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LINKING COEVOLUTIONARY HISTORY TO ECOLOGICAL PROCESS: DOVES AND LICE

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Abstract.—Many host-specific parasites are restricted to a limited range of host species by ecological barriers that impede dispersal and successful establishment. In some cases, microevolutionary differentiation is apparent on top of host specificity, as evidenced by significant parasite population genetic structure among host populations. Ecological barriers responsible for specificity and genetic structure can, in principle, reinforce macroevolutionary processes that generate congruent host-parasite phylogenies. However, few studies have explored both the micro- and macroevolutionary ramifications of close association in a single host-parasite system. Here we compare the macroevolutionary histories of two genera of feather lice (Phthiraptera: Ischnocera) that both parasitize New World pigeons and doves (Aves: Columbiformes). Earlier work has shown that dove body lice (genus *Physconelloides*) are more host specific and have greater population genetic structure than dove wing lice (*Columbicola*). We reconstructed phylogenies for representatives of the two genera of lice and their hosts, using nuclear and mitochondrial DNA sequences. The phylogenies were well resolved and generally well supported. We compared the phylogenies of body lice and wing lice to the host phylogeny using reconciliation analyses. We found that dove body lice show strong evidence of cospeciation whereas dove wing lice do not. Although the ecology of body and wing lice is very similar, differences in their dispersal ability may underlie these joint differences in host specificity, population genetic structure, and coevolutionary history.

Key words.—Columbidae, cospeciation, host, macroevolution, parasite, Phthiraptera, specificity.

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Comparing the phylogenies of interacting groups, such as hosts and parasites, is a topic of considerable recent interest (see reviews by Brooks and McLennan 1991; Klassen 1992; Hoberg et al. 1997; Paterson and Gray 1997; Page and Charleston 1998; Page 2003). Phylogenies of interacting species are often congruent, or nearly so, due to repeated cospeciation events (Hafner et al. 1994; Moran and Baumann 1994; Page et al. 1998). In other cases, phylogenies show a complete lack of congruence, owing to host switching, extinction, and other macroevolutionary events that erode congruence (Barker 1991; Hoberg et al. 1997; Johnson et al. 2002a). These events may be governed by simple ecological factors, such as barriers to parasite dispersal, which reinforce the host specificity and population genetic structure of parasites. In short, ecological factors that dictate microevolutionary patterns may also be responsible for long-term macroevolutionary patterns, despite the vast expanse of time involved (Clayton et al. 2003). Unfortunately, few studies have explored both the micro- and macroevolutionary ramifications of close association in a single host-parasite system.

In this paper we compare the histories of two genera of feather lice (Phthiraptera: Ischnocera) that parasitize New World pigeons and doves (Aves: Columbiformes). The terms ''pigeon'' and ''dove'' refer to relative body sizes (large and small, respectively) and have no formal meaning; thus we refer to all species as ''doves'' for sake of simplicity. New World doves are parasitized by two common genera of feather lice known as ''body'' lice (genus *Physconelloides*) and ''wing'' lice (genus *Columbicola*). These two genera, which are not closely related (Cruickshank et al. 2001), have both been subjected to recent taxonomic revisions (Clayton and Price 1999; Price et al. 1999; Adams 2002).

Body lice and wing lice are ecological ''replicates'' in many respects (Johnson and Clayton 2003). Both groups are permanent parasites that complete their entire life cycle on the host, even gluing their eggs to the feathers with a glandular cement (Clayton 1991). Body lice lay their eggs and spend most of their time on the host's abdominal feathers. They escape from host defense (preening) by burrowing into the downy portions of these abdominal feathers (Clayton et al. 1999). Wing lice lay their eggs and spend most of their time on feathers of the wings and tail. Wing lice are elongate in shape and escape from preening by inserting in the space between barbs of the large flight feathers (Clayton et al. 1999). Body and wing lice both feed on feathers. Both kinds of lice are usually transmitted to new hosts during periods of direct contact between host individuals, such as parent birds and their offspring in the nest (Clayton and Tompkins 1994).

Despite their similarities, body lice and wing lice also have some important differences. For example, dove body lice are significantly more host specific than dove wing lice (Johnson et al. 2002b). Most species of body lice are found on a single species of host, whereas many wing lice occur on multiple species of hosts. This difference in host specificity may arise, in part, from differences in the dispersal ability of the two groups of lice (see Discussion).

Dove body lice also show significantly more population genetic structure than dove wing lice, which may also be attributable to differences in dispersal ability (Johnson et al. 2002b). Considering louse populations on the same host species, body lice tend to show population genetic differences between geographic localities, whereas wing lice do not. Furthermore, in cases where species of body lice are distributed across multiple host species, there is substantial genetic struc-

ture in body louse populations across those hosts, whereas wing lice show much less structure (Johnson et al. 2002b).

We compared the coevolutionary histories of *Physconelloides* body lice and *Columbicola* wing lice by reconstructing phylogenies for representatives of these two genera and their hosts, using nuclear and mitochondrial DNA sequences. We restricted our analysis to host taxa for which we had samples of both genera of lice. We tested the explicit prediction that body lice, which have the greatest specificity and population genetic structure, also show the most cospeciation. This pattern is not a foregone conclusion. Host specificity is an ecological index to a parasite's distribution among host species. Although specificity is a necessary condition for cospeciation, it is not a sufficient condition. The specificity shown by a given parasite does not mean that its ancestors were host specific, much less that they underwent cospeciation with their hosts (Brooks 1985; Hoberg 1986; Hoberg et al. 1997). Specificity describes a pattern of current association that may or may not reflect macroevolutionary history.

Methods

DNA Sequencing

Samples of 13 species of doves and their associated wing and body lice were obtained from a variety of localities in the New World, including the United States, Mexico, Peru, and Brazil. In the case of the United States and Mexico, sampling of the dove fauna was comprehensive at single localities, such that we had the potential to detect any deviation from host specificity at a locality, if it existed (see Johnson et al. 2002b). For the 13 species of doves, we sequenced a 1045 base-pair portion of the mitochondrial cytochrome *b* (cyt *b*) gene and the entire β-fibrinogen intron 7 (FIB7) nuclear gene as described by Johnson and Clayton (2000). In addition, we sequenced a 379 base-pair portion of the mitochondrial cytochrome oxidase I (COI) gene using the primers L6625 and H7005 (Hafner et al. 1994).

For lice, we extracted DNA and prepared voucher specimens by removing the head from the body of each louse. We used a Qiaquick Tissue Extraction Kit (Qiagen, Valencia, CA) following manufacturer's protocols to extract DNA from both the head and body in the same tube. We suspended DNA in a final volume of 50 μl of water. The head and body were then reassembled as a mounted slide, thus providing a morphological voucher specimen corresponding to each DNA sequence.

For both genera of lice, we amplified the mitochondrial COI and 12S rRNA genes and the nuclear elongation factor—1 alpha (EF1α) gene using PCR. We used the primer combinations L6625 / H7005 (Hafner et al. 1994) for COI, 12Sai/12Sbi (Simon et al. 1994) for 12S, and EF1a-For 3 / EF1a—Cho10 (Danforth and Ji 1998) for EF1α. We purified PCR products using a Qiagen PCR Purification Kit. DNA sequence data was collected and analyzed using an ABI Prism 377 automated DNA sequencer (Perkin Elmer Applied Biosystems, Foster City, CA). We aligned and reconciled complementary chromatograms using Sequencher 3.1 (GenBank accession numbers AY273875-AY273888; Johnson et al. 2001, 2003). We aligned sequences of 12S using a secondary structure model developed specifically for lice (Page 2000, Page et al., 2002).

Based on COI sequences, Johnson et al. (2002b) identified divergent mitochondrial haplotype lineages (9–18% uncorrected sequence divergence) within some morphologically described species of lice. These divergent haplotypes often clustered by host, and divergences within each haplotype cluster were generally low (< 1% sequence divergence). The host specificity of these divergent haplotypes suggests that these groups should be used as terminals in cophylogenetic analyses. These haplotype groups are indicated by numbers after the species name. Given the low divergences in COI within clusters of haplotypes, we only sequenced one individual of each haplotype for the other genes (EF1α and 12S). We used COI sequences from 2–20 individuals of each louse species (Johnson et al. 2002b) to first identify the divergent lineages and thus the taxa for which sequences of 12S and EF1α were needed.

Phylogenetic Analysis

We conducted all phylogenetic analyses using PAUP* (Swofford 2002). For all taxa, we first conducted partition homogeneity tests (Farris et al. 1994, 1995, Swofford 2002) among gene regions to determine if they could justifiably be combined in an analysis (Bull et al. 1993). This test was not significant ($P > 0.10$) in all cases, therefore we conducted subsequent analyses by combining the gene regions for each group. For Columbiformes, outgroup analyses including other groups of birds (Johnson and Clayton 2000; Johnson 2001) indicated that the small ground doves (*Columbina* and *Claravis*) are sister to all other doves; therefore, we rooted the tree on these two genera. For *Columbicola* we used a representative of the louse genus *Oxylipeurus* to root the tree (Cruickshank et al. 2001). For *Physconelloides*, we used a representative of *Goniodes* to root the tree (Johnson et al. 2001).

For each group, we first reconstructed a tree using equally weighted parsimony. To evaluate support for various nodes in the tree, we performed 1000 replicates of bootstrap analyses (Felsenstein 1985). To evaluate the sensitivity of tree topology to method of analysis, we also used maximum-likelihood analysis. To select the model used in maximum-likelihood searches, we preferred the simplest model that could not be rejected in favor of a more complex one (Huelsenbeck and Crandall 1997) using the program ModelTest (Posada and Crandall 1998). The parameter estimates from ModelTest were used in maximum-likelihood analyses with ten random addition replicates and tree bisection reconnection branch swapping. We constructed 100 maximum-likelihood bootstrap resampling replicates with TBR branch swapping.

Cophylogenetic Analysis

In cophylogenetic analyses, we used comparisons of host and parasite trees resulting from equally weighted parsimony and maximum-likelihood searches. By using both combinations of phylogenies, we were able to assess the robustness of the cophylogenetic results to method of phylogenetic analysis. We used reconciliation analysis (Page 1990a) as implemented in TreeMap (Page 1995) to determine the maxi-

mum number of cospeciation events that could be inferred between the host and parasite trees. We randomized the parasite tree 10,000 times to determine if the number of cospeciation events reconstructed was more than expected by chance (Page 1990b, 1995). We calculated the fraction of host nodes that were inferred to be cospeciation events for both *Columbicola* and *Physconelloides* (after Clayton et al. 2003). These values were compared using the *z*-statistic for comparison of proportions. To evaluate the effect of host-specificity per se on the inferred number of cospeciation events, and on whether more events are present than expected by chance, we broke host associations for both *Columbicola* and *Physconelloides* to make them each 100% host specific (each parasite species associated with only one host species). We removed host-parasite associations in such a way as to maximize the number of cospeciation events that would be inferred in the tree comparisons under reconciliation analysis. We counted the number of cospeciation events for these ''perfectly'' host-specific associations, then determined for each genus whether there were more cospeciation events than expected by chance.

Results

Doves

Combined unweighted parsimony analysis of all three genes produced a single tree (Fig. 1a). This tree is consistent with the broader tree for Columbiformes of Johnson and Clayton (2000). The tree topology is robust to bootstrap resampling, with eight of ten branches recovered in over 70% of bootstrap replicates. Major clades include small ground doves (*Columbina* and *Claravis*), midsized ground doves (*Geotrygon*, *Leptotila*, and *Zenaida*), and arboreal pigeons (*Patagioenas*, which was split from *Columba* by Johnson et al. (2001)). Monophyly of all genera represented by more than one species was supported. Likelihood-ratio tests revealed that a model incorporating six substitution types (general time reversible), unequal base frequencies, invariant sites, and rate heterogeneity according to a gamma distribution could be supported in favor of simpler models. Likelihood searches resulted in a single tree (Fig. 1b), identical to the parsimony tree. Again, eight of ten branches were recovered in over 70% of bootstrap replicates.

Wing Lice

Unweighted-parsimony analysis of the combined gene regions for wing lice (*Columbicola*) produced a single tree (Fig. 2a). Four of eight nodes in this tree were recovered in over 80% of bootstrap replicates. The major lineages of *Columbicola macrourae* did not form a monophyletic group, but this was not strongly supported. Likelihood-ratio tests showed that the same Maximum-likelihood model used for doves was appropriate for wing lice. Maximum-likelihood analyses using this model produced a tree similar in most respects to the parsimony tree (Fig 2b). However, the positions of *C. passerinae* and *C. gracilicapitis* were reversed, and the rooting of the *C. macrourae* + *C. adamsi* + *C. extinctus* clade was altered slightly. Four of eight branches in this tree were recovered in over 50% of bootstrap replicates.

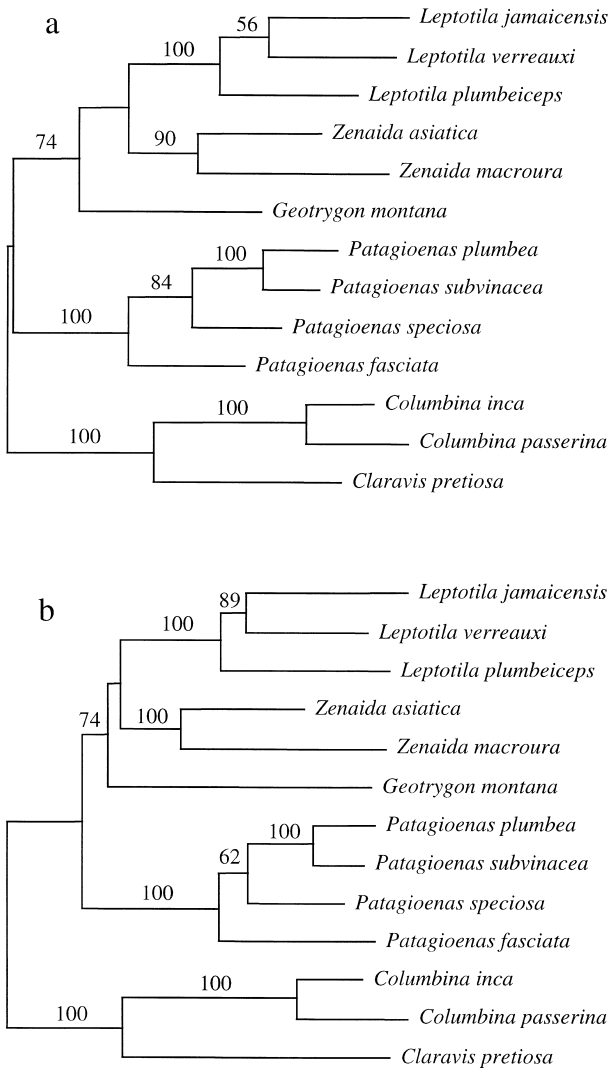
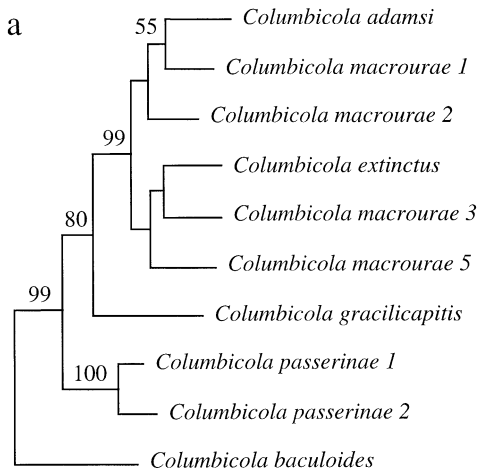


FIG. 1. (a) Phylogeny for Columbiformes based on unweighted parsimony analysis of mitochondrial cytochrome *b*, cytochrome oxidase I, and nuclear β-fibrinogen intron 7 sequences. Length = 1241, RC = 0.341. Numbers above branches indicate bootstrap support. Branch lengths proportional to the number of reconstructed changes over the tree. (b) Phylogeny of Columbiformes based on maximum-likelihood analysis of mitochondrial cytochrome *b*, cytochrome oxidase I, and nuclear β-fibrinogen intron 7 sequences (-ln likelihood = 9420.92). Model included six substitution types (A-C = 2.61, A-G = 13.33, A-T = 1.38, C-G = 1.09, C-T = 20.62, G-T=1.00), unequal base frequencies (A = 0.286, C = 0.287, G = 0.161, T = 0.266), invariant sites (I = 0.561), and rate heterogeneity according to a gamma distribution (shape parameter = 0.905). Numbers above branches indicate bootstrap support. Branch lengths proportional to branch lengths estimated under the maximum-likelihood model.

Tendeiro (1965, 1983–1984) divided the genus *Columbicola* into 10 species groups on the basis of morphology. Adams (2002) further divided *Columbicola* into 24 species groups, also on the basis of morphology. Only five of these groups are distributed in the New World, and four of these are represented in our study. The two species groups represented by more than one taxon (*macrourae* and *passerinae*) are monophyletic in both the parsimony and likelihood trees (Fig. 2).



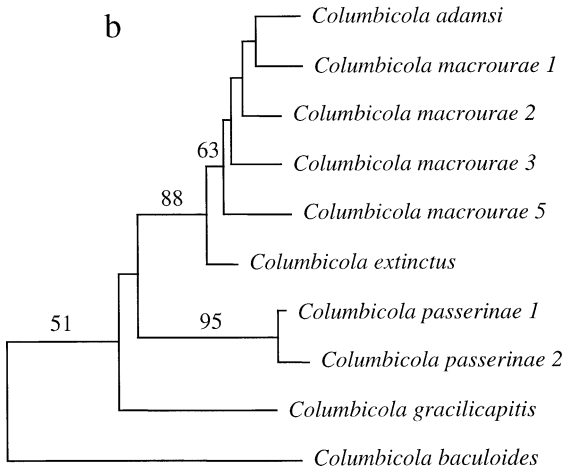
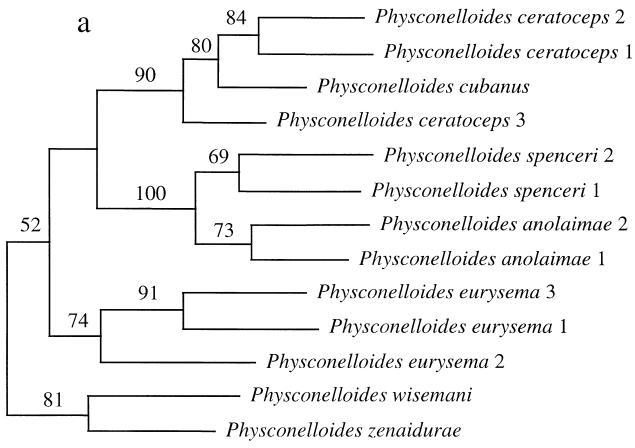


FIG. 2. (a) Phylogeny for *Columbicola* based on unweighted parsimony analysis of mitochondrial COI, 12S, and nuclear EF1α sequences. Length = 1186, RC = 0.290. Numbers after names indicate cryptic species of lice (Johnson et al. 2002b); other conventions as in Figure 1a. (b) Phylogeny of *Columbicola* based on maximum-likelihood analysis of mitochondrial COI, 12S, and nuclear EF1α genes (-ln likelihood = 6094.80). Model included six substitution types (A-C = 0.75, A-G = 8.47, A-T = 1.24, C-G = 2.46, C-T = 11.63, G-T = 1.00), unequal base frequencies (A = 0.322, C = 0.166, G = 0.197, T = 0.316), invariant sites (I = 0.291), and rate heterogeneity according to a gamma distribution (shape parameter = 0.342). Numbers after names indicate cryptic species of lice (Johnson et al. 2002b); other conventions as in Figure 1b. Both trees are rooted on *Oxylipeurus chiniri*.



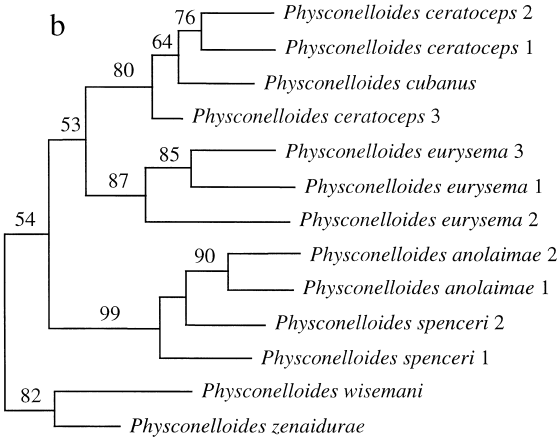


FIG. 3. (a) Phylogeny for *Physconelloides* based on unweighted parsimony analysis of mitochondrial COI, 12S, and nuclear EF1α sequences. Length = 819, RC = 0.229. Conventions as in Figure 2a. (b) Phylogeny of *Physconelloides* based on maximum-likelihood analysis of mitochondrial COI, 12S, and nuclear EF1α genes (-ln likelihood = 4911.08). Model included six substitution types (A-C = 2.71×10^{-6}, A-G = 12.04, A-T = 2.89, C-G = 0.18, C-T = 5.72, G-T = 1.00), unequal base frequencies (A = 0.303, C = 0.155, G = 0.212, T = 0.330), invariant sites (I = 0.582), and rate heterogeneity according to a gamma distribution (shape parameter = 0.731). Conventions as in Figure 2b. Both trees are rooted on *Goniodes* sp.

Body Lice

Unweighted parsimony searches of the combined data set for body lice (*Physconelloides*) produced a single tree (Fig. 3a). Eight of 11 nodes were recovered in over 70% of bootstrap replicates. Likelihood-ratio tests indicated that the same ML model used for doves and wing lice was appropriate for body lice. Maximum-likelihood analyses using this model produced a tree (Fig. 3b) that was in most respects similar to the parsimony tree. The relationships among the major clades (species groups, see below) were slightly rearranged, as were relationships within the *spenceri* clade. Eight of 11 nodes were supported in over 60% of bootstrap replicates.

Price et al. (1999) divided the genus *Physconelloides* into five species groups on the basis of morphology. Four of these groups are distributed in the New World and each of these is represented in our tree by more than one taxon. All four of these groups are monophyletic with high support (> 70%) in the equally weighted parsimony and maximum-likelihood analyses.

Cophylogenetic Analysis

Reconciliation analysis (Page 1990a) of the *Columbicola* and dove phylogenies using TreeMap (Page 1995) reconstructed three or four cospeciation events in the case of like-

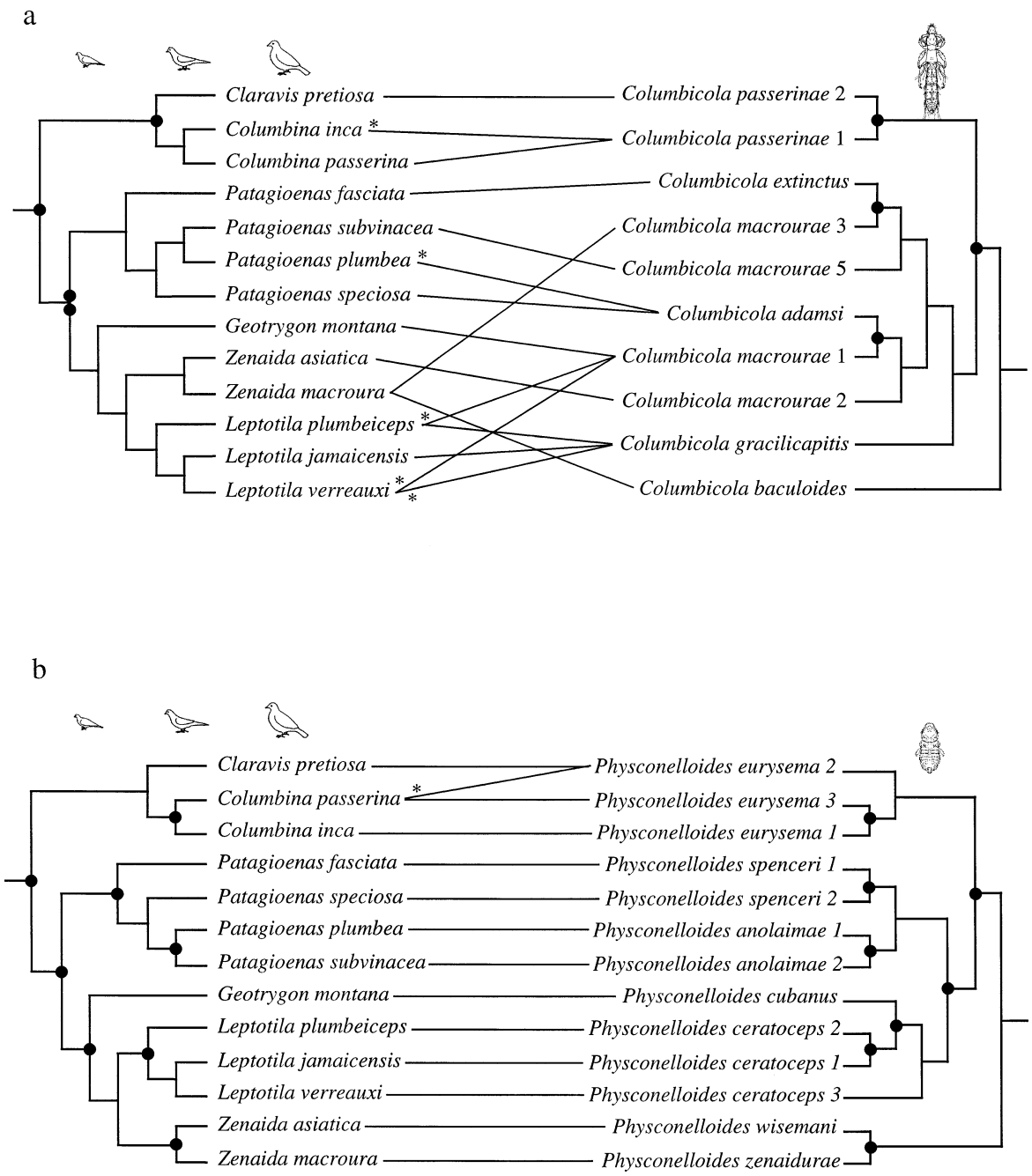


FIG. 4. (a) Cophylogenetic analysis of *Columbicola* with respect to their hosts (Columbiformes) using the unweighted parsimony trees. Four inferred cospeciation events are indicated by circles. Randomization of the *Columbicola* tree indicated that four events are not more than expected by chance ($P = 0.153$). Lines between hosts and parasites indicate associations. Asterisks indicate those associations removed in the analysis of the impact of specificity on cospeciation. (b) Cophylogenetic analysis of *Physconelloides* with respect to their hosts (Columbiformes) using the unweighted parsimony trees. Eight inferred cospeciation events are indicated by circles. Randomization of the *Physconelloides* tree indicated that eight events are many more than expected by chance ($P = 0.0006$). Lines between hosts and parasites indicate associations. Asterisks indicate those associations removed in the analysis of the impact of specificity on cospeciation.

lihood and parsimony trees, respectively (Fig. 4a). In both comparisons, only three of 12 host nodes (25%) had a cospeciation event associated with them. These events were reconstructed as being near the base of the tree, and no host terminal sister taxon comparisons had cospeciation events associated with them. For *Columbicola*, three or four cospeciation events is not more than expected by chance ($P = 0.52$ and $P = 0.15$, respectively).

For *Physconelloides*, reconciliation analysis reconstructed eight cospeciation events in comparisons of both parsimony and likelihood trees (Fig. 4b). In both comparisons, eight of 12 host nodes (67%) had a cospeciation event associated with

them. This proportion is significantly greater than that for *Columbicola* ($z = 2.04$, $P = 0.04$). These cospeciation events were spread throughout the host tree, and three of them were associated with terminal host-parasite sister pairs. Using randomizations of the parasite tree, eight cospeciation events are considerably more than expected by chance ($P = 0.0006$ in both cases).

To test whether the increased number of cospeciation events recovered in *Physconelloides* was simply a direct result of higher host specificity, we broke host-parasite associations in both the *Columbicola* and *Physconelloides* cophylogenetic analyses. We removed associations in such a way to make every species of louse completely host specific and to maximize the number of cospeciated nodes that would be inferred in the analysis (see Fig. 4). When we forced *Columbicola* to be 100% host specific, we still recovered only three or four cospeciation events, ($P = 0.64$ or $P = 0.26$). In contrast, when we forced *Physconelloides* to be 100% host specific, the number of inferred cospeciation events increased from eight to nine in both parsimony- and likelihood-tree comparisons. Nine events were many more than expected by chance ($P < 0.0001$).

Discussion

Columbicola wing lice are less host specific, and have less population genetic structure, than *Physconelloides* body lice. Our goal was to see if these microevolutionary patterns correspond to similar macroevolutionary patterns, in which case we predicted that body lice would have a phylogeny more similar to the host phylogeny than wing lice. Although some level of host specificity is necessary for cospeciation to occur, specificity is not a sufficient condition for cospeciation. Just because a parasite is host specific does not mean that it has cospeciated with the host. Although ecological factors reinforcing specificity and population genetic structure *may* favor a history of cospeciation (Clayton et al. 2003), this hypothesis must be tested.

Our results were consistent with the predicted difference in cophylogenetic history. New World wing lice have an evolutionary history that is largely independent of host history, whereas the history of New World body lice strongly mirrors host history. This difference held even when host associations were modified, such that each species of louse was made (artificially) 100% host specific. Our study is one of the first to compare phylogenies of different parasite lineages living on the same hosts. As such, host factors are held constant, allowing differences in aspects of parasite biology to be explored. In this case, the differences in host specificity and underlying differences in population genetic structure are correlated with coevolutionary history.

The differences in host specificity and population genetic structure presumably have an ecological basis, such as differences in the dispersal ability of wing and body lice. Although both groups of lice depend on physical contact between hosts for transmission, this may not be the only route of transmission. Feather lice are known to attach ''phoretically'' to parasitic flies (Diptera: Hippoboscidae), particularly when abandoning a dead or dying host (Clayton et al. 2003). Because these flies are not as host specific as lice, it is conceivable that phoresis is a route of dispersal between species of hosts. Several records of *Columbicola* attached to flies have been published, compared to only one case of *Physconelloides* (Keirans 1975). Wing lice may therefore be able to move among host species more easily via phoresis than body lice. This hypothesis could be tested experimentally.

Other factors may contribute to an increased ability of wing lice to disperse between host species, compared to body lice. For example, feather lice are also thought to disperse among host taxa on detached feathers or via shared dust baths (Clayton et al. 2003). Dove wing lice survive longer than dove body lice off the body of a host (Rem and Zlotorzycka 1981; Dumbacher 1999; Clayton, unpubl. data). Wing lice also leave the body of a dead host more quickly than body lice (Petryszak et al. 1996). These differences may contribute to some difference in the ability of dove wing and body lice to disperse by means other than phoresis. Again, experiments are needed to test relative dispersal abilities.

In conclusion, the ability of a parasite lineage to switch hosts over macroevolutionary time may be influenced by the same factors that govern host specificity and population genetic structure. Because host switching erodes patterns of congruence (Page and Charleston 1998; Clayton et al. 2003), lineages with high dispersal ability should show less congruence, all else being equal. Experimental approaches and additional comparisons of parasite lineages that vary in dispersal ability are needed to test further the impact of ecological factors on coevolutionary history.

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