

CHAPTER ONE

Introduction

“The student who intends working on the Mallophaga should take warning that he will be tried almost beyond endurance by the paradoxes and complexities that beset his subject but he will also find, in the dual and inter-related aspect of insect and bird, an infinite fascination.”

(Rothschild and Clay, 1952: pp. 156-157)

Lice and the people that study them have played an important role in our understanding of the patterns and processes of coevolution. This is readily apparent from many of the seminal works that have appeared on coevolution throughout this century. Even the idea of a shared history between parasites and their hosts is as old as modern evolutionary thought. In a letter to Henry Denny, the first (and only) person to make a special study of the louse fauna of Britain, Charles Darwin (7 November, 1844) remarked in reference to the bird lice of Europe and North America “what an interesting investigation would be the comparison of the parasites of the closely allied and representative birds of the two countries”. However, it took over 100 years before empirical data on such observations were articulated into coherent ideas on coevolution. Kellogg (1896b), and later Fahrenholz (1913) began to examine the evolutionary relationships between parasites and their hosts based on their studies of avian lice. Earlier, Von Ihering (1891) used evidence from flatworms and their crayfish hosts to postulate that southern South America and New Zealand once shared a freshwater connection. These studies spawned a century of research into questions on the evolutionary relationships of parasites and their hosts that continues to this day.

The first biologists to look in detail at these host-parasite interactions worked extensively on chewing lice (Mallophaga). These authors included the likes of Kellogg, Fahrenholz, Johnston and Harrison, whose interest in the group stemmed initially from

a desire to understand more about their natural history, but were struck by the related patterns of distribution between the lice and their hosts. These patterns became apparent after extensive observations on their taxonomy and distribution. They noted that certain louse groups were restricted to particular groups of host (Fahrenholz, 1913; Kellogg, 1896b), and that in some cases, the host identity could be predicted from the identity of the louse (Hopkins, 1942). These observations of correlated evolution (coevolution) required explanation, and each of these early researchers concluded that it was the common genealogy of their hosts, rather than independent evolution of the lice that was the chief explanation for this distribution. This was first noted by Kellogg, who writes in his 1896 monograph: “The occurrence of a parasitic species common to European and American birds...must have another explanation than any yet suggested. This explanation, I believe, is, for many of the instances, that the parasitic species has persisted unchanged from the common ancestor of the two or more now distinct but closely allied bird-species” (Kellogg, 1896b p. 50-51). This same conclusion was apparently arrived at independently by Fahrenholz (1913), Johnston (1913), and Harrison (1914) (see Klassen, 1992) and provided the foundation for modern coevolutionary studies.

1.1: Concepts of Coevolution:

The word ‘coevolution’ was not used until the late 1950s and early 60s (Thompson, 1989), but prior to this, concepts of coevolution were expressed in a variety of so called ‘parasitological’ rules, first summarised by Eichler (1942; 1948) which formed a conceptual framework by which ideas on coevolution could be better understood. Implicit in these rules was the idea that host specificity governed parasite speciation, and consequently parasites were thought to have great predictive value in resolving host relationships. Eichler’s dogged insistence on this, and in particular, his reliance upon host taxonomy to delimit parasite species did much to tarnish his reputation, and that of the emerging field of coevolution. Yet his ‘parasitological rules’, particularly the rule he attributed to Fahrenholz (parasite phylogeny mirrors host phylogeny), provided much needed hypotheses which permitted many of these developing ideas on coevolution to be tested.

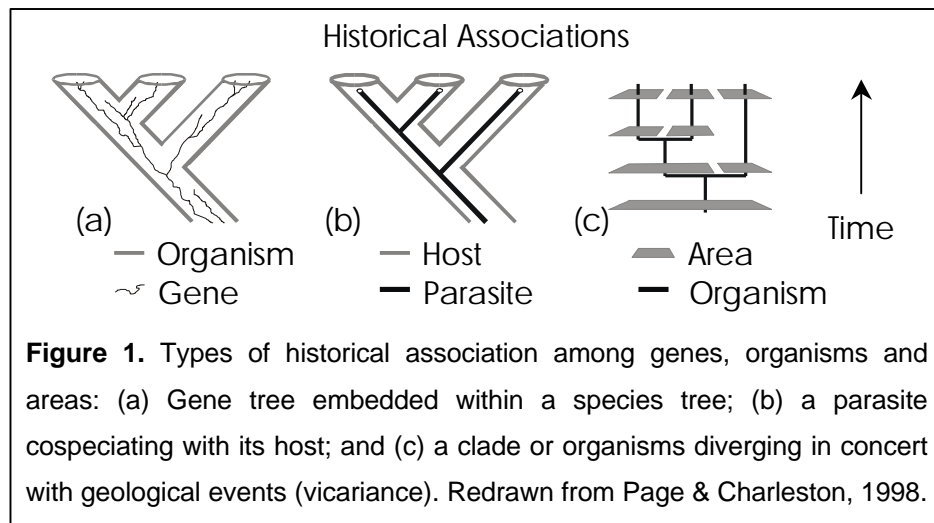
The first step towards critical appraisal of these hypotheses arose with the advent of cladistics (Hennig, 1966), and increasingly attention switched amongst those

studying host-parasite relations from coevolution, to a perceived subset of coevolutionary processes known as cospeciation. Cospeciation, like all coevolutionary processes, requires reciprocal changes in the host and parasite taxa. However, with cospeciation these changes take the form of contemporaneous cladogenic events in both host and parasite lineages. In contrast, coevolution in its most restrictive sense refers to specific adaptive responses (anagenesis) between ecologically interacting species. These generate successive changes in host and associate which result in a kind of evolutionary 'arms-race'. This definition, championed by Janzen (1980) and Thompson (1989) highlights a clear distinction between coevolution and cospeciation. To these authors, demonstrating coevolution not only requires that the two forms are adapted to each other, but also that their ancestors evolved together, exerting selective forces on one another. In contrast, some authors (e.g., Brooks & McLennan, 1991) have defined coevolution in a much broader sense, encompassing both the degree of phylogenetic association (i.e., cospeciation) with the degree of mutual modification (coevolution *sensu* Thompson, 1989). To distinguish these phenomena, they have applied the term coadaptation to processes that were conventionally called coevolution (*sensu*, Janzen, 1980 and Thompson, 1989). However, this is unfortunate as mutual adaptation (coadaptation *sensu*, Janzen, 1980) does not necessarily imply coevolution, since two lineages may evolve independently, yet at some stage be mutually adapted to each other. To avoid confusion, Janzen (1980) and Thompson's (1989) definitions of coevolution, coadaptation and cospeciation are adopted from here on.

Studies of cospeciation are particularly attractive because they are more easily quantified than coevolution or coadaptation. Cospeciation events are putatively indicated by topological congruence between the host and associates phylogenetic histories, and confirm a long and intimate association between organisms that may be biologically very distinct. Kellogg recognised this as early as 1913 when he wrote "...the parasite species has been handed down practically unchanged to the present...bird species from their common ancestor of earlier days. *The parasite species dates from the days of its ancestor*" (italics mine) (Kellogg, 1913 p. 157). This sets the stage for studies on the historical ecology of coadaptation and community evolution. Cospeciation events mark a single point in time in the host and associates evolutionary history, acting as a marker that can be used to calibrate the rate of molecular sequence evolution in the two groups. With the advent of modern molecular biology, it has become possible to pin actual dates on these events.

1.2: Types of Historical Association:

The association of two or more lineages over evolutionary time is not unique to studies of host-parasite biology (Page & Charleston, 1998). Parallels exist within the fields of biogeography and molecular biology, with each discipline facing fundamentally similar problems. In particular, analogous processes between host and associate, be they host and parasite, organism and area, or organism and gene, lend themselves to a more general problem despite differences in the mechanisms underlying these processes (Fig. 1).



This realisation was partly recognised by Von Ihering (1891) and Kellogg (1896b). Later, Metcalf (1923) referred to what he called the ‘host-parasite method,’ in reconstructing the biogeographic relationships among Anura (frogs and toads) (Klassen, 1992). However, the analogy with molecular biology was to come considerably later. This stemmed from the realisation that multiple copies of some genes are present in an organism’s genome due to gene duplications. This process is analogous to ‘within host speciation’ by a parasite on its host, and sympatry between organisms in an area. Recognising duplication events is important if we are to correctly infer ancestral relationships, be they for genes, hosts or areas. This is often a primary goal in the reconstruction of historical associations among ancestral lineages. The analogy between these different categories of association, with each a special case of a more generalised problem, has led to the development of a single analytical tool which can be applied to each kind of association (see section 1.4).

1.3: Prerequisites for Testing Cospeciation

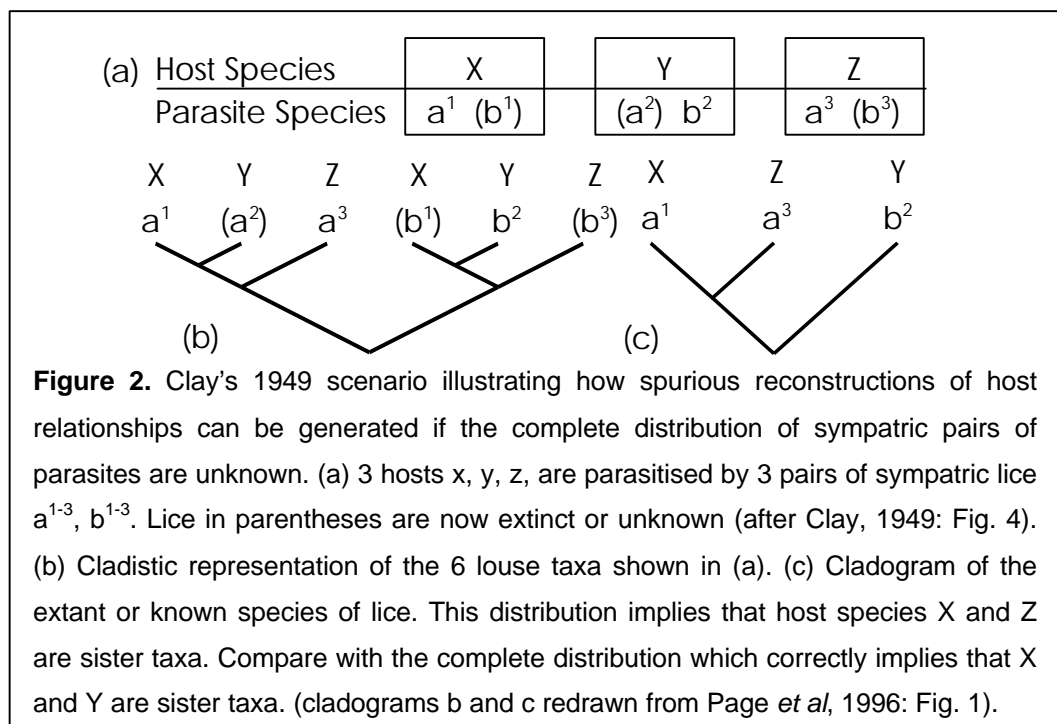
The prevalence of cospeciation in host-parasite systems is an empirical question that requires considerable amounts of data. Such information could then be applied to addressing questions concerning the processes involved in structuring host-parasite assemblages. Suitable data for such studies are lacking, partly because it is only recently that a methodological framework for quantitatively studying cospeciation has been developed (see next section). However, more fundamentally there are a number of basic requirements needed for testing cospeciation. These were initially outlined by Page *et al.* (1996), and I provide further comment on these here.

Accurate taxonomy and phylogeny of host and parasite clades: All hypotheses of cospeciation ultimately depend upon accurate recognition of taxa and accurate hypotheses of relationships between these clades. Failure in either of these regards can lead to spurious interpretations of the data. Unfortunately, many parasite taxa are poorly known taxonomically and even less well understood phylogenetically, whilst host taxa (typically fish, mammals or birds) may be much better studied, but authorities often fail to agree on their taxonomy and phylogeny.

Accurately delimiting terminal taxa (usually species) within host and parasite lineages is critically important to studies of cospeciation, yet species concepts held by different taxonomists often differ greatly. Excessive ‘splitting’ between taxa over emphasises the importance of host taxonomy in the separation of parasite species, whilst broader species limits can obscure patterns of host specificity. These influence our perception of the extent to which cospeciation shapes host-parasite assemblages. Unfortunately, it is often not clear where intraspecific variation ends and where interspecific variation begins, hence species concepts (particularly amongst phthirapteran taxonomists) are often applied inconsistently. Recent advances in systematics, such as new methods in the analysis and use of morphometric data (e.g., landmark and Fourier based techniques), new molecular techniques, and analytical tools to analyse data quality have the potential to provide more robust taxonomies and phylogenies. However, a lack of basic taxonomic data is likely to be the main limitation on future studies of host-parasite cospeciation.

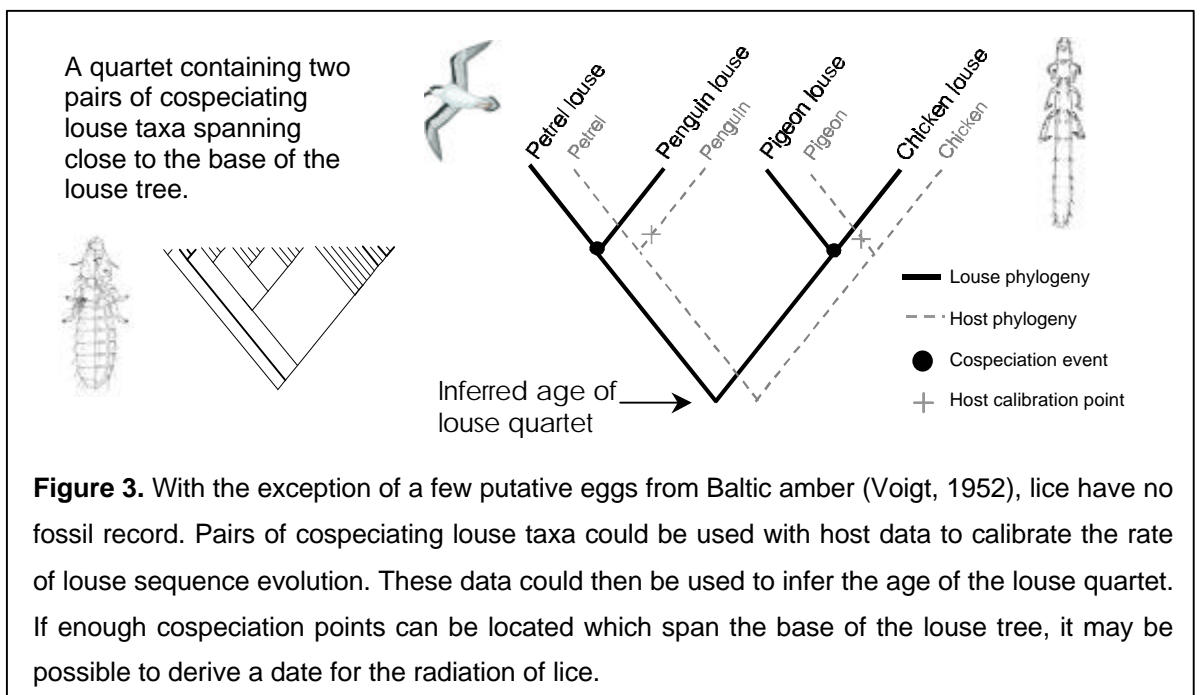
Exhaustive sampling of parasite clades: Parasites commonly occur in low numbers or have a patchy distribution amongst host taxa (Rékási *et al.*, 1997) and may escape detection (sampling error). This can generate a false absence of parasites from

their hosts ('pseudosorting' *sensu* Paterson *et al.*, 1999) and like other sorting events can lead to spurious reconstructions of host relationships if undetected. This was recognised by Hopkins (1948) and Clay (1949), who gave a hypothetical example of how a naive interpretation of a parasite's host distribution can imply incorrect host relationships (Fig. 2). Consequently, the strongest tests of hypotheses for host-parasite cospeciation come from exhaustively sampled clades of parasites. Given a choice, studies of cospeciation are better conducted on all representatives of a clade, such as a single genus, than to sample the same number of species from a range of different clades. Unfortunately, this opposes the instinct of most taxonomists to capture the broad outline of a parasite phylogeny, by sampling a range of disparate taxa.



Molecular phylogenies: Molecular phylogenies can potentially provide the answer to many key questions in studies of host-parasite cospeciation. This is because the fundamental units of molecular evolution (i.e. nucleotide substitutions in the DNA sequence), are comparable for the same genes between host and parasite. Homologous genes can readily be found in most taxa, whereas homologous morphological features may be extremely difficult to find in taxonomically disparate clades (Page *et al.*, 1998). Consequently, molecular phylogenies based on comparable genes allow us to compare the rates of sequence divergence between hosts and parasites. Also, if these data are compatible with a molecular clock hypothesis, temporal congruence between events in

the host and parasite phylogeny can be established. This is useful as it allows us to distinguish between the two primary explanations of incongruence between host-parasite phylogenies, i.e. host switching and multiple lineages (Page *et al.*, 1996). Further to this, if the rate of sequence evolution in either the host or parasite lineage can be calibrated, it may be possible to date the speciation of the parasite lineages from its common ancestor, based on the estimated speciation date of their hosts, or vice versa. This assumes that the host and parasite lineages have cospeciated (Page *et al.*, 1998). Possible sources of calibration data include the fossil record of either taxon or the use of a previously established calibration rate in a related taxon. More significantly, if enough cospeciation points can be identified and calibrated in the host-parasite system, the rate of sequence evolution can be extrapolated back to their common ancestor to establish a date of radiation for the whole group. A hypothetical example of how this might be applied to the investigation of a date for the radiation of lice, is shown in Fig. 3.



Host transfer experiments: Controlled transfer experiments offer the prospect of identifying the constraints on natural host switching (Page *et al.*, 1996). This is particularly important in studies of host-parasite biology as establishing the likelihood of host switching events is of critical importance to many models of cospeciation. From a broader perspective, host transfer experiments may also help elucidate many of the factors governing a parasite's host specificity. For example, a number of physiological,

chemical and ecological properties of hosts have been proposed as mechanisms for maintaining the host specificity of lice. Preliminary studies undertaken by Tompkins and Clayton (1999) have shown that feather barb size governs the specificity of swiftlet lice. This has implications for understanding the circumstances in which host switching will occur, and further studies are needed to identify the adaptive constraints of host specificity in other louse groups.

These prerequisites of host-parasite studies are all essentially concerned with methods of acquiring data that may be compatible with a hypothesis of cospeciation. However, objective methods of analysing these data, particularly with respect to rigorous comparison of host-parasite phylogenies, are needed. This has led to the development of sophisticated methods of analysis which take into account individual evolutionary processes to reconstruct the history of host-parasite associations.

1.4: Testing Cospeciation - A Methodological Perspective:

The birth of cladistics provided a method of visualising the relationship between host and parasite, however it is only recently that methods have been developed to quantify the extent to which host-parasite lineages have diverged. The first step was the development of methods to quantify the degree of topological congruence between two trees. In the field of host-parasite biology these measures of fit were used under the assumption that significant discordance between host and parasite trees implied a history of host switching and not cospeciation (Fahrenholz's rule). Such measures were useful indicators of cospeciation. However, they lacked the sophistication required to explain all of the biological events in the history of a host-parasite association. In particular, reconstruction of these associations needed to recognise cospeciation events, host-switches, within-host speciation and parasite extinction. The identification of these processes provides an accurate measure of the fidelity with which a parasite lineage has tracked its host.

Brooks Parsimony Analysis (BPA) was a first attempt to incorporate these processes into such a reconstruction. Using Wagner parsimony the additive binary coded parasite tree is fitted into a host tree. Thus, parasites are treated as characters of their hosts to construct a host phylogeny. This reconstruction attempts to explain the parasite distribution under the assumption that the most parsimonious explanation is the

most likely. In other words, it minimises the overall number of ‘ad hoc hypotheses,’ accommodating all four of the biological processes required to measure the fidelity with which the parasite has tracked its host. Unfortunately, BPA can generate spurious reconstructions that are biologically impossible (Page, 1990; 1994). This problem arises because of the way BPA accommodates host-switching events, treating characters created by additive binary coding as independent. Consequently, under some circumstances when a host switch occurs, BPA also requires the deceased ancestors of extant parasite to disperse (Page, 1993). In addition, BPA has a tendency to overestimate the number of host switching events, since this is the standard interpretation of incongruence between the BPA and original host tree. In fact, this incongruence could be equally well interpreted as a parasite sorting or speciation event (Paterson & Gray, 1997).

A collection of methods known as component analysis (Nelson & Platnick, 1981; Page, 1990) avoids the assumption that incongruence indicates host switching. These attempt to reconcile the host and parasite trees under the initial assumption that no host switching has occurred. Host switching events are subsequently detected indirectly in the reconciliation analysis as they significantly contribute to the lack of fit between the host and parasite tree (Paterson & Gray, 1997). A reconciled tree depicts the most parsimonious explanation of the phylogeny of the associate (i.e. the parasite in the case of reconstructing host-parasite relations) embedded within the phylogeny of its host. This requires the postulation of a number of duplication (within host speciation) and sorting (parasite extinction) events. In addition to visualising the relationship between host and associate, allowing cospeciation events to be readily identified, reconciled trees provide a quantitative measure of the extent to which the host and associate trees have diverged. They can also be used as predictive tools, with missing lineages corresponding to sorting events. These may represent as yet undiscovered or extinct parasite lineages. This approach has been criticised because of its emphasis on maximising cospeciation, at the explicit cost of duplication and sorting events. Under this scenario, virtually any incongruent host-parasite phylogeny can be reconciled if enough ‘within host speciation’ and ‘parasite extinction’ events are postulated. However, because they are not subject to problems caused by false incongruence (i.e. overestimating host switching and underestimating cospeciation) and avoid some of the spurious reconstructions generated by other methods, they are widely used in instances where the evolutionary histories of hosts and associates need to be reconciled.

The most recent modification to this method was proposed by Charleston (1998). His solution can accommodate all temporally congruent host switching events by employing a mathematical structure called a ‘jungle,’ which describes all possible ways in which an associate tree can be mapped to that of its host. Costs for cospeciation, host switching, within host speciation and parasite extinction can then be applied to the connections (vertices) in the ‘jungle’ to find the most parsimonious subgraph(s) describing the least costly associations of the host and associate. This approach is a significant advance in our ability to reconstruct the ancestral relations of host-parasite lineages, however it has two main problems. Firstly, from a computational perspective, the cost of incorporating temporally congruent host switching events into the reconstruction has significantly increased the complexity of the problem. This is particularly the case if the likelihood of host switching is deemed high, although as Charleston points out, “the problem is inherently complex and this complexity has been previously ignored,” (Charleston, 1998 p. 210). Also, the technique requires that the costs of the four main processes underlying the model be known. These play an important role in finding optimal solutions, although in certain cases the costs do not appear to matter all that much (M. Charleston, pers. comm.). However, estimating these values is very difficult (Charleston, 1998). A first step towards estimating these costs has been developed by Huelsenbeck *et al.*, (1997) in developing a statistical test of host-parasite cospeciation. Nevertheless, estimates of these costs are likely to vary significantly between different host-parasite groups, and consequently calculating these costs is likely to remain problematic.

1.5: Lice as Model Organisms for Studying Cospeciation

Lice are wingless obligate ectoparasites, present on almost all birds and about a quarter of all mammal species. They are highly host specific and relatively non-pathogenic. These facts, combined with their widespread host distribution, particularly within the class Aves, suggest a long and relatively stable evolutionary relationship. This has led many authors to claim that lice adopted a parasitic lifestyle early in their hosts evolution, and that they subsequently radiated (cospeciated) with their hosts (e.g., Clay, 1957; Hopkins, 1942; Lyal, 1985b; Mauersberger & Mey, 1993; Page *et al.*, 1996). Lice are particularly attractive for studying these relationships because, unlike many parasites, their host associations are highly tractable. There is a long tradition of

documenting these patterns, which goes back at least three centuries (see next section). This represents a valuable resource for those studying cospeciation, which is unparalleled by any other metazoan parasite group, yet most of the early pioneers of louse systematics failed correctly to explain these congruent host-louse associations. This is not surprising given the prevailing views on evolution and speciation held at that time, and it was not until rigorous taxonomic studies were made by the likes of Kellogg (1896b) and Harrison (1914), that specific investigations into the distribution of lice were made.

Early studies of louse-host relationships typically had a very broad focus, concentrating on either select examples of louse relationships that might help resolve particularly contentious issues of host taxonomy (e.g., Fahrenholz, 1913; Kellogg, 1913 and Harrison, 1915), or documenting general trends of distribution amongst diverse host taxa (e.g., Clay, 1950; Rothschild and Clay, 1952; Hopkins, 1957 and Clay, 1957). Examples of the latter became particularly common as specialists began to concentrate on particular host groups. The lice of pelagic seabirds have long been singled out by entomologists as putative indicators of host relationships (Edwards, 1951). This was initially highlighted in a series of papers by Thompson (1938a; 1938b; 1939; 1940a; 1940b; 1940c; 1946; 1947) and studied in depth by Timmermann for both Charadriiformes (Timmermann, 1957) and Procellariiformes (Timmermann, 1965). Select examples of similar studies for other host groups include an investigation by Ward into the lice of South American tinamou (Tinamiformes) (Ward, 1957), Passeriformes by Clay (1946) and Galliformes by Kettle (1981). Inferences concerning cospeciation were drawn entirely from the known distribution of the lice, in conjunction with a limited understanding of louse taxonomy. However, the assumptions on which these studies were based were often flawed. In particular, the apparent host specificity of many louse taxa may have been exaggerated by the circular reasoning, common among earlier taxonomists who described new species on the basis of their host associations. Clearly a phylogenetic framework was needed if inferences of cospeciation were to accurately be drawn from these data.

The first critical attempts to examine an hypothesis of cospeciation based on a phylogeny of lice were conducted by Lyal (1987) and Kim (1988). Both studies focused on cospeciation of mammalian lice. Lyal re-evaluated the taxonomy of ischnoceran family Trichodectidae and generated a morphological phylogeny based on the 351 species of the group that he considered valid. Kim's (1988) phylogeny focused on the

sucking lice (suborder Anoplura). He examined 47 generic exemplars in an attempt to build the first general picture of anopluran relationships. Both studies supported a general hypothesis of cospeciation, however, critical appraisal of their results was not possible as the techniques needed to quantitatively analyse these data had not yet been developed. Nevertheless, a substantial proportion of the speciation events in both studies could be explained by cospeciation (almost 75% in the case of Lyal's study), particularly for small clades towards the tips of the cladogram. In several cases these showed close phylogenetic parallelism between lice and their mammalian hosts. This was an important finding as future studies of cospeciation were to be directed at these terminal clades. Specifically, these investigations focused on species belonging to one or two closely related genera, as the small numbers of terminal taxa would lend themselves to more rigorous tests of cospeciation.

The most famous example of host-lice cospeciation is also the most extensively studied. This focuses on two trichodectid genera (*Geomydoecus* and *Thomomydoecus*) and corresponds to the first molecular phylogeny ever produced for lice. These are hosted by several species of pocket gophers belonging to the rodent family Geomyidae. Both the hosts and their lice have been extensively studied taxonomically (e.g., Demastes, 1994; Hafner *et al.*, 1983; Hafner *et al.*, 1987; Hellenthal & Price, 1988; 1989; Price, 1975; Price & Emerson, 1971), and ecological characteristics of the hosts (highly asocial and well-dispersed) suggest that the lice would have few opportunities for colonisation of new host species. Cospeciation between these groups has been investigated using morphology (Page *et al.*, 1995; Timm, 1983), allozymes (Demastes & Hafner, 1993; Hafner & Nadler, 1988) and nucleotide sequences (Hafner *et al.*, 1994). In each case, significant evidence for cospeciation has been demonstrated and in most of the more recent studies, quantitative methods of reconstructing the history of the associations have been employed. Consequently, the gopher-lice system has become a 'text-book' example of cospeciation (e.g., Ridley, 1996) and is used as a model for developing many of the methods for reconstructing host-parasite relationships (e.g., Charleston, 1998; Huelsenbeck *et al.*, 1997).

Not all studies of host-lice relationships have revealed a predominance of cospeciation. Barker (1988; 1991) investigated the evolution of host-parasite associations among species of boopiid lice (suborder Amblycera) on rock wallabies (Marsupialia: *Pterogale*). He proposed that after an initial cospeciation event, the present distribution of lice could only be explained by extensive host switching and

extinction (Barker *et al.*, 1992). This was partly due to a range expansion and development of host hybrid zones. This finding is consistent with anecdotal evidence which suggests that amblyceran lice are less host specific than other louse groups. However, an investigation into the louse genus *Dennyus* suggests that cospeciation is the prevailing process amongst some amblyceran taxa. A phylogeny of these lice parasitic on swiftlets (Aves: Collocaliinae) was constructed based on mitochondrial cytochrome *b* sequences (Page *et al.*, 1998). The phylogeny was congruent with a previous phenetic analysis of morphometric data for the lice (Clayton *et al.*, 1996), and indicates some degree of cospeciation when compared to a previous estimate of host phylogeny. This study on *Dennyus*, and a further study of ischnoceran lice belonging to the *Philoceanus*-complex (*sensu* Smith, submitted) by Paterson (1994) represent the only phylogenies of avian lice. Paterson's study focused on the coevolutionary history of seabirds (orders Procellariiformes and Sphenisciformes) and their lice. Using 12S rRNA sequence data, Paterson attempted to quantify the cost of fitting the louse to the host tree using reconciliation and BPA. These results support a general history of cospeciation (Paterson *et al.*, in press).

Over the past decade quantitative studies of cospeciation have largely been based on molecular phylogenies of lice. This is in part to do with the increasing ease with which PCR based techniques are used to generate nucleotide sequence data. As has already been mentioned, these data lend themselves to studying disparate rates of molecular evolution in the host-parasite clades. This is important if temporal congruence between speciation events in host-parasite cladograms is to be established. Studies of mitochondrial DNA sequences suggest that the cytochrome *b* gene in *Dennyus* (Page *et al.*, 1998) and cytochrome oxidase I gene in gopher lice (Hafner *et al.*, 1994) have evolved two to three times more rapidly than in their hosts. A similar figure was proposed using a maximum likelihood approach to testing cospeciation in the gopher lice (Huelsenbeck *et al.*, 1997). Mitochondrial data based on 12S rRNA suggest a value of approximately four times the rate of their hosts (Paterson, 1994). Given that these groups of lice are taxonomically very disparate, the prospect is raised that this pattern may be general among lice. Few other insect groups, with the exception of the Hymenoptera (wasps, ants and bees), show comparable amounts of divergence (Page *et al.*, 1998). Generation time has been proposed as an explanation for this disparity in rates, as this is of a similar difference in magnitude between the hosts and their lice (Hafner *et al.*, 1994). However, Page *et al.* (1998) suggested that the small effective

population size of lice, coupled with founder events occurring during transmission to new host individuals may be an important factor. The explanation for these disparate rates of evolution is important as it may help elucidate the mechanisms that help structure host-parasite populations.

1.6: Louse Biology and Taxonomic history

Lice belong to the superorder Psocodea. This group comprises two orders (Lyal, 1985b): the paraphyletic “Psocoptera” (psocids, booklice, barklice) and the Phthiraptera (lice). “Psocoptera” are free-living insects feeding on microflora and organic debris. Some are associated with birds and mammals, dwelling in nests or found amongst their plumage or fur, but none are parasitic (Smithers, 1996). Phthiraptera have no free-living stage and are all obligate ectoparasites of birds and mammals, feeding on feathers, fur, sebaceous exudates or blood. Their sister group lies within the “Psocoptera” (probably the Liposcelidae) (Lyal, 1985b), however relations within both groups remain contentious. Phthirapteran relationships are the most ambiguous with little consensus amongst the principal workers in the field.

Like many higher insect groups the taxonomic history of Phthiraptera is complex, and perhaps for this reason there have been few attempts to describe it. However, to understand why this insect group has attracted so much attention over the past two decades, and perhaps more importantly why we still know so little about them, it is useful to review their systematic history. This is particularly relevant within the context of this thesis, which focuses on the most neglected group of lice – the avian Ischnocera.

The most detailed historical account of louse taxonomy was given by Fahrenholz (1936), and this was later summarised by Ferris (1951) with particular reference to the sucking lice (Anoplura). The following review focuses principally on the systematic history of chewing lice (Mallophaga) and is largely based on these accounts with additional reference to the work of Königsmann (1960), Clay (1950) and Lakshminarayana (1976). Due to the antiquity of several texts referred to in the following section, it has not been possible to check every reference at first hand. In these cases I have attempted to corroborate the details with Kéler’s bibliography of chewing louse literature (Kéler, 1960), and in the event that a discrepancy has been found, the reference has been confirmed by an additional source.

According to Kéler (1960), the earliest written reference to chewing lice was made by Herakleitos Ephesius (500 BC). Later, the works of Aristotle (350 BC), Diophanes (100 BC) and Plinius (70 AD) all make reference to the lice of birds, however like most of these early references, human lice (albeit indirectly) featured more prominently in their writings than their avian or mammalian relatives. Since these early descriptions, occasional references to chewing lice have been noted in the early literature. Kéler (1960) cites on average two references each century for the first 500 years of the last millennium.

It was Redi (1668) who made the first attempt to make a special study of the insect parasites on birds and mammals (Clay & Hopkins, 1950), and illustrated many chewing and sucking lice with considerable accuracy (Kim & Ludwig, 1978a). However, the basis of our present system of classification starts with the treatment by Carolus Linnaeus (Carl von Linné) in the tenth edition of his *Systema Naturae* (1758). Linnaeus adopted the ancient Latin name *Pediculus* into which, according to Ferris (1951), went almost everything that could conceivably be called a louse, including the chewing and sucking lice, the Psocoptera, and even a hippoboscid fly. This genus was placed in the order Apterata, along with the mites, fleas and the primitively wingless group now called the Thysanoptera. Fabricius (1775) in his “*Systema Entomologiae*” followed Linnaeus with a similar arrangement, placing the genus in his order Antliata, but the distinction between the chewing and sucking lice was not made until the treatment by de Geer (1778). He placed chewing lice in the genus *Ricinus* and sucking lice in the genus *Pediculus* (Johnston & Harrison, 1911). The first use of the term Anoplura was made by Leach (1815) in Brewster’s *Edinburgh Encyclopaedia*. This new order contained a single genus of chewing louse (*Nirmus*) and three genera of sucking lice (*Pediculus*, *Haematopinus* and *Phthirus*), and was maintained in his “*Zoological Miscellany*” (1817) when he placed the chewing lice in the family Nirmidae and the sucking lice in the family Pediculidae.

Christian Ludwig Nitzsch (1782-1837), who is considered by many to be the pioneer of our systematic knowledge on lice, described numerous species of chewing and sucking lice in at least nine publications throughout the 19th century. Unfortunately Nitzsch paid no heed to the rules of nomenclature that were originally formulated in Linnean times (Clay & Hopkins, 1950). In his paper entitled “*Die Familien und Gattungen der Thierinsekten (Insecta Epizoica)*,” published in 1818 (the only one published by himself in which he gives specific names), he recognised the distinction

between chewing and sucking lice, placing them in the orders Orthoptera Epizoica and Hemiptera Epizoica respectively. Unfortunately, he considered it necessary to rename almost all species which he mentioned that had already been named by previous authors. This created considerable difficulty for more recent authors attempting to apply the principle of priority to scientific names, as almost all subsequent authors (with the possible exception of Piaget, 1880) accepted and used Nitzsch's names without question (Clay & Hopkins, 1950) until Harrison's 1916 catalogue.

Further changes in the arrangement and/or ordinal names of chewing and sucking lice were made by Dumeril (1823), Latreille (1825) and Kirby & Spence (1826) (Ferris, 1951). The most significant of these were the changes made by Latreille (1825) who redefined the order Parasita which he originally erected in 1806, restricting it to the families Mandibulata (bird lice) and Siphunculata (sucking lice) (Lakshminarayana, 1976).

The name Mallophaga was first used by Nitzsch (1818) although Ferris (1951) mistakenly attributes it to Burmeister (1838). Lice feature in volume one of Burmeister's "Handbuch der Entomologie" (Burmeister, 1838), published in five volumes between 1835-1840. In this work, sucking lice were placed in the order Rhynchota and chewing lice in the order Mallophaga. Within the latter, he proposed the new subfamilies Philopterinae and Liotheinae. Denny (1842) restored Leach's order Anoplura in his monograph on British lice ("Monographia Anoplurorum Britanniae"), and according to the full title of his monograph, divided genera according to the views of Leach, Nitzsch and Burmeister. He reduced Rhynchota and Mallophaga to the rank of suborder, and elevated Philopteridae and Liotheidae to familial status within the latter. Piaget, in his monograph "Les Pédiculines" (1880), avoided the use of ordinal names, but maintained Denny's chewing louse families (Liotheidae and Philopteridae), and placed sucking lice in the Pediculidae (Ferris, 1951). He gave each of these families equal rank. Haeckel (1896) united both groups under the name Phthiraptera. This name was later taken up by Weber (1939) and Eichler (1941), and continues to be used today, despite Latreille's redefined ordinal name 'Parasita' (Latreille, 1825) having priority (Lakshminarayana, 1976).

Further changes in the ordinal names of lice were proposed by Cholodkovsky (1904), Shipley (1904) and Börner (1904) all in the same volume of the journal "Zoologischer Anzeiger". With the exception of those workers who specialised on the sucking lice, the majority of specialists were of the opinion that lice constituted a single

group of ordinal rank. Mjöberg (1910), in a work entitled “Studien über Mallophagen und Anopluren” employed the subordinal names Mallophaga for the chewing lice and Anoplura for the sucking lice, placing them both in the order Siphunculata. Lancelot Harrison was also of this view and in 1916 made the first real attempt to strictly apply the rules of nomenclature (albeit in several cases incorrectly) in a checklist of lice. In this paper, Harrison adopted Mjöberg’s 1910 familial classification, which was based broadly on schemes proposed by Kellogg (1896a; 1908a; 1908b). Harrison included Mjöberg’s chewing louse family Gonioididae, although he reduced it to the rank of subfamily. Earlier, Kellogg (1908a) had published a similar list of Mallophaga in Wytsman’s “Genera Insectorium.” However, he never published any synonyms, significantly reducing the value of his list to taxonomists. Kellogg published several studies on the chewing lice of North America prior to this list, including comparative studies on the morphology of the various chewing louse groups. In one of his 1896 papers (Kellogg, 1896a) he divided chewing lice into the suborders Amblycera and Ischnocera. Subsequently these names have become universally accepted and have since been referred to as suborders and occasionally superfamilies. Kellogg (1896a; 1908a; 1908b) included the families Gyropidae and Liotheidae in the suborder Amblycera, and the families Trichodectidae and Philopteridae in the suborder Ischnocera. In his 1896 paper (Kellogg, 1896a) he stated that his classification scheme mainly followed Nitzsch, ranking Nitzschian families as suborders, Nitzschian genera as families and Nitzschian subgenera as genera.

Despite the comparative stability brought about by the publication of Harrison’s 1916 checklist, and an increasing appreciation of the rules of nomenclature by louse taxonomists, the systematics of this group were still very confused. This led Theresa Clay, one of the leading louse taxonomists of the 20th century to later remark “perhaps no group of insects has suffered so much at the hands of authors who were ignorant of, or careless about, the rules of nomenclature as have the Mallophaga” (Clay and Hopkins, 1950: p. 223).

Aside from numerous alpha taxonomic problems, debate still continued as to the affinities of the chewing and sucking lice. Chief among those arguing for a separate order for the sucking lice was Gordon Ferris. In a series of papers entitled “Contributions towards a monograph of the sucking lice,” published over a period from 1920 to 1935, he maintained this view, and in his 1951 monograph “The Sucking Lice,” remarked:

“...the idea that the biting lice and the sucking lice are related finds but little actual morphological support, although there is a suggestion of some sort of remote relationship. The feeling of relationship seems to arrive chiefly from the fact that the biting lice offer the only known source from which the sucking lice could have been derived. The writer [Ferris] is not impressed by Webb’s insistence upon the evidence afforded by the tracheal system, in the light of the very profound differences in the feeding mechanism. The opinion is here maintained, therefore, that the sucking lice should be recognised as the Order Anoplura.” (Ferris , 1951: p. 61).

One cannot help but feel Ferris’s desire to maintain ordinal status for the Anoplura was more a measure of his personal affection for the group than for any scientific rationale. What Ferris failed to recognise was that these groups of organisms could be both morphologically very different, and yet still closely related.

The discovery of an unusual species of louse found on elephants added additional complexity to the problems of untangling the higher taxonomic groups of lice. This species was originally thought to belong to the Anoplura, and placed in the anopluran family Haematomyzidae by Enderlein (1904). However, a re-examination by Ferris (1931) showed that this species had mandibulate mouthparts like the chewing lice. Therefore Ferris referred the species to the Mallophaga, placing it in the new suborder Rhyncophthirina. The ischnoceran family Trichophlopteridae was established by Mjöberg (1919) for a monotypic louse confined to lemurs. This species was unusual as it represented the only member of the Ischnocera found on a mammal that did not belong to the family Trichodectidae. The family Heptapsogasteridae was described by Carriker (1936) for an unusual group of Ischnocera confined to the tinamiform birds of South America.

Weber (1939) in volume 59 of “*Biologisches Zentralblatt*,” took up Haeckel’s name Phthiraptera, placing under it the suborders Mallophaga, Rhyncophthirina and Anoplura. Eichler (1941) also adopted this arrangement, as did Webb (1946) (although under the ordinal name Anoplura) and Hopkins (1949). The single most important contribution to the stabilisation of the taxonomy of chewing lice was the publication of a checklist of the genera and species of Mallophaga by Hopkins and Clay (1952). This was largely made possible by a complete revision of the early taxonomic work on

chewing lice between 1758-1818, in a series of four papers entitled “The early literature on Mallophaga” (Clay & Hopkins, 1950; 1951; 1954; 1960). The 1952 checklist presented an extremely conservative classification of the chewing lice, which was divided into the suborders Amblycera, Ischnocera and Rhyncophthirina. A basic familial classification of these groups was also presented, however their doubts over this most simplistic classification are reflected by the fact that the entire checklist is arranged alphabetically by louse genus.

Kéler and Eichler independently attempted the most comprehensive schemes of classification for chewing lice in a series of papers spanning much of their academic careers. Both were considered extreme ‘splitters’ by Anglo-American taxonomists and consequently much of their work has been overlooked. Particular publications of note include Kéler’s monographs on the ischnoceran families Trichodectidae and Gonioididae (Kéler, 1938; 1939 respectively) and Eichler’s synopsis of his classification of Phthiraptera (Eichler, 1941; 1963). Specifically Eichler has been much criticised for never publishing any clear justification of his classification. Nevertheless, their schemes serve as useful starting places for a more thorough review of louse classification.

It is almost fifty years since Hopkins and Clay’s checklist was published. In this time, further revisions of higher louse systematics have been almost absent. In 1976 Lakshminarayana attempted to change the subordinal names of the four suborders to keep their suffixes in line with the most recently described suborder Rhyncophthirina. He proposed the names Amblycerophthirina, Ischnocerophthirina, and Siphunculophthirina, however this appears to have been completely ignored by all louse taxonomists except Lakshminarayana! Perhaps the most significant development has been the gradual reduction in the use of the term “Mallophaga” due to an increasing realisation that this group is paraphyletic. Nevertheless, this term is still frequently used by the non-specialist biologists, and it will perhaps take another fifty years before the name is completely eradicated from general use. The most comprehensive single review of a higher louse taxon was conducted by Lyal. He developed a cladistic phylogeny and taxonomy of the ischnoceran family Trichodectidae (Lyal, 1985a) and examined in detail the cospeciation implications of his findings (Lyal, 1987).

To bring this discussion up to date it is worth noting that a recent checklist of sucking lice was published by Durden and Musser (1994), and a new checklist of chewing lice is currently in preparation by Roger Price, Ronald Hellenthal and Ricardo Palma (R. Price pers. comm.). The latter is largely the result of the monumental efforts

by these authors (particularly Roger Price) throughout much of their academic careers to confirm the status, and check the host associations of the thousands of species of chewing lice described by nearly 300 authors since the time of Linnaeus. As of May 1999, the chewing louse checklist contains over 4,400 valid species of lice, and documents over 11,000 host-lice associations (R. Price pers. comm.). These figures will undoubtedly rise as more new species are described prior to the official publication of the list.

1.7: Higher Order Relationships of Lice

The extent of knowledge on louse relationships at the outset of my doctoral research is summarised in Fig. 4, although the number of recognised species in each of the major clades has been brought up to date. Phthiraptera are currently recognised as comprising four major groups (suborders): Anoplura (colloquially known as sucking lice), Rhyncophthirina (a monogeneric group found only on elephants and warthogs), Ischnocera and Amblycera. Every conceivable relationship between these taxa has been proposed at some time. Historically “Mallophaga” and Anoplura have been awarded ordinal status. Morphological data supporting the monophyly of “Mallophaga” were proposed by Kim and Ludwig (1978b; 1982), although these results were controversial (Haub, 1980). Lyal (1985b) conducted a detailed review of the morphological data supporting the monophyly of the four suborders and their relative relationships. His study confirmed the monophyly of all four suborders, although ischnoceran monophyly was the least well supported. The subordinal phylogeny established by Lyal (1985b) is concordant with comments in Clay (1970) and Königsmann (1960) who both considered the Amblycera to be sister taxa to a monophyletic group comprising the Ischnocera, Rhyncophthirina and Anoplura.

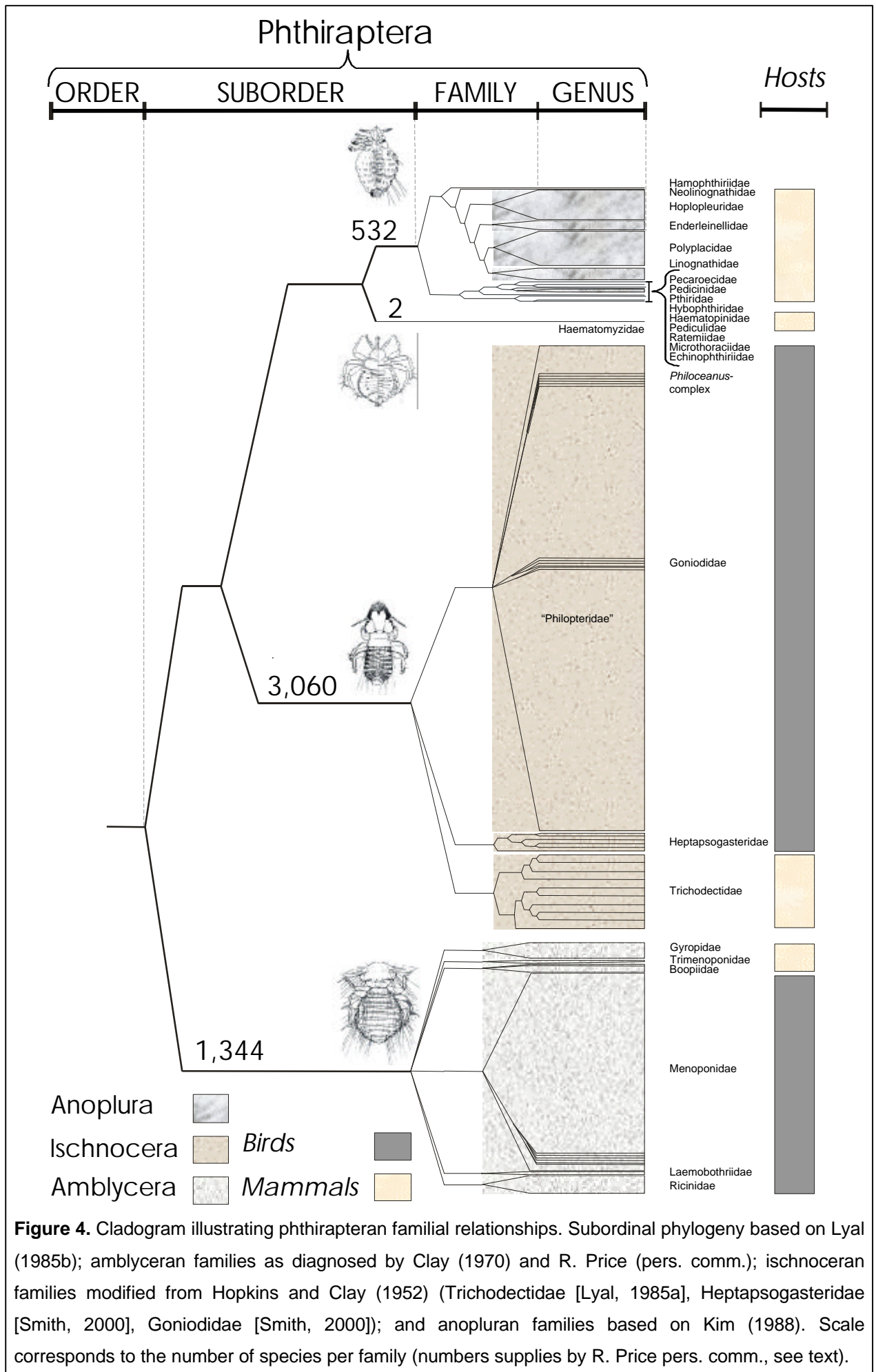
Familial classifications within each of the suborders are less problematic, with the notable exception of the Ischnocera. Anopluran lice have a significant medical and veterinary importance, which in part, explains why they are the best-studied suborder of Phthiraptera. Ferris, between 1920 and 1935 provided the foundation for modern taxonomic work on the Anoplura, and when republished as a monograph (Ferris, 1951) he recognised 6 families. In the light of new species descriptions, this was expanded to 15 families by Kim and Ludwig (1978a), and more recently a cladistic morphological phylogeny has been proposed by Kim (1988). Rhyncophthirina comprise just two

species in a single genus. The subordinal status of these species was awarded by Ferris (1931) on account of their peculiar morphology, and both their monophyly and rank was supported by Lyal (1985b). Amblyceran classification has been the subject of several detailed studies, most notably by Clay (1970) who has done much to stabilise their familial groupings. She also considered possible relationships of genera in the largest amblyceran family, the Menoponidae (Clay, 1969). Phylogenetic relationships between these families have yet to be studied in detail.

The number of families making up the Ischnocera is a matter of some contention. Eichler (1963) recognised twenty-one families whilst Hopkins and Clay (1952) accepted just three. This discrepancy can partly be explained by the diversity of form exhibited amongst the genera, as ischnoceran lice vary considerably in terms of their size and general morphology. This diversity makes even generic differences hard to define, and comparative morphological studies within this group are exceedingly difficult. No clear justification of the scheme proposed by Eichler (1963) was ever published, and it has subsequently been rejected by most authorities due to the assumption that it was unduly biased towards the host classification. Clay attempted to define a preliminary classification of Ischnocera in producing a 'natural' generic key for the group during the 1960s. This study was built on work previously published in a paper titled "An introduction to a classification of the avian Ischnocera (Mallophaga): Part I" (Clay, 1951). Despite this provocative title, her paper did not contain any details of an ischnoceran classification, instead focusing on reviewing character complexes that might be phylogenetically informative at a suprageneric level. According to Ledger (1980 p. 87), Clay never published her key (the sequel to this series) due to her dissatisfaction with certain aspects of it. Specifically, it seems she doubted the validity of some of the groupings proposed. Part of the key was published with the permission of Clay in Ledger, (1980 pp. 91-97), however Ledger's study focused on host taxa endemic to sub-Saharan Africa, and consequently many louse genera were excluded. As a result the meaning of many of the 'natural' groups proposed by Clay was lost. Nevertheless, a complete copy of the original manuscript ("A key to the genera and generic groups of the Ischnocera [Mallophaga]") is present in the collection of Theresa Clay's correspondence maintained at the BMNH, although figures one to twelve are missing.

The most recent studies on Ischnocera all recognise at least three monophyletic groups (Lyal, 1985b; Mey, 1994; Smith, 2000). These are the Trichodectidae restricted

to mammalian hosts, the Heptapsogasteridae present on tinamiform birds and the Gonioididae of Galliformes and Columbiformes. A fourth group (the Philopteridae *sensu* Eichler, 1963) comprise some 70% of ischnoceran species and are present on almost all families of birds. It is generally accepted that this is a miscellaneous collection of genera and is almost certainly para- or polyphyletic. However, the relationships amongst these taxa have never been studied. A monotypic taxon (the Trichophilopteridae) represented by a single species present on Madagascan primates (Lemuridae and Indridae) may be related to the avian Philopteridae. This species bears a number of significant morphological characters that are apparently intermediate between the Philopteridae of birds and the Trichodectidae of Mammals. Consequently the affinities of this genus are unclear, and it has been variably placed amongst both these groups and in an independent family within Ischnocera (Emerson & Price, 1985; Ferris, 1933; Stobbe, 1913).



1.8: Thesis Motivation

Previous sections of this introduction have reviewed some of the extensive work that has been undertaken over the past three centuries towards a better understanding of the biology and coevolution of Phthiraptera. Kéler, in his bibliography of chewing louse literature (Kéler, 1960) records over 2000 separate references in twenty-one different languages between 500 BC - 1959, charting the history of chewing-louse research. My own personal bibliography records a further 500+ additional references published between 1960-1999*, and these figures exclude numerous publications on the 530+ spp. of Anoplura currently described. Despite this, our knowledge of the group still amounts to little more than a patchy understanding of their basic taxonomy and biology. Particularly incomplete is our understanding of the higher level relationships of Phthiraptera, especially within the avian groups. Avian lice account for nearly 80% of all phthirapteran species, and of these, the majority (70%) belong to the suborder Ischnocera. This lack of phylogenetic information is surprising given its potential for unravelling their coevolutionary relationships with their hosts, yet at the outset of my doctoral research there were no satisfactory classifications or phylogenies for any avian Ischnocera. This is unfortunate, as the group has attracted increasing attention from researchers conducting ecological and comparative studies, principally with a view to examining the extent of cospeciation and / or coadaptation between the lice and their hosts.

Aim - The principal aim of this thesis was to investigate the suprageneric relationships of the suborder Ischnocera with particular reference to avian taxa. Such studies do not lend themselves to rigorous cospeciation analysis and this has not been the central aim of this work. Instead, much of this thesis has been devoted to documenting basic homologies amongst the major character systems of the head, thorax and abdomen. These are used to build the first cladistic hypotheses of relationships amongst the avian Ischnocera, and will provide a framework for further generic level revision of the major complexes outlined in this study.

* Access to my searchable bibliography is available on-line at the following address:
http://taxonomy.zoology.gla.ac.uk/~vsmith/bibliography/bib_frame.html

Structure of Thesis - The layout of this thesis is in the form of a series of interconnecting but self-contained chapters that have been prepared for submission to various journals. Their format has been standardised and their order and current status is outlined below:

• **Chapter two:** *Basal ischnoceran louse phylogeny (Phthiraptera: Ischnocera: Gonioididae and Heptapsogasteridae)*. A phylogenetic analysis of generic relationships for avian chewing lice of the families Gonioididae and Heptapsogasteridae (Phthiraptera: Ischnocera) is presented. These lice, hosted by galliform, columbiform and tinamiform birds were putatively basal in the phylogeny of Ischnocera, although subsequent morphological and molecular studies suggest this is not the case. Congruence of the phylogeny with host relationships is discussed.

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• **Chapter three:** *Reconstructing character state trees: An example based on louse head shape*. Issues concerning the development and use of multistate characters are explored in deriving a character to describe louse head shape. Character states based on an elliptic Fourier analysis of head shape for 69 taxa of nymphal and adult ischnoceran lice were delimited using UPGMA cluster analysis. Rates of ontogenetic change in shape were explored and different estimates of character state relationships were compared with the ischnoceran louse phylogeny described in chapter four.

Present Status: In prep. for submission to *Cladistics*.

• **Chapter four:** *Avian Louse Phylogeny (Phthiraptera: Ischnocera): A cladistic study based on morphology*. The first cladistic study based on a broad cross section of avian Ischnocera is presented. A tentative familial classification is proposed. The phylogeny is partly congruent with previous attempts to resolve higher ischnoceran louse clades, and is broadly consistent with host relationships.

Present Status: Submitted to *Zoological Journal of the Linnean Society*

• **Chapter five:** *Conclusion and Prospects*. The work presented in this thesis is brought into context with previous studies on phthirapteran systematics and possible directions for future research are outlined. Bird lice are an excellent study system because a wealth of phylogenetic and comparative data is available for their avian hosts and the

equivalent phylogenetic and distributional data is beginning to accumulate for lice. Their role as model organisms for studying cospeciation is explored, and their potential in helping to understand the factors which influence the evolution of diversity are considered.

• **Appendix:** *CD-ROM of Electronic Louse Resources*. An extensive collection of electronic resources has been generated during the course of my Ph.D. Specifically this CD contains an image library of over 500 scanning electron micrographs, a Java based interactive guide to louse anatomy and a bibliographic database containing over 1000 references with extensive notes for each publication. Chapters, illustrations and reprints from this thesis have been added and the data sets generated during the course of my Ph.D. are stored on this disk. These resources are integrated via HTML and can be accessed through a Java-aware web browser. This should start automatically upon insertion of the CD-ROM in a PC. Apple Mac users should open the file "index.html" in a web browser. On-line versions of these resources are available from my home page (<http://taxonomy.zoology.gla.ac.uk/~vsmith/vince.html>) and serve as an erratum to this CD-ROM.

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