POINTS IN QUESTION

Lice and Cospeciation: A Response to Barker

Although historically lice (Insecta: Phthiraptera) and scientists who have studied them have played a dominant role in the development of ideas on speciation and coevolution (Paterson, Gray & Bliss, 1995), in recent texts on coevolution (e.g., Cock & McLenan, 1991, 1995; Thompson, 1994) they have been largely ignored (or have suffered the ignominy of being called "mites"). This is despite the fact that lice provide the clearest evidence of host-specific cospeciation (Hafner & Nadler, 1988; Hafner et al., 1993; Hafner et al., 1994). Barker's (1996a) review of the phylogeny and evolution of host associations of lice is therefore welcome and timely.

PATRICK GRAY

He presents a good overview of higher-level louse taxonomy, and the conditions under which we expect cospeciation or host-switching to dominate. However, in assessing the available evidence on host-louse coevolution we believe Barker has overlooked some important studies, and as an unpalatable conclusion based on the data he does cite. Furthermore, his review fails to grasp the complexity of the possible phylogenetic and ecological relationships between hosts and lice.

TESTING THE HYPOTHESIS OF COSPECIATION

- "cospeciation?"

Barker (1996a, p. 1288) concludes that "cospeciation and subsequent coevolution, undeniably occur...are less common than previously thought...or may be not the prevailing patterns in the Phthiraptera." Barker cites 3 studies in support of this claim: Lyal's (1987) study of 351 trichodectid lice for which he estimated that 20.7% of the speciation events involved host switches; Hafner & Nadler (1988), whose data suggest that most host switches are due to 9 speciation events (Page, 1990); and his own studies (Barker, 1991) of 11 species of rock-wallaby lice for which he found little evidence for cospeciation.

Hafner et al. (1996) is right to bemoan the ready acceptance of cospeciation as an axiom, but at that same time his conclusion that cospeciation is not the prevailing pattern contradicts the very evidence he cites.

Furthermore, Barker overlooks 2 major studies of host-host relationships: Kim's (1988) study of mammalian Anoplura, and Paterson, Gray & Wallia (1993) study of lice found on penguins, petrels and albatrosses. Kim (1988: p. 106) concluded that Anoplura have a complicated history of association with mammals which was initiated by a series of "cercarial" colonizations occurring at different times, followed by close coevolution with sporadic host changes.

Paterson et al. (1993, 1995) examined the coevolutionary history of seabirds and their lice. Component analysis of phylogenies constructed for seabirds and lice revealed little evidence for host switching in the evolutionary history of this host-parasite system. The pattern found was one of multiple louse lineages present on the ancestral seabird species with occasional episodes of cospeciation and extinction. Subsequent research using 12S mitochondrial DNA sequence data for both seabird and louse species has confirmed that the proposed cospeciation events occurred relatively concurrently and that the rate of molecular evolution, unlike morphological evolution, has been greater in the lice (Paterson & Gray, in press).

WHAT IS EVIDENCE FOR COSPECIATION?

Farenholz's fallacy

Farenholz's rule, that host and parasite phylogenies should mirror each other, is often viewed as a cornerstone of coevolution research. Conversely, failure to find identical host and parasite phylogenies is seen as prima facie evidence for host switching. While strict adherence to Farenholz's rule encourages the dismissal of unexpected host records as due to "stragglers" (Ruma, 1993) and hence may lead to underestimates of host-switching, such adherence can also lead to a naive equation of incongruent host-parasite phylogenies with host-switching. However, incongruence between host and parasite phylogenies can arise from a number of causes, such as the presence of multiple lineages of
parasites coupled with parasite extinction, or failure of parasites to colonize both decendants of a host species that underwent an extinction event ("missing the host")—as illustrated by the failure (Page, 1993a; Paterson & Gray, 1995, in press), or collection failure (Page & Paterson, 1994). Failure to recognize these factors may lead to overestimates of host-switching. For example, the ancestral host seabird lineage splits into two separate main lineages (Page et al., 1993; Paterson et al., 1994) with the genus Stenonema, which is partially distributed in the oceans and in the open sea. This group of species has a diadromous geographic distribution on the outermost part of the ocean. The marine seabirds, the founding population for pteropods inhabiting the open sea, did not include species that are marine seabirds. Furthermore, the subsequent history of the oceanic seabirds and of the marine seabirds that are marine seabirds would become a part of the oceanic seabirds. Interestingly, this group of species may have been distributed among several of the oceanic seabirds.

The genus Stenonema may be distributed among the marine seabirds, the marine seabirds, and the marine seabirds, which is a diadromous geographic distribution on the outermost part of the ocean. The marine seabirds, the founding population for pteropods inhabiting the open sea, did not include species that are marine seabirds. Furthermore, the subsequent history of the oceanic seabirds and of the marine seabirds that are marine seabirds would become a part of the oceanic seabirds.

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Disadvantages of host-switching and the advantages of host-switching are discussed in detail in Chapter 7. The following discussion of host-switching in the marine seabirds, the founding population for pteropods inhabiting the open sea, did not include species that are marine seabirds. Furthermore, the subsequent history of the oceanic seabirds and of the marine seabirds that are marine seabirds would become a part of the oceanic seabirds.

Wallaby bite

Based on the extensive studies of hosts listed on rock-wobble (Page & Rogers) Barker (1994, p. 1288) concluded that the bite has been conserved entirely or even closely with their hosts. "Taken together, this conclusion seems reasonable: the phylogeny for wallabies and their lios do indeed show poor correspondence. Much of this incongruence reflects disagreements between host use patterns and the distribution of host-sharing lios found in the literature (Page & Rogers, 1994, p. 1288)." However, the data and models are not as robust as it appears. Further, the analysis is not as robust as it appears. The data and models are not as robust as it appears. Further, the analysis is not as robust as it appears. The data and models are not as robust as it appears.

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host-parasite phylogenies, host-switching and multiple lineages. Figure 2a depicts a pair of incongruent host and parasite phylogenies. The incongruence may be due to host-switching or the presence of multiple lineages. By themselves the cladograms do not allow us to decide between these explanations although the relative likelihood of either host-switching or multiple lineages and extinction scenarios may be assessed. A host-switching explanation for Fig. 2a suggests that the ancestor of P2 colonized H1 from H2 and displaced the parasite species (P4) already present on H1 (Fig. 2b). This scenario requires 2 evolutionary events, one host-switching event and the extinction of P4. A multiple lineage explanation suggests that 2 lineages were present on the ancestral hosts and 3 sorting events occurred (Fig. 2c). Which scenario is supported may be determined by the biology of the host-parasite relation, i.e. how common are host-switching events relative to sorting events?

If we have information on relative time of divergence between the host and parasite species then we may be able to choose between these explanations. In Fig. 2d this information supports host-switching (evolutionarily recent parasite colonizing new host) whereas Fig. 2b supports multiple lineages (the persistence of relict parasites on their original hosts). Such information on timing can be provided by molecular clocks.

A disadvantage of molecular data is that they are expensive to collect, which places constraints on sampling taxa, conflicting with the previous requirement of exhaustive sampling. Pocket gopher lice provide a good illustration; while a complex morphological and morphometric phylogeny for all 127 known taxa is available (Page, Price & Hohenatal, 1995), only lice have been sequenced (Hafner et al., 1994). Quantitative comparison of host and parasite phylogenies: Quantifying the similarity between host and parasite phylogenies makes possible analysis of their statistical tests of coevolution, rather than relying on qualitative assessments. Given a measure of IT between the 2 trees, i.e. how similar the trees are, the

Points in Question
Lice, Coevolution and Parasitism

The debate about the evolution of lice (Barker, 1994), which has been a focus of research for over 50 years, revolves around two main points: what proportion of extant and ancestral lineages of lice are specialized with their hosts (coevolved) and, is the phylogeny of lice a reliable indicator of the phylogeny of their hosts? There are two main schools of thought on the ways associations among lice and their hosts have evolved. The first school proposes that coevolution is typical for extant and ancestral lineages and that host-switching is uncommon. They argue that host-switching can be identified by morphological and chemical tests (e.g., Barker, 1994) and that the phylogeny of lice may be used to infer the phylogeny of their hosts, hence the name "comparative parasitologists" (Paterson, Gray & Wallis, 1995). In an application of phylogenetic approach to the systematics of lice, we have been engaged in exploring over 150 years, for example, Jardine (1841), (1941), and papers cited by Paterson, Gray & Wallis (1993). People in the second school, like myself, Lyal (1986) and Ríos (1993) consider that host-switching has been more common and coevolution less common than is generally accepted. We deduce, therefore, that host-switching has had profound effects on louse-host associations since lice evolved from free-living insects, possibly in the Cretaceous (Lyal, 1985). It is often difficult, however, to distinguish between host-switching and other events that lead to incongruence of parasite and host phylogenies, for example, where there are multiple evolutionary lineages of parasites and some species of parasites become extinct, despite the existence of extant tests to prove these points (Page, 1994). Therefore, the inference of host phylogeny from the phylogenies of their parasites is likely to be unreliable; therefore, it is better to apply molecular and cladistic analyses of morphological and anatomical features directly to infer the phylogeny of animals. Nevertheless, techniques which estimate and test association, host-switching and parasite extinction, and that identify multiple lineages of parasites (e.g., Page, 1994) will continue to be useful, but the extent of occurrence of louse-switching is likely to be underestimated; therefore, it is better to apply molecular and cladistic analyses of morphological and anatomical features directly to infer the phylogeny of animals. Nevertheless, techniques which estimate and test association, host-switching and parasite extinction, and that identify multiple lineages of parasites (e.g., Page, 1994)
polarity of characters states—the author simply stated that "polarity was determined by examination of the pattern of character development and by comparison to an out-group" the fitchecnna (p. 952). In effect, the study may have missed some of the species of lice that are most closely related to humans because the phylogenetic relationships were not taken into account.

Points in question

Is the use of out-groups to infer evolutionary relationships valid in the absence of direct evidence from fossils or other sources of evidence? Why or why not?


POINTS IN QUESTION

More “Misconceptions” About the Measurement of Aggregation

I commented on the paper by R. Poulin on
aggregated parasite distributions (International Jour-
nal for Parasitology 1993, 23: 937-944) in Interna-
tional Journal for Parasitology 1995, 25: 863-864. How-
ever, it seems to me that most points brought forward
in my comments were not really resolved in his reply or
are regarded as not important. The two out-
standing points in my view will be addressed here in
more detail than in my earlier comments.

First, I argued that the index of discrepancy (DI) as
proposed by Poulin does not present a new look at
parasite aggregation. The definition of aggregation
is not changed, has 0 ≤ 1 argued further that
expressing degree of aggregation as some propor-
tion of the total parasite population harboured by some
portion of the host population is essentially the
same as the index D. Poulin states that such a measure
tend to correlate with the index D, but only within
some. I would argue that the expression of the index
as a proportion of the host population in the same
way as expressing it by the index D. The problem Poulin referred to arises
when prevalence is very low. If, for example, the
selected fixed proportion of hosts is set at 0.8, any
parasite distribution for which prevalence is 20% or
less cannot be discriminated any longer by the
proportion of parasites harboured by 80% of the
hosts since that proportion will be zero (see Fig. 1).

However, this problem can be simply circumvented
by choosing another proportion of hosts at which to
look at. Alternatively, we can choose a fixed propor-
tion of the parasite population and find out what
proportion of the hosts belong to it (in Fig. 1 set
0.2 on the vertical axis). Another alternative is to
draw the diagonal from 0, 0 to 1, 0 and look at the
intersections (in Fig. 1 identified by the closed circles).

Admitted, D is more elegant since it expresses degree
of aggregation in a single value, whereas expressing it
in proportions of hosts and parasites requires 2
values. None the less, both measures uniquely belong
to one and the same line and therefore can be used
interchangeably, provided of course that the above
stated conditions do apply and that they are not
fruits of my vivid imagination.

A related point to the above is Poulin’s statement
that the index D is a more adequate measure of
aggregation than other measures, among them the
coefficient k in the negative binomial distribution. He
found a negative correlation (r) of −0.744 between k
and D, and concluded that “they probably quantify
related things”. This leaves room for assuming that D
partly measures something else than k. I wonder
whether that’s the case. Knowing that the range
of possible values for D has an upper boundary (unity)
as opposed to the range of possible values for k, it
might be suspected that the relationship between k
and D is nonlinear. If you plot D against k, it becomes
clear that the relationship is indeed nonlinear. So, the
correlation Poulin presented is misleadingly low. If
you take a simple natural logarithmic transformation
for k, the correlation between k and D already
becomes −0.897. The remaining unexplained varia-

bility between the 2 parameters may well be
accounted for by the fact that D is calculated from
the observed frequency distribution, whereas k is a
coefficient from a fitted negative binomial distribu-
tion. I suspect that “the related things k and D

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