A Different Tempo of Evolution in Birds and their Parasitic Lice

Roderic D. M. Page, Patricia L. M. Lee, S. Anette Becher,
Richard Griffiths, and Dale H. Clayton

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Host-Parasite Cospeciation

A key question in the study of coevolution is the tempo and mode of evolution of the interacting partners. Is the association an ancient one, reflecting a long and intimate interaction between the two organisms, or is it a recent event due perhaps to a parasite colonising a new host? What is the relative rate of evolution between host and parasite? Answering these questions requires the comparison of evolutionary trees (phylogenies) for host and parasite (Figure 1). To the extent that the trees match, host and parasite have cospeciated, that is, parasite and host speciated at the same time. Mismatches between the host and parasite phylogenies signal processes other than cospeciation, such as host switching, speciation by parasites independently of their hosts, and parasite extinction (Page, Clayton et al. 1996). Because cospeciating taxa are, by definition, contemporaneous, we can compare amounts of evolutionary divergence in cospeciating pairs of hosts and parasites to measure relative rates of evolution in the two clades. Because host and parasite are often taxonomically distant (e.g., birds and insects), with differing generation times, population sizes, and metabolic rates, they are ideal systems to investigate the influence of these factors on rates of evolution (Page and Hafner 1996).

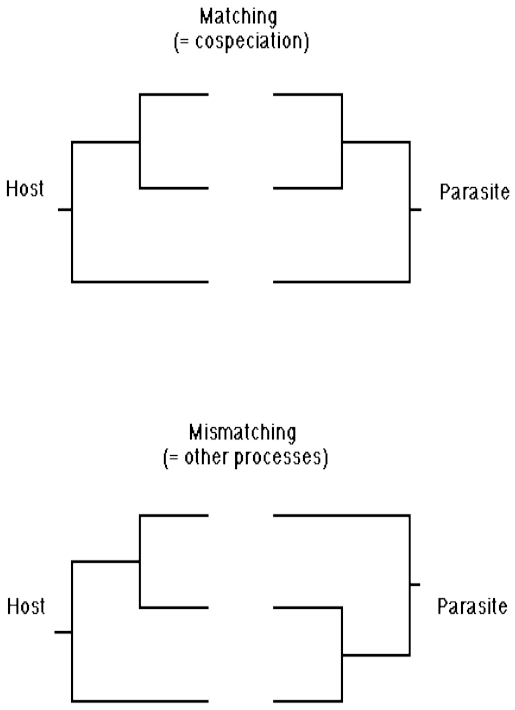

Figure 1 Matching and mismatching pairs of host and parasite phylogenies. Matching (top) is evidence for host-parasite cospeciation; mismatching (bottom) is evidence for processes other than cospeciation.

Swiftlets and lice

The two dozen species of swiftlets and their lice show great promise as a model system for studying cospeciation. The lice are host specific, and transmission of *Dennyus* lice between individual hosts is known to be strictly vertical (between parent bird and its offspring) (Lee and Clayton 1995), suggesting that opportunities for colonizing new host taxa are quite limited. Swiftlets predominantly nest in caves (Figure 2), often in large colonies. This makes it feasible to undertake transfer experiments to test the survival of lice moved to foreign hosts.

Figure 2 *Aerodramus* swiftlets nesting in a cave in Malaysia. These small insectivorous birds navigate in the cave by echolocation. Nests of *A. fuciphagus* are commercially harvested as the essential ingredient of "bird's nest soup"

Figure 3 Specimens of the common swift *Apus apus* (top) and two rows of swiftlets (genera *Aerodramus* and *Collocalia*) from Malaysia. Ernst Mayr (1937) regarded the classification of swiflets as "the most difficult problem in the taxonomy of birds."

Why use molecular data?

Swiftlet species are often difficult to distinguish morphologically (Figure 3), indeed the best guide to the identity of an individual is often its nest. Swiftlet nest structure is useful taxonomically, but is not phylogenetically informative (Lee, Clayton et al. 1996).

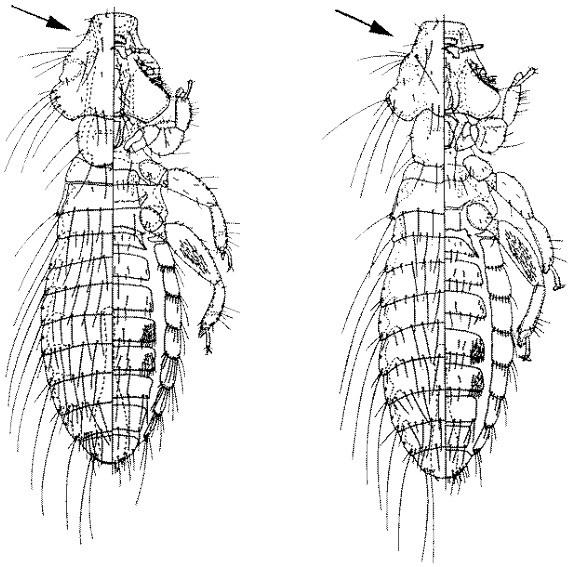

Figure 4 The principal difference between *distinctus* and *thompsoni* species-group lice is the shape of the preantennal margin of the head. The mitochondrial DNA of these two species groups differs by 25-30%; greater than the difference between swifts and hummingbirds.

Dennyus lice show limited morphological variation, and some taxa were only discovered by using multivariate morphometrics. This morphological conservatism prevents cladistic analysis, so the only morphological estimate of relationships available is a cluster analysis of morphometric data (Figure 5).

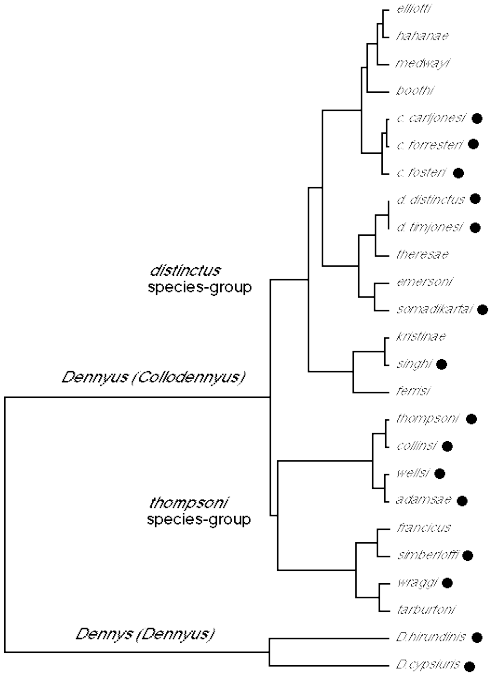

Figure 5 UPGMA dendrogram for female *Dennyus* lice from swifts and swiftlets (Clayton, Price et al. 1996). The tree was constructed from the first five principal components for 29 morphometric variables. The lice we sequenced are indicated by (.).

While molecular data are useful in cases like this where morphological data is limited, there are two other compelling reasons to use DNA sequences in studies of host-parasite cospeciation:

- Homologous characters can be obtained for both hosts and parasites. In such taxonomically disparate taxa as birds and insects there are few homologous morphological characters which can be compared, whereas there are many genes that are homologous. Furthermore, molecular data permit the use of the same units (e.g., numbers of nucleotide substitutions per site) to measure evolutionary change, which is essential if we wish to compare rates of evolution.
- Molecular information can provide data on the relative ages of the host and parasite clades.

Information on lineage age can help distinguish between host switching and the persistence of relict parasite lineages as alternative explanations of incongruence between host and parasite phylogenies.

Data and Analysis

DNA sequences for an homologous region of the mitochondrial (mtDNA) cytochrome b gene were obtained from swiftlets and their lice using standard techniques (Lee, Clayton et al. 1996; Page, Lee et al. submitted). *Dennyus* lice feed on both feathers and blood, so to minimise the chances of mistaking host DNA for louse DNA the lice were starved for 24 hours prior to death. Sequences obtained from the insects were different from any bird sequence we obtained, and readily aligned with other insects (Figure 6). Different tree building methods yielded similar trees, differing only in resolving relationships among some distinctus species-group lice for which the phylogenetic signal is fairly weak. Conformity to molecular clocks was tested using maximum likelihood tests. Host and parasite trees were compared using TREEMAP (Page 1994). For contrasting views on the most appropriate of comparing host and parasite trees see Hoberg et al. (1997) and Paterson and Gray (1997).

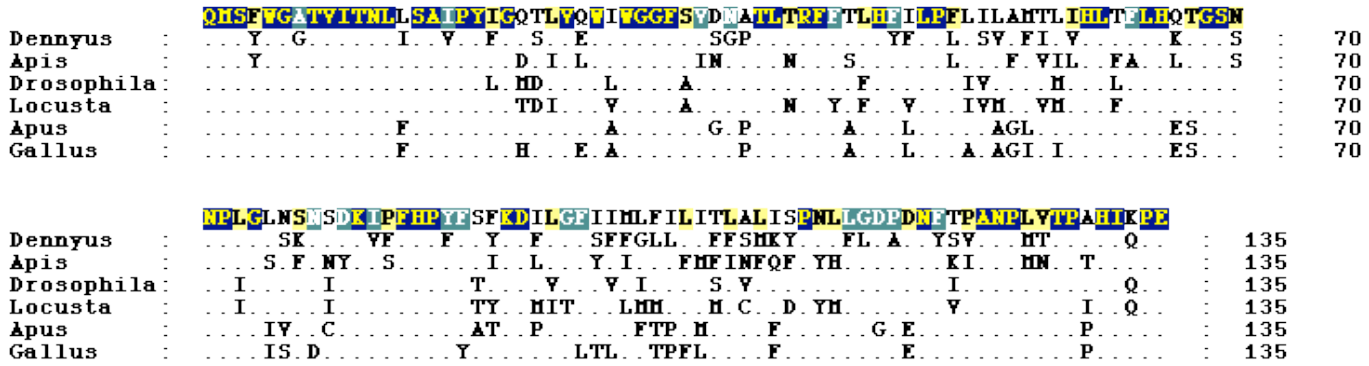

Figure 6. Aligned partial protein sequences for the mitochondrial cytochrome b gene for the louse *Dennyus hirundinis* and its swift host (*Apus apus*) compared with sequences for three other insects - honeybee (*Apis*) , fruit fly (*Drosophila*), and locust (*Locusta*) - and the chicken (*Gallus*). The top line is the consensus sequence.

Have swiftlets and lice cospeciated?

Detailed reconstruction of the history of a host-parasite association requires robust, fully resolved trees. Because of some areas of uncertainty in the louse phylogeny we can confidently compare only part of the trees (Fig. 7).

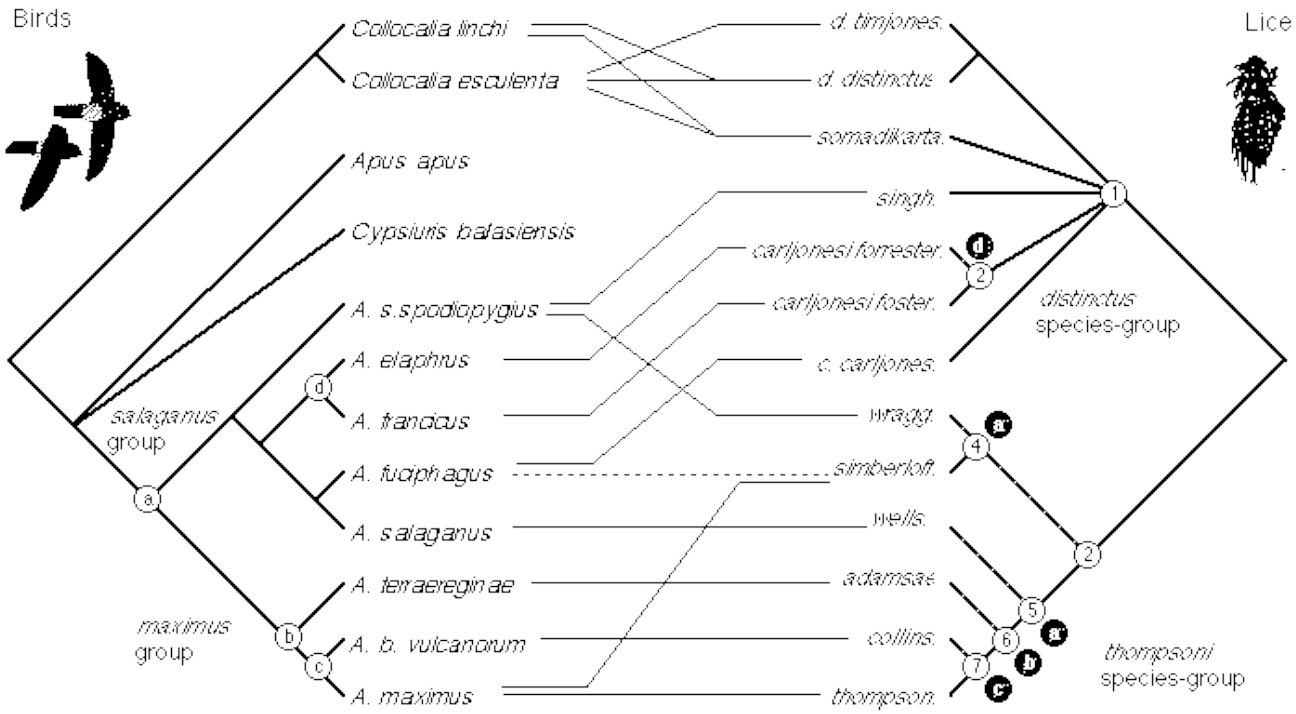

Figure 7Cladograms for *Dennyus (Collodennyus)* lice and their hosts. For nodes 3-7 the corresponding nodes in the host cladogram are indicated by the letters a-d. A is the genus *Aerodramus*. Although the *D. simberloffi* louse we sequenced was obtained from an individual of *Aerodramus fuciphagus* (indicated by the dashed line) the primary host of this louse is *A. maximus* (Clayton, Price et al. 1996).

Within the well resolved *thompsoni* species-group several putative cospeciation events can be indentified. The swiftlet species pair *Aerodramus maximus* and *A. brevirostris* harbor a related pair of lice (*Dennyus collinsi* and *D. thompsoni*), and the nearest relative of these two birds (*A. terrereginae*) hosts the sister taxon of these lice (*D. adamsae*). The sister pair of Indian Ocean Ocean birds, *A. elaphrus* and *A. francicus* harbor a sister pair of lice, *D. fosteri* and *D. forresteri*.

Louse mtDNA is rapidly evolving

Although Dennyus lice are very morphologically conservative, their mitochondrial DNA is highly divergent. The distinctus and thompsoni species groups differ only in minor details of head shape and setation (Figure 4), and yet show 25-30% DNA sequence divergence - greater than the divergence between swifts and and their sister taxon the hummingbirds.

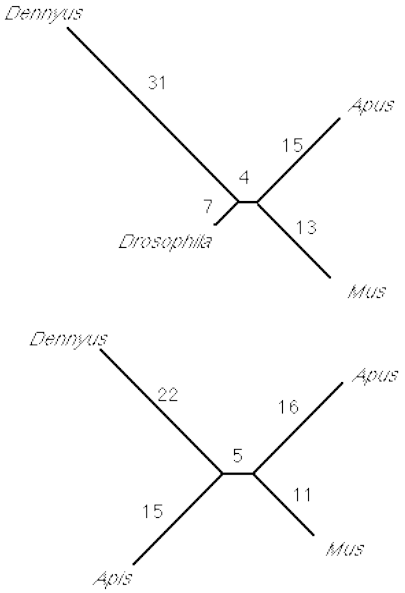

Figure 8 Comparisons of amino acid divergence in *Dennyus* and two other insects, relative to their last common ancestor. Each edge is labelled with the number of amino acid replacements that can be assigned unambiguously to that edge using parsimony. The louse cyt b (*Dennyus hirundinis*) sequence has diverged ~4.5 times more from a common ancestor than has that of *Drosophila yakuba*, whereas the ratio of louse and honeybee (*Apis mellifera*) divergence is ~1.5.

Comparisons of cytochrome b amino acid sequences between lice and other insects (honeybee, fruitfly, mosquito and locust) show that *Dennyus* is among the most divergent insects known (Figure 8). This variation in rate of insect mtDNA evolution means that calibrations of absolute rate of evolution in other insects (for example, that based on the age of Hawiaiin island *Drosophila*) will not apply to lice, hence it is difficult to independently estimate the age of the lice relative to their hosts. However, we can directly compare amounts of sequence divergence in birds and lice.

Lice evolve more rapidly than their hosts

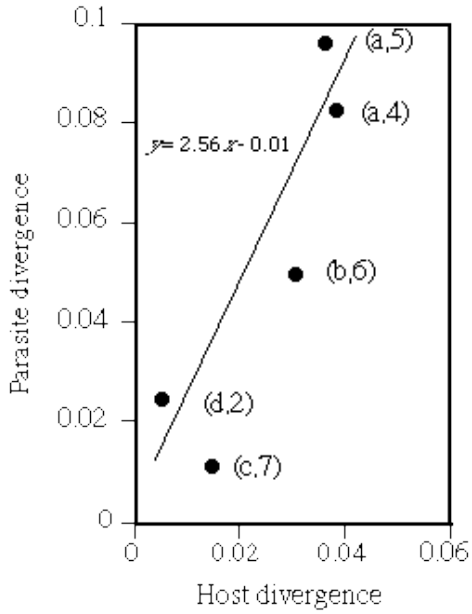

Figure 9 Plot of divergence in pairs of host and parasite nodes. The cyt b gene in lice is evolving more than twice as fast as the same gene in their avian hosts.

Comparing overall rates of molecular evolution in host and parasites requires molecular clocks in both taxa (of course, these clocks may tick at different rates in the two clades). Both swiftlet and louse cyt b sequences are consistent with a clock (based on maximum likelihood tests). We compared the amount of divergence in each putative pair of cospeciation events in the host and bird trees. Plotting parasite divergence against host divergence shows a 2-3 fold greater rate of evolution in the lice (Figure 9). This parallels the disparity in

rates of evolution in mammalian lice and their hosts (Hafner, Sudman et al. 1994; Page 1996; Huelsenbeck, Rannala et al. 1997).

Summary

The mitochondrial DNA of swiftlet lice is evolving more rapidly than that of their hosts. Possible explanations for this disparity include the difference in host and parasite generation time, different selection pressures, and different population sizes. There seems to be little relationship between generation time and rate of molecular evolution in insects, and the ratio of synonymous and nonsynonymous substitutions (a measure of selection) is similar in birds and lice. Louse populations tend to be highly structured, with each host individual being effectively an "island" colonised by small numbers of lice, suggesting that lice may undergo repeated founder events. This may contribute to the fast rates observed in lice. Current work by the authors seeks to test whether the difference in rate of nucleotide substitution between Dennyus and swiftlets applies to other mitochondrial and nuclear genes, and whether lice from other birds show a similarly accelerated rate of evolution.

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Roderic D. M. Page (r.page@bio.gla.ac.uk)
Richard Griffiths (rg25d@udcf.gla.ac.uk)
Division of Environmental and Evolutionary Biology, IBLS, University of Glasgow, Glasgow G12 8QQ, UK. Patricia L. M. Lee (p.lee@vax.ox.ac.uk)
Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, UK. S. Anette Becher
School of Biological and Medical Sciences, University of St Andrews, St Andrews KV16 9TH
Dale H. Clayton (clayton@biology.utah.edu)
Dept. of Biology, University of Utah, Salt Lake City, UT 84112, USA.