversity is unavoidable. In the alpha taxonomy of free-living organisms, geography plays an important role in organizing specimens into populations. In the same way, hosts organize individual lice into populations with recognizable boundaries. Whether these boundaries are meaningful requires careful examination of morphological features. However, the danger in taxonomic work on parasites comes when host taxonomic boundaries do not correspond to biologically meaningful boundaries for the parasites. For example, often alpha taxonomic revisions of lice are undertaken on the basis of a circumscribed host group, rather than on morphological features of the lice themselves. This creates the tendency for description of generic boundaries solely on the basis of host occurrence. In this study we highlight a group of lice that

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perhaps epitomizes this practice and point out the dangers of using host information in louse taxonomy.

The *Degeeriella* complex as defined by Clay (1958) is a group of genera sharing some common morphological features, such as a medially interrupted ventral carina. Members of the *Degeeriella* complex parasitize a wide diversity of avian groups. This complex has been well recognized by louse taxonomists (Clay, 1958; Eichler, 1963) and its monophyly, together with the closely related *Otidoecus* complex, is strongly supported by morphological (Smith, 2001) and molecular (Cruickshank et al., 2001) data. Within the *Degeeriella* complex, species are divided into several genera, and generic boundaries generally correspond to host orders or families. Exceptions do occur; for example, *Picicola* occurs on both the avian orders Piciformes and Passeriformes. However, circumscription of genera by single host groups is the rule. Clay (1958) indicates for the *Degeeriella* complex that "it has not been possible to find characters of generic or suprageneric importance," suggesting that genera in the *Degeeriella* complex are not currently defined on the basis of morphological synapomorphies.

Some authors have questioned the validity of many of the genera in the *Degeeriella* complex (Clay, 1958; Dalgleish, 1969), although none have provided a revision that would assign genera to perceived natural (i.e., monophyletic) groups. For example, Clay (1958) indicated that members of the genus *Capraiella* are closer to members of the *Degeeriella fulva* species group than are other members of *Degeeriella*. Dalgleish (1969) suggested that the *thripias* species group of *Picicola* is closely related to the *rufa* species group of *Degeeriella*, which are parasites of falcons (Falconidae). The goal of our current study is to assess the monophyly of these and other genera within the *Degeeriella* complex to determine whether concerns about the overuse of host taxonomy in louse classification are well founded.

To examine relationships within the *Degeeriella* complex we obtained sequences of both nuclear elongation factor-1α (EF-1α) and mitochondrial cytochrome oxidase I (COI) genes. We included members of 8 of the 16 genera within this complex and multiple representatives of the genera *Picicola*, *Cuculicola*, *Degeeriella*, *Cotingacola* and *Austrophilopterus*, including representatives of the "problem taxa" identified by Clay (1958) and Dalgleish (1969) as discussed above. We constructed phylogenies based on these sequences and assessed the monophyly of the above five genera.

2. Materials and methods

2.1. Samples

We removed lice from various species of birds using an ethyl acetate fumigation method (Clayton et al., 1992). We included samples of 22 members of the *Degeeriella* complex (Table 1). As part of the ingroup, we also sampled two species of the *Otidoecus* complex, which is believed to be very closely related to the *Degeeriella* complex (Clay, 1958; Cruickshank et al., 2001). Members of seven other genera of lice were used as an outgroup (Table 1).

2.2. Sequencing

We stored specimens of lice dry at −70 °C or in 95% ethanol at −20 °C. For individual lice, we removed the head from the body and placed both parts in a digestion buffer from a Qiagen tissue kit at 55 °C for 56 h. The head and the body were then removed from the buffer and mounted in balsam on a microslide as a voucher for the DNA sequence. This procedure preserves all the features necessary for identification. The remainder of DNA extraction proceeded according to manufacturer's protocols (Qiagen).

We performed PCR on the DNA extracts, amplifying both the EF-1α and the COI genes. The primers EF1-For3 and EF1-Cho10 (Danforth and Ji, 1998) were used for EF-1α and the primers L6625 and H7005 (Hafner et al., 1994) for COI. Gene amplification and sequencing protocols followed Johnson and Clayton (2000). Because these sequences are protein coding, alignment was straightforward (GenBank Accession Nos. AF444846–AF444876 and AF447184–AF447211).

2.3. Analysis

We used PAUP* version 4.0 b8 (Swofford, 2001), unless otherwise indicated, for all phylogenetic analyses. To evaluate the relative rates of substitution in these nuclear and mitochondrial genes, and their potential for multiple substitution, we plotted pairwise divergences for COI against those for EF-1α. In phylogenetic analyses we used the genus *Haematomyzus*, representing the suborder Rhynchophthirina, to root the entire tree, the remainder of which are members of the suborder Ischnocera. Both independent and combined analyses were used to explore differences and similarities in trees derived from alternate gene regions. We used symmetric difference distances (Penny and Hendy, 1985) to compare tree topologies from each gene analyzed separately.

We used the partition homogeneity test (Farris et al., 1994, 1995; Swofford, 2001) to determine whether the EF-1α and COI genes contained significantly different signals. The partition homogeneity test can produce significant results if one gene has experienced many multiple substitutions or contains random information (Dolphin et al., 2000; Barker and Lutzoni, 2002). COI evolves at a much faster rate than EF-1α, so for distantly related taxa, it may retain little phylogenetic signal. To determine whether this might be the case, we

Table 1
Samples sequenced

Species	Host	Host order	Locality
Ingroup (*Degeeriella* and *Otidoecus* complexes)			
Austrophilopterus pacificus	*Andigena nigrirostris*[a]	Piciformes	Peru
Austrophilopterus sp.	*Selenidera gouldi*[a]	Piciformes	Brazil
Austrophilopterus sp.	*Ramphastos brevis*[a]	Piciformes	Ecuador
Austrophilopterus subsimilis	*Ramphastos sulfuratus*[a]	Piciformes	Mexico
Austrophilopterus torquatus	*Pteroglossus torquatus*[a]	Piciformes	Mexico
Picicola snodgrassi	*Melanerpes carolinensis*[a]	Piciformes	Louisiana
Picicola porisma	*Colaptes auratus*[a]	Piciformes	New Mexico
Picicola sp.	*Chelidoptera tenebrosa*[a]	Piciformes	Brazil
Picicola sp.	*Galbula albirostris*[a]	Piciformes	Brazil
Picicola sp.	*Monasa nigrifrons*[a]	Piciformes	Bolivia
Picicola sp.	*Nystalus chacuru*[a]	Piciformes	Bolivia
Picicola capitatus	*Dendropicos fuscescens*[a]	Piciformes	South Africa
Picicola sp.	*Mesopicus pyrrhogaster*[a]	Piciformes	Ghana
Capraiella sp.	*Eurystomus gularis*[a]	Coraciiformes	Ghana
Degeeriella carruthi	*Falco sparverius*[b]	Falconiformes	Utah
Degeeriella fulva	*Buteo regalis*[b]	Falconiformes	Utah
Cotingacola stotzi	*Querula purpurata*	Passeriformes	Brazil
Cotingacola sp.	*Querula purpurata*	Passeriformes	Brazil
Trogoninirmus sp.	*Trogon melanocephalus*[a]	Trogoniformes	Mexico
Cuculicola sp.	*Chrysococcyx klaas*[c]	Cuculiformes	Ghana
Cuculicola atopus	*Piaya cayana*	Cuculiformes	Mexico
Rhynonirmus sp.	*Scolopax bukidnonensis*	Charadriiformes	Philippines
Colinicola docophoroides	*Callipepla californica*	Galliformes	Utah
Cuclotogaster hopkinsi	*Francolinus africanus*	Galliformes	South Africa
Outgroup			
Colilipeurus colius	*Colius indicus*	Coliiformes	South Africa
Penenirmus zumpti	*Lybius torquatus*[a]	Piciformes	South Africa
Quadraceps punctatus	*Larus cirrocephalus*	Charadriiformes	South Africa
Brueelia marginella	*Momotus momota*[a]	Coraciiformes	Mexico
Nyctibicola longirostris	*Nyctibius jamaicensis*	Caprimulgiformes	Mexico
Chelopistes texanus	*Ortalis vetula*	Galliformes	Mexico
Haematomyzus elephantis	*Elephas maximus*	Proboscidea	India

Note. Host habits.
[a] Hole nester.
[b] Bird of prey.
[c] Brood parasite.

also conducted a partition homogeneity test using only members of the *Degeeriella* and *Otidoecus* complexes (i.e., excluding the seven outgroup species). The partition homogeneity test involving only the ingroup taxa was not significant (see Results), so we decided to combine gene regions for purposes of estimating the phylogeny within the *Degeeriella* and *Otidoecus* complexes.

We first used unweighted parsimony to reconstruct a tree for the *Degeeriella* complex. Bootstrap analysis with 1000 replicates was used to evaluate the relative support for nodes in this tree (Felsenstein, 1985). To evaluate the sensitivity of the tree topology to method of analysis, we also estimated a maximum-likelihood model that best fit the data using the likelihood ratio test procedure outlined by Huelsenbeck and Crandall (1997) as implemented in Model Test (Posada and Crandall, 1998). This analysis resulted in a model with six substitution categories (general time reversible), unequal base frequencies, invariant sites, and rate heterogeneity according to a gamma distribution (eight rate categories). We used the estimated likelihood model parameters in searches using 10 random-addition replicates and TBR branch swapping. We evaluated the support for this tree by conducting 100 bootstrap replicates with single random-addition replicates and TBR branch swapping. For comparison, we also used Bayesian maximum-likelihood methods with Markov Chain Monte Carlo searching (Larget and Simon, 1999), using the program MrBayes (Huelsenbeck, 2001). We used four search chains, allowing each to run 200,000 "generations." Trees were saved every 100 generations and we computed a 50% consensus tree of trees from generations 50,000 to 200,000.

3. Results

Parsimony analyses of both gene regions independently produced different trees, but eight nodes were in common (not shown). The symmetric difference distance between parsimony trees from genes analyzed independently ranged from 32 to 40 (mean 36). Phylogenetic relationships identified by each gene region were similar to those recovered in combined analyses, which are discussed below. Maximum-likelihood analyses of each gene independently produced trees that were slightly more similar to each other than those from parsimony analyses (symmetric difference distance range from 33 to 34, mean 33.5).

When all taxa were included, a partition homogeneity test indicated that EF-lα and COI are heterogeneous partitions ($P < 0.001$). Dramatic differences in homoplasy can potentially cause gene partitions to be heterogeneous (Barker and Lutzoni, 2002; Bull et al., 1993; Dolphin et al., 2000). In our case, the homoplasy from EF-lα (consistency index = 0.435) was much less than that from COI (consistency index = 0.264). Plots of pairwise sequence divergence comparisons for COI against those for EF-lα indicated that COI evolves at a faster rate and likely experiences more multiple substitutions (not shown). No nodes showed conflict above the 50% bootstrap level in trees produced from independent analysis of the EF-lα and COI genes. Thus, while differences between trees from independent analyses were not strongly supported, the partition homogeneity test was still quite significant. A lack of bootstrap support for conflict suggests that the hetero-

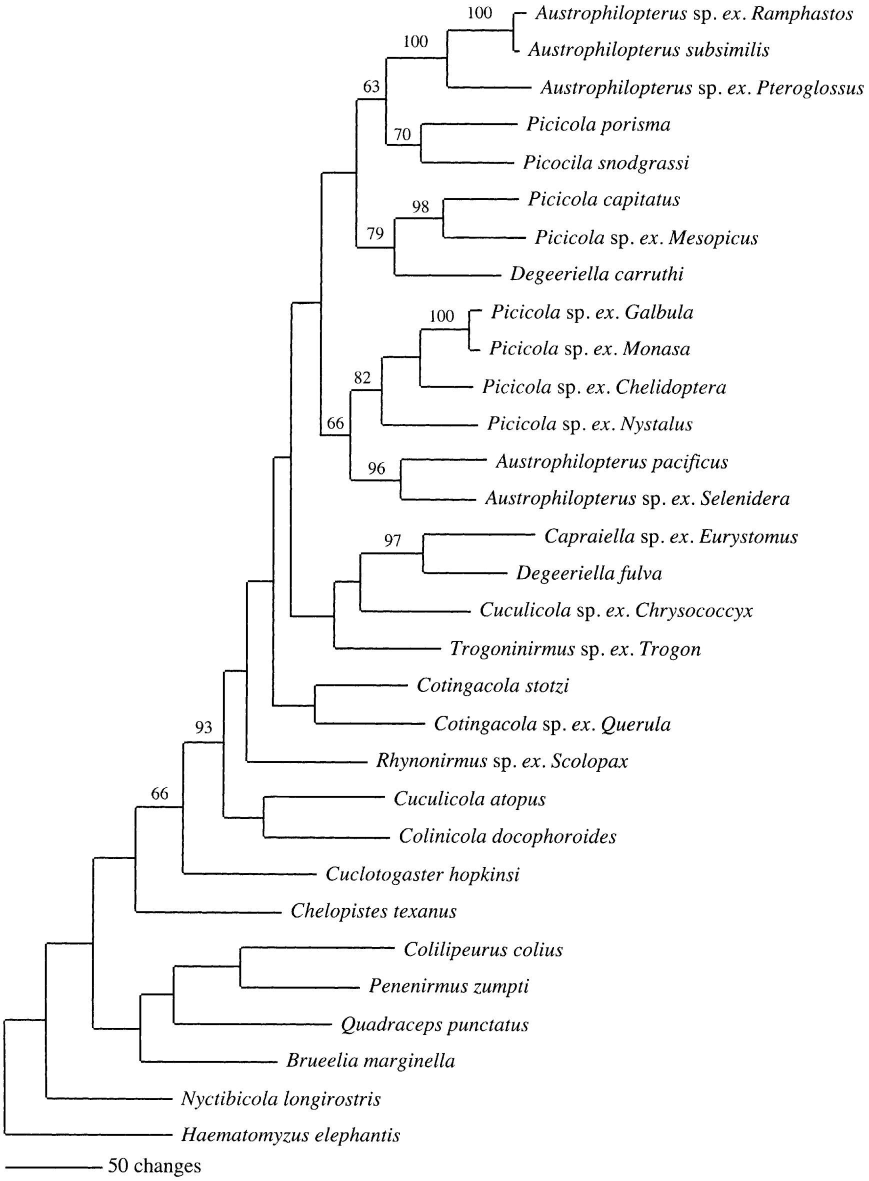

Fig. 1. Single tree (length = 2161, rescaled consistency index = 0.118) derived from parsimony analysis of combined COI and EF-lα DNA sequences. Numbers above branches indicate bootstrap support from 1000 replicates.

geneity is likely due to an underlying difference in rates, rather than phylogenetically meaningful differences (Barker and Lutzoni, 2002). A partition homogeneity test using only the ingroup taxa resulted in a nonsignificant *P* value ($P = 0.13$), indicating that differences in homoplasy most affect heterogeneity for comparisons of highly divergent taxa. Because 50% bootstrap topologies did not differ between gene regions, and because heterogeneity was not evident for ingroup comparisons, we decided that combined analysis should provide the best estimate of the tree topology for the ingroup.

Unweighted parsimony analysis of combined gene regions produced a single tree (Fig. 1). This tree indicates monophyly for a group containing both the *Degeeriella* and the *Otidoecus* complexes, but does not recover monophyly of either complex by itself. Specifically, *Rhynonirmus* (traditionally a member of the *Otidoecus* complex) falls within the *Degeeriella* complex with strong support (bootstrap 93%). Within the *Degeeriella* complex, several relationships are well supported. *Degeeriella*, *Austrophilopterus*, *Cuculicola*, and *Picicola* are all paraphyletic or polyphyletic. *Degeeriella carruthi* is sister to *Picicola* from African woodpeckers and this is strongly supported (bootstrap 79%). Meanwhile, *D. fulva* is closely related to *Capraiella* (bootstrap 97%), resulting in polyphyly of *Degeeriella*. In addition, *Picicola snodgrassi* plus *Picicola porisma* are sister to one clade of *Austrophilopterus* (bootstrap 63%), resulting in

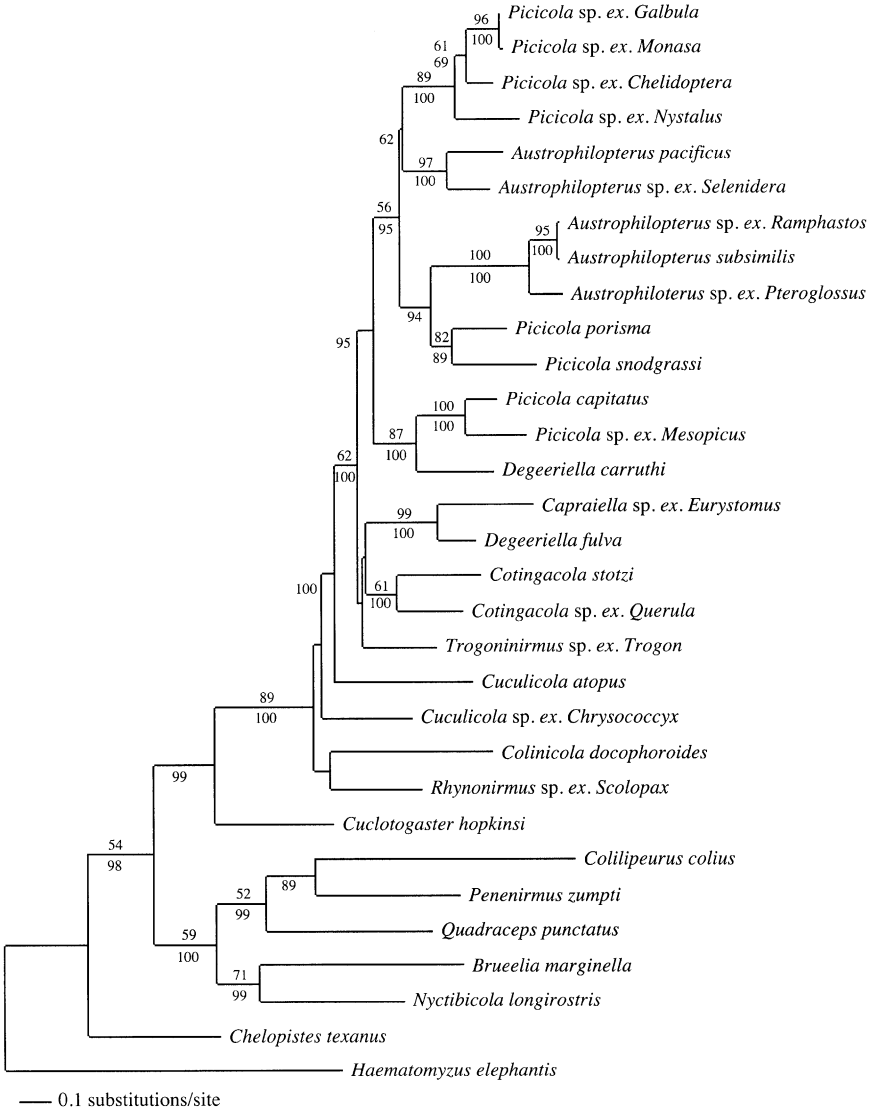

Fig. 2. Tree derived from maximum-likelihood analysis of combined COI and EF-1α DNA sequences ($L = 9062.31132$). Model includes six substitution types ($A\text{-}C = 2.451$, $A\text{-}G = 11.443$, $A\text{-}T = 1.370$, $C\text{-}G = 5.201$, $C\text{-}T = 17.469$, $G\text{-}T = 1.00$), unequal base frequencies ($A = 0.303, C = 0.134, G = 0.196, T = 0.367$), invariant sites (0.205), and rate heterogeneity according to a gamma distribution (shape parameter $= 0.203$). Numbers above branches indicate support from 100 bootstrap replicates. Numbers below branches indicate support values from Bayesian analyses.

paraphyly of both *Austrophilopterus* and *Picicola*. Two species of *Cuculicola* included in this study do not appear to be closely related, although this result does not receive strong support. The two species of *Cotingacola* are sister taxa in this tree, indicating potential monophyly of *Cotingacola*. Within *Picicola*, one clade uniting species occurring on puffbirds (Bucconidae) and jacamars (Galbulidae) is strongly supported. However, lice occurring on puffbirds are paraphyletic with respect to those occurring on jacamars. Another large clade unites *D. carruthi* and all species of *Picicola* and *Austrophilopterus*, but this receives weak support (bootstrap $< 50\%$).

Maximum-likelihood analyses of combined gene regions produced results similar (Fig. 2) to that of the combined unordered parsimony analysis. Support is high for a clade containing all members of the *Degeeriella* complex plus *Rhynonirmus*, making the *Otidoecus* complex paraphyletic. Another deep branch uniting all species of *Austrophilopterus* and *Picicola* and *D. carruthi* receives strong support from Bayesian analysis (Fig. 2), even though it does not receive strong bootstrap support in either parsimony or likelihood analyses. Well-supported clades from the parsimony analysis within the *Degeeriella* complex are also recovered in the likelihood analysis. This includes well-supported paraphyly for *Degeeriella*, *Austrophilopterus*, and *Picicola*. In addition, *Cuculicola* is again paraphyletic, but this was not strongly supported. Monophyly of *Cotingacola* is supported in the likelihood analysis.

4. Discussion

Combined analyses of nuclear EF-1α and mitochondrial COI genes produced well-resolved phylogenies for members of the *Degeeriella* complex. Paraphyly was recovered for four of five genera sampled by more than one species. While not all nodes in the tree received strong support, the paraphyly of three of these genera (*Degeeriella*, *Austrophilopterus*, and *Picicola*) was relatively strongly supported (bootstrap $> 60\%$ in each case). This confirms earlier suspicions (Clay, 1958; Dalgleish, 1969) that many genera within the *Degeeriella* complex, defined largely on host association, do not reflect evolutionary relationships.

Several relationships recovered by both parsimony and likelihood analyses are of note. Two species of *Picicola* from African woodpeckers (Picidae) are sister to *D. carruthi* from *Falco*. Dalgleish (1969) indicated that this relationship was the case based on morphology, noting that the structure of the genitalia of the *Picicola thripias* species group (found on African woodpeckers) is more similar to that of species of *Degeeriella* from Falconidae than it is to other members of *Picicola*. *P. snodgrassi* and *P. porisma* from New World woodpeckers are sister to one clade of *Austrophilopterus*, also entirely New World in distribution. A second clade of *Austrophilopterus* is sister to a clade of *Picicola* from puffbirds (Bucconidae) and jacamars (Galbulidae), and all of these hosts are New World in distribution. The taxa of *Picicola* on puffbirds and jacamars represent the subgenus *Tyrannicola*, which also occurs on Passeriformes (Oniki and Emerson, 1981; Williams, 1979). Puffbirds and jacamars are closely related (Sibley and Ahlquist, 1990) and the clade of *Picicola* on these species appears to reflect the relationship at that level. Considering the relationships among species of *Austrophilopterus*, toucans in the genera *Andigena* and *Selenidera* are closely related (Barker and Lanyon, 2000) as are their respective lice. However, the host genera *Ramphastos* and *Pteroglossus* are not sister taxa (Barker and Lanyon, 2000), yet their lice appear to be sisters.

A large clade containing all species of *Austrophilopterus* and *Picicola* as well as *D. carruthi*, was recovered in both analyses, and this group was strongly supported in Bayesian maximum-likelihood analyses. The former two genera, as included in this study, are all on Piciformes, indicating some influence of host relationship on the phylogenetic relationships among species of lice in this group. Relationships among species outside this large group of primarily piciform lice are generally less clear, but several consistent groupings are evident. First, our single sample of *Capraiella* (from a roller in Africa) is sister to *D. fulva* (from a hawk in North America), and this is strongly supported. This general relationship was also recognized based on similarities in the morphology of male genitalia and in head shape (Clay, 1958). Clay suggested that *Capraiella* is closely related to the *D. fulva* species group and that the retention of *Capraiella* as a separate genus is placed in doubt. The sequence divergence for EF-lα between these two species is only 2.6% and the divergence for COI is 21.9%, which are extremely low compared to divergences between other species. Another consistent relationship is that two species of *Cotingacola* from the same host species (*Querula purpurata*) are sister taxa. However, more sampling of this genus from other host species is needed to assess its monophyly. Relationships among other poorly sampled genera are less clear, but little correspondence between host relationships and louse phylogeny is evident. For example, the two species of *Cuculicola* are never sister taxa in any analysis.

Given the paraphyly of many genera in the *Degeeriella* complex, taxonomic revision is warranted. In the past, many species in this complex have been placed in the single genus *Degeeriella*. The genetic divergences between members of the *Degeeriella* complex are comparable to divergences within other well-marked genera of Ischnocera (Cruickshank et al., 2001). However, *Rhynonirmus*, a member of the closely related *Otidoecus* complex, appears to come out within the *Degeeriella* complex. This makes it difficult to simply sink all genera in the *Degeeriella* complex into *Degeeriella* without further study. Perhaps several genera can still be recognized by identifying more thoroughly some of the subgroups within the *Degeeriella* complex. For example, we consistently recovered monophyly of a group of lice on Piciformes (plus *Degeeriella* from Falconidae). Perhaps groups such as these can be recognized as separate genera upon more phylogenetic study. For the time being, it seems reasonable to perhaps lump all members of the *Degeeriella* and *Otidoecus* complexes into *Degeeriella*, given the generally low morphological variation between species in these groups (Clay, 1958) and the relatively low sequence divergences among these groups.

The extreme diversity of host groups within the *Degeeriella* complex and the general lack of monophyly of genera defined on the basis of host association raise questions about why this group of lice tends to show little correspondence to host phylogeny at deep taxonomic scales. Other groups of lice often show considerable cospeciation with their hosts (Hafner et al., 1994; Johnson and Clayton, 2002; Page et al., 1998). Several factors probably play a role in reducing concordance with host relationships in the *Degeeriella* complex. First, avian Ischnocera are often found attached to flies in the family Hippoboscidae, which are also parasites of birds. These flies have wings, can fly between hosts, and are generally less host specific than lice (Corbet, 1956). There are many records of hitchhiking (phoresis) of lice in the *Degeeriella* complex on hippoboscid flies (Keirans, 1975). Thus, phoresis may provide an opportunity for dispersal of lice between host species, promoting host switching and a breakdown of host specificity. Another group of lice with a large number of records of phoresis (*Brueelia*) also shows little evidence of cospeciation (Clayton et al., 2002). However, other genera of lice with fewer instances of phoresis tend to exhibit a greater correspondence between host phylogeny and parasite phylogeny (Clayton et al., 2002). Together these studies implicate phoresis in playing a potentially important role in the dispersal of lice between host species.

In addition to phoresis, other biological factors may be important in influencing the lack of correspondence to host phylogeny of the *Degeeriella* complex. Some of the host groups whose lice do not form monophyletic groups possess biological features that would promote opportunities for host switching. First, members of the Falconiformes (hawks and falcons) prey on other birds. Lice may transmit between host species (from prey to predator) during predation (Clay, 1949). One might expect selection to favor lice that leave their dead host for its predator, given that continued survival on the prey is not possible. Species of *Degeeriella* (parasites on Falconiformes) are closely related to lice from other host groups, often showing little genetic divergence. This result indicates that transfer of lice between prey and predators may be relatively common in the history of the radiation of the *Degeeriella* complex. However, ecological studies of the transfer and survival of lice from prey to predators are needed to test this hypothesis.

Another case of unique biological features involves cuckoos. Most cuckoos are brood parasites of many species of birds, laying their eggs in the nests of other birds. Cuckoo hosts raise the young cuckoos by feeding and brooding them. A large fraction of the transmission biology of lice involves vertical transmission between parents and offspring (Lee and Clayton, 1995). Cuckoo nestlings and fledged juveniles have been documented to carry lice from their foster bird hosts (Lindholm et al., 1998). These observations indicate that opportunities for host switching do exist between cuckoo hosts and cuckoos, and thus multiple independent origins of cuckoo lice from avian hosts might be expected.

Finally, many of the hosts of species of lice in the *Degeeriella* complex nest in holes, including nearly all species of Piciformes, Trogoniformes, and Coraciiformes. Competition for nest holes in bird species can be extremely intense, and interspecific nest hole takeovers can be common (Merilä and Wiggins, 1995). Lice can often be recovered from the nests of birds (Nordberg, 1936) and so may survive away from the body of the host for a short period of time in a nest. This time may be enough for a host switch to occur in conjunction with a nest hole takeover. In addition, lice glue their eggs to host feathers, and feathers from birds are often used to line the nest. Thus, an interspecific nest takeover may occur before the louse eggs have hatched, allowing nymphs a chance to transfer to a different species of host. Studies of owl lice (*Strigiphilus*) indicate that species of lice are often shared by sympatric species of owls that nest in holes (Clayton, 1990). The role of nest holes in dispersal of lice between host species needs to be examined in more detail.

In summary, the current definitions of genera in the *Degeeriella* complex of lice do not represent monophyletic groups. These genera are largely defined on the basis of host association, and phylogenetic analysis reveals that lice from a particular host group are not always closely related. The life history characteristics of hosts of lice in the *Degeeriella* complex provide several avenues for host switching, which may explain why louse phylogeny does not more tightly mirror host phylogeny in this group.

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