

## Untangling Coevolutionary History

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Organisms in nature exist in complex environments where they interact with a diversity of other species. Just as interactions between species are fundamental to ecological studies, they also are integral to understanding many macroevolutionary patterns of diversification. Chief among these are the coevolutionary patterns apparent between closely interacting groups, such as hosts and parasites, or mutualists. A variety of historical processes play a role in the diversification of interacting taxa. These processes occur on a variety of scales, ranging from the intracellular to the community level, and across a diverse array of taxa, ranging from viruses to vertebrates.

Recent phylogenetic studies reveal that the phylogenies of interacting taxa are often very similar, sometimes identical. This similarity is most often generated by repeated instances of cospeciation, the simultaneous speciation of interacting taxa. Alternatively, a number of processes can reduce the congruence between phylogenies of closely interacting taxa. These processes include host switching, duplication, sorting events, and failure of one lineage to speciate in response to speciation in the other lineage. Recent cophylogenetic studies have revealed a diversity of patterns, ranging from complete congruence to no significant similarity between phylogenies of interacting taxa (Page, 2003).

Coevolutionary biologists can help provide explanations for this diversity by integrating cophylogenetic studies with knowledge of the ecological and physiological mechanisms underlying species interactions. Research on coevolution often merges ecology, systematics, population genetics, physiology, and molecular biology. At the 2002 joint Society of Systematic Biologists (SSB)/Society for the Study of Evolution (SSE) annual meeting we had an opportunity to bring together coevolutionary biologists working on a diverse array of taxa. These workers have summarized their presentations in this issue of *Systematic Biology*. We are grateful to the SSB for providing support for the symposium and its publication. Our goal has been to inspire comparisons across studies to understand the processes responsible for different patterns of coevolutionary history.

As background for this compilation of empirical studies, we review here the processes believed to be important in coevolutionary history (see also Page and Charleston, 1998; Page, 2003). For ease of description, we use hosts and parasites to illustrate these processes, but any pair of interacting taxa could be used. We provide specific examples from a single host–parasite system con-

sisting of pigeons and doves (Aves: Columbiformes) and their parasitic lice (Insecta: Phthiraptera).

The first process, cospeciation, is the simultaneous speciation of hosts and parasites. Repeated instances of cospeciation generally increase the congruence between host and parasite phylogenies; cospeciation is usually inferred directly from such congruence. For tightly interacting organisms, some workers consider cospeciation to be a null model of sorts, because forces isolating host populations also tend to isolate their parasite populations. An example of cospeciation can be seen in body lice (*Physoconelloides*) found on New World doves (Fig. 1).

One of the processes that reduces the congruence between host and parasite phylogenies is host switching. Incomplete host switching is simply an expansion of a parasite's host range, such as when a parasite colonizes an additional species of host (Fig. 2). Incomplete host switching reduces the parasite's level of host specificity; where a parasite species once occurred on a single host species, it now occurs on two host species. Host switching can be completed either by extinction of the parasite on the original host, speciation between the parasite populations on the new host and those on the original host, or both. Incomplete host switching has occurred in body lice (*Physoconelloides*) of small New World ground doves (Fig. 2).

Sorting events are another group of factors that, in combination with other processes, can reduce the similarity between host and parasite phylogenies. Sorting can involve extinction, in which a parasite lineage is lost from a host lineage, or "missing the boat," in which a parasite lineage is "missing" from a host lineage during founder event speciation. An apparent sorting event has occurred in the wing lice (*Columbicola*) of the New Zealand pigeon (*Hemiphaga novaeseelandiae*). Wing lice have never been found on New Zealand pigeons despite intensive sampling (Paterson et al., 1999; Clayton, unpubl. data), whereas the closest relatives of the New Zealand pigeon do have wing lice (Adams, 2002).

Yet another factor that can reduce phylogenetic congruence is duplication, which occurs when a parasite lineage speciates in the absence of host speciation. Duplication can occur via sympatric speciation of parasites or via allopatric speciation of parasite populations across the geographic range of a host. Although there are few examples of recent duplication events in lice (Johnson and Clayton, 2003), a duplication event seems to have occurred in the body lice of the Band-tailed

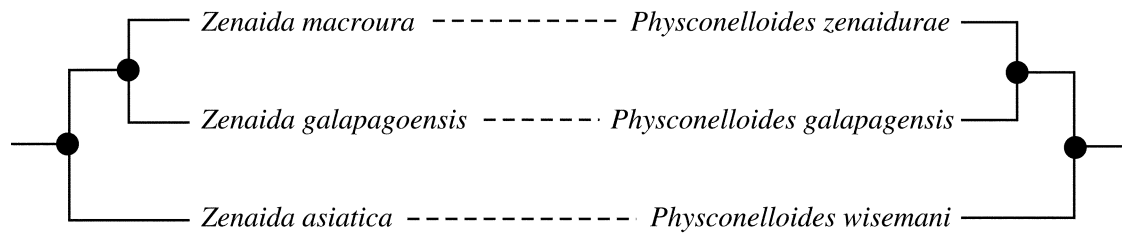


FIGURE 1. Phylogenies of New World midsize ground doves (*Zenaida*) and their associated body lice (*Physconelloides*) illustrating perfect (one for one) cospeciation. Trees are from Johnson and Clayton (2003). Dashed lines connect hosts with associated parasites. Solid circles indicate inferred cospeciation events.

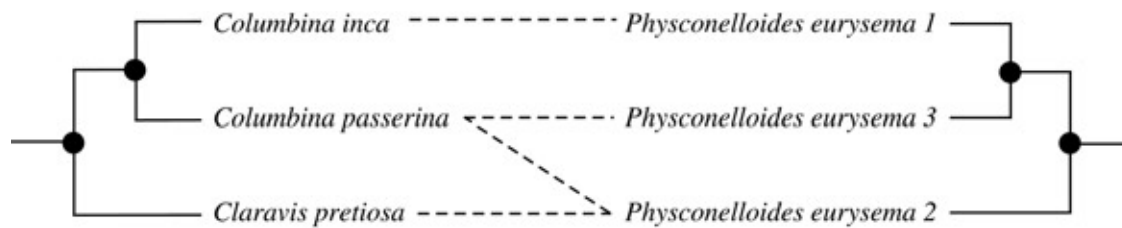


FIGURE 2. A recent incomplete host-switching event in small New World ground doves (*Claravis* and *Columbina*) and their body lice (*Physconelloides eurysema* 1–3). *Physconelloides eurysema* 2 has expanded its host range by colonizing *Columbina passerina*. Trees are from Johnson and Clayton (2003). Numbers indicate cryptic species of lice documented by Johnson et al. (2002). Conventions as in Figure 1.

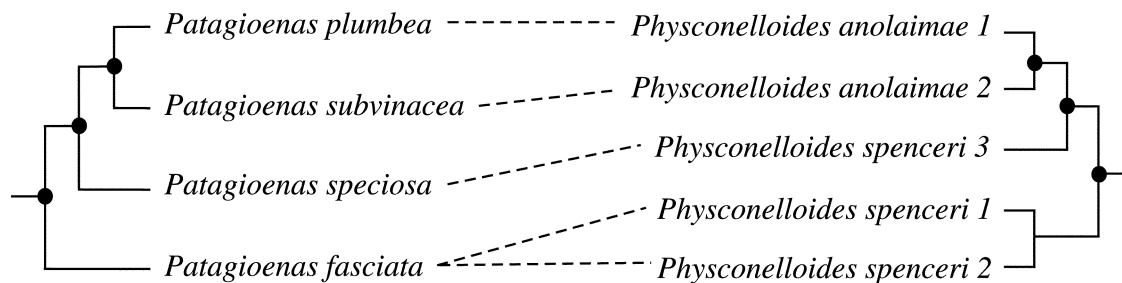


FIGURE 3. Duplication event in the body lice (*Physconelloides*) of the Band-tailed Pigeon (*Patagioenas fasciata*). Broader trees for *Patagioenas* and lice are from unpublished data. Conventions as in Figures 1 and 2.

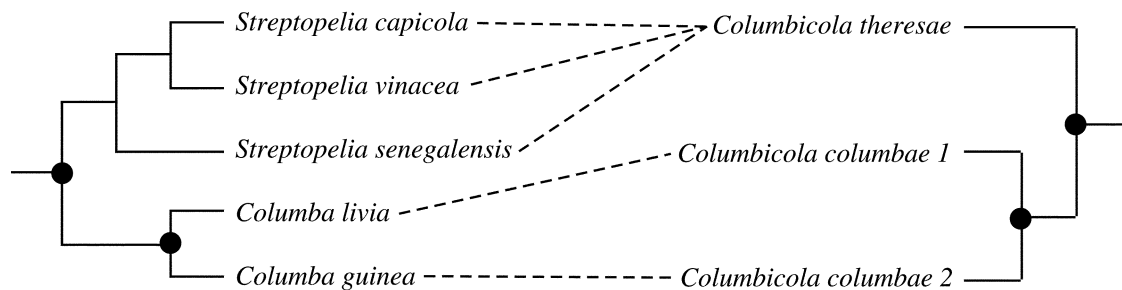


FIGURE 4. Failure to speciate in the wing lice (*Columbicola theresae*) of African turtle doves (*Streptopelia*). Trees are from Johnson et al. (2003). Conventions as in Figures 1 and 2.

Pigeon (*Patagioenas fasciata*). At the mitochondrial DNA sequence level, Band-tailed Pigeons in North and South America show no detectable divergence. However, populations of Band-tailed Pigeon body lice (*Physoconelloides spenceri*) show a pronounced mitochondrial divergence between North and South America (approximately 9% uncorrected sequence divergence, similar to the divergence between species of lice). Populations of these lice appear to be isolated from each other, but populations of their hosts are not (Fig. 3). Such divergence is the fuel for a duplication event.

The converse of duplication is failure to speciate, i.e., parasite populations may "fail" to speciate in response to host speciation. This situation can occur when parasites retain the ability to disperse between diverging species of hosts (Johnson et al., 2003) and tends to erode the similarity between host and parasite phylogenies, as seen in the wing lice (*Columbicola*) of African turtle doves (*Streptopelia*) (Fig. 4).

In summary, coevolutionary history is shaped by a combination of these five processes, which in turn are influenced by ecological factors. The articles that follow provide a wealth of examples of interacting systems with phylogenies exhibiting the range of patterns of congruence. These authors have addressed the ecology of their systems in sufficient detail to provide an understanding of at least some of the reasons for the level of phylogenetic congruence observed. Compilation of additional examples in the future should allow us to predict a priori what the phylogenies of interacting groups will look like in relation to one another.

Degnan et al. (this issue) demonstrated that endosymbiotic mutualistic bacteria cospeciate extensively with their ant hosts. Parasitic microorganisms, such as the avian malaria parasites examined by Ricklefs et al. (this issue), show evidence of phylogenetically restricted host associations, but this restriction is far from complete. Rather, host switching seems to be an important component of the interaction between avian malarial organisms and birds, because these parasites are spread by vectors. Percy et al. (this issue) used plants and their insect herbivores to show that cospeciation alone may not account for phylogenetic congruence between plants and herbivorous insects. Rather, insect herbivores may switch among closely related hosts, giving the illusion of repeated cospeciation. This study shows why estimates of the timing of speciation events, in addition to phylogenies, are needed to make a compelling case for a history of cospeciation. Weiblen (this issue) has provided a nice example of the integration of cophylogenetic study with

an examination of coadaptation between traits important in a mutualistic host–pollinator system. In a comparison of the phylogenies of behavioral parasites, brood parasitic finches, and their avian hosts, Sorenson et al. (this issue) found no evidence for cospeciation, even though coadaptation appears to be very important in this system. Weckstein (this issue) has provided a counterexample to many of the ectoparasitic louse systems studied to date by showing that the lice of toucans do not cospeciate with their hosts. Rather, biogeography seems to play a crucial role in explaining these host–parasite associations. The concluding contribution to the symposium (Clayton et al., this issue) again is focused on host–louse systems, illustrating that ecological information is essential for understanding why lice show nearly the full range of variation in coevolutionary histories possible in host–parasite systems. This ecological approach can be extended to other systems to provide a general framework for untangling the tangled trees of coevolutionary history.

#### ACKNOWLEDGMENTS

Our work was supported by NSF-CAREER award DEB-9703003 to D.H.C., NSF DEB-0107891 to K.P.J., and NSF-PEET DEB-0118794 to D.H.C. and K.P.J. We thank the Society of Systematic Biologists for financial support for the symposium. We are grateful to Susan Perkins, David Reed, and Jennifer Wernegreen for comments that improved the manuscript.

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Final acceptance 12 September 2003

Associate Editor: David Reed