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The Biology, Ecology, and Evolution of Chewing Lice

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BIOLOGY

Introduction

Chewing lice are small, dorsoventrally compressed insects and are parasites of virtually all birds (Fig. 1) and some mammals (Fig. 2). Many chewing lice are host specific, being found on only a single species of host. All chewing lice are permanent ectoparasites and complete their entire life cycle on the body of the host, where they feed mainly on feathers, dead skin, blood, or secretions. Chewing lice on mammals apparently do not ingest hair, rather they feed on skin and skin products (Waterhouse 1953). Some species of lice feed on the eggs and molting stages of mites and other lice, including members of their own species (Nelson and Murray 1971). Lice also ingest microbes, such as bacteria and fungi, which are of unknown nutritive value.

Chewing lice have a hemimetabolous life cycle that includes a large egg, three nymphal stages, and the adult (Marshall 1981a). Louse populations are normally controlled by host grooming and other factors. When not kept in check, however, dramatic increases in louse populations can severely degrade host condition, reproductive success, and survival (Durden 2001, Clayton and Adams In press). Chewing lice are relatively easy to detect through careful visual examination, and their population sizes can be measured accurately both on live and dead hosts (Clayton and Walther 1997, Clayton and Drown 2001). Lice are usually identified on the basis of sclerotized features visible in cleared, slide-mounted specimens (Kettle 1974, also see Checklist Introduction).

Chewing lice are named for their mandibulate, chewing mouthparts. Chewing lice ("Mallophaga") do not form a monophyletic group but are paraphyletic with respect to sucking lice in the insect order Phthiraptera (Fig. 3). Modern classifications divide Phthiraptera into four suborders, three of which make up the chewing lice:

Suborders & Families	Genera	Species
Amblycera		
Menoponidae[B]	68	1,039
Boopiidae[M,1]	8	55
Laemobothriidae[B]	1	20
Ricinidae[B]	3	109
Gyropidae[M]	9	92
Trimenoponidae[M]	6	18
Ischnocera		
Philopteridae[B,2]	138	2,698
Trichodectidae[M]	19	361
Rhynchophthirina		
Haematomyzidae[M]	1	3
Anoplura (16 families)[M]	49	532

Table 1. Higher level classification of lice (Insecta: Phthiraptera). Data for chewing lice (Amblycera, Ischnocera, and Rhynchophthirina) are from checklist data (see Checklist Introduction). Data for sucking lice (Anoplura) are from Durden and Musser (1994a). [B]Found on birds; [M]Found on mammals; [1]One genus (*Therodoxus*) occurs on birds (cassowaries); [2]One genus (*Trichophilopterus*) occurs on mammals (lemurs) and sometimes is placed in the separate family Trichophilopteridae.

Amblycera, Ischnocera, and Rhynchophthirina. Most species of Amblycera and Ischnocera are parasites of birds, although about 12% of the species, along with the three species of Rhynchophthirina, are parasites of mammals (Table 1). Amblycera are generally more mobile than Ischnocera. For example, Amblycera will abandon a dead or distressed host in search of a new one. Most Ischnocera are so specialized for life on hair or feathers that they do not venture away from the host. Avian chewing lice are often called "feather lice," a phrase that is perhaps best applied to ischnoceran lice on birds, since they are true feather specialists.

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Members of the fourth suborder, Anoplura, parasitize mammals and are called sucking lice because they have piercing-sucking mouthparts. Sucking lice are easy to distinguish from chewing lice because they have heads that are narrower than their prothorax. With the exception of Rhynchophthirina, the sister group to Anoplura (Fig. 3), chewing lice have large, heavily sclerotized heads that are as wide as the prothorax, if not wider (Figs. 1-2). Durden and Musser (1994a) provide a comprehensive checklist of the 532 valid species of Anoplura described through January 1993. Durden and Musser (1994b)

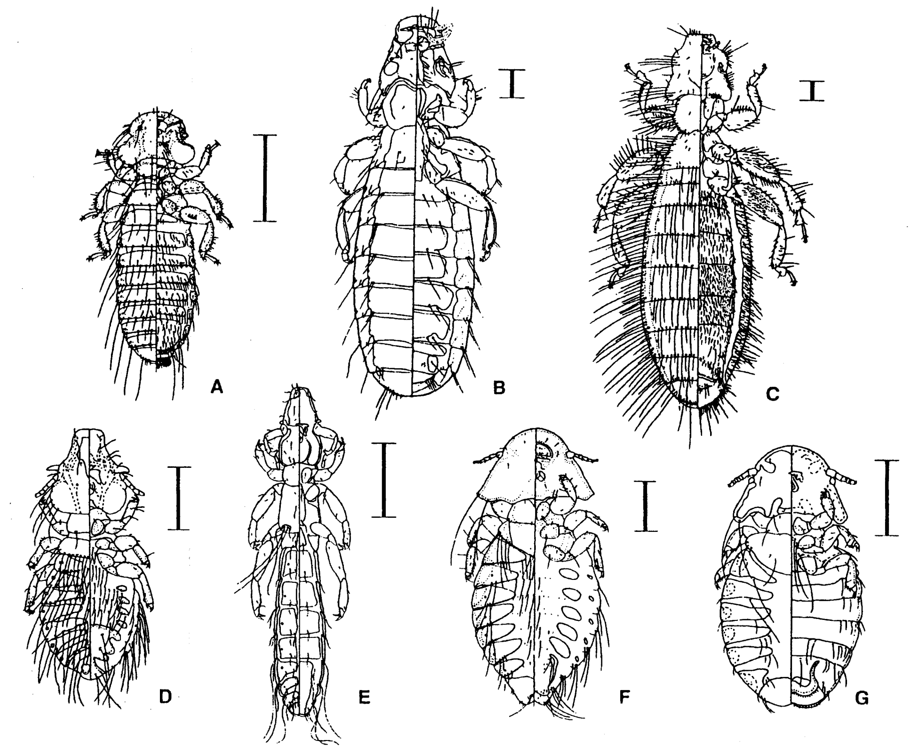

Figure 1. Representatives of the four families of avian chewing lice (see Table 1). Dorsal morphology to left of midline, ventral morphology to right. Scale bars = 0.5 mm. (A) *Colpocephalum holzenthali* (Amblycera: Menoponidae), F, ex Barred Forest-falcon (*Micrastur ruficollis*); (B) *Ricinus* sp. (Amblycera: Ricinidae), F, ex Passeriformes sp; (C) *Laemobothrion maximum* (Amblycera: Laemobothriidae), F, ex hawk (*Buteo* sp.); (D) *Philopterus* sp. (Ischnocera: Philopteridae), M, ex Passeriformes sp.; (E) *Columbicola columbae* (Ischnocera: Philopteridae), M, ex Rock Dove = feral pigeon (*Columba livia*); (F) *Goniodes australis* (Ischnocera: Philopteridae (Goniodidae of some authors; see text)), F, ex Mallee Fowl (*Leipoa ocellata*); (G) *Heptapsogaster* sp. (Ischnocera: Philopteridae (Heptapsogasteridae of some authors; see text)), F, ex Tinamiformes sp. [(A) after Clayton and Price (1989); (B) after Ledger (1980); (C) after Nelson and Price (1965); (D) after Price and Hellenthal (1998); (E) original drawing by Richard Adams; (F) after Emerson and Price (1986); (G) original drawing by Richard Adams].

provide a host list, and Durden (2001, 2002) succinctly reviews the biology of Anoplura.

Morphology, Physiology, and Behavior

Adult chewing lice vary in length from 0.8 mm to 11 mm. In most species the females are larger than the males, often by 20%. The body is dorsoventrally flattened with a horizontally positioned head. This shape is an adaptation for lying flat against feathers or hair, which increases the tenacity of the louse in the face of host movement and grooming. Chewing lice vary in color from nearly white, through shades of yellow and brown, to black. Some taxa match the color of their host, suggesting that lice may use cryptic coloration to avoid detection by the host (Rothschild and Clay 1952). This interesting hypothesis has yet to be tested.

The three suborders of chewing lice are easily identified. Amblycera have maxillary palps, a primitive condition shared with their psocopteran ancestors.

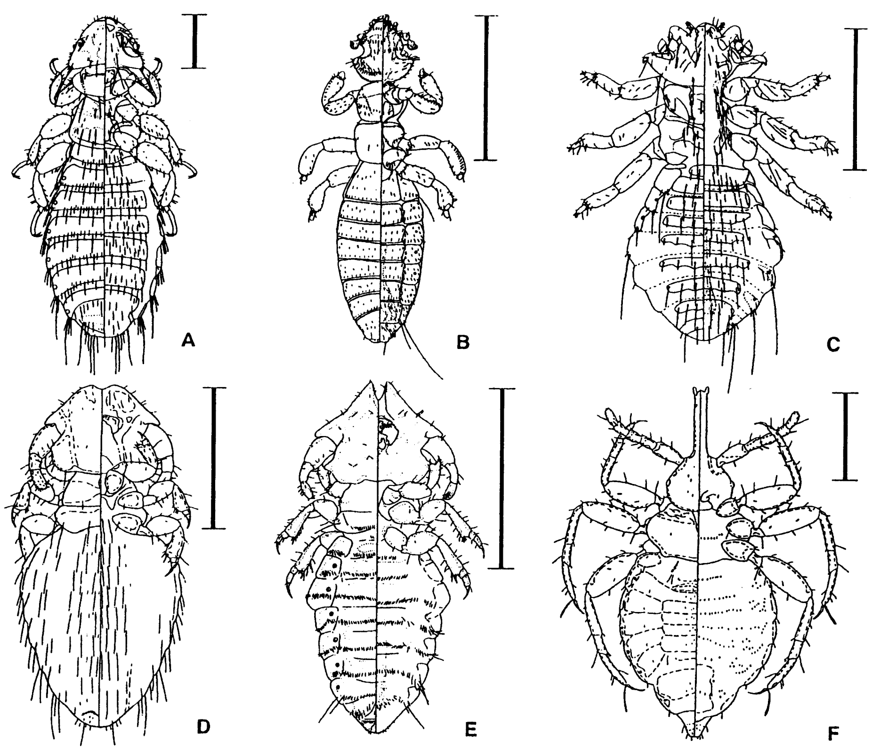

Figure 2. Representatives of the five families of mammalian chewing lice (see Table 1). Dorsal morphology to left of midline, ventral morphology to right. All drawings are of male lice. Scale bars = 0.5 mm. (A) *Heterodoxus spiniger* (Amblycera: Boopiidae) ex Domestic Dog (*Canis familiaris*); (B) *Gliricola wenzeli* (Amblycera: Gyropidae) ex Central American Spiny Rat (*Proechimys semispinosus*); (C) *Harrisonia uncinata* (Amblycera: Trimenoponidae) ex Central American Spiny Rat (*P. semispinosus*); (D) *Neotrichodectes minutus* (Ischnocera: Trichodectidae) ex Long-tailed Weasel (*Mustela frenata novaeboracensis*); (E) *Cebidicola extrarius* (Ischnocera: Trichodectidae) ex Red Howler Monkey (*Alouatta seniculus*); (F) *Haematomyzus elephantis* (Rhynchophthirina: Haematomyzidae) ex African and Indian elephants (*Loxodonta* and *Elephas*). [A-E after Emerson and Price (1975); F after Durden (2001).

Ischnocera and Rhynchophthirina, which are more derived clades, lack maxillary palps. Members of the Amblycera have four segmented antennae, with a pedunculate third segment. The antennae are concealed in lateral grooves, making them difficult to see. Ischnocera and Rhyncho-phthirina have fully exposed, filiform antennae with 3 to 5 segments. Some male Ischnocera have large, dimorphic antennae (Figs. 1E, 2D, E) that are used to clasp the female during copulation, which can last for hours or even days (Rózsa Pers. comm.)! Amblycera have opposable mouthparts that move in a vertical plane, perpendicular to the ventral surface of the head. Some Amblycera, such as ricinid bird lice (Fig. 1B), have chewing mouthparts that are essentially modified to suck blood (Clay 1949a, Nelson 1972). In contrast to Amblycera, the mouthparts of Ischnocera move in a horizontal plane parallel to the head. Rhynchophthirina, which are parasites of elephants, warthogs, and bush pigs, have chewing mouthparts borne on the end of a long proboscis, giving them a weevil-like appearance (Fig. 2F).

Ischnocera have only two apparent thoracic segments because the mesothorax and metathorax are fused to form a pterothorax (see Checklist Introduction, Fig. 2). In contrast, Amblycera have a distinct suture that divides the mesothorax and metathorax. The abdomens of chewing lice have 11 segments, but only 8 to10 of these are visible because of fusion or reduction. The abdominal segments have dorsal, ventral, and lateral plates to help maintain structural integrity. The thorax has a single pair of respiratory spiracles and the abdomen has up to six pairs of spiracles, all linked to an elaborately networked tracheal system (Fig. 4A). The thorax supports three pairs of well-developed legs with two tarsal claws per leg in the case of bird lice, but only one claw per leg in the case of most mammal lice. This reduction in the number of claws in mammal chewing lice is paralleled both in the sucking lice and in hippoboscid flies that parasitize mammals (Kettle 1977). The reduction in claw number presumably relates to the simpler structure of hair compared to feathers.

Chewing lice are morphologically and behaviorally adapted for particular microhabitats on the host. As such, they can be assigned to informal categories on the basis of overall morphology and how they avoid host grooming. For example, one scheme for bird lice includes the following categories: 1) agile Amblycera that run quickly

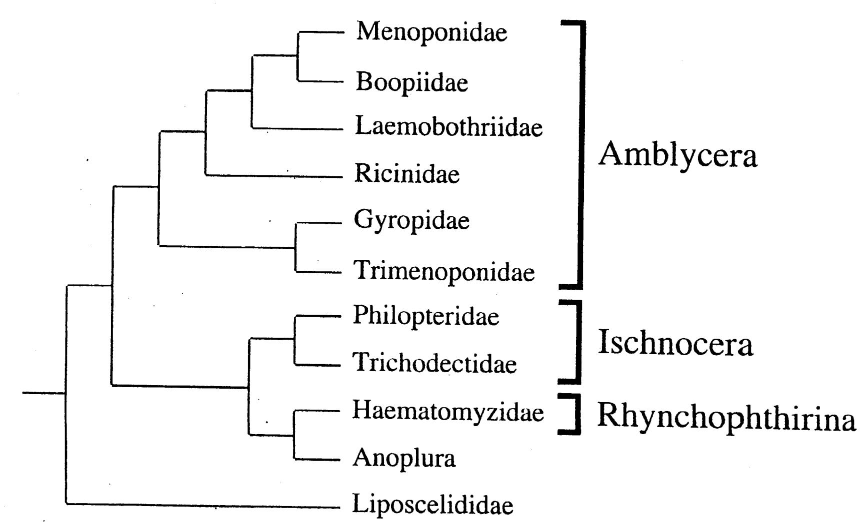

Figure 3. Composite phylogeny of the suborders of Phthiraptera, resolved to family level in chewing lice only. Phylogenetic relationships among the suborders are based on morphological (Lyal 1985a) and molecular (Johnson and Whiting 2002, Barker et al. In press) characters. Phylogenetic relationships within Amblycera are based on morphological characters (Marshall In press). See text for more discussion.

across the skin or feathers (Fig. 1A); 2) very large Amblycera that slip sideways between the feathers (Fig. 1B, C); 3) sluggish, triangular-headed Ischnocera that avoid preening by dwelling mainly on the head and neck (Fig. 1D); 4) elongate Ischnocera that hide between the barbs of wing and tail feathers (Fig. 1E); 5) sluggish Ischnocera that burrow into the downy regions of the abdominal feathers (Figs. 1F, G). These categories have no formal taxonomic significance, and not all bird lice can be placed neatly into one of the categories. However, the scheme does illustrate some of the major adaptive zones occupied by most bird lice.

Chewing lice feed by shearing or scraping feathers or skin with their mandibles. Particles of food are pushed into the preoral cavity by the labrum. The maxillae and labium are much reduced in size and play only a minor role in feeding. Like Psocoptera, many Ischnocera and some Amblycera have lingual sclerites that are posted vertically between the labrum and labium. These sclerites are part of an efficient water-vapor uptake system that extracts water directly from the air (Rudolph 1983), enabling lice to feed solely on feathers and dry flakes of dead skin and other debris.

Lice have sense organs in their mouths, as well as on their antennae. The antennal sense organs of Ischnocera are more specialized than those of Amblycera (Clay 1970). A few species of chewing lice have small eyes, which are probably little more than light sensors. Lice are repelled by light, while being attracted to the warmth and odor of the host. Most lice have sensory hairs, or setae, distributed over the body. The number, length, and distribution of setae are important taxonomic characters. Backward pointing setae apparently also protect lice from being dislodged by host grooming. Additional features of external morphology, especially those that are important taxonomic characters, are illustrated in Figure 2 of the Checklist Introduction.

The internal morphology of chewing lice is dominated by the alimentary canal, which includes the esophagus, crop, midgut, smaller hindgut, four Malpighian tubules, and rectum. The crop differs considerably among the suborders of chewing lice, reflecting differences in diet. In Amblycera, many of which feed on skin products and blood, the crop is merely an enlargement of the esophagus (Fig. 4A). In Ischnocera, most of which feed on feathers, the crop is a diverticulum off the esophagus that runs nearly the entire length of the abdomen (Fig. 4B). In Rhynchophthirina, which are thought to feed mainly on blood, the crop is underdeveloped. Pieces of ingested feathers and other material are often plainly visible in the crops of chewing lice. When a louse feeds, its crop pulsates, breaking up food particles by rubbing them against comb-like teeth in the crop walls. In an interesting parallel to their avian hosts, some lice have grit in their crops, which helps pulverize food during digestion. Although mechanical action initiates digestion, lice rely on powerful enzymes in the gut to complete the digestive process.

Endosymbiotic bacteria may also play a role in the nutritional physiology of chewing lice. Rickettsia-like bacteria are present in many avian Ischnocera, but absent from Trichodectidae and most Amblycera (Ries 1931, Reed and Hafner 2002). The bacteria are present in Rhynchophthirina and probably all Anoplura. They reside in specialized cells called bacteriocytes, or mycetocytes, which are sometimes concentrated in structures called mycetomes (see figures in Eichler et al. 1972). The bacteria undergo transovarial transmission by migrating from the bacteriocytes into developing eggs in the female louse. The importance of these bacteria is suggested by early ablation experiments in which human lice (Anoplura) deprived of bacteria did not feed properly, survive, or reproduce (reviewed in Buxton 1947). It is also worth noting that, with the exception of blood feeders, bacteria are mainly present in lice with diets that are particularly difficult to digest, such as feathers. Blagoveshtchensky (1959) suggested that the bacteria provide vitamins or other necessary supplements. More work is needed on this interesting topic.

The reproductive tract of chewing lice is large and taxonomically informative, particularly in the case of the external male genitalia. The genitalia are structurally complex and large (Fig. 4C), encompassing up to half the length of the male abdomen. A typical configuration includes a flattened or rod-like basal apodeme, which supports an endophallus and associated sclerotized structures, all of which get everted during copulation. The apparatus is often bordered by a pair of sickle-shaped parameres that help locate the female genital opening and protect the delicate endophallus during copulation (Lyal 1987). Male Amblycera have three pairs of testes, whereas male Ischnocera and Rhynchophthirina have only two pairs. The testes are connected to the vas deferens. These, in turn, coalesce to form the seminal vesicle, which stores sperm.

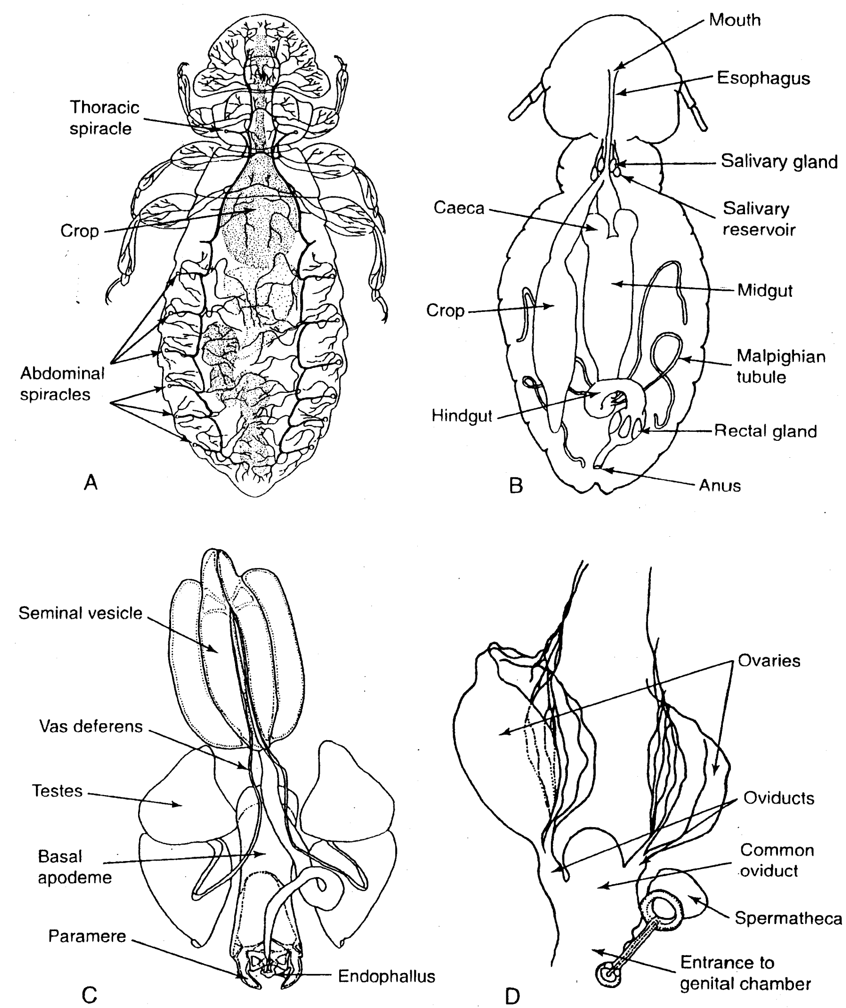

Figure 4. Internal features of chewing lice. (A) Tracheal system (bold) and alimentary canal (stipled) of *Myrsidea cucullaris* (Amblycera: Menoponidae) ex European Starling (*Sturnus vulgaris*); (B) Alimentary canal of *Bovicola bovis* (Ischnocera: Trichodectidae) ex Domestic Cow (*Bos taurus*); (C) Male reproductive tract of *Craspedorrhynchus spathulatus* (Ischnocera: Philopteridae) ex Black Kite (*Milvus m. migrans*); (D) Female reproductive tract of *Philopterus ocellatus* (Ischnocera: Philopteridae) ex Carrion Crow (*Corvus corone sharpii*) [A adapted from Harrison (1915b); B adapted from Marshall (1981a); C and D adapted from Smith (2001)].

The female reproductive tract contains several ovaries (Fi.g 4D) with eggs in various stages of development. The ovaries are connected by oviducts to a common oviduct, or uterus, that leads to the genital chamber. In many taxa, a spermatheca is connected to the genital chamber by a thin duct. Male lice deposit a spermatophore in the spermatheca during insemination. The spermatophore may be in continuous use until it is replaced at a future insemination (Khalifa 1949). Female lice have no ovipositor, but they do have finger-like gonopods that help position the eggs during laying. Most species of lice attach their eggs individually or in clumps to basal regions of the hair or feathers with a glandular cement. Many species deposit their eggs in regions that are relatively protected from host grooming, such as the scruff of the neck (Rust 1974), or between the barbs of feathers (Nelson and Murray 1971).

The eggs, also known as nits, are whitish in color. They require 4 to10 days of incubation, depending on the species. Eggs are often easier to detect than hatched lice because they glisten in reflected light, particularly before they hatch. Some species produce eggs that are heavily sculptured or equipped with projections that facilitate attachment and/or gas exchange (Balter 1968, Foster 1969a, Marshall 1981a, Cohen et al. 1991). The distal end of the egg has a cap known as the operculum. When a nymph is ready to hatch, it sucks air in through its mouth. This air passes down the alimentary canal and accumulates behind the nymph, below the operculum. When sufficient air has accumulated, the resulting pressure pops the operculum open. Hatching is further aided by a platelike structure, the hatching organ, situated at the upper end of the prenymphal skin. Hatched eggs remain attached to the hair or feathers and are grayish and flattened in appearance.

Each nymphal stage requires 3 to 12 days for completion and is successively larger (Marshall 1981a). Nymphs lack reproductive organs and they have less sclerotization and fewer setae than adults. Some chewing lice have nymphs that look much like miniature adults. However, other species have early nymphal stages that differ considerably in appearance from the adults. These differences can be taxonomically useful, which is why it is desirable to preserve specimens of all life history stages, not just adults. Adult lice live about a month, with females producing an average of 1 egg per day, for a total of 12 to 20 eggs. Lice have chromosomes that are quite small with no localized centromere (holokinetic). The chromosomes are few in number, ranging from n = 2 to n = 12. Conspecific males and females have the same number of chromosomes, but identifiable sex chromosomes are missing. The mechanism of sex determination in lice is unknown (Kettle 1977, Tombesi and Papeschi 1993, Tombesi et al. 1999). Males have achiasmatic meiosis, and spermatogenesis follows a particular course with mitotic divisions following meiosis, rather than preceding it, as in most insects. These factors markedly constrain genetic variability, which may be related to the predictable environment in which lice live.

Although most groups of ectoparasites tend to have even sex ratios (Marshall 1981a), lice sometimes have skewed ratios, usually with a female bias (Clayton et al. 1992). In an analysis of published data, Marshall (1981b) reported 31 of 50 species (62%) with significantly female biased sex ratios (none showed a male bias). In some ischnoceran lice, males are rare, or absent altogether, indicating parthogenetic reproduction (Marshall 1981a, b, Westrom et al. 1976). The causes and consequences of biased sex ratios in chewing lice deserve further study.

ECOLOGY

Population Dynamics and Community Ecology

Chewing louse populations are profoundly affected by variation in temperature and humidity near the host skin. A good deal of work has been done on this topic, particularly for the lice of domesticated mammals; see reviews by Marshall (1981a) and Price and Graham (1997). Chewing lice are so attuned to conditions on the body of the host that few species can survive for more than a few days off the host. Indeed, most taxa are difficult to culture in vitro, even when provided with ample food in incubators with carefully regulated temperature and humidity. Marshall (1981a) reviews the literature concerning attempts to culture lice in vitro. Humidity near the skin is a function of ambient humidity, at least in the case of birds (Moyer et al. 2002). Birds in humid regions of the world have more lice than birds in arid regions, even when lice on birds of the same species are compared across broad geographic distributions (Moyer et al. 2002, Moyer et al. 2003).

Like many macroparasites, chewing lice have aggregated populations that often conform to a negative binomial distribution (Eveleigh and Threlfall 1976, Fowler and Williams 1985, Clayton and Tompkins 1995, Lee and Clayton 1995, Rózsa et al. 1996, Clayton et al. 1999). In other words, most individual hosts have few lice, whereas a few individual hosts have many lice. Lee and Clayton (1995) discuss factors underlying such distributions, and Rózsa et al. (1996) show that aggregation is reduced in lice on colonial species, presumably because of an increase in opportunities for horizontal transmission.

Successful transmission is one of the greatest challenges faced by any parasite. The close physical association of lice with their hosts means that the greatest opportunity for transmission is during periods of direct contact between hosts. The rate of transmission of chewing lice has been measured directly between copulating birds (Hillgarth 1996), and between parent birds and their offspring (Clayton and Tompkins 1994). Lee and Clayton (1995) showed that transmission from adult to nestling swifts (*Apus apus*) involved significantly more immature than adult lice. This fact, in conjunction with the fact that populations of lice on juvenile hosts tend to undergo a period of rapid expansion, explains why juvenile hosts often have more immature than adult lice (Eveleigh and Threlfall 1976). However, the reverse may be true for populations of lice on adult hosts. For example, Clayton et al. (1992) recorded significantly more adult than immature lice on adults of many species of Amazonian birds.

Some species of chewing lice may have life cycles that are synchronized with those of the host (Marshall 1981a). Foster (1969b) reported data showing an increase in populations of blood feeding lice concurrent with the host breeding season. She went on to suggest that breeding in the lice may have been triggered by host reproductive hormones, as in the case of rabbit fleas (Rothschild and Ford 1964). The synchronization hypothesis requires direct testing because increases in lice could be due to host life history tradeoffs, such as an inability to devote sufficient time to preening during the breeding season. Marshall (1981a) reviews the population ecology of lice, including a variety of factors thought to influence population dynamics and age structure.

Although direct contact between host individuals facilitates transmission of lice, it is probably not the only route of transmission. Ischnoceran lice are capable of leaving the host by "hitchhiking" on hippoboscid flies, a phenomenon known as phoresis (Keirans 1975). Corbet (1956) found lice attached to 43.5% of 156 hippoboscid flies that he removed from European Starlings (*Sturnus vulgaris*). Although phoresis has been recorded for a few ischnoceran genera, it is unclear how common the phenomenon is among Ischnocera. Phoresis is quite rare among Amblycera, apparently because attaching to flies is difficult with vertically oriented mouthparts (Keirans 1975). Since hippoboscids are not as host specific as lice, phoresis may be a route by which some species of lice can wind up on the "wrong" species of host. Clay (1949b) and Timm (1983) suggested three additional routes by which bird lice could move between host species: 1) dispersal of lice (or eggs) on detached feathers, 2) shared dust baths, and 3) shared nest holes. The fact that birds steal nest material from other species of birds suggests yet another possible dispersal route (Fey et al. 1997). Clayton (1990a) showed that sharing of lice by unrelated species of owls is restricted to cases involving sympatric species of hosts with overlapping microhabitat.

Opportunities for dispersal notwithstanding, many chewing lice are quite host specific. Clayton et al. (1992) used carefully standardized collecting methods to compare the louse communities on 127 species of birds in 26 families, all from one region of Amazonian Peru. Of the lice that could be identified to species, nearly all were confined to one species of host. This is not to say, however, that all chewing lice are host specific. Some species occur on more than one genus, family, or even order of host. For example, Price (1975) recorded *Menacanthus eurysternus* from 118 bird species belonging to 70 genera and 20 familes. In short, specificity should *never* be assumed. Chewing louse systematics has suffered greatly at the hands of taxonomists who have tended to describe new species on the basis of host associations, rather than on the basis of the lice themselves. This circular practice is in large part responsible for the regrettably high number of synonymies in chewing louse taxonomy.

Chewing louse communities vary considerably in their species richness, ranging from one species per host, as in the case of ostrich lice, to more than 20 species, as in the case of tinamous, which are terrestrial, Neotropical birds. Over 20 species of lice are known from the single species *Crypturellus soui*, and up to 9 species have been collected from a single individual of this species (Ward 1957)! Why such variation exists is not well understood. In the case of tinamous, which are one of the oldest lineages of birds (Sibley and Ahlquist 1990), the explanation may be that there has been more time for speciation and colonization events to take place. An historical approach that incorporates phylogenies for both tinamous and lice would be useful here.

A recent phylogenetically independent comparative analysis of the louse communities on more than 50 species of neotropical birds revealed no features of host morphology or ecology that correlate significantly with louse species richness (Clayton and Walther 2001). However, richness itself was a significant predictor of the mean abundance of lice on different host species, as was host body size and the degree to which the upper mandible of the bill overlaps the lower mandible (a feature of host defense; see below). As pointed out by Rózsa (1997), the correlation of louse abundance with body size could be explained by 1) more resources on larger hosts, 2) more refugia from preening on larger hosts, or 3) greater longevity of larger hosts, which would provide a larger window of opportunity for infestation by lice. These possibilities should be tested.

Interspecific competition between lice may also play a role in the structuring of louse communities. Clayton et al. (2003) reported experimental data showing that interspecific competition does, in fact, occur in lice. Competitive exclusion could also conceivably influence the probability of successful host switching in lice (Page et al. 1996). Louse communities and populations may also be influenced by predatory mites and hyperparasites of lice, such as bacteria or fungi (Marshall 1981a). Unfortunately, little is known about the impact of these organisms on lice. Host defenses also have a striking effect on the population dynamics and community structure of lice, as discussed next.

Host Defense

Birds and mammals combat lice using a variety of defenses. The simplest defense is to avoid getting lice in the first place. This may be the principle advantage birds gain from choosing louse-free individuals as mates (Clayton 1991a). Other behaviors that may help to control lice include dusting, sunning, anting, and "fumigation" of nests with green vegetation (Hart 1997, Moyer et al. 2003). Additional research is needed to determine the precise importance of these behaviors in louse control.

The most important defenses against lice are oral grooming and scratching. Oral grooming includes combing with the teeth in mammals and preening with the bill in birds. The rasping surface of the tongue in some mammals is thought to increase the efficiency of grooming. Saliva could conceivably also play a role in the control of lice through grooming, by reducing the abundance of bacteria upon which lice feed (Murray 1990). This interesting possibility has not been tested. Allogrooming, in which one individual grooms another, plays a significant role in controlling lice on mammals, such as mice (Bell and Clifford 1964). Some birds also allopreen, but the effectiveness of this behavior for controlling lice remains untested (Moyer et al. 2003).

Regions that cannot be orally groomed are scratched with the feet in both mammals and birds. The effectiveness of scratching is revealed by the fact that lice increase dramatically in number on the forepart of the body of mice that are missing the toes on their hind feet (Bell et al. 1962). Similarly, natural "experiments" confirm that scratching is critical for controlling louse populations on regions that birds cannot preen. Birds that cannot scratch because of leg injuries tend to have large numbers of lice and nits on the head and neck, but not on regions that they can still preen (Clayton 1991b).

The importance of preening for controlling lice has been shown by experiments that impair preening (Brown 1972, Clayton et al. 1999). Birds that cannot preen efficiently usually experience huge increases in their louse populations (Moyer et al. 2003). The importance of preening is also apparent from recent comparative studies. Clayton and Walther (2001) compared the diversity of lice among 52 species of Neotropical birds. Phylogenetically controlled comparative analyses revealed a correlation suggesting that birds with longer overhangs are better at controlling lice by preening. The size of the bill overhang can vary markedly among related species of birds. (Extreme overhangs, such as the hooked bills of raptors and parrots, are feeding adaptations that may do little to improve preening efficiency).

The importance of the bill overhang for controlling lice has recently been confirmed experimentally. Removal of the (1 to 2 mm) overhang triggered a significant increase in louse load, similar to that caused by separating the bird's mandibles with a bit (Moyer and Clayton 2003). Additional recent work provides clues as to how the bill overhang actually functions in controlling lice. In a series of measurements using magnetic transducers glued to the mandibles of captive pigeons, Clayton et al. (unpub. data) showed that the lower mandible moves forward slightly during preening. This forward motion creates a shearing force that damages lice. Birds are unable to generate the same force without the bill overhang.

Another factor that may help hosts control lice and other ectoparasites is periodic molting of feathers or hair (Blagoveshtchensky 1959). Murray (1957) documented an 80% reduction in louse eggs on molting domestic horses, and Baum (1968) reported an 85% drop in the abundance of hatched lice on molting Eurasian Blackbirds (*Turdus merula*). However, in a recent study in which Moyer et al. (2002) experimentally manipulated the molt of feral pigeons, molt had no impact on louse populations, partly because the lice used freshly emerging pin feathers

as refuges. Hence, the defensive role of molt against lice cannot be assumed, but must be tested.

Feather toughness may also play a role in controlling populations of feather lice. Feathers containing melanin—the pigment responsible for gray or black feather color—are known to be more resistant to mechanical abrasion than feathers without melanin (Bonser 1995). Kose et al. (1999) studied the interaction between the Barn Swallow (*Hirundo rustica*) and its louse (*Machaerilaemus malleus*), which chews holes in the tail feathers, which are dark with white spots (Møller, 1991). The lice fed more on the white than dark regions of the tail, resulting in more extensive damage to the white spots (Kose et al. 1999, Kose and Møller 1999). Although these results are consistent with the hypothesis that melanin deters louse feeding, they are not a direct test. Such a test would require that melanin be manipulated and the feeding response of lice evaluated.

Another possible defense against lice is feather chemistry. The feathers and skin of several species of birds in the genus *Pitohui* contain the same neurotoxin as that found in the skin of poison dart frogs (Dumbacher et al. 1992). When given a choice in lab experiments, lice avoid feeding or resting on *Pitohui* feathers. Lice also have higher mortality when fed toxic feathers as compared to nontoxic control feathers (Dumbacher 1999).

The immune system may also be an effective defense against chewing lice, even in the case of surface feeders that do not feed on blood (James 1999). Very little is known about immunity to chewing lice, compared to other ectoparasites (Nelson et al. 1977, Wikel 1996). Recent reviews are provided by Durden (2001) for mammal lice and Moyer et al. (2003) for bird lice.

Effects of chewing lice

Chewing lice have severe effects on poultry and livestock when present in large numbers. For example, poultry lice can reduce food consumption, body mass, and egg production (Nelson et al. 1977; Arends 1997). These effects are largely a result of irritation. For example, infestations of the chicken head louse, *Cuclotogaster heterographus*, cause severe restlessness and debility (Kim et al. 1973) and they sometimes kill chicks outright (Loomis 1978). Brown (1974) showed a significant increase in the grooming rates of chickens infested with the louse *Menacanthus stramineus*. In contrast, Clayton (1990b) found no increase in the grooming rates of Rock Doves (*Columba livia*) infested with large numbers of wing lice (*Columbicola columbae*) and body lice (*Campanulotes compar*). These species, which do not venture onto the host's skin, appear to cause little, if any, irritation. Despite their potential effects, poultry lice are considered a relatively minor problem in modern operations because they are relatively easy to control. However, lice are still a problem for poultry kept under traditional conditions, particularly when birds are crowded or in poor health. Arends (1997) and Price and Graham (1997) review the impact of lice on poultry and other domesticated birds and provide information on how to control louse infestations.

Chewing lice are also important pests of domesticated mammals, such as cattle. When present in large numbers, the cattle louse (*Bovicola bovis*) (Fig. 4B) is so annoying that patches of skin can become raw and encrusted as a result of excessive host grooming. The lice congregate beneath loose scabs on the raw skin, and large patches of hair are typically lost. Cattle can destroy fences, barns, and other structures by rubbing against them to relieve the severe irritation (Price and Graham 1997). Large infestations retard the growth of young cattle and can limit milk production in dairy cows. The extensive hair and skin loss may even interfere with thermoregulation (DeVaney et al. 1988). Kunz et al. (1991) estimate that 10% of cattle in the northern U.S. have heavy *B. bovis* infestations, resulting in losses of many millions of dollars. Price and Graham (1997) review the impact of these and other chewing lice on domesticated mammals. They also review methods of controlling mammal louse infestations.

Little is known about the impact of chewing lice on wild mammals. Large infestations have seldom been implicated as the cause of serious pathology (Nelson et al. 1975, 1977, Durden 2001). However, chewing lice are known to cause minor problems, such as alopecia and furmatting in coyotes (*Canis latrans*), with up to 50,000 lice on a single animal (Foreyt et al. 1978). Large infestations of *Haematomyzus elephantis* (Fig. 2F) lead to severe dermatitis, pruritus, and dry scaly skin in elephants (Raghavan et al. 1968). A careful assessment of the impact of chewing lice on wild mammals would require experimental work in which the consequences of high loads are carefully measured. Durden (2001) reviews what is currently known about the impact of lice on wild mammals.

More is known about the impact of lice on wild birds. Samuel et al. (1982) recorded severe hemorrhagic ulcerative stomatitis and death in juvenile American White Pelicans (*Pelecanus erythrorhyncus*) infested with the menoponid louse *Piagetiella peralis*. Kose et al. (1999) recently showed that the menoponid louse *Machaerilaemus malleus* chews holes in the tail feathers of Barn Swallows (*Hirundo rustica*). These holes may increase feather breakage, as well as transmissivity of the feathers to air, which could alter aerodynamic efficiency (Bonser 2001). The holes may also increase the potential costliness of long tails, which function as sexually selected "handicaps" signaling freedom from parasites (Kose et al. 1999). In another swallow study, Brown et al. (1995) reported significant reductions in the long-term survival of Cliff Swallows (*Hirundo pyrrhonota*) infested with lice, fleas, and bugs, compared to parasite-free (fumigated) controls. However, it was not possible to assess what fraction, if any, of the survival effect could be attributed specifically to the lice versus fleas and bugs.

Feather damage from chewing lice can have other consequences, as demonstrated in free-ranging feral pigeons, or Rock Doves (*Columba livia*). Populations of the ischnoceran lice *Columbicola columbae* and *Campanulotes compar* increase dramatically on pigeons with impaired preening ability. These two species, which feed on abdominal contour feathers, reduce the density of the plumage, leading to an increase in thermal conductance, which, in turn, causes birds to increase their metabolic rates by an average of 8.5% in order to maintain normal core body temperatures (Booth et al. 1993). Heavily infested birds draw on fat reserves to sustain the elevated metabolic rate, leading to a chronic decline in body mass over several months. The end result, not surprisingly, is a significant drop in over winter survival, since birds cannot keep up with the energetic cost. The impact of feather lice on energetics may also be responsible for the significant drop in the rate of male courtship display, and thus the ability of heavily infested males to attract mates (Clayton 1990b). Studies of several other bird species have demonstrated similar reductions in the attractiveness of lousy males to females (reviewed by Clayton 1991a).

The time and energy required for efficient grooming to control lice may also be costly. Heavy infestations of amblyceran lice cause increased grooming rates in poultry (Brown 1974). Species of birds with more species of lice spend more time grooming than birds with fewer species of lice (Cotgreave and Clayton 1994). In other words, the species richness of a bird louse community may influence the amount of time the bird must devote to grooming defense. More time devoted to grooming may mean less time available for other activities, such as foraging and territory defense. Increased grooming can also reduce vigilance, which could increase the risk of being killed by a predator (Redpath 1988).

Finally, chewing lice can affect birds and mammals indirectly by serving as vectors or intermediate hosts of other parasites, such as microbes, fungi, and helminth worms. The menoponid louse *Trinoton anserinum* transmits a common heartworm to swans and geese (Seegar et al. 1976; Cohen et al. 1991), and the dog louse *Trichodectes canis* is an intermediate host of a tapeworm that parasitizes canids (Kim et al. 1973). Viruses and bacteria have been isolated from chewing lice, although the role of lice, if any, in transmission has not been established. Saxena et al. (1985), Price and Graham (1997), and Durden (2001) all provide reviews of chewing lice as intermediate hosts and vectors, and Bartlett (1993) summarizes her work on the role of chewing lice as vectors of nematodes in aquatic birds.

Biogeography

There is relatively little known about the biogeographic distributions of chewing lice, at least compared to what we know about their hosts. For many louse specimens in collections, only the host species is recorded with little information on the specific locality where the specimen was collected. It is important for future workers to provide more information on collecting locality. With this caveat in mind, for some species of lice there are interesting biogeographic patterns. While chewing lice may be quite host-specific, there are examples where a species of louse may be absent from part of the host geographic range. This may be because 1) that species is replaced by another congeneric species (perhaps because of competition), 2) some other factor (perhaps environmental) results in that species being absent, 3) that species was absent on hosts colonizing a new, isolated area, or 4) the species went extinct in that region.

Clay (1964) outlines a case where two species of *Sula* harbor one species of *Pectinopygus* (Philopteridae) in the Atlantic Ocean and two different species in the Pacific and Indian Oceans. The distribution of *Heterodoxus* (Boopiidae) species on rock wallabies in eastern Australia also contains interesting biogeographic patterns. At a given locality, each species of rock wallaby only harbors a single species of louse (Barker 1991). However, across the range of a rock wallaby, there may be several species of lice. Often one species of *Heterodoxus* replaces the other across the range of the host. In several cases a species of louse is restricted to an isolated and peripheral

part of the host range (Barker 1991). In addition, a single species of *Heterodoxus* may occur on several species of rock wallabies. These non-specific lice are always on species of rock wallabies with adjacent biogeographical distributions, suggesting that species of *Heterodoxus* have distributions independent from their host species, but still restricted in biogeographic extent.

There appear to be several cases where the environment restricts the distribution of louse species into only a part of the host distribution. The wallaby louse, *Heterodoxus spiniger*, has become established on domestic dogs. However, this species is only found on dogs in the tropical and subtropical regions, suggesting that climate limits its distribution (Clay 1976). Humidity affects the distribution of dove lice. In arid regions, such as southern Arizona, species of *Columbicola* and *Physconelloides* are absent (or nearly so) on doves, while in more humid regions, prevalence is over 50% (Moyer et al. 2003). In fact, prevalence appears to vary with humidity in dove lice such that in dry regions some lice disappear entirely, leaving gaps in the geographic distribution of these louse species (Moyer et al. 2002).

Finally, lice may be absent from part of a host range because they were absent from the individuals that colonized that region or they went extinct in that region. Birds on islands, such as New Zealand, tend to have fewer species and genera of lice than their continental relatives (Paterson et al. 1999), presumably because the birds that colonized New Zealand did not bring all the usual species of lice with them. This is also true for introduced species (Paterson et al. 1999). For example, *Sturnidoecus sturni* does not occur on European Starlings (*Sturnus vulgaris*) introduced to North America, while it is a common parasite of starlings in Europe (Clay 1976). Similarly, feral pigeons (*Columba livia*) in North America do not harbor any species of *Coloceras*, even though *Coloceras* is found throughout much of the native range of these birds.

EVOLUTION

Origins of Lice

Fossils of lice older than the Quaternary are unknown (but see Rasnitsyn and Zherikhin 1999, Kumar and Kumar 1999, 2001 for possible recent findings). Thus, the age and origins of lice have been a matter of contention. Various authors have suggested origins of lice ranging from the late Cretaceous (60 mya) to the late Carboniferous (280 mya) (Kéler 1957, Kim and Ludwig 1978a, b, 1982, Hopkins 1949, Stenram 1964, Lyal 1985a). This debate has largely been a matter of speculation based on current host distributions (Hopkins 1949) because of the lack of fossil material and uncertainties regarding the closest relatives of lice. Currently, it is generally agreed that lice share a common ancestor with Psocoptera (book lice and bark lice), or some member within Psocoptera (Lyal 1985a, Whiting et al. 1997). Phthiraptera has been placed together with Psocoptera in the group Psocodea within the group Paraneoptera (also containing Hemiptera and Thysanoptera) (Kristensen 1991). These relationships are generally supported by limited morphological and molecular data (Whiting et al. 1997, Yoshizawa and Saigusa 2001).

Phthiraptera and Psocoptera share several important morphological synapomorphies, which are taken as strong evidence of their close relationship. These include the atmospheric water-vapour uptake system described earlier (Rudolph 1982, 1983), among eight other synaporphies identified by Lyal (1985a). While a close relationship of Phthiraptera and Psocoptera has generally not been controversial, the exact placement of lice with respect to Psocoptera has. Kim and Ludwig (1982) suggest that lice were derived from Permopsocida, an extinct group of presumed psocopteran ancestors (Smithers 1972). Considering extant taxa, this scenario would place lice as the sister taxon to all Psocoptera. In contrast, a cladistic analysis of morphological characters (Lyal 1985a) indicated that lice are the sister taxon to the Liposcelididae, a single family within the suborder Troctomorpha. Recent molecular evidence (K. Yoshizawa and K. P. Johnson, unpublished) generally supports Lyal's view, with the psocopteran genus *Liposcelis* perhaps being the closest relative of Phthiraptera. These two hypotheses have different implications for the age of lice. Kim and Ludwig (1982) posit an origin of louse ancestors in the Carboniferous or Permian, while Lyal's (1985a) result requires lice to be no older than the origins of the family Liposcelididae (perhaps late Cretaceous). Information from molecular data, assuming a molecular clock can be calibrated for lice, may also resolve this issue.

The monophyly of Phthiraptera has rarely been explicitly questioned. However, various authors allude to the idea that the various lineages of lice might be independently derived from similar psocopteran ancestors (Clay 1957, Kim and Ludwig 1978a, 1982, Ledger 1980). Lyal (1985a) lists 24 synapomorphies for Phthiraptera, but many of these are related to their parasitic habit. Molecular data produced to date (K. P. Johnson and K.

Yoshizawa unpublished) are still ambiguous on the question of Phthiraptera monophyly, at least with respect to *Liposcelis*.

A potential scenario for the origin of parasitism by lice involves a transition between facultative commensalism in a psocid-like louse ancestor to obligate parasitism in lice (Hopkins 1949, Waage 1979, Lyal 1985a, Barker 1994). Members of Psocoptera are known from the pelage and nests of mammals (Pearlman 1960, Mockford 1971), the nests of birds (Hicks 1959, Rapp 1961, Wlodarczyk 1963), and the plumage of birds (Mockford 1967). Often these records involve *Liposcelis*, a genus of small wingless Psocoptera, potentially the closest living relative of lice. Based on current knowledge of louse phylogeny, it is not clear whether birds or mammals were the primary hosts of the ancestral lice, and there has been considerable speculation on this topic (reviewed in Lyal 1985a and Barker 1994).

Phylogenetics of Phthiraptera

Chewing and sucking lice were traditionally classified in the separate orders Mallophaga (chewing lice) and Anoplura (sucking lice), largely on the basis of differences in their mouthparts. Recent workers agree, however, that chewing lice are paraphyletic, with Anoplura being the sister taxon to Rhynchophthirina (Fig. 3; reviewed in Barker 1994). For this reason, chewing and sucking lice are now classified in the single order: Phthiraptera. Kim and Ludwig (1978a, 1982) argued that the Anoplura are distinct from Mallophaga and should be retained as a separate order. Their argument was later disputed by Lyal (1985a), who presented considerable morphological evidence for the paraphyly of chewing lice (Fig. 3).

Recent molecular data have been used to address the relationship of the four suborders of Phthiraptera. Analyses of partial sequences of the nuclear elongation factor 1- (EF1) gene did not provide good resolution for the relationships among the suborders (Cruickshank et al. 2001). Only the monophyly of Amblycera was consistently recovered with this gene. In contrast, analyses of the 18S nuclear ribosomal gene recovered the monophyly of Amblycera, Anoplura, and Ischnocera with strong support (Johnson and Whiting 2002). In addition, a sister relationship between Anoplura and Rhynchophthirina, as proposed by Lyal (1985a), was strongly supported. When the tree for Phthiraptera is rooted with *Liposcelis* (Barker et al. In press) the phylogenetic arrangement of Lyal is strongly supported (Fig. 3). These data indicate that the chewing lice are a paraphyletic group and that the term "Mallophaga" should no longer be used, but instead subsumed within Phthiraptera, and reference made to the four suborders (Barker 1994). Classification of the sucking louse suborder Anoplura is detailed elsewhere (Kim and Ludwig 1978b, Durden and Musser 1994a), and the three chewing louse suborders are treated below.

Phylogenetics of Amblycera

Classification of the Amblycera at the family level has been relatively stable. Generally six families are recognized (Table 1), three parasitizing birds (Ricinidae, Laemobothriidae, and Menoponidae) and three parasitizing mammals (Trimenoponidae, Gyropidae, and Boopiidae) (Hopkins and Clay 1952, Clay 1970). A single species of Boopiidae (*Therodoxus oweni*) parasitizes cassowaries, which are large flightless birds. The three families of bird lice are widely distributed geographically, while the mammalian Amblycera have more restricted geographic distributions. Trimenoponidae and Gyropidae were historically confined to South America, while Boopiidae is generally confined to Papua-Australian marsupials. One species of Boopiidae, *Heterodoxus spiniger*, has spread on dogs (and dog relatives) throughout tropical and subtropical areas (Clay 1976), probably in prehistoric times (Murray and Calaby 1971). A seventh family, Abrocomophagidae, was described (Emerson and Price 1976) after the Clay (1970) monograph; however, this family is not recognized in the by recent workers (Price and Timm 2000). Eichler (1963) elevated many of the families to superfamily rank and recognized smaller groupings as 16 families. His classification has not been widely adopted by other workers because he provided little justification for his classification.

Clay (1970) suggested a close relationship between the Gyropidae and Trimenoponidae, separating the Gyropidae into three subfamilies (Gyropinae, Protogyropinae, and Gliricolinae). A cladistic reanalysis of Clay's morphological characters (Marshall In press) supports a major split between the Gyropidae + Trimenoponidae and all other Amblycera (Fig. 3). A more thorough phylogenetic analysis of 147 morphological characters for 44 genera of the remainder of Amblycera finds that bird lice (Ricinidae and Laemobotriidae) form the basal families in the sister clade to Gyropidae + Trimenoponidae, with Boopiidae the sister taxon to Menoponidae (Fig. 3). Marhsall's analysis found

support for monophyly of Ricinidae, Boopiidae, and Menoponidae.

Limited molecular phylogenetic analysis of the Amblycera (Johnson and Whiting 2002, Barker et al. In press) provides a different picture. With nuclear 18S sequences, the monophyly of Boopiidae is strongly supported (Barker et al. In press). With the exception of the genus *Trinoton*, monophyly of the Menoponidae also is supported. *Trinoton* may be the sister taxon of all other Amblycera (18S, Johnson and Whiting 2002, Barker et al. In press), or, together with Laemobothriidae, form the sister taxon to all other Amblycera (combined 18S, EF1 , and COI genes, Johnson and Whiting 2002). Resolving differences between molecular and morphological trees requires additional data.

Menoponidae is the largest family of Amblycera, but attempts to provide a subfamilial classification within this group have been difficult. Clay (1969) recognized the *Colpocephalum* and *Menacanthus* complexes, but these account for only a portion of menoponid diversity. Marshall (In press) provided a phylogenetic analysis of morphological characters for 35 menoponid genera. The tree was well-resolved and supports four major groupings of Menoponidae. One of these clades includes representatives of the *Colpocephalum* complex (genera *Osborniella*, *Eomenopon*, *Piagetiella*, *Ciconiphilus*, *Cuculiphilus*, *Ardeiphilus*, *Odoriphila*, *Psittacomenopon*, *Comatomenopon*, and *Colpocephalum*). Another large group represents an expanded *Menacanthus* complex including several genera from galliform birds (*Numidicola*, *Menopon*, *Amyrsidea*, *Somaphantus*, and *Menacanthus*), among others.

At the generic level, amblyceran taxonomy is relatively stable. Clay produced keys to the genera of Menoponidae (1969) and Boopiidae (1970). Relationships among genera and monophyly of genera remain largely untested. However, some relationships are supported by both morphological and molecular analyses. The genera *Dennyus* and *Myrsidea* are closely related, as indicated by both morphology (Marshall In press) and the EF1 gene (Cruickshank et al. 2001). The genus *Ancistrona* also appears to be related to these two genera (Marshall In press; Cruickshank et al. 2001). Analysis of a limited number of EF1 sequences recovered monophyly of *Hohorstiella*, *Actornithiphilus*, *Dennyus*, *Myrsidea*, and *Menacanthus*, but not *Austromenopon*. Considerable phylogenetic work is needed to provide a complete classification of Amblycera below the level of family.

A few species-level phylogenies have been constructed for Amblycera using both morphological and molecular data. Barker (1991) examined the relationships among the species of *Heterodoxus* (Boopiidae) infesting rock wallabies using morphology and allozymes. The phylogeny was generally well-resolved and species of lice in close biogeographic proximity were generally closely related. The phylogenetic relationships among several of the species of swiftlet lice in the genus *Dennyus* (subgenus *Collodennyus*) have also been investigated using both morphological (Clayton et al. 1996) and molecular data (mitochondrial cytochrome *b* DNA sequences, Page et al. 1998). These trees agree on a split between the *distinctus* and *thompsoni* species groups of *Dennyus*, and in general the congruence between the molecular and morphological trees is remarkable.

Phylogenetics of Ischnocera

Unlike Amblycera, classifying the suborder Ischnocera has been exceedingly difficult and contentious at all levels. Ischnocera can first be divided into two major groups, those occurring on birds and those occurring on mammals. The monophyly of the ischnoceran lice on mammals (Trichodectidae), excluding the enigmatic lemur louse *Trichophilopterus*, is generally agreed upon. The Trichodectidae is often considered to be the sister taxon to avian Ischnocera (Blagoveshtchensky 1956, Mey 1994, Smith 2001), although this remains to be conclusively demonstrated. In contrast, classification of the avian Ischnocera has been especially problematic. Clay (1951) reviewed the morphological characters of avian Ischnocera, but was unable to produce a classification that she felt reflected natural (monophyletic) groupings. Within avian Ischnocera, most species are classified in the family Philopteridae, including *Trichophilopterus*. However, many attempts have been made to recognize various other groups. The family Heptapsogasteridae is often recognized for a distinctive group of lice occurring on tinamous (Carriker 1936, Hopkins and Clay 1952, Barker 1994, Smith 2000). This group is characterized by a unique seven-segmented abdomen. Some workers recognize a separate family for *Trichophilopterus* (Trichophilopteridae) (Eichler 1963). The family Goniodidae (Eichler 1963, Smith 2000, Johnson et al. 2001a) is also often recognized (informally called the *Goniodes* complex, Ledger 1980).

Beyond these groups, the identification of further groups within avian Ischnocera has been difficult. Other, largely informal, groupings include the *Philoceanus*, *Cummingsiella*, *Otidoecus*, *Brueelia*, *Acidoproctus*, and *Degeeriella* complexes (Clay 1958, Ledger 1980, Smith 2001). Eichler (1963) classifies the avian Ischnocera into 17 families and the mammalian Ischnocera into 4 families (splitting the Trichodectidae into 3 families). This classification has not been widely accepted because little justification is provided for the classification, and it is generally perceived to rely too heavily on host classification (reviewed in Smith 2001).

Recent phylogenetic work on Ischnocera has addressed some of these problems. The Trichodectidae are particularly well studied. Lyal (1985b) analyzed 187 morphological characters for 351 species and subspecies of Trichodectidae. Based on his cladistic analysis, Lyal divided the Trichodectidae into five subfamilies: Bovicolinae, Eutrichophilinae, Dasyonyginae, Trichodectinae, and Neotrichodectinae. Based on this phylogeny, Lyal constructed a classification of species down to the level of subgenus, but did not resolve the relationships among the many species of *Geomydoecus*. However, Page et al. (1995) further examined the relationships within the Neotrichodectinae gopher lice. They used 58 morphological characters to construct a phylogeny for all 122 species and subspecies of the genera *Geomydoecus* and *Thomomydoecus* for. While not completely resolved, together these studies provide the most complete phylogeny and classification for any major group of lice.

Relationships within the Trichodectidae also have been examined using molecular data. EF1 DNA sequences support the monophyly of Trichodectidae as well as the sister relationship of Bovicolinae to the other Trichodectidae (Cruickshank et al. 2001). At the species level, phylogenies have been constructed for gopher lice in the genus *Geomydoecus* based on allozymes (Hafner and Nadler 1990) and mitochondrial COI sequences (Hafner et al. 1994).

In contrast to mammalian Ischnocera, phylogenetic relationships among major lineages of avian Ischnocera have been remarkably difficult to resolve. Smith (2001) conducted an extensive study of 138 morphological characters for 51 genera of avian Ischnocera. Phylogenetic analysis of these data generally separated avian Ischnocera into two major groups: those with a circumfasciate head and those with a non-circumfasciate head. While this tree was well-resolved, many aspects of the tree were not strongly supported. Importantly, however, the monophyly of some key groups was recovered, including the *Goniodes*, *Philoceanus*, and *Degeeriella* complexes. Surprisingly, the monophyly of the Heptapsogasteridae was not recovered, although this was likely an artifact of taxon and character sampling (Smith 2000, 2001).

Molecular analysis of ischnoceran relationships, while providing information on some relationships, has not yet produced clear results on the overall phylogeny of Ischnocera. Analyses of sequences of the EF1 gene (Cruickshank et al. 2001) recovered monophyly of the Trichodectidae, most of Goniodidae, and the *Philoceanus* and *Degeeriella* complexes. However, the relationships among these and other groups of avian Ischnocera were wholly unresolved. Studies of other genes (12S, Page et al. 2002; 18S, Johnson and Whiting 2002) provided little additional resolution of ischnoceran relationships. In both the morphological (Smith 2001) and molecular (Cruickshank et al. 2001) studies of avian Ischnocera, Goniodidae and Heptapsogasteridae are imbedded within other avian Ischnocera. Thus, recognition of these families would result in paraphyly of "Philopteridae." Much more work is needed to provide a stable family-level classification of Ischnocera.

Phylogenetic work within subgroups of avian Ischnocera has also been conducted. Morphological characters have been used to study relationships among the genera of Heptapsogasteridae and Goniodidae (Smith 2000). While morphological characters provided considerable resolution within Heptapsogasteridae, resolution within Goniodidae was generally poor. Monophyly of the Strongylocotinae (*sensu* Eichler 1963, i.e., *Strongylocotes*, *Austrokelloggia*, *Kelloggia*, and *Ornicholax*) was recovered, but other genera formed a grade with respect to the apical Strogylocotinae. Within the resolved portion of the Goniodidae, columbiform and galliform lice were not monophyletic. Mey (1999) analyzed 51 morphological characters among taxa of goniodids on megapodes (Galliformes: Megapodiidae) and produced a well-resolved phylogeny. Further investigation of relationships within Goniodidae using EF1 and COI DNA sequences (Johnson et al. 2001a) indicated that the genus *Chelopistes* (and *Labicotes*) should be removed from conceptions of Goniodidae. *Chelopistes* was found to be the sister taxon of *Oxylipeurus*, as suggested by Clay (1976). In addition, the genus *Passonomedea* was found to have close affinities with Heptapsogasteridae, which in turn may be the closest relative of the Goniodidae (Smith 2000). Within the Goniodidae, species can be separated into the *Goniodes* and *Coloceras* complexes (more formally Goniodinae and Physconelloidinae). Monophyly of the *Coloceras* complex was strongly supported, while

monophyly of the *Goniodes* complex was less clear (Johnson et al. 2001a).

At the generic level, monophyly of several ischnoceran genera has been questioned, and there are many issues that still need to be resolved regarding generic-level classification. A few statements from Clay highlight this point: "...generic separation [within the Heptapsogasteridae] becomes an almost insoluble problem" (Clay 1951, p. 175); "...even the apparently well-defined genera *Goniodes* and *Goniocotes* seem to grade into each other" (Clay 1951, p. 175). Smith (2001) sampled two species from each of four genera in his broader morphological study. In each case, he found support for the monophyly of those genera. However, a broader scale morphological assessment of generic monophyly in avian Ischnocera has not been conducted.

Limited molecular assessment of generic monophyly in avian Ischnocera is available. Using a limited taxon sample of EF1 sequences (Cruickshank et al. 2001), monophyly of the genera *Pectinopygus*, *Geomydoecus*, *Docophoroides*, *Columbicola*, *Anatoecus*, *Anaticola*, *Chelopistes*, *Penenirmus*, *Philopterus*, *Paragoniocotes*, *Quadraceps*, *Saemundssonia*, and *Austrophilopterus* could be supported, while that of *Heptapsogaster* and *Rallicola* could not. However, this study included only a very limited taxon sample of each genus (generally two or three species) and thus does not provide a powerful test of generic monophyly in avian Ischnocera. Johnson et al. (2002b) assessed the monophyly of several of the genera using the EF1 and COI genes within the problematic *Degeeriella* complex. The genera *Picicola*, *Austrophilopterus*, *Degeeriella*, and *Cuculicola* were all paraphyletic using these data. Many of these problems within the *Degeeriella* complex were also identified by previous workers using morphological information (Clay 1958, Dalgleish 1969).

A few studies have examined species-level relationships within avian Ischnocera. Paterson et al. (2000) studied the relationships of some seabird lice (13 species in the genera *Austrogoniodes*, *Halipeurus*, *Harrisoniella*, and *Trabeculus*) using sequences from the mitochondrial 12S gene. This tree supported monophyly of those genera and was generally well-resolved. A study of phylogenetic relationships among species in the genus *Penenirmus* (Johnson et al. 2001c) indicated that the species of *Penenirmus* on passerine songbirds formed a monophyletic group. The species of *Penenirmus* on barbets were distributed among several different lineages, some very closely related to those on woodpeckers. In contrast, a molecular phylogenetic study of the genus *Brueelia* revealed little correspondence with host taxonomy (Johnson et al. 2002a).

Phylogenetics of Rhynchophthirina

The Rhynchophthirina contains only three species in a single genus (*Haematomyzus*), which is placed in the family Haematomyzidae. Strong morphological (Lyal 1985a) and molecular evidence (Johnson and Whiting 2002, Barker et al. In press) supports the sister relationship of Rhynchophthirina and Anoplura.

Cophylogenetics of Lice and Hosts

Lice, because of their high level of host-specificity, have become a model system for cophylogenetic studies. Much can be learned about the history of host-parasite association by comparing the phylogenies of hosts and parasites. Fahrenholz's Rule (Eichler 1941) has been used to describe the expectation that louse phylogeny should mirror host phylogeny (Fahrenholz 1913). There has been much debate over the relative importance of this rule in louse evolution (Timm 1983, Lyal 1985b), but clearly certain groups of lice are confined to phylogenetically restricted groups of hosts (Hopkins 1942). Several workers have suggested that the phylogenetic relationships of lice can potentially be used as an indication of the phylogenetic relationships of their hosts (Harrison 1915a, Hopkins 1942, Clay 1950, Mey 1999). For example, the phylogenetic position of flamingos is uncertain. Traditionally, they have been placed in the order Ciconiiformes, which includes storks. However, Hopkins (1942) pointed out that flamingos share four genera of lice with waterfowl (Anseriformes) but none with storks. Because closely related hosts often harbor the same genera of lice, Hopkins (1942) took this as strong evidence that flamingos and waterfowl are closely related. However, this example was later reinterpreted as a case of multiple host switches from waterfowl to flamingos (Sibley and Ahlquist 1990).

Much of the recent attention regarding Fahrenholz's Rule has centered around the phenomenon of cospeciation, the simultaneous speciation of both host and parasite lineages. Comparisons of host and associated louse trees (cophylogenetic analysis) may reveal portions of the trees that are identical, and this is taken as evidence of cospeciation (Brooks 1988, Page 1990, 1991). However, other evolutionary events besides cospeciation may occur (Page 1990, 1994). These include 1) host-switching, 2) sorting events (extinction and "missing the boat"), 3) duplication (speciation of the parasite in the absence of host speciation), and 4) failure of the parasite to speciate in response to host speciation (Johnson and Clayton 2003, Clayton et al. 2003, Johnson et al. 2003a).

To date, several studies comparing louse phylogenies with host phylogenies have been conducted. Gopher lice (*Geomydoecus*: Trichodectidae) exhibit substantial cospeciation with their gopher hosts (Hafner and Nadler 1988, Hafner et al. 1994). Gopher lice have often been used as a model system for developing cophylogenetic methods (Page 1994, Huelsenbeck et al. 1997, Johnson et al. 2001b). However, not all groups of lice exhibit the remarkable degree of cospeciation shown by *Geomydoecus*. Swiftlet lice (*Dennyus*: Menoponidae) are not as host-specific, but even so show a significant degree of cospeciation (Page et al. 1998). Seabird lice (*Halipeurus*, *Trabeculus*, and *Austrogoniodes*: Philopteridae) show evidence of cospeciation, but also show evidence for host-switching and duplication and sorting events (Paterson et al. 2000). Wallaby lice (*Heterodoxus*: Boopiidae) show no evidence of cospeciation with their hosts; rather, hosts and parasites seem to be responding to different isolating events (Barker 1991). The phylogeny of avian lice in the genus *Brueelia* also shows no congruence with host phylogeny despite considerable host-specificity (Johnson et al. 2002a). Explaining variation in the degree of cospeciation across lice is a significant challenge, but knowledge of underlying biological and ecological factors may provide predictive power (Clayton et al. 2003).

Population Genetics

Relatively few studies have been made of the population genetics of lice, but those that have been conducted generally indicate that louse populations are genetically structured. In studies of genetic variation of allozymes within species of *Heterodoxus* (Boopiidae), 4 of 11 species could be further subdivided into two operational taxonomic units, perhaps cryptic species (Barker et al. 1991a). Furthermore, populations of species of *Heterdoxus* found on a single colony of rock wallabies were shown to be highly homozygous and differentiated from other populations (Barker et al. 1991a). In the case of *Heterodoxus octoseriatus*, genetic differentiation was arranged north to south and generally corresponded to the ranges of two host subspecies (Barker et al. 1991b).

Genetic host races or cryptic species have also been documented in dove lice in Texas and Mexico (Johnson et al. 2002c). Study of mitochondrial COI sequences in *Physconelloides* and *Columbicola* (Philopteridae) found that four of five species distributed on multiple host species had within species genetic divergence exceeding 9% (up to 19%). In some cases these haplotypes were host-specific while in others they were distributed on more than one host species (Johnson et al. 2002c). In addition, genetic differentiation was also observed between localities in species of *Physconelloides*, but this generally was low (< 2% sequence divergence). In general, *Physconelloides* (body lice) showed much more genetic structure than *Columbicola* (wing lice) across the same host species.

Genetic variation has also been studied in louse populations in hybrid zones. Studies of allozyme variation in the gopher louse *Geomydoecus actuosi* (Trichodectidae) across a contact zone of gopher subspecies revealed that genetic differentiation in lice mirrored that of their hosts (Nadler et al. 1990). *Geomydeocus* populations, like those of *Heterodoxus*, were found to have very low levels of heterozygosity. Moreover, louse populations on different individual hosts were significantly differentiated from each other, revealing a substantial level of inbreeding (Nadler et al. 1990).

Macroevolutionary Trends: Morphology

Body size and shape vary considerably across groups and species of lice. One pervasive pattern, termed Harrison's Rule (after Harrison 1915a), is that louse body size tends to be correlated with host body size. Harrison (1915a), working on kiwi lice (*Rallicola*), noted "But, in general, when a genus is well distributed over a considerable number of nearly related hosts, the size of the parasite is roughly proportional to the size of the hosts." Harrison's Rule has been investigated and found to be very strong in a wide variety of groups of lice, and very few exceptions have been found. In Menoponidae, there is a strong relationship between the head width of species of *Actornithophilus* and host body length (Clay 1962, Kirk 1991). The size of tinamou lice ("Heptapsogasteridae") also is correlated with that of their hosts (Ward 1957). Another genus of avian Ischnocera (*Philopterus*) also shows a general correlation of host and louse body sizes (Kettle 1977).

These early investigations of Harrison's Rule did not take into account the phylogenetic non-independence in cross species comparisons (Felsenstein 1985). Recent studies of the size relationships of gopher lice (*Geomydoecus*) control for the phylogeny of the lice using

regression of independent contrasts. Harvey and Keymer (1991) showed that the overall body size of *Geomydoecus* species is correlated with that of gophers, when the phylogeny of the lice is taken into account. This relationship has been investigated further (Morand et al. 2000, Reed et al. 2000) by comparing the hair diameter of the gophers to the width of a head groove in the trichodectid lice. Hair diameter is correlated with body mass in mammals (Reed et al. 2000). There is a very tight match between hair diameter and head groove width (Morand et al. 2000). Since trichodectid lice often attach to mammal hair by means of the groove (the hair fits through the groove), this may be a mechanism that maintains host specificity in these lice. It may be difficult for trichodectid lice to survive on a mammal host that is different in size from their usual host (Reed et al. 2000).

The ability to stay attached to the host may also drive Harrison's Rule in other groups of lice. Phylogenetically controlled analyses of Harrison's Rule in swift lice (*Dennyus*) also reveal a strong correlation (Clayton et al. 2002). Species of *Dennyus* stay attached to bird feathers by means of a tarsal claw (Tompkins and Clayton 1999). Since swifts are presumably inefficient preeners, given their small bills, this close match between louse and bird size may be maintained by selection for tenacity, i.e. staying attached during host flight (Tompkins and Clayton 1999). The correlation between louse and host size in another avian louse genus, *Columbicola*, is more likely selected for by host preening. Since wing lice escape preening by inserting between the barbs of wing feathers (Clayton 1991b), preening-imposed selection would be expected to favor a match between parasite and feather barb size (Clayton et al. 2002). In keeping with this hypothesis, Clayton et al. (1999) demonstrated experimentally that host preening does, in fact, exert direct selection on *Columbicola* body size. Although the selective agents responsible for Harrison's Rule may vary, the pattern of correlated body size holds across different avian and chewing mammalian lice. Harrison's Rule is therefore one of the more robust macroevolutionary patterns demonstrated for lice to date.

While overall body size varies with host size in chewing lice, body shape is generally quite stable within major groups (e.g. Amblycera and Trichodectidae). However, within avian Ischnocera (Philopteridae), body form is remarkably varied (Clay 1949b). This variation generally corresponds with specialization to three particular microhabitats (niches) on the bird body. "Wing lice" have a long and slender body form and escape from host preening by inserting themselves between the barbs of the wing feathers (Fig. 1E, Clayton 1991b). In contrast, "head lice" have an oval abdomen with a triangular head, and often possess a dorsal anterior head plate (Fig. 1D, Smith 2001). Head lice escape from host preening by remaining in the head feathers, because a bird cannot preen its head with its bill. A third form, often called "fluff lice" or "body lice," occupies the lush feathers of abdominal regions, where they escape from preening by burrowing in the downy basal regions of these feathers (Clayton 1991b). Lice occupying this microhabitat generally have a short rounded body form like head lice, but with a rounded, circumfasciate head (Fig. 1F, G, Smith 2001). Body lice have a restricted host distribution, being common only on Tinamiformes, Galliformes, Columbiformes, and Psittaciformes, among a few others.

Many groups of birds are parasitized by several genera of lice, each occupying different microhabitats on the body (Clay 1949b). This diversity could have arisen in one of two ways. First, the major microhabitat specializations may have evolved early in the radiation of Philopteridae, and these forms of lice simply radiated and assorted with their hosts. Alternatively, these forms may have repeatedly evolved on various host groups by character displacement, leading to repeated convergent evolution of microhabitat specialization. Phylogenies constructed from morphological data tend to indicate that lice of similar microhabitat specializations are closely related (Smith 2001), supporting the assortment hypothesis. However, phylogenetic study based on morphology may have difficulty detecting repeated convergence in body form, if it has occurred. In contrast to morphological study, investigation of these patterns using preliminary molecular phylogenetic information on Philopteridae indicates a mixture of the two patterns (Cruickshank et al. 2001, Johnson et al. 2001a). In some cases lice sharing the same microhabitat and body form seem to be closely related. For example, most body lice tend to be closely related in the groups "Goniodidae" and "Heptapsogasteridae." However, one body louse, genus *Chelopistes*, from New World Galliformes is most closely related to a genus of wing louse from New World Galliformes, *Oxylipeurus* (Cruickshank et al. 2001, Johnson et al. 2001a), together being very distant from "Goniodidae." Similarly, wing (*Anaticola*) and head (*Anatoecus*) lice from waterfowl are closely related, as are wing (*Quadraceps*) and head (*Saemundssonia*) lice from Charadriiformes (e.g. gulls) (Cruickshank et al. 2001). These patterns need to be investigated in more detail as better phylogenetic information becomes available for avian Ischnocera.

Macroevolutionary Trends: Molecules

There are several unusual features of louse molecular evolution. First, in comparisons of rates of mitochondrial evolution between lice and their hosts (birds and mammals), lice are found to have elevated rates of substitution (Hafner et al. 1994, Page et al. 1998, Paterson et al. 2000). Lice experience mitochondrial substitutions with a rate at least five times faster than their hosts. This difference appears not to be simply a difference between insects and vertebrates, because comparisons with other insects also reveal a substantially elevated mitochondrial rate (Simmons and Weller 2001). The relative rate of mitochondrial to nuclear substitution also appears to be very high in lice (Johnson et al. 2001a, c, 2003b), often leading to significant incongruence, as a result of high mitochondrial homoplasy, between phylogenies derived from mitochondrial and nuclear genes (Johnson et al. 2001a, 2002b, Johnson and Whiting 2002).

Elevated mitochondrial molecular evolution is evidenced not only in the substitution rates, but also in structural arrangements. The secondary structures (stems and loops) of louse 12S and 16S genes are highly variable (Paterson et al. 2000, Page et al. 2002). In domain III of 12S, there is more length variation within chewing lice than across all other insects (Page et al. 2002). In addition to variation in the number and length of stems and loops in structural rRNA genes, the gene order of the louse mitochondrion is highly unusual (Shao et al. 2001a). The complete mitochondrial genome of *Heterodoxus macropus* shows at least nine rearrangements in protein coding genes as compared to the relatively conservative arrangement across other insects. All of the tRNA genes changed position relative to the ancestral gene arrangement of insects (Shao et al. 2001a). There are also inversions in several protein coding and tRNA genes. A partially rearranged mitcohondrial genome is found in some other lice, and also in Psocoptera and Thysanoptera (Shao et al. 2001b).

Not only is molecular evolution of the louse mitochondrion highly unusual, but there are also unusual aspects of molecular evolution in some nuclear genes. For example, the 18S rRNA gene has large, unusual insertions in many genera of lice (Johnson and Whiting 2002), making this gene difficult to sequence for some lice. The elongation factor 1- gene also lacks introns found in Psocoptera and Thysanoptera (Cruickshank et al. 2001, D. Morris Pers. comm.). The causes of the anomalous aspects of louse molecular evolution are still unknown, but more work on the subject may be revealing.

SUMMARY

Chewing lice are proving to be a model system for studying the interface between ecology and evolution. The relatively simple life cycle of lice and their close association with their hosts make them ideal for experimental study. In addition, the interaction between lice and their hosts generally involves a few, readily studied factors. The discrete nature of louse populations also makes quantification straightforward and allows relatively simple ecological and genetic population models to be directly applied to louse populations. The fast rate of evolution at the molecular level should provide a wealth of molecular markers for genetic studies. The fact that many groups of lice cospeciate with their hosts implies a long-term history of association, which allows the history of selective forces to be reconstructed. Finally, chewing lice exhibit a range of variation across species in host-specificity, body form, and dispersal ability. This variation facilitates comparative studies, in combination with experiments, to unlock the causes of macroevolutionary patterns. The description of chewing louse diversity provided in this volume is the first step in understanding how such diversity came to be.

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