

CHAPTER FIVE

Conclusions & Prospects

Understanding the factors which influence diversification is a major challenge in evolutionary biology, and as a large proportion of living things, parasites play a major role in this endeavour. They form important ‘model systems’ because many aspects of their environment are more readily measured than in free living organisms, and host specific parasites are particularly attractive because their habitat (the host) is clearly circumscribed. Hence, inferring the evolution of the habitat is equivalent to reconstructing the evolution of the hosts. Lice in particular have had a considerable influence over evolutionary theories about host-parasite associations, due largely to their unique biology. Since they spend their entire life cycle on a single host, lice are unusually tractable organisms for research in population biology. Their close association with their host can yield pronounced host specificity and cospeciation. Indeed, lice are commonly used as model systems for the development of analytical methods to assess the patterns and rates of cospeciation. Their tractability in ecological time, combined with their history of cospeciation, also make them one of the best groups for research on the ecological factors which govern speciation. Finally, a wealth of phylogenetic and comparative data is available for their hosts (mammals and birds). Unfortunately, the same cannot be said for lice, and their potential role as models for research is greatly hampered by the poor state of louse systematics.

5.1: Taxonomy

As outlined in the introduction to this thesis, most studies of louse taxonomy were principally motivated by the desire to show cospeciation. By necessity this tended to focus systematic research on lice to a few, select groups. Hence, with the exception of a handful of well studied genera, phylogenetic relationships of lice are poorly understood at all levels. Work presented in this thesis in chapters two and four, in addition to a comparable molecular study conducted with colleagues at the Universities of Glasgow

and Utah (Cruickshank *et al.*, in prep.), are a first step towards resolving the phylogeny of avian Ischnocera. Combined, these studies have examined the phylogeny of over 160 species (98 genera), amounting to approximately one fifteenth of all avian ischnoceran species. In conjunction with comparable studies of the mammalian Ischnocera (Lyal, 1985; Page *et al.*, 1995) (where the phylogeny for over 90% of trichodectid species is known), places ischnoceran systematics on a much firmer footing. However, this is only a first step towards improving ischnoceran taxonomy and considerable barriers to advancing ischnoceran louse systematics remain.

Clearly many more louse taxa need to be sampled at all phylogenetic levels. Whilst arguably the systematics of Ischnocera (especially avian Ischnocera) are the least understood, the taxonomy of Amblycera and the relationships between the chewing and sucking lice remain highly contentious. The alpha taxonomy for most of the 300+ genera of lice is in a state of disrepair, and has required the synonymisation of nearly 2000 louse species during its brief history (R. Price pers. comm.). Similarly, many of the checklists available for lice are hopelessly out of date. Checklists represent one of the most valuable resources compiled by taxonomists, documenting patterns of distribution which evolutionary biologists seek to explain. Although a recent checklist of anopluran lice is available (Durden & Musser, 1994), the most recent inventory for chewing lice (>90% of all louse species) is half a century old (Hopkins & Clay, 1952). Much of the data necessary to compile a checklist of chewing lice is available. However, these data remain largely unpublished and are principally confined to the hands of a few senior taxonomists close to retirement. Clearly dissemination of these unpublished data will be a priority if lice are to continue playing a role in the development of evolutionary theories about host-parasite associations. The recent emergence of information networks has made the task of managing systematic knowledge much easier, and provides an obvious medium for distributing these data. Greater emphasis on louse phylogeny will also be required if the value of these data is to be fully realised. At the subordinal level, questions over the status of the “Mallophaga” and relationships amongst louse suborders have yet to be resolved. Familial relationships within the chewing lice are just beginning to be investigated and offer the prospect of helping us understand more about the evolution and biogeography of their hosts. Rigorous studies of louse cophylogeny are perhaps best confined to terminal clades as these permit more extensive sampling of both host and louse taxa. As a stop gap, new phylogenetic tools such as ‘supertrees’ will permit more extensive

cophylogenetic studies, although this will not demean the value of well sampled clades for assessing cospeciation.

5.1.1: Comparing Subsets of Characters

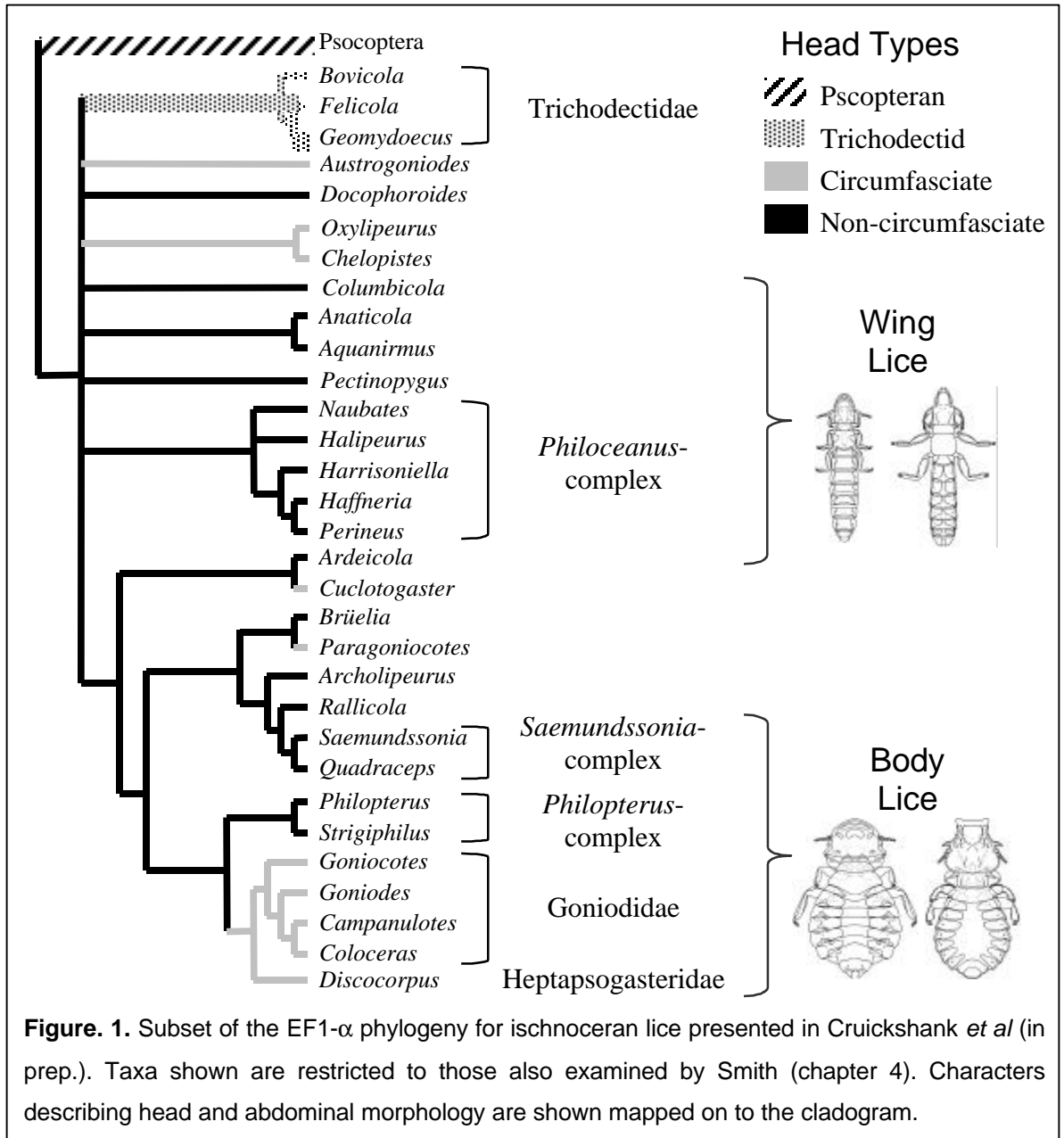
An integrated approach combining molecular and morphological data will be necessary to answer many key questions about the evolution of lice. Molecular data in particular, have the power to answer more sophisticated questions than morphological data alone, simply because the units of change (i.e. nucleotide substitutions) are comparable between taxa. This is despite the fact that these comparisons may be made in taxa as distantly related as a host and parasite. However, I am not suggesting that molecular data are intrinsically better, or easier to interpret, than morphological data, as my co-authors on a recent molecular phylogeny of lice might testify. Both are equally as effective (or ineffective) at resolving particular phylogenetic questions. The key difference lies in the type of questions we can ask of these data.

Much of the debate concerning the virtues of molecular versus morphological data hinges on the assessment of homoplasy or the convergence of characters. It has been proposed that homology assessment based on morphological data is a simpler problem than that faced by molecular systematists, because independent sources of data (e.g., outgroups and ontogeny) are available to a comparative morphologist to help resolve questions of homology (Patterson, 1987). In contrast, homoplasy in molecular data has been reduced to a statistical concept, simply because the limited scope for character change, combined with known problems such as transition to transversion bias, AT richness, or variation in substitution rates between taxa, mean that homoplasy is an ever present issue in DNA sequences. The effects of homoplasy, and the chance that they may be confounding phylogenetic reconstructions are of great concern to molecular and morphological systematists alike. This is typically viewed as noise in a data set that makes delimiting phylogenetic reconstructions difficult, yet patterns of homoplasy provide an opportunity for a variety of evolutionary studies. Specifically, identifying the presence and causes of homoplasy has the potential to uncover evolutionary processes that have implications for all systematists. Such studies are only possible with the presence of multiple corroborative data sets, and present the opportunity to compare the phylogenetic histories of different subsets of characters. Data presented in this thesis (Chapters two and four), combined with a recent molecular estimate of louse phylogeny (Cruickshank *et al.*, in prep.) provide just such an opportunity.

Until recently, workers comparing the performance of data sets have focused on the virtues of molecular and morphological data in tree construction, often with the aim of showing that one is superior to the other. However, where two or more independent data sets are available, a comparative approach to evolutionary patterns can be adopted. Subsets of characters that can be considered independent of one another can be optimised on to the preferred phylogeny and compared to investigate how different aspects of the clade's biology have evolved over time. This approach is not confined simply to the morphological versus molecular dichotomy, but can be expanded to include different kinds of molecular data (e.g., first versus third codon positions; coding versus non coding regions), different parts of an organism's morphology (for example, head versus abdominal characters) or even different stages in the life history of an organism (such as nymphal versus adult morphology). These kinds of comparisons are useful for investigating whether specific traits have evolved independently or in concert with one another, and whether some characters are more prone to homoplasy than others.

Molecules versus Morphology

The phylogenies generated from the molecular data of Cruickshank *et al.* (in prep.) and my morphological data (Chapter four) are in some respects strikingly incongruent, particularly for the deep nodes in the tree which resolve the relationships of the major generic complexes. Perhaps the most striking incongruence concerns the lack of support for the division between avian Ischnocera with a circumfasciate and non-circumfasciate head (Fig. 1). This division is a basal split within the morphological phylogeny, and underpins many traditional ideas on the classification of Ischnocera. However, the molecular phylogeny suggests that these head types have evolved on multiple occasions. Conversely, characters documenting various aspects of abdominal morphology, such as the division between short fat (head) and long, thin (wing) lice, appear to fit the molecular data much better than the morphological data. This discordance is particularly problematic given that characters describing head morphology play a major role in resolving the basal nodes of the morphological tree (unlike those of the abdomen). Testing for homoplasy in these character suites and removing characters which are highly homoplasious might help resolve much of the incongruence between the molecular and morphological phylogenies.



These issues might be explored by comparing the fit of these data partitions within the morphological data (such as the head, thoracic and abdominal characters) on the molecular phylogeny. This could be done using measures such as the consistency and retention index, and would help establish whether particular suites of characters were more homoplasious than others. Homoplasy in the molecular data might similarly be explored by comparing different partitions of the molecular data, on the morphological phylogeny. For example, it is generally accepted that rapidly evolving nucleotide sites are phylogenetically less informative than more slowly evolving ones, especially for recognising more ancient groupings. For this reason, third codon positions are often regarded as a less reliable indicator of phylogeny than first or second positions, and are regularly down weighted in phylogenetic analyses. However, several recent studies have challenged the logic behind this, suggesting that third positions increase phylogenetic structure (e.g., Björklund, 1999; Källersjö *et al.*, 1999). This issue might be explored by comparing the fit of the first, second and third positions on the morphological tree. If our orthodox notions about the utility of different codon positions hold true, third positions are likely to be more homoplasious than first or second positions.

Nymphal versus Adult Morphology

One of the most interesting future directions would be to explore the comparative patterns of evolution for the nymphal and adult morphologies. Specifically, it would be interesting to address whether these morphologies are evolving in tandem or independently. Lice as permanent obligatory ectoparasites pass through a direct life cycle, and their habitat (the host) provides a relatively constant environment throughout this period. However, the precise microhabitat of instars during different stages in their development is not known. Shifts in microhabitat between the nymphal and adult stages may explain why the nymphs of some lice are almost unrecognisable from their adults. In fact, it is not unknown for the nymphs of some taxa to have been mistakenly described as new species (e.g., Carriker, 1936). In contrast, the nymphal morphology of other species may be identical to that of their adult stage (Chapter 3) - perhaps because the microhabitat shifts between instars and adults are less significant, or because their environment (the host's feathers or fur) are more uniform.

Total Evidence versus Taxonomic Congruence

In order to address these questions outlined above, a robust phylogeny for lice would be required. This would allow the molecular, morphological and ontogenetic characters to be independently assessed. However, currently available louse phylogenies (e.g., Chapter 4 and in Cruickshank *et al.*, in prep.) are neither independent or especially robust, and there is no *a priori* reason for believing that one data set should be more correct than the other. In fact, we have good reason for believing that both phylogenies contain significant amounts of homoplasy. For example, saturation curves for the EF1- α data suggest that part of the molecule is heavily saturated with genetic change, thus compromising the phylogenetic utility of this gene. Similarly, the low consistency and retention indices for the morphological data suggest a high level of homoplasy. Combining these data into a single phylogenetic hypothesis might provide a solution to this problem. However, exactly how phylogenetic information should be combined is a source of considerable debate within the systematic community (Allard & Carpenter, 1996; Allard *et al.*, 1999; Huelsenbeck *et al.*, 1996; Kluge, 1998; Page, 1996; Page & Charleston, 1999).

Advocates of the ‘total evidence’ approach, in which all data are combined into a single phylogenetic analysis, do not recognise the divisions between different types of phylogenetic data. They argue that this method derives a hypothesis of phylogenetic relationships that is the best supported overall (Kluge & Wolf, 1993). In contrast, those arguing for taxonomic congruence (consensus) combine the phylogenies generated from different ‘types’ of data in a single consensus tree. Thus seeking to uncover the source of incongruence between these data ‘types’. It is not my intention to discuss the merits of these different approaches. Instead, I simply seek to point out that these issues would have to be considered when producing a working hypothesis of louse relationships. However, this topic of taxonomic congruence versus total evidence, might itself form the basis of an investigation using the molecular and morphological louse data.

5.2: Diversification

In the previous section I have attempted to identify some of the major questions in louse systematics which have yet to be addressed, and shown how might we make better use of the currently available data. In particular, by describing how these data might be used to compare the phylogenetic history of different subsets of characters, I have

touched on many questions which are relevant to current problems in systematics and taxonomy. Yet addressing the causes of incongruence between these characters sets provides an opportunity to consider some of the most important questions in evolutionary biology, such as the correlates of diversification and evolution of specialisation.

5.2.1: Host correlates of Louse Diversification

The host specificity of lice, coupled with a history of cospeciation in at least some host lineages, mean that changes in the characters of their host (such as body size, metabolic rate, sociality, trophic level) are likely to be correlated with characteristics of the lice. By reconstructing the evolutionary history of these characters, we can relate changes in parasite diversity to changes in host attributes. Bird lice are particularly suitable for such studies, since their hosts are some of the most intensively studied organisms on the planet. The biology of many bird groups is thoroughly documented, and provides an opportunity to survey a range of host characteristics which may correlate with their parasite load.

The number of louse species present on a particular bird taxon varies considerably. For example, the world's largest bird (the ostrich) has just a single louse species, whilst its much smaller relatives, the tinamou, play host to one of the most diverse louse faunas known. Thus, body size (at least in this case) does not seem to be a good predictor of louse species richness. However, a more detailed examination of the habitat of the lice (the host's feathers) may provide an explanation for this. The feather types present on tinamou are diverse, differentiated into contour, secondary and downy feathers as in many birds, and the structure of tinamous is highly specialised, perhaps more so than in any extant bird (Chandler, 1916). In contrast, the plumage of the ostrich is relatively simple, and not differentiated into numerous feather types (Chandler, 1916). Therefore, perhaps the diversity and specialisation of the feather structure is a better predictor of louse species richness than simply the size of their host. Other aspects of the host's biology might be investigated in a similar manner in an attempt to find the host correlates of louse diversification. These include bird sociality (are social birds in mixed colonies host to more louse species than eusocial taxa); trophic level (are bird predators more 'lousy' than their prey) and behaviour (do common behaviours such as communal dust bathing affect louse species richness). Perhaps even the biochemistry of feather structure, or their bacterial flora can affect louse taxonomic diversity

(Dumbacher, 1999).

5.2.2: Louse Specialisation

Many lice show apparent adaptations to specific parts of the host's body, perhaps the most classic example being the division between long thin (wing) and short fat (body) lice of birds. Other examples would include the development of a head groove in gopher lice (adapted to the width of hair shafts on part of host's body) (Reed, 1994), or the long thin abdomen of some amblyceran lice (e.g., *Rediella*), adapted for living inside the shafts of their host's feathers (Clay, 1962). Have lice evolved these attributes numerous times on different hosts, or do they represent ancient specialisations by the lice to different host niches? Preliminary data suggests that many aspects of louse morphology (e.g., head asymmetry, antennal sexual dimorphism and the osculum) have evolved more than once (Chapter 4 and in Cruickshank *et al.*, in prep.). If this result is supported, we can ask how these morphologies have evolved repeatedly, and whether there is any direction to this change. For example, do head lice repeatedly evolve from wing lice, or vice versa?

Ontogeny can be a useful tool in predicting whether adult characters have evolved convergently or in parallel. An adult character state derived via different transformation series in different taxa suggests some degree of convergence. Conversely, identical character transformation series in unrelated taxa suggest that these characters have evolved in parallel. This distinction is important as the parallel persistence of major traits through evolutionary time suggests a strong selection pressure on those characters. These may have functional importance and help us understand why certain transformations might be more common than others. Studies using Fourier techniques outlined in chapter three have highlighted both parallel and convergent evolutionary transformations for a character describing head shape. This work might be extended using more sophisticated landmark-based morphometrics (e.g., thin plate splines), perhaps helping to evaluate the findings of the Fourier analysis and potentially highlighting character transformations which are functionally important.

5.2.3: Modes of Speciation

Lice also provide an excellent framework to test the relative frequencies of sympatric and allopatric speciation. The presence of multiple, related species on the same host has been used to argue that sympatric speciation is more common than is

generally recognised (e.g., de Meeûs *et al.*, 1998). Implicit in this argument is the notion that these multispecies assemblages comprise suites of closely related parasites that have evolved *in situ*. An alternative hypothesis is that these assemblages are distantly related, and have either been associated with their hosts for a long time, or have independently colonised their present host. Asking whether the louse faunas of different hosts are monophyletic might easily test these hypotheses. If they are, then we can ask whether some host clades are more prone to such assemblages than others, and if so, are there aspects of their hosts biology that might explain this. A related question to this issue concerns the morphological divergence of lice on the same host. We would expect as the number of louse species on a host increases, so would the morphological disparity between them, leading to greater specialisation and the eventual occupation of different niches. Morphometric techniques (such as elliptic Fourier analysis) allow us to quantify the degree of similarity between shapes, and might be used to test this.

5.3: Cophylogeny

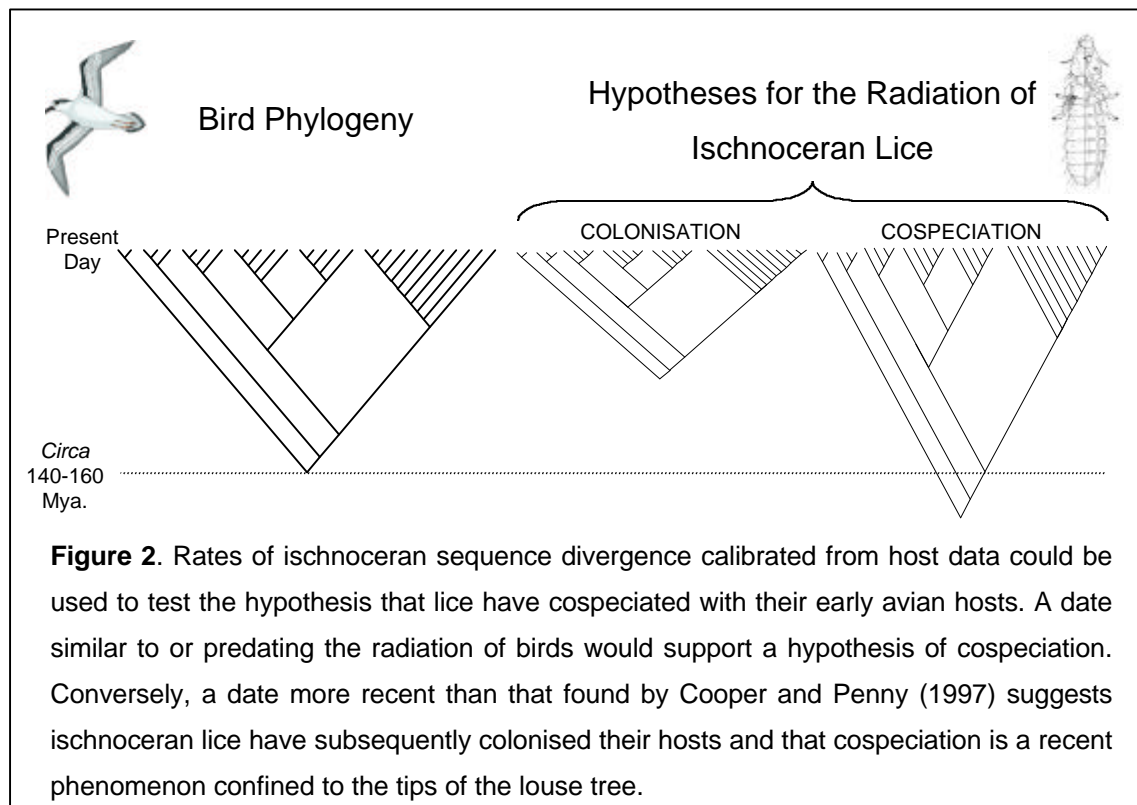
One of the most fundamental correlates of louse diversification is likely to be host speciation. In strictly cospeciating host-parasite assemblages, host phylogeny will determine parasite phylogeny. This has been most convincingly shown with bacterial endosymbionts and their hosts, such as in a series of studies by Moran *et al.* with aphid endosymbionts (Moran *et al.*, 1993; Moran *et al.*, 1995) and in the chemoautotrophic bacteria of deep sea clams (Peek *et al.*, 1998). However, lice are unique, because they are one of the few metazoan parasites which apparently exhibit cospeciation (Hafner & Nadler, 1988; Lyal, 1987; Page *et al.*, 1996; Paterson, 1994). The notion that cospeciation has been the dominant force shaping host-lice assemblages, taken to extremes by some (e.g., Eichler, 1982), has shaped our ideas about the evolution of this insect group, however, several recent studies have challenged this hypothesis (e.g., Barker, 1991; 1994). In this final section, I will attempt to define some of the key questions which could be addressed if the affects of host speciation on lice are to be better understood.

Rigorous tests of host-parasite cospeciation require robust, fully resolved phylogenies which have been extensively sampled (Page *et al.*, 1996). For lice, such studies are only practical on a small scale. Consequently, most studies of host-lice cospeciation are confined to the terminal branches of the wider louse tree. More

ambitious studies are precluded by the lack of any detailed phylogeny for all 5000+ species, and has prompted the suggestion that cospeciation may be a phenomenon confined to small terminal louse clades (Chapter 2). Whilst a complete phylogeny for all lice is both impractical and unlikely given their species richness, we might ask whether aspects of their biology and evolutionary history are at least compatible with a history of cospeciation.

5.3.1: Heirlooms or Souvenirs?

Several observations refute a strict one to one hypothesis of cospeciation. For example, many birds and mammals are host to more than one species of louse, whilst many mammals completely lack lice. There are also many more species of hosts than there are lice (although this is somewhat dependent upon our rather conservative species concepts in Phthiraptera and assumes that we have described all extant louse species). Finally, our limited understanding of the deep branch louse relationships suggests that the lice of the major host groups (birds and mammals) are not monophyletic. Despite these points, they do not rule out cospeciation as a dominant process. Lice may be a very ancient group, and it is likely that many other forces including extinction, host switching and within host speciation will complicate the overall picture. An improved test would be to determine the relative age of lice with respect to their hosts. If lice are as old, or older than their hosts, then cospeciation may have been a factor in their early diversification. Conversely, if lice post-date the radiation of their hosts, cospeciation could not have affected the early radiation of lice. Such a test is dependent upon finding sufficient cospeciation points within the louse clade, and would have to be restricted to practical clades of lice, such as the avian Ischnocera (Fig. 2). The methodology is the same as that used by Cooper and Penny (1997) to test whether the radiation of modern birds pre- or post-dates the K/T boundary. By substituting birds for the K/T boundary, and targeting lice hosted by birds for which there is a good estimate of the host's geological age, a reliable estimate of louse divergence time could be made using programs such as QDate (Rambaut & Bromham, 1998).



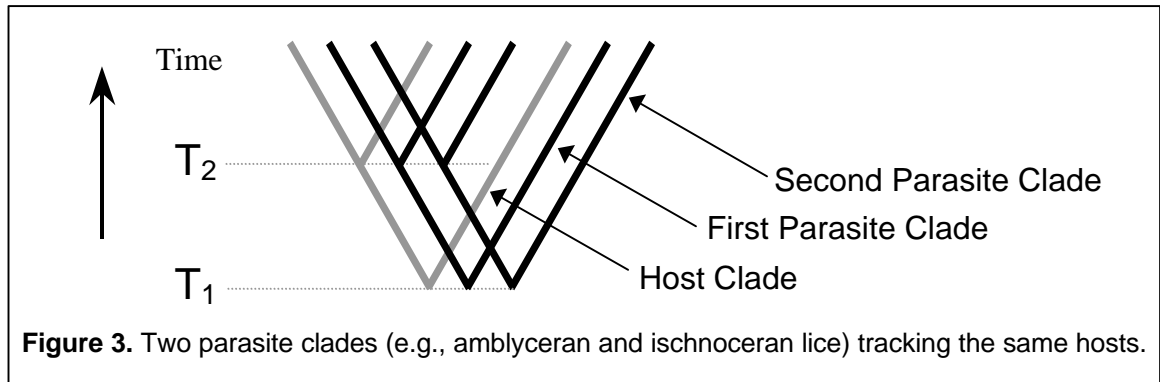
5.3.2: Comparative Cophylogenies

One of the challenges facing evolutionary studies is the lack of experimental replication. In many cases, inferences about the coevolution or cospeciation of a host and associate are based on reconstructions of past events (e.g., via reconciled trees or Brooks parsimony analysis) rather than by direct experimental manipulation. Since each taxon has its own phylogenetic history, it is difficult to make generalisations and test hypotheses, based on limited reconstructions. More importantly, since it is rarely possible to directly observe these processes, how can we be sure these reconstructions are correct?

One solution to this problem is to find ‘natural experiments’ – instances where the patterns observed in one organism corroborate those observed in another. This approach can be applied to the study of host-parasite coevolution when multiple clades of parasite occur on the same host (Fig. 3).

Comparing these patterns in different clades can test hypotheses about rates of diversification and character evolution. Since multiple clades of lice occur on the same host clade, they offer the possibility of a replicated ‘natural experiment’. For example, because the major suborders of avian lice (Amblyceran and Ischnocera) have a similar

distribution across birds, it is possible to compare their phylogenetic histories with their hosts. Comparing the degree to which the two suborders have cospeciated would help to gain insight into the factors affecting coevolution and cospeciation.



5.3.3: Transmission and Specificity

A great deal of anecdotal evidence concerning the population biology and ecology of lice would suggest that they are likely to cospeciate. Their limited transmissibility has led to the suggestion that they are passed like genetic heirlooms from parent to offspring, whilst their inability to survive away from the host and host specificity suggests that transfer to non-specific hosts is likely to be rare. However, reliable data addressing these issues are in scant supply.

Louse Transmission

Tracking parental lineages of lice on parental lineages of host would be one way in which some of these issues might be explored. It is generally assumed that most transmission between conspecific hosts is vertical, and it has been shown that transmission does occur in this way (Hillgarth, 1996). Further evidence comes from observations on the density of chewing louse populations on hosts prior to the fledging of nestlings in birds (e.g., Ash, 1960) or shortly after the birth of a litter in mammals (e.g., Rust, 1974). A decline in louse density on the host's parents is thought to be caused by the dispersal of lice to their offspring. However, a recent study based on pocket gophers and their trichodectid lice did not support a strict hypothesis of maternal transmission (Demastes *et al.*, 1998). This study suggests that at least in pocket gophers, lice may be transmitted predominantly, but not exclusively from mother to offspring, or that louse transmission may be altogether independent of pocket gopher genealogy. Understanding the frequency of vertical to horizontal transmission in lice is important,

because a high rate of horizontal transmission would increase the chance of host switching. This has implications for understanding the prevalence of cospeciation in host-lice systems. Studies on the acquisition of feather lice by brood parasites such as the cuckoo (*Cuculus canorus*) suggest that their host specific lice are acquired horizontally (Brooke & Nakamura, 1998), and recent work conducted by Kevin Johnson and Dale Clayton at the University of Utah might suggest that some bird lice are able to cross the species barrier during transmission (K. Johnson, pers. comm.). Their study based on mitochondrial sequence data, found ischnoceran lice with the same haplotype on as many as four species of columbiform host in the same locality. This suggests that horizontal transmission (which in this case is crossing the host species boundary) may be more common in some host-lice systems than was originally thought.

Other opportunities for horizontal transmission, apart from direct body to body contact need to be explored. Phoresy has long been touted as a possible mechanism for louse transfer. However, data on its frequency and prevalence among louse taxa are in scant supply. Phoresy is in effect a risky process of redistribution in which an individual of one species attaches to the body of another, gaining a mode of transportation but without feeding on its 'host' during transit. This has been occasionally reported between lice and hippoboscids (Clay & Meinertzhagen, 1943), and on rare occasions between lice and fleas (Smit, 1954). It is thought to be particularly common on dead or dying hosts. In these circumstances, the lice, detecting a drop in the body temperature of their host, move to the surface of the feathers or fur (often on the host's head), where they are most likely to be in contact with another possible host. In a last ditch attempt to escape a dead host, some lice are thought to attach to hippoboscids so that they might be transferred. However, only two genera of ischnoceran lice (*Philopterus* and *Brüelia*) have been reliably reported attached to hippoboscids, and limited experiments to observe this attachment behaviour have failed (Clay & Meinertzhagen, 1943). Nevertheless, there is no doubt that phoretic associations between lice and hippoboscids do occur, as is dramatically illustrated in the scanning electron micrographs shown in Fig. 4 overleaf.

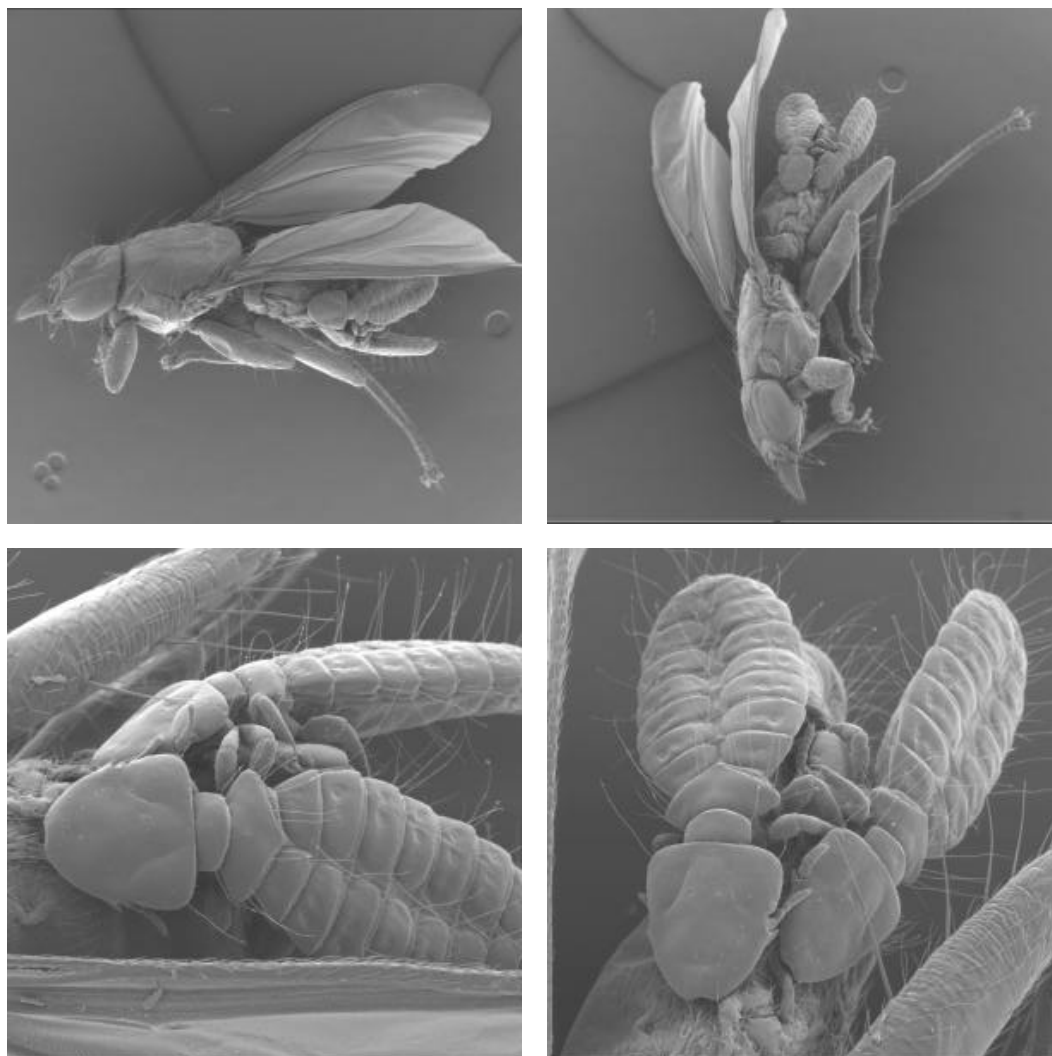


Figure 4. Scanning electron micrographs illustrating phoresy between chewing lice and a hippoboscid fly. These specimens were collected from a blackbird (*Turdus merula*) in Agadir, Morocco, and show the lice (*Brüelia* sp.) firmly attached to the abdomen of the fly.

Phoretic associations between lice and hippoboscids are often cited as a means of possible transfer between hosts, particularly when no other means of transfer seems likely (e.g., Brooke & Nakamura, 1998). However, until there is confirmation of phoresy involving more than two louse genera, it seems unlikely that it will play a major role in interpreting how lice are transmitted.

Causes and Consequences of Host Specificity

Understanding the causes and mechanism of host specificity in lice is perhaps the last major challenge to determining their propensity for cospeciation. The host specificity of parasites is likely to be a major contributor to their diversity, and this is sometimes taken as *prima facie* evidence for their adaptive specialisation (Secord & Kareiva, 1996). In lice, if they cannot survive or reproduce on 'foreign' hosts, then they are considered to be specialised. However, specificity may simply be maintained by limited dispersal among host species and therefore adaptation may not necessarily play a role. This can be tested by comparing the fitness (i.e., the survival) of host specific lice on 'foreign' host taxa with the fitness of controls transferred to individuals of the usual host. If parasite fitness on the usual and foreign hosts does not differ, specificity is not governed by adaptive constraints. To date such studies with lice have been limited to work on the swiftlet louse genus *Dennyus*. Tompkins and Clayton (1999) found that the survival of lice in most transfers to 'foreign' hosts were greatly reduced. However, perhaps more significantly, louse survival was proportional to the mean difference in feather barb size between the donor and recipient host species. Also, in transfers where lice survived, microhabitat shifting was observed, in which transferred lice moved to feather barbs which were of the same size as on the original host. Thus, it seems these lice are adapted to a particular resource on the hosts body and that this governs the specificity of swiftlet lice. Survival after host transfer also did not appear to be correlated with host phylogeny. This implies that ecological and mechanical attributes of the host are likely to play more important role in the host specificity of lice, than the host's phylogenetic history. If this is the case, why should small changes in feather barb size be so critical to louse survival? Perhaps this increases the chance that the lice may be preened off their hosts, or are more likely to fall off their host's feathers during flight. Alternatively, differences in the microclimate along feather barbs may play a role? Clearly more effort needs to be directed towards examining the causes and mechanisms of host specificity in these and other louse groups, particularly for

ischnoceran lice which are putatively more host specific than amblyceran lice such as *Dennyus*.

5.4: Summary

“The student of Mallophaga...can be compared to the palaeontologist. He delves into the past, not by quarrying into the rocks for fragments of bones, but by studying the morphology and distribution of these living fossils. As he pieces together the story of their evolution, he likewise unfolds the story of the evolution of the birds.”

(Rothschild and Clay, 1952: p. 146)

Within the host-lice framework there remains the potential for the discovery of a range of micro- and macroevolutionary patterns and processes which have implications for diverse groups of organisms. These questions can only be addressed with robust taxonomies, and a lack of systematic data is likely to be the main barrier to answering many of these questions in subsequent research. This thesis has attempted to lay the groundwork for revision of many avian louse clades within the suborder Ischnocera, and in doing so has touched upon many of the problems and controversies which are relevant to the theory and practice of modern systematics. Within this framework I hope to have shown that morphology still has a part to play in unravelling the “paradoxes and complexities” which beset this subject, and as Rothschild and Clay noted in my introduction to this thesis, this subject will remain an “infinite fascination”.

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