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Preface

Cospeciation is an interwoven process that impacts many organisms. It is important to study because no organism lives in a vacuum by itself. All organisms interact with other organisms on a daily basis. Some interactions are fleeting, whereas others may become more and more important as time progresses. This study attempts to discover if the interactions between parasitic chewing lice and their avian hosts are important enough to cause cospeciation.

The first chapter of this work includes a literature review covering broad aspects that affect speciation. As this is a rather broad subject, I focused on antagonistic relationships and what I feel are the major factors that impact them: transmission and virulence. I focused especially on the specific interactions of chewing lice and their avian hosts, as they present an interesting system for a cospeciation study.

After the basics of cospeciation and the factors the influence it have been laid out, in chapter 1, I use phylogenetic analyses of two genera of chewing lice, *Brueelia* and *Myrsidea* from *Catharus* thrushes to experimentally test whether they have cospeciated. I chose *Catharus* thrushes because they are common captures at the Shaw Woods Avian Monitoring Project (SWAMP) and I knew that they were often heavily infested with lice. Also there was a published phylogeny of the *Catharus* thrushes for me to compare to my parasite phylogeny.

Chaper 1: How do Ecological Features Influence Evolutionary Outcomes in Host-parasite Systems?

This chapter focuses on close-knit relationships and the factors that influence the cophylogenetic history of two organisms. I attempt to draw links between ecological and evolutionary processes to elucidate the patterns of organisms that are likely to cospeciate. First, I introduce the basics behind coevolution and why it might lead to cospeciation. Next, I review the two most important ecological factors affecting two organism's cophylogenetic history: virulence and transmission. I look at other cophylogenetic patterns that may arise in host-parasite systems, and offer an explanation for why these patterns may occur instead of cospeciation. Throughout this chapter, I focus heavily on bird-louse systems, but include selective examples from other systems.

Coevolution And Specialization

Coevolution occurs when organisms respond to each other's adaptations with reciprocal adaptations. Where species of hosts and parasites have coevolved exclusively, there should be high host-specificity, concordant geographic ranges, and congruent phylogenies, i.e. cospeciation (Barker, 1991). Although coevolution does not necessarily always lead to cospeciation (Hoberg and Brooks, 1997), specialization is likely to increase the rate of speciation that may occur in both host and parasite (Price, 1980). The new species will likely have adaptations that make it better suited to its coevolved partner. Over time, these adaptations may accumulate so that one partner will not be able to survive without the other. Coevolution supports cospeciation, and enough specialization may lead to cospeciation.

Coevolutionary Arms Races

Highly coevolved antagonistic interactions are sometimes termed coevolutionary arms races, and these interactions were the inspiration for the coevolution concept. Coevolution was originally outlined by Ehrlich and Raven (1964) in a study on butterflies and their host plants. They found that the plants they studied were usually fed upon by a single, phylogenetically coherent group, or several closely related groups of butterflies, and that these butterflies and plants were specifically adapted to one another (Ehrlich and Raven, 1964). Through occasional mutations and recombinations, plants produce chemical compounds that protect them from attacks of phytophagous insects (Ehrlich and Raven, 1964; Farrell and Mitter, 1998). In response, the phytophagous insects may evolve a defense that neutralizes the chemical compound and leaves them free to feed on the plant (Ehrlich and Raven, 1964; Farrell and Mitter, 1998). As the plants and insects acquire adaptations, the number of species of insects that can consume the plant diminishes, as does the number of plants the insect can consume (Ehrlich and Raven, 1964). As these organisms become specifically adapted to each other, a certain dependence forms, and if the interaction is tight enough, cospeciation is likely to occur.

Coevolutionary arms races are also common in predator-prey relationships. In Lake Tanganyika there is a group of endemic gastropods and their predators, the potamonautid crab (Thompson, 1994). These two organisms have acquired some obvious adaptations that showcase their coevolutionary history. The claws of the crabs are large and robust relative to other freshwater species and the gastropods have responded with thicker lips, more sculpting on their shells, and stronger shells compared to other freshwater species to defend against the larger claws of their predators (Thompson, 1994). As the gastropod developed a thicker shell, the crab developed larger claws to break that shell, and then the gastropod developed an even thicker shell, which led to selection for even larger claws in the crab. Although they are highly coevolved, as of yet, no one has tested to see if the two organisms have cospeciated.

Why parasites are likely to coevolve with their hosts

Similar to the herbivore-plant and predatory-prey systems, the nature of the host-parasite relationship provides strong incentive for parasites and their hosts to coevolve. Parasites are organisms that depend upon

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other host organisms for food and shelter, and in the pursuit of these things they cause damage to the host. Extreme specialization is the norm in parasites due to a number of factors specific to living life on the body of another (Thompson, 1994). These factors include: long-term attachment to host, induced host defenses, unbalanced nutrition, intake of large amounts of one or several toxic compounds and avoidance of enemies (Thompson, 1994). When confronted with these factors, the parasite needs to be extremely well-adapted to its host or it will die. At the same time, the host also faces selective pressures to adapt defenses against these harmful organisms and ensure their health. Throughout time, reciprocal adaptations by host and parasite lead to coevolution.

Coevolution leads to organisms with specific adaptations to each other. Over time, these adaptations may result in the two organisms becoming exclusive partners. Extreme specialization by parasites tends to result in the parasites only being able to survive on one or a few host species (Moller et al., 2005; Poulin, 1997). When this specialized parasite is transferred to a novel host, it may not be able to survive in the new habitat. The novel host may have a toxin or defense that the parasite is unable to defend against. Even if a parasite has evolved to detoxify the toxin of its original host, it is unlikely to be able to detoxify a wide variety of toxins. As the coevolutionary arms race draws parasite and host into a tight interaction, the likelihood that the two will cospeciate increases.

Chewing lice and their avian hosts

Of all parasites, lice may be expected to coevolve with their hosts. These insects are found on virtually all bird species and many of these are host specific, occurring on only one host (Johnson and Clayton, 2003; Janovy, 1997). Lice might be expected to coevolve with their hosts for reasons such as: they lack a free-living stage in their life cycle, they are wingless, they are completely dependent upon their host, and transmission is generally only through direct contact (Barker, 1991). The obvious, coevolved characteristics between lice and their hosts make them perfect for cospeciation studies.

Bird Defenses

Birds have developed a variety of defenses in their fight to control parasite infestations. Unfortunately for birds, parasites evolve more quickly than their hosts, and this may result in their anti-parasite defenses being perpetually obsolete (Hafner et al., 1994; Whiteman et al., 2005). For the most part, louse populations are controlled through host grooming as well as a number of other defenses including anting, dust-bathing, sunning, and potential avoidance behavior through sexual selection (Johnson and Clayton, 2003; Marshall, 1981). Some birds will even go so far as to leave a heavily infested nest, even if it has eggs or nestlings in it (Emlen, 1986). A coevolutionary balance between host defense and parasite resistance may explain why most birds have small populations of lice that have little or no negative effects on the birds, because lice generally only reduce the host's fitness when they are in large numbers (Clayton, 1991b). The defenses birds have evolved help them to keep louse populations from approaching levels where they would become harmful.

Once a bird has become infested with lice, the most obvious and effective defense for their removal is grooming. Selective pressure is exerted by the lice for efficient preening ability (Clayton et al., 1999). Birds that are host to a large number of parasites must spend more time preening and this leads to less time available for foraging or other important activities (Hart, 1997). The bill overhang on the beak is specially adapted for rooting out and damaging lice and defects in bill shape often lead to increased parasite load (Clayton et al., 2005; Moyer, Peterson, and Clayton, 2002; Clayton and Walther, 2001). Birds have adapted this deadly overhang specifically to root out louse infestations and keep their populations from getting out of hand. Unfortunately, the lice are also well-adapted to the body of their host, and it is unlikely that a bird will be able to remove every last louse.

Having a healthy mate is essential to the success of a pair's offspring. In species where pairs mate for a season, or life, it is worth the effort to ensure an unparasitized mate. These mated pairs may allopreen, or preen each other, often in places they cannot reach themselves such as the head (Hart, 1997). Birds that do not have an allopreening partner are sometimes able to damage parasites on their head by scratching with their feet, however it is not as effective (Marshall, 1981). Unmated birds are unlikely to invest in the health of another bird unless it has a direct benefit for them, such as the increased health and reproductive ability of their mate.

Anting is a rather unique adaptation that has been shown to decrease louse loads. Anting is when a bird exposes itself to acid- or toxin-secreting ants, or to other pungent substances such as limes (Clayton and Vernon, 1993). Clayton and Vernon (1993) observed a common grackle (*Quiscalus quiscula*) preening with bits of a lime. They experimentally tested louse susceptibility to limes in a Petri dish and found that lice exposed to limes were killed (Clayton and Vernon, 1993). Anting is a way for birds to kill lice without rooting out each one individually. It is kind of similar to dousing themselves with a pesticide and may be an effective way to get rid of lice.

Another rather amazing adaptation for reducing louse infestations is sunning. Moyer and Wagenbach (1995) observed Black Noddies (*Anous minutus*) sunning in large groups with one wing extended and their tail feathers fanned. They experimentally reproduced these wings and placed ischnoceran lice on them and found that air temperatures slightly above 40 degrees Celsius can be lethal to lice and their eggs. Birds were observed to groom extensively preceding or following sunbathing, likely to remove the dead lice (Blem and Blem, 1993; Moyer and Wagenbach, 1995). Sunbathing in Swallows (Hirudinidae) can often lead to heat stress, including behaviors such as gaping and panting (Blem and Blem, 1993). Obviously, these birds are not comfortable; it is unlikely an adaptation to warm themselves, but an adaptation to kill lice (Blem and Blem, 1993). Blem and Blem (1993) treated a number of birds with pesticide and then observed the behavior of the birds and found that the treated birds spent less time sunning than untreated birds. Sunning, like anting, is a way to kill a large number of lice without spending the time to root out each one individually while preening.

Secondary sexual characteristics may have evolved to cue females to the parasite levels of males. Species with the most evident sexually selected traits are often the most subject to attack by debilitating parasites (Hamilton and Zuk, 1982). Although lice are

generally not debilitating, there may be heritable genetic resistance to louse infestations (Potti and Merino, 1995; Clayton, 1991a). However, low parasite load does not necessarily mean that an individual is resistant to parasites; it may only mean that this particular individual was never exposed (Clayton, 1991a). Parasite infestation can actually lower the testosterone levels in the host, preventing it from developing secondary sexual characteristics (Hilgarth and Wingfield, 1997). Testosterone has been shown to be an immunosuppressant and increased levels may result in a decreased ability to fight infections (Hilgarth and Wingfield, 1997). If a young male bird is infested with parasites, he must reduce the amount of testosterone in his system to fight the infestation and therefore he will not be able to develop his secondary sexual characteristics. If the testosterone is not reduced, the secondary sexual characteristics can develop but he would leave himself open to infestation and may be overcome by it.

Reduced reproductive success is correlated with male parasite infestation in some birds (Lehmann, 1993). Female barn swallows (*Hirundo rustica*) are attracted to long tails in their mates (Kose and Moller, 1999). The number of holes in tail feathers caused by lice is negatively correlated with tail length in male barn swallows, and therefore reduced reproductive success (Kose and Moller, 1999). Lice preferred white spots to other areas of the tail feathers and males with longer tails had less damage to white-spots, possibly due to genetic resistance (Kose and Moller, 1999). Females chose to mate with males with longer tails and these males may have been chosen because they have genetic resistance to louse infestations that the females would like to pass on to their offspring.

Infestation level does not always reduce the mating chances of males. Increased parasite load does not always equal decreased showiness in passerines; sometimes there are no signs that point to a heavily infested individual (Walther et al., 1999). In these cases, females do not seem to prefer unparasitized males (Walther et al., 1999). Brown et al. (1995) found no relationship between flea or chewing louse load and the quality of their host, the Cliff Swallow's (*Hirundo pyrrhonota*) phenotype, which suggests that there is not sexual selection for parasite resistance. The theory that secondary sexual characteristics developed to alert females to parasite infestations in males has not been proven. If this theory is true, parasites that inflict obvious damage may be selected against and less damaging parasites may thrive.

Chewing Lice

Just as birds have adapted to remove lice, lice have adapted to thwart these defenses. Lice have evolved many resistance tactics to counter a bird's preening bill including: small size, flattened shape, heavily sclerotized integuments, spines, ctendia, numerous setae, strong mouthparts, grasping claws, and avoidance behavior (Clayton, 1991b; Lehane, 2005). These adaptations allow the louse to hide from the bill and prevent them from being dislodged.

Host-specificity in lice may be partially due to extreme specialization to the body of their host. Lice tend to stay within a specific feather barb diameter and are only able to survive upon hosts of a particular size (Tompkins and Clayton, 1999). The main reason lice are unable to survive on hosts of varying size is their inability to escape a preening bill when they no longer fit between the host's feather barbs (Clayton et al., 2003). Lice are only able to survive on birds of a particular size, which leads to high host-specificity.

Grooming-imposed selections upon lice differ with the area of the body the louse inhabits. Lice on the wings, which are the most vulnerable to grooming, tend to be elongate, compressed forms that flatten against feathers or insert between the barbs very quickly (Clayton, 1991b). Those that live on the head and neck tend to be round-bodied and sluggish with no apparent adaptations for avoidance (Clayton, 1991b). These lice are safe from the beak of the bird and therefore have not adapted to get away from it quickly like the lice on the wings have. The lice that live on the wings and body of their host are forced to conform to the topology of the host in order to be able to avoid the host's defenses (Kethley and Johnston, 1975). Host body size is the major selection factor acting upon lice, but where they occur on the body also affects the lice.

After molting, there appear to be fewer lice, but actually the number has not decreased, they are just hidden from human eyes. Lice have evolved to actively seek refuge inside the sheath that encases developing feathers when the bird begins molting (Lehane, 2005; Moyer, Gardiner and Clayton, 2002). By hiding in the sheath, they are not dropped with the feather and are able to continue on their host. This is a significant adaptation for survival on an avian host. If they dropped with the feathers every time the bird molted, the louse populations would be significantly decreased every molting cycle.

Some lice have also adapted behaviors that make them better able to infest the next generation. Some blood-feeding lice may synchronize their life cycle with that of their host (Janovy, 1997; Moller et al., 2003). *Ricinus picturatus* and *Menacanthus* sp. showed peak reproduction during their host's, the Orange-crowned Warbler (*Vermivora celata*), nesting period (Janovy, 1997). This way they are able to increase the chances of nestlings picking up their parent's lice. Non-blood-feeding lice reproductive-cycles were not dependent upon the host; the blood-feeders may be responding to host hormones that signal when they should start reproducing (Janovy, 1997). These types of adaptations can only occur when the lice are in contact with the host's blood.

Lice are well-adapted to living life on the body of their host and consequently are not well-equipped to survive off of the host. Louse populations are extremely sensitive to changes in temperature and humidity, and by living so near to the host's skin, there is some control of these factors as compared with the outside environment (Moyer, Drown, and Clayton, 2002; Johnson and Clayton, 2003). Birds that live in humid regions are likely to have a greater number of lice than those that live in dry regions (Moyer, Drown, and Clayton, 2002; Johnson and Clayton, 2003). These lice are so adapted to the temperature and humidity controls on the body of their hosts that few can survive for more than a few days off of their host (Johnson and Clayton, 2003). Rem and Zlotorzycka (1981) found that lice lived 3-11 days in an empty tube at room temperature with unknown humidity, although it is unknown how long they retain the ability to infest another host. Although these lice were able to survive a surprisingly long time without food, they likely did not experience extreme changes in temperature or humidity, which could have killed them, so this study may not represent an accurate representation of how long a louse can live off of its host.

Amblycerans and Ischnocerans

The two main suborders of lice that infest birds are Amblycera and Ischnocera. Amblycerans feed mainly on host skin as well as blood and skin secretions; however, they may also eat other lice and feather mites especially when they are in high abundance (Marshall, 1981; Moller and Rozsa, 2005; Whiteman and Parker, 2004a). Blood has high nutritional value and it is easy to digest, which allows blood feeders to have greater fecundity (Lehane, 2005). Amblycerans are generally less host-specific, less restricted to a particular region of the host's body, more vagile than ischnocerans and when they do co-occur with ischnocerans, amblycerans are the more abundant (Whiteman and Parker, 2004a). Although there are major differences between amblycerans and ischnocerans, both suborders respond to selective pressures imposed by their hosts, and both show evidence that they have coevolved with their hosts.

Ischnocerans live on their hosts' feathers and, unlike amblycerans, they have no contact with their host's immune system. Ischnocerans feed on feathers and/or skin debris, but not blood (Marshall, 1981; Moller and Rozsa, 2005; Crompton, 1997). They have no direct contact with the host's immune system and mainly encounter the host's mechanical defenses (Whiteman et al., 2005). Since ischnocerans have no contact with the host's immune system, there may be more selective pressure for birds to evolve defenses against amblycerans.

Although there may be more selective pressure for a host to adapt to amblycerans, amblycerans are thought to be better able to find new hosts. Amblycerans are generally more mobile than ischnocerans and will often abandon a dead host in search of a new one, whereas the ischnocerans will die with their host (Johnson and Clayton, 2003; Kierans, 1975; Marshall, 1981). Amblycerans are known to migrate to the head feathers of dead hosts even though they are not normally found there and were able to survive for up to 14 days, just hoping a chance would come along for them to find a new host (Rem and Zlotorzycka, 1981). It is possible that although amblycerans try to find new hosts, they are frequently denied the chance.

Factors that hinder cospeciation

Chewing lice and their hosts have coevolved, but have they cospeciated? Extreme specialization by both host and parasite will not always lead to cospeciation. Factors such as parasite virulence and transmission ability may hinder cospeciation. Phylogenetic congruence may be hidden by sorting or duplication events (Banks et al., 2006). False congruence could come from a series of sequential host switches successively colonizing the host's closest relatives and then speciating, although this is unlikely to be common (Banks et al., 2006; Paterson and Gray, 1997; Paterson et al., 2000). Furthermore, a large founding population of hosts would be necessary for all louse species to be present when speciation occurs (Paterson et al., 1999). House Sparrows (*Passer domesticus*) were introduced to North America and only 35 of the original 69 ectoparasite species of the European species are present on the North American species (Paterson et al., 1999). With factors working for and against cospeciation, partially congruent phylogenies may be common.

Paterson et al. (2000) demonstrated partial congruence between a louse phylogeny and their seabird hosts. Cospeciation is also the main explanation for the history of seabirds and their lice (Paterson et al., 2000). It is not strict cospeciation however; there is some intrahost speciation and also some sorting events with little host-switching (Paterson et al., 2000). Host-switching is rare due to limited contact between hosts and the lack of a vector (Paterson et al., 2000). These organisms have partially cospeciated, but other cophylogenetic patterns explain the rest of the relationships.

Virulence

Traditionally, virulent pathogens/parasites were thought of as those that had been associated with their host for only a short period of time. Pathogens were thought to evolve towards non-virulence the longer they were associated with a host, because non-virulence ultimately benefits the pathogen (Smith, 1934; Swellengrebel, 1940). This view predicts that non-virulent pathogens are more likely to have cospeciated with their hosts than virulent ones.

Although, in theory, a pathogen has high fitness if it is benign, the view that all pathogens are evolving toward becoming more benign has lost favor in recent decades. Even in the 1940's, some believed that long associations could also lead to increased virulence (Ball, 1943). In the 1990's Paul Ewald really revolutionized the field. By showing that easily transmitted pathogens tend to be highly virulent (Ewald, 1993). He showed that the length of the association between host and parasite/pathogen is not the determining factor; long associations are just as likely to result in non-virulence as virulence (Ewald, 1983, 1998). A pathogen or parasite that has been associated with its host for a long period of time can still have high fitness while being virulent if it is easily transmitted to a new host.

The mode of transmission and the ability to survive outside/off of the host greatly influence the evolution of virulence (Ewald, 1993, 1998). The more difficult it is for a pathogen or parasite to be transferred to a new host, the less virulent it can afford to be. If it incapacitates its host, its host will be unable to transfer it to a new host and the pathogen or parasite will die with its host. However, if there is a vector that facilitates the transfer of the pathogen or parasite between host individuals, the pathogen or parasite can afford to incapacitate the host, because it can still colonize a new host (Ewald, 1983). Along the same lines, if a pathogen or parasite is able to survive for a long time off of the host, it can afford to be more virulent. It can sit and wait for a new host to come along without being adversely affected (Ewald, 1995). Hosts and parasites will not ultimately end up in a coexisting state with neither harming the other in all cases; it depends a lot on transmission (Anderson and May, 1982). Essentially, the more easily something is transmitted, the more virulent it can afford to be. These easily transmitted, virulent organisms may have been associated with their hosts for a short or a long period of time, but there is certainly incentive for the host to adapt defenses to protect against them.

Parasite virulence

Although a lot of work has been done on the virulence of pathogens, ectoparasites have not received as much attention. Ectoparasites generally do not kill their host, so virulence in parasites may be measured as parasite

reproduction, parasite infectiousness or parasite-induced mortality rate of the host (Toft, 1991). Ectoparasites may harm their hosts by lowering body mass, blood loss, feather loss; they may serve as vectors for other pathogens, and may also increase time spent in self-maintenance behavior and, therefore, reduce the amount of time that the host can spend on other activities (Brown et al., 1995). Although parasites generally do not kill, they do have a negative impact on their hosts. A host with few parasites is bound to be healthier than a host with many parasites.

Virulence and Chewing Lice

As discussed before, lice generally have small populations on a host due to their host's defenses. Lice are also the only parasitic insects that complete their entire life cycle on a host and show only low levels of pathogenicity (Moller and Rozsa, 2005; Crompton, 1997). However, much of this data has come from studies that merely correlate host condition with parasite loads, and therefore may not tell the whole story (Booth et al., 1993). The effect of infestations may not be evident until a burst of energy is needed, such as when the host needs to escape from a predator (Hart, 1997). Unfortunately, heavily infested birds are uncommon in nature which makes them difficult for correlational studies to observe.

On the other hand, experimental studies that have manipulated the louse loads on birds have been able to look at many heavily parasitized individuals. Booth et al. (1993) showed that birds with high loads of ischnoceran lice suffered significant feather mass reduction and an increase in metabolic rate and whole thermal body conductance. Barbosa et al. (2002) found a significant positive relationship in barn swallows between the number of lice and the percentage of time spent in flapping flight. Since lice are not thought to produce any mechanical constraints on flight, these high parasite loads have been linked to increased thermoregulation costs and therefore lower fat stores, which lead to less energy that can be devoted to flying. Although lice likely have a negative impact on their host, it is generally not readily detectable.

Are Amblycerans or Ischnocerans More Virulent?

There is some debate over whether amblycerans or ischnocerans are more virulent, and since most studies measuring virulence are correlational, there is not a lot of data to definitively support either as more virulent. Large populations of either louse suborder can induce a wide variety of negative effects; however, lice generally are in low enough populations that they have no detectable effect on host fitness (Clayton and Tompkins, 1994; Tompkins et al., 1996). Certain factors, such as contact with the immune system suggest that amblycerans are more virulent, although further study is necessary.

This contact with the immune system most certainly results in a coevolutionary arms race between amblycerans and their hosts. A strong correlation exists between amblyceran lice and negative body condition in their hosts (Whiteman and Parker, 2004a). One of the reasons for this may be that amblyceran lice feed on blood, and in large enough numbers, they may cause anemia (Brown et al. 1995; Clayton and Tompkins, 1994). Also, amblyceran lice may deliver foreign pathogens to the host as they feed (Brown et al. 1995). Both of these are significant reasons for a host to develop defenses against amblyceran lice. As they feed, amblycerans interact with their host's immune system, and host antibodies have been shown to reduce amblyceran louse fecundity and survivorship and regulate the population growth rate (Whiteman et al., 2005; Mumcuoglu et al., 1997; Lehane, 2005). However, it is suspected that host antibodies may actually have developed to defend against a more virulent pathogen, and just happen to negatively affect amblyceran lice (Moller and Rozsa, 2005). Whether or not the hosts developed these defenses specifically to defend against amblycerans, it is certain that amblycerans interact with, and are affected by, their hosts' immune systems.

Interaction with the immune system may increase the likelihood of speciation in lice. As T-cell mediated immune response increased, the number of other host species parasitized by a flea species decreased, and the number of flea species per host increased with host immune response (Moller et al., 2005). Amblycerans often have higher species richness than ischnocerans (Moller and Rozsa, 2005). This is possibly a result of increased speciation stimulated by host antibodies.

However, ischnocerans are not benign. They eat the feathers of their host and when in high loads, their host's feathers weighed 19% less than low-load birds (Clayton et al., 1999). Heavy ischnoceran louse loads on Rock Pigeons (*Columba livia*) corresponded with a decreased feather mass of 30% and increased metabolic rate of 8.5% (Booth et al., 1993). The pigeons had to increase their metabolic rate to compensate for increased thermal conductance and maintain body temperature, so high-load birds steadily lost body mass and appeared unable to compensate for increased metabolic rate (Booth et al., 1993). Ischnocerans certainly seem capable of inflicting damage; however, in most cases the host's defenses will keep them in small enough numbers to prevent major harm.

Transmission

Transmission not only has an influence on virulence, it also has a more direct impact on the cophylogenetic histories of hosts and parasites. Hosts act as temporary islands for parasites and effective transmission to a new host is essential for the survival of the parasite genes (Ewald, 1983). There are three main types of transmission patterns: vertical, horizontal and host-switching. Each of these supports a different cophylogenetic history which will be outlined below.

Vertical Transmission

Vertical transmission is the transfer of parasites from parents to offspring through direct contact. This common dispersal method essentially guarantees the survival of the parasite in the next generation, resulting in high fitness. Vertically transferred organisms, whether they be parasite or symbionts, are relatively benign since they rely on their host to pass them to their offspring (Lipsitch et al., 1996). A solely vertically transferred organism is likely to cospeciate with its host. Vesicomyid clams have had a long term association with endosymbiotic sulfur-oxidizing bacteria (Peek et al., 1984). These bacteria are transferred cytoplasmically through the eggs and there has been nearly completely vertical transmission for as long as they have been associated with one another (Peek et al., 1984). These two organisms have cospeciated almost strictly (Peek et al., 1984). Although strict

vertical transmission will not always result in cospeciation, cospeciation is extremely likely.

Another example of strict vertical transmission also results in cospeciation. Aphids and their endosymbiotic bacteria, *Buchnera* have cospeciated (Moran, 2001; Clark et al., 2000). *Buchnera* are transferred from mother to progeny and there has been strict vertical transfer over the last 100 million years (Moran, 2001). There is not even any evidence of horizontal transmission among closely related groups (Moran, 2001). Vertically-transmitted endosymbionts tend to cospeciate with hosts to a greater extent than do ectoparasites, because they are tied to their hosts and have few transmission opportunities.

Horizontal Transmission

Some parasites that are vertically transferred can also be horizontally transferred. Horizontal transfer is transfer between individuals of the same species. It can occur through direct contact during mating, copulation, pair preening, pair feeding, working in a nest chamber, chick feeding, or phoresy (Darlova et al., 2001). Since they are not dependent upon living on individual host organisms for long periods of time in order to be transferred to the next generation for survival, they can also afford to evolve to become more virulent. Furthermore, since they are able to transfer between unrelated individuals, there are more opportunities for a chance switch to a new species to occur, resulting in incongruent phylogenies of host and parasite. When looking at an evolutionary time scale, unlikely everyday events become commonplace. An extremely rare, chance encounter between two unrelated species may be enough to transfer a parasite to a novel host, thereby changing the cophylogenetic history of the organisms. Although horizontal transfer does not necessarily entail switching between host species, it may make it more likely.

Host-switching

When a parasite is transferred to a novel host species it is called host-switching. Vectors are a common implement in host-switching as they provide an easy way for parasites to be transferred to novel hosts and this relatively easy transfer often allows for greater virulence in vector-borne parasites (Day, 2002; Sol et al., 2000). Some parasites, like malaria are transferred solely by vectors such as mosquitoes (Ricklefs and Fallon, 2002). Mosquitoes have broad host ranges and this creates ample opportunities for host-switching in mosquito-carried blood pathogens (Ricklefs and Fallon, 2002). This rampant host-switching would probably result in a phylogenetic tree of malaria parasites looking nothing like a phylogenetic tree of their hosts.

Thriving on a novel host is not as simple as getting an opportunity to switch to a new host. Presumably, most host-switches are unsuccessful if parasites encounter preexisting competitors and no potential mates (Rosza, 1993). The novel host may also kill the new parasite quickly if the parasite is not adapted to the novel host's defenses. Despite the general likelihood of death, many ectoparasite phylogenies reflect a history of many successful host-switches (Rosza, 1993). Host-switching can completely prevent cospeciation between a parasite and its host if it is common enough.

Transmission in Chewing Lice

Direct contact is the main mode of transmission for lice. Lice are generally transmitted as nymphs or adults through direct contact between parents and their young and between mates (Janovy, 1997). Horizontal transfer through direct contact may be the most common mode of transfer. Louse loads correspond on mates, suggesting that when the mates come into direct contact, their lice are able to transfer from one body to the other and the loads become evenly split over time. (Potti and Merino, 1995). Common Cuckoos (*Cuculus canorus*) also support frequent transfer through direct contact. They are brood parasites, so their young have no contact with their parents. Although there is no direct contact between the two, there are multiple cuckoo-specific lice that seem to be acquired through direct body contact before the breeding season (de L Brooke, 1998; Lindholm et al., 1998). Direct contact, whether it is vertical or horizontal, is believed by most to be the main way lice find new hosts.

Horizontal transmission is not limited to direct contact. Additional non-vertical routes for louse transmission between birds of the same species include: dispersal of lice or eggs on detached feathers, shared dust baths or shared nest holes or stolen nest material (Johnson and Clayton, 2003; Whiteman and Parker, 2004b). If a louse does manage to get on a new host through one of these methods, competition among the lice already present on that host may limit the success of host-switching (Barker, 1994). While these methods are unlikely to be common, they may occasionally result in horizontal transfer of lice or even a host-switch.

Since lice are transferred mainly through direct contact, they should be confined to their host species. Valera et al. (2003) found that mites and *C. hemapterus* parasites were able to transfer between European bee-eaters (*Merops apiaster*) and Rock Pigeons (*Columba livia*) living in a mixed colony, whereas the lice species remained exclusively on their respective hosts. It is possible that the other two parasites were transferred via a vector that was unavailable to the lice. However, if the two species were coming into direct contact with each other, it is possible that lice were being transferred but were unable to survive on novel host species.

Horizontal transmission may be a more important dispersal route for amblycerans than ischnocerans (DeVaney et al., 1980, Whiteman and Parker, 2004b). Amblycerans may be more adept at transfer during brief periods of direct contact. This speed would allow them to make use of even a brief point of contact between two hosts. The amblyceran levels were similar between individual birds living in a polyandrous group, whereas the ischnoceran levels differed, suggesting a greater ease of transmission for amblycerans than ischnocerans (Whiteman and Parker, 2004b). However, this may only be true for polyandrous species that come into direct contact with their mates on a regular basis. Species that do not come into frequent direct contact may not share this characteristic and horizontal transfer of amblycerans among them may be no more common than in ischnocerans.

Phoresy on Hippoboscid Flies

The one relatively common event that may prevent cospeciation between some chewing lice and their hosts is phoresy on hippoboscid flies. Ischnocerans are able to attach to hippoboscid flies (Hippoboscidae)

and hitch rides between birds (Kierans, 1975). Amblycerans, on the other hand, are unable to attach to hippoboscid flies due to the shape of their mandibles (Marshall, 1981; Kierans, 1975). Ischnocerans are quite capable of attaching to hippoboscids; in fact, there is an account of 31 ischnocerans being found on a single fly (Marshall, 1981). *Brueelia* and *Sturnidoecus*, both ischnocerans, are the louse genera most often collected from flies (Kierans, 1975). In contrast, there has only been one record ever of an amblyceran on a hippoboscid fly (Kierans, 1975). The host-switching opportunity provided by phoresy may result in *Brueelia* and *Sturnidoecus* having fewer cospeciation events with their hosts than do amblyceran lice

There is no hippoboscid phoresy in the two chewing louse systems in which host-louse cospeciation has been demonstrated. Gopher and swiftlet lice (Amblycera) have cospeciated with their hosts, and this may be due to all of the factors that have been discussed that make lice ideal for cospeciation, and the lack of a vector that would enable host-switching (Hafner et al., 1994; Johnson, Williams, et al., 2002). If the lack of a vector, like the hippoboscid fly, results in cospeciation in lice, amblycerans should cospeciate. However, ischnocerans, with their well-documented ability to phorese on hippoboscid flies, should not cospeciate with their hosts.

Hippoboscid flies are generally considered to be generalist parasites similar to mosquitoes. However, Tella et al. (1998) found that hippoboscids can have high host-specificity, even in a mixed colony of birds. Hippoboscid fly and bird interactions are not extremely well-studied, so the host-specificity of the flies is not well known. It is possible that hippoboscid flies are only another form of horizontal transfer. If these flies are highly host-specific, they will only transfer attached lice to hosts of the same species. Although the more accepted view is that lice will be more likely to be transferred to a novel host (Kierans, 1975). Either way, phoresy on hippoboscid flies enables lice to be transferred to new host individuals without the need for direct contact between host individuals, which may increase the likelihood of host switching opportunities to some extent. Even if it is a rare occurrence for a louse to be transferred to a novel host and to be able to survive on it, the possibility is there. Over an evolutionary time span, it may even become likely.

Possible Cophylogenetic Patterns of Amblycerans and Ischnocerans

Current host-parasite associations can be explained by one of two overarching cophylogenetic histories. Association by descent is when associations have in the absence of host-switching (Banks and Paterson, 2005; Hoberg and Brooks, 1997). This association often results in cospeciation. Weckstein (2004) suggested that association by descent should be rare in bird lice because of factors such as host-switching, extinction, failure to speciate, or independent speciation of the parasite (Weckstein, 2004). Each of these factors can change the topology of the parasite tree and prevent congruence with the host tree.

The other overarching cophylogenetic history is association by colonization. Association by colonization occurs when host switching is the predominant explanation for the parasite's distribution (Banks and Paterson, 2005; Hoberg and Brooks, 1997). Generally when association by colonization is predominant, the host and parasite phylogenies will not be congruent. However, there is the extremely unlikely possibility that the parasites colonized each new host species as they speciated and therefore it appears as if the two have cospeciated (Banks and Paterson, 2005).

Amblycera: Myrsidea

Amblycerans are more likely to cospeciate with their hosts than ischnocerans are. They feed on the blood of their hosts, which may make them more virulent than ischnocerans (Marshall, 1981; Whiteman and Parker, 2004a; Brown et al. 1995; Clayton and Tompkins, 1994). They are also incapable of attaching to hippoboscid flies, which may result in them being more host specific than ischnocerans (Kierans, 1975). Increased virulence and the inability to easily transfer to a novel host increases the likelihood that these lice will cospeciate with their hosts.

However, phylogenetic congruence is imperfect or absent for most kinds of interactions because even a very low rate of horizontal transfer among host lineages over long periods of time would reduce or eliminate the pattern of cospeciation (Clark et al., 2000; Barker, 1991). Incongruence does not necessarily suggest host-switching, though (Banks and Paterson, 2005). A false incongruence could be caused by parasite lineage sorting events such as extinction, absence from founding population or sampling error (Paterson and Gray, 1997; Paterson et al., 2000). It is unlikely that the parasite and host tree will be perfectly congruent in this case, especially since the main mode of transfer for amblycerans seems to be horizontal. Over an evolutionary time scale, there will likely be opportunities for a host-switch to occur, thus preventing total congruence between the host and parasite tree.

Ischnocera: Brueelia

Brueelia are even less likely to cospeciate with their hosts. *Brueelia* feed on feathers and are frequently transferred among birds by hippoboscid flies (Marshal, 1981; Kierans, 1975). The relative non-virulence of *Brueelia* likely results in less cospeciation with their hosts. Despite this, approximately 90% of *Brueelia* species are believed to occur on only a single host species (Johnson, Williams, et al., 2002). However, strict cospeciation will only occur when opportunities for host-switching are absent (Barker, 1994). *Brueelia* phoresy on hippoboscids reduces the likelihood of much congruence between the parasite and host trees.

Cruickshank et al. (2001) suggested that ischnocerans should be host specific, and therefore should cospeciate. However, Johnson, Adams, and Clayton (2002) found that *Brueelia* do not appear to have cospeciated with their hosts. They found a general lack of phylogenetic congruence between *Brueelia* and their hosts, which they attributed to host switching events that might have occurred through hole-nests or by phoresy on hippoboscid flies (Johnson, Adams, and Clayton, 2002). Based on transmission ability and virulence, *Brueelia* should cospeciate with their hosts less frequently than *Myrsidea*.

Chapter 2: Comparative Phylogenetic Histories of Two Louse Genera Found on *Catharus* Thrushes and Other Birds

Abstract

I reconstructed phylogenies of *Brueelia* (Ischnocera) and *Myrsidea* (Amblycera) chewing lice from a variety of birds to determine the evolutionary history of the parasites with respect to their hosts. In particular I concentrated my sampling on chewing lice from *Catharus* thrushes, which are common migrant passerines of Eastern North America. If thrush-louse associations are species-specific and ancient, their phylogenies should be concordant, reflecting cospeciation. Alternatively, lice may have switched host species in recent evolutionary time, resulting in non-matching louse and thrush phylogenies. I collected lice from five species of North American thrushes, and additional Neotropical migrant species, captured or collected in Northeastern Illinois in the spring of 2006. I extracted DNA from the lice, amplified and then sequenced three genes: CO1, 12s (mitochondrial), and EF1α (nuclear). I reconstructed the louse phylogenies from these DNA sequences using maximum parsimony, maximum likelihood, and Bayesian methods. *Brueelia* do not appear to have speciated, much less cospeciated with their thrush hosts. *Myrsidea* show a greater degree of diversification than *Brueelia*, but also do not appear to have cospeciated with thrushes. The lack of differentiation and/or cospeciation suggests that host switching or failure to speciate is rampant in this system. The relationships between chewing lice and their hosts may be better explained by biogeography, habitat, or even barb-size correspondence.

Introduction

Chewing lice are prime candidates for cospeciation studies because they lack a free-living stage which makes these parasites completely dependent upon their host (Crompton, 1997). Specific adaptations such as dorsoventral flattening and hiding in the sheath of developing feathers during molting allow lice to survive the defenses of their hosts (Lehane, 2005; Tompkins and Clayton, 1999; Moyer, Gardiner and Clayton, 2002). The strong selective pressure to conform to the topology of the host body to avoid defenses limits the number of host species on which a louse can survive (Kethley and Johnson, 1975; Clayton et al., 2003). Lice are fit to live on their specific hosts, but not many other places.

Not only have lice adapted to living their entire lives on birds, but birds have responded with adaptations of their own to defend against these parasites. Preening is a bird's first line of defense (Marshall, 1981; Hart, 1997), and the bill shape is specifically adapted for removal of lice (Clayton et al., 2005; Moyer, Peterson, and Clayton, 2002). Other defenses include anting (Marshall, 1981), sun bathing (Moyer and Wagenbach, 1995; Blem and Blem, 1993), and dust bathing (Marshall, 1981). Also, sexual selection may cue potential mates to infestation levels and potential genetic resistance to louse infestations (Hilgarth and Wingfield, 1997; Read, 1988; Potti and Merino, 1995; Moller, 1988; Kose and Moller, 1999; Hamilton and Zuk, 1982; Clayton, 1991a). This highly specialized, coevolved system is an ideal arena for cospeciation between chewing lice and their hosts. Coevolution may lead to exclusivity and cospeciation, as it has between gophers and their chewing lice (Hafner et al., 1994).

Of the two suborders of lice present on birds: Ischnocera and Amblycera, amblycerans are more likely to cospeciate with their hosts. Ischnocerans, that eat only feathers, are seen as less virulent than amblycerans, which feed on blood (Marshall, 1981). The more virulent amblycerans may exert a stronger selection pressure on their host which would make them more likely to cospeciate with their hosts than ischnocerans. Lice of both suborders are generally transmitted through direct contact by parent-offspring interaction, sexual contact or predator-prey contact (Potti and Merino, 1995; Rozsa, 1993, Janovy, 1997; de L. Brooke et al., 1998; Lindholm et al., 1998). However, ischnoceran lice are also capable of being transmitted through phoresy on hippoboscid flies (Kierans, 1975; Marshall, 1981). The ability of ischnoceran lice to hitch a ride on hippoboscid flies may result in enough host switching or gene flow opportunities to prevent cospeciation. Amblyceran lice, on the other hand, are unable to attach to hippoboscids due to their mandible shape, and may therefore be more likely to cospeciate (Kierans, 1975; Marshall 1981). Many host-switches presumably end with death due to non-specific hosts, potential competitors, and few, if any, reproductive opportunities (Rozsa, 1993). However, a few studies have found high host specificity in louse flies (Kierans, 1975; Tella et al., 1998) suggesting that phoresy on flies might allow for a successful switch to a host of the same or similar species.

Based on transmission ability, ischnoceran lice seem to have greater opportunities for host switching and amblyceran lice, therefore, should be more likely to cospeciate. Although amblycerans are unable to attach to hippoboscid flies, they are generally thought to be less host-specific than ischnocerans (Whiteman and Parker, 2004a). They are possibly transferred through loose feathers or shared dust baths (Whiteman and Parker, 2004b). Lice may also be transferred through chance contact and amblycerans are much more likely to leave a dead host than are ischnocerans (Marshall 1981; Kierans 1975). However, lice are unable to survive for an extended period of time off a host (Rem and Zlotorzycka, 1981), so presumably most lice die when their host dies.

Decreased transmission ability of amblycerans is not the only factor that may contribute to them cospeciating with their hosts. The greater virulence of amblycerans may also make them more likely than ischnocerans to cospeciate. Amblyceran lice come into direct contact with the host's immune system through their blood meals, whereas ischnoceran lice are restricted to feeding on feathers, and therefore have no contact with the host's immune system (Marshall 1981; Crompton 1997; Moller and Rozsa, 2005). Amblyceran lice are known to induce an immune response in their hosts (Lehane 2005; Whiteman et al. 2005; Mumcuoglu et al. 1997) and it has been found that as the immune response increases against fleas, the number of host species parasitized decreases (Moller et al. 2005). This interaction has led many to believe that amblycerans are more virulent than ischnocerans (Whiteman and Parker, 2004a; Barbosa et al. 2002). However, this has been challenged by the negative effects ischnocerans cause by increasing the metabolic rate of their host through feather mass reduction (Booth et al. 1993; Hart 1997). Amblycerans are generally believed to be more virulent than

ischnocerans, but it is possible that in heavy infestations ischnocerans are just as virulent as amblycerans.

Although some louse groups are known to cospeciate with their hosts (Hafner et al., 1994; Paterson et al., 2000), other cophylogenetic patterns can occur. In ischnocerans, the general lack of virulence and frequent transfers through hippoboscid flies may result in the lice infesting many of the hosts in a particular region, regardless of the host's taxonomy. For example, *Austrophilopterus* (Ischnocera) lice, which are known to ride on hippoboscid flies, inhabit multiple species of *Ramphastos* toucans in a given geographic area (Weckstein, 2004). Biogeography, not cospeciation, is the major factor influencing speciation in these lice. The overarching factor that may limit successful host-switches between avian species in a particular area may be barb correspondence (Clayton et al., 2003; Tompkins and Clayton, 1999). Lice hide from preening bills in between feather barbs, so size correspondence with the space between barbs is important.

The louse genera *Myrsidea* (Amblycera) and *Brueelia* (Ischnocera) both infest New World Thrushes in the genus *Catharus*. Multiple data sets indicate that *Catharus* thrushes are a monophyletic group (Outlaw et al., 2003; Winker and Pruett, 2006). Therefore, I chose to use this monophyletic group of hosts to explore patterns of speciation with their chewing lice. I used phylogenies of *Brueelia* and *Myrsidea* to assess patterns of host specificity and their phylogenetic history with respect to the host's phylogenetic history. Based on *Brueelia*'s increased transmission abilities and lesser virulence I predicted that *Brueelia* would cospeciate less than *Myrsidea,* which are less able to transfer to a new host and more virulent due to contact with the host's immune system.

Methods

Mist-netting
Birds were captured in Shaw Woods at the Skokie River Nature Preserve in Lake Forest, IL (42º 15' 37.2" N, 87º 51' 34" W) as part of the Shaw Woods Avian Monitoring Project (SWAMP) (Gordon et al., 2002). Twelve standard mist nets (35mm mesh and 12 meters in length) were set up in brush-cleared lanes. The nets were open from 5 am to 10 am 27 days between May 1st and May 31st, 2006. Captured birds were removed from the nets and placed in cloth bags to be carried back to the banding station. The five focus species of my study, *Hylocichla mustelina*, *Catharus minimus*, *Catharus ustulatus*, *Catharus fuscescens*, and *Catharus guttatus*, were banded with standard bands from the U.S. Federal Bird Banding Laboratory, deloused, and then released. Following the procedure of Walther and Clayton (1997) and Clayton and Drown (2001), thrushes were dusted with pyrethrin flea powder (Hartz), which was then rubbed into their feathers for approximately 5 minutes. As the lice were killed, they fell off the bird onto a white piece of paper. They were then collected with a paint brush and placed in a vial of 95% ethanol and stored frozen at -20 ºC. The paper and brush were carefully kept clean to eliminate the possibility of cross-contamination between birds.

Delousing Salvaged Specimens
Window-killed thrushes, and other Neotropical migrant species, salvaged by the Field Museum of Natural History in spring, 2006 from the downtown Chicago area, were placed in ziplock bags for 5-10 minutes with a drop of ethyl acetate on a cotton ball to kill the lice. The specimen's feathers were then rigorously ruffled over a clean piece of white paper until no more lice fell off the bird. Then the lice were picked up with a paint brush and placed in a vial of 95% ethanol and stored frozen at -20 ºC.

Louse Specimens
Louse identifications were made using the Price et al. (2003) chewing lice checklist and the taxonomic descriptions cited within. DNA was amplified and sequenced for 39 *Brueelia* chewing lice. Lice included: 12 individuals from *Catharus* thrushes of 4 different species, and 26 other *Brueelia* and *Sturnidoecus* lice, from a range of host species (Table 1). *Sturnidoecus* was included because there is evidence that it is actually a *Brueelia* (Johnson, K. P., unpublished data). Outgroup (ischnocheran) taxa for the *Brueelia* phylogeny included *Paragoniocotes*, *Neopsittaconirmus*, and *Struthiolipeurus*. DNA from 34 *Myrsidea* chewing lice from 6 individual *Catharus* hosts was amplified and sequenced, and the other 28 lice were from a range of hosts (Table 2). Outgroup (amblyceran) taxa for the *Myrsidea* phylogeny included *Ricinus* and *Dennyus*.

Louse DNA extraction
Each louse to be extracted was placed in a clean dish of fresh ethanol under a dissection scope and the head was plucked from the body using a set of sterilized forceps. The head and body were then placed in a 0.5 mL tube which was left open until the ethanol dried. The genomic DNA was then extracted using the Qiagen Dneasy micro-kit following the manufacturer's protocols. All specimens were extracted, amplified and sequenced in the Pritzker Laboratory at the Field Museum of Natural History. The head and body of each specimen from each extraction was mounted on a slide and placed in the Field Museum's insect collection.

Amplification of Louse Genes
379-385 base pairs (bp) of the mitochondrial gene cytochrome oxidase I (COI) were amplified with primers L6625 and H7005 (Hafner et al. 1994) using the temperature protocols in Weckstein et al. (2004). 483 bp of 12s were amplified using primers 12sai and 12sbi (Simon et al., 1994). 347 bp of the nuclear elongation factor 1α (EF-1α) gene were amplified using primers EF1-For3 and EF1-Cho10 (Danforth and Ji, 1998) using the temperature protocols in Weckstein et al. (2004). Most PCR products were amplified using Taq Gold (AmpliTaq Gold; Perkin-Elmer Corporation, Foster City, CA) and Taq beads (Promega, Madison, WI) were used to amplify a few EF-1α sequences. PCR-products were purified with either Exonuclease and Shrimp Alkaline Phosphotase enzymatic reactions (United States Biochemical) or by cutting bands from a low melt agarose gel and digesting them with gelase (Epicentre Technologies, Madison, WI).

Sequencing of Louse Genes
I cycle sequenced 1µL of purified PCR product with 1µL ABI Big Dye kit (version 3.2, Applied Biosystems, Foster City, CA) and 1µLxµM primer, and ran these sequenced products on an ABI Prism 3730 automated DNA sequencer (Perkin-Elmer Applied Biosystems). Sequencher (version 4.5, Genecodes Co., Ann Arbor, MI) was used to reconcile and align double-stranded

Table 1: Voucher numbers, localities, host associations and host habitat and range information for all *Brueelia* louse specimens used in this study. Habitat and range information was taken from MacKinnon and Phillipp 1993; Dickinson et al., 1991; Morris and Hawkins, 1998; Erize et al., 2006; Ridgely and Gwynne, 1989; Fjeldsa and Krabbe, 1990; Howell and Webb, 1995; Sinclair and Ryan, 2003; Ridgely and Tudor, 1989; Evans Mac Yong, 2000; Lowther et al., 2001; Jones and Donovan, 1996; Moskoff, 1995; and Roth et al., 1996

Number	Louse species	Voucher number	Host Family	Host species	Locality	Habitat	Range
1	*Brueelia antiqua*	Bran.6.13.2006.1	Turdidae	*Catharus guttatus*	Illinois: Cook Co	forest and edge, understory	S U.S., Mexico to Canada
2	*Brueelia sp.*	Brsp.Cafu.6.13.2006.2	Turdidae	*Catharus fuscescens*	Bolivia: Chaco	second growth understory	N S. Am. to N U.S. and Canac
3	*Brueelia zeropunctata*	Brze.6.13.2006.3	Turdidae	*Catharus ustulatus*	Panama	old 2nd growth, above-ground forager	Mexico and N S. Am. to Cana
4	*Sturnidoecus sp.*	Brsp.Cafr.6.13.2006.4	Turdidae	*Catharus fuscator*	Panama	interior forest, understory	N S. Am.
5	*Brueelia sp.*	Brsp.Cami.6.13.2006.5	Turdidae	*Catharus minimus*	Illinois: Cook Co	second growth understory	S Am. to N Alaska, and N Car
6	*Brueelia sp.*	Brsp.Cafu.6.13.2006.6	Turdidae	*Catharus fuscescens*	Illinois: Cook Co	second growth understory	N S. Am. to N U.S. and Canac
7	*Brueelia zeropunctata*	Brze.6.13.2006.7	Turdidae	*Catharus ustulatus*	Illinois: Cook Co	old 2nd growth, above-ground forager	Mexico and N S. Am. to Canac
8	*Sturnodoecus sp.*	Stsp.Hymu.6.13.2006.8	Turdidae	*Hylocichla mustelina*	Illinois: Lake Co	forest and edge, understory	Middle Am., Mexico to Canad
9	*Brueelia sp.*	Brsp.Cafu.6.13.2006.9	Turdidae	*Catharus fuscescens*	Illinois: Lake Co	second growth understory	N S. Am. to N U.S. and Canac
10	*Brueelia zeropunctata*	Brze.6.13.2006.10	Turdidae	*Catharus ustulatus*	Illinois: Lake Co	old 2nd growth, above-ground forager	Mexico and N S. Am. to Canac
11	*Sturnodoecus sp.*	Stsp.Hymu.6.13.2006.11	Turdidae	*Hylocichla mustelina*	Illinois: Lake Co	forest and edge, understory	Middle Am., Mexico to Canad
12	*Brueelia sp.*	Brsp.Door.6.13.2006.13	Emberizidae	*Dolichonyx oryzivorous*	Illinois: Cook Co	marshes, tall grass	N. Am. to S S. Am.
13	*Brueelia sp.*	Brsp.Mege.6.27.2006.17	Emberizidae	*Melospiza georgiana*	Illinois: Cook Co	marshes, brushy fields	E US to C Mexico
14	*Brueelia anamariae*	Bana.6.27.2006.18	Troglodytidae	*Troglodytes aedon*	Illinois: Cook Co	scrubby woodland, open areas	N. Am. to S. Mexico
15	*Brueelia sp.*	Brsp.Zoal.6.27.2006.19	Emberizidae	*Zonotrichia albicollis*	Illinois: Cook Co	brush and woodland	N N. Am. to N Mexico
16	*Brueelia brunneinucha*	Brbr.6.27.2006.20	Mimidae	*Dumetella carolinensis*	Illinois: Cook Co	humid to semihumid evergreen	Panama to SE US
17	*Brueelia sp.*	Brsp.Zole.6.27.2006.21	Emberizidae	*Zonotrichia l. leucophrys*	Illinois: Cook Co	brush and woodland edge	C Mexico to NW N. Am.
18	*Brueelia sp.*	Brsp.Seau.6.27.2006.22	Parulidae	*Seiurus aurocapillus*	Illinois: Cook Co	scrubby woodland	N S. Am. to E N. Am.
19	*Brueelia dorsale*	Brdo.6.27.2006.24	Mimidae	*Toxostoma rufum*	Illinois: Cook Co	brushy scrub, woodland understory	SE US to E N. Am.
20	*Brueelia vulgata*	Brvu.6.27.2006.28	Emberizidae	*Junco hyemalis*	Illinois: Cook Co	arid to semiarid pine, grassy areas	N Mexico to N N. Am.
21	*Brueelia zeropunctata*	Brze.6.27.2006.29	Turdidae	*Catharus ustulatus*	Illinois: Cook Co	old 2nd growth, above-ground forager	Mexico and N S. Am to Canac
22	*Brueelia antiqua*	Bran.6.27.2006.30	Turdidae	*Catharus guttatus*	Illinois: Cook Co	forest and edge, understory	S U.S., Mexico to Canada
23	*Brueelia sp.*	Brsp.Cafu.6.27.2006.31	Turdidae	*Catharus fuscescens*	Illinois: Lake Co	second growth understory	N S. Am to N U.S. and Canad
24	*Brueelia sp.*	Brsp.Paele.7.14.1999.3	Paridae	*Parus elegans*	Philippines	forest edge or second growth	Philippines
25	*Brueelia sp.*	Brsp.Rhnig.7.14.1999.11	Dicruridae	*Rhipidura nigrocinnamomea*	Philippines	forest understory	Philippines
26	*Brueelia sp.*	Brsp.Sifro.7.14.1999.1	Sittidae	*Sitta frontalis*	Philippines	pine and evergreen forest	SE Asia, Philippines
27	*Brueelia sp.*	Brsp.Fihyp.7.14.1999.2	Muscicapidae	*Ficedula hyperythra*	Philippines	forest understory	SE Asia
28	*Brueelia laticeps*	Brlat.1.17.2000.14	Ramphastidae	*Andigena nigrirostris*	Peru	cloud forest, small thickets	Venezuela, Ecuador, Colombi
29	*Brueelia laticeps*	Brlat.1.17.2000.15	Ramphastidae	*Aulacorhynchus prasinus*	Peru	humid montane forest	C Mexico to N S. Am.
30	*Brueelia moriona*	Brmor.4.7.1999.8	Corvidae	*Cyanocorax morio*	Mexico	forest, semi-open areas	E Mexico to W Panama
31	*Brueelia sp.*	Brsp.Cahae.10.12.1999.9	Icteridae	*Cacicus haemorrhous*	South America	canopy woodlands	Guianas, Venezuela, Colombi
32	*Brueelia sp.*	Brsp.Pasub.2.3.1999.5	Cisticolidae	*Parisoma subcaeruleum*	Africa	Savanna, acacia thickets	SW Africa
33	*Brueelia sp.*	Brsp.Mecan.1.15.2000.12	Picidae	*Melanerpes candidus*	Brazil	open woods savanna	C South America
34	*Brueelia sp.*	Brsp.Camex.2.1.2000.8	Fringillidae	*Carpodacus mexicanus*	Utah	arid to semiarid, open areas	W North America to Mexico
35	*Brueelia sp.*	Brsp.Parnig.1.12.1999.11	Paridae	*Parus niger*	Africa	forest and broadleaf woodland	SE Africa
36	*Brueelia sp.*	Brsp.Pynig.1.12.1999.8	Pycnonotidae	*Pycnonotus nigricans*	Africa	arid savanna, riverine bush	SW Africa
37	*Brueelia sp.*	Brsp.Costr.7.14.1999.10	Campephagidae	*Coracina striata*	Philippines	forest canopy and second growth	SE Asia, Borneo, Philippines
38	*Brueelia sp.*	Brsp.Memon.10.5.1999.10	Capitonidae	*Megalaima monticola*	Borneo	forest and village fruit groves	N Borneo
39	*Brueelia sp.*	Brsp.Irpu.6.27.2006.23	Irenidae	*Irena puella*	Malaysia	tropical moist forest	SE Asia, Philippines
	Outgroup						
	Paragoniocotes sp	Pasp.Aras.AF348870	Psittacidae	*Aratinga astec*			
	Neopsittaconirmus circumfasciatus	N.circumfasciatus.AY314819	Psittacidae	*Platycercus elegans*			
	Struthiolipeurus nandu	A.nandu.AF545768	Rheidae	*Rhea americana*			

Table 2: Voucher numbers, localities, host associations and host habitat and range information for all *Myrsidea* louse specimens used in this study. Habitat and range information was taken from MacKinnon and Phillipps, 199 Dickinson et al., 1991; Morris and Hawkins, 1998; Erize et al., 2006; Ridgely and Gwynne, 1989; Fjeldsa and Krabbe, 1990; Howell and Webb, 1995; Sinclair and Ryan, 2003; Ridgely and Tudor, 1989; Evans Mack and Yong, Lowther et al., 2001; Jones and Donovan, 1996; and Roth et al., 1996

Number	Louse species	Voucher number	Host Family	Host species	Locality	Habitat	Winter or Resident Range
1	*Myrsidea pricei*	Mypr.6.14.2006.1	Turdidae	*Catharus guttatus*	Illinois: Cook Co	forest and edge, understory	S U.S., Mexico to Canada
2	*Myrsidea pricei*	Mypr.6.14.2006.2	Turdidae	*Catharus guttatus*	Illinois: Cook Co	forest and edge, understory	S U.S., Mexico to Canada
3	*Myrsidea simplex*	Mysi.6.14.2006.3	Turdidae	*Catharus fuscator*	Panama	interior forest, understory	N S. Am.
4	*Myrsidea sp.*	Mysp.Hymu.6.14.2006.4	Turdidae	*Hylocichla mustelina*	Illinois: Cook Co	forest and edge, understory	Middle Am., Mexico to Canada
5	*Myrsidea incerta*	Myin.6.14.2006.5	Turdidae	*Catharus ustulatus*	Illinois: Cook Co	old 2nd growth, above-ground forager	Mexico and N S. Am. to Canada
6	*Myrsidea sp.*	Mysp.Hymu.6.14.2006.6	Turdidae	*Hylocichla mustelina*	Illinois: Lake Co	forest and edge, understory	Middle Am., Mexico to Canada
7	*Myrsidea incerta*	Myin.6.14.2006.7	Turdidae	*Catharus ustulatus*	Illinois: Lake Co	old 2nd growth, above-ground forager	Mexico and N S. Am. to Canada
8	*Myrsidea incerta*	Myin.6.14.2006.8	Turdidae	*Catharus minimus*	Illinois: Lake Co	second growth understory	S Am. to N Alaska, and N Canada
9	*Myrsidea sp.*	Mysp.Seau.6.14.2006.10	Parulidae	*Seiurus aurocapillus*	Illinois: Cook Co	scrubby woodland	N S. Am. to E N. Am.
10	*Myrsidea ptilostomi*	Mypt.6.14.2006.12	Corvidae	*Ptilostomus afer*	Ghana	open savvana, short-grass	Middle of Africa
11	*Myrsidea sp.*	Mysp.Gybu.6.14.2006.13	Lybiidae	*Gymnobucco calvus*	Ghana	forest and secondary growth	W Africa
12	*Myrsidea minuscula*	Mymin.7.25.2005.9	Philepittidae	*Philepitta castanea*	Madagascar	evergreen humid forest, understory	Madagascar
13	*Myrsidea willardi*	Mywil.7.25.2005.10	Philepittidae	*Philepitta schlegeli*	Madagascar	humid evergreen forest, mid and canopy	Madagascar
14	*Myrsidea palmeri*	Mysp.Ancur.8.16.2005.5	Pycnonotidae	*Andropadus curvirostris*	Ghana	closed-canopy forest	W Africa
15	*Myrsidea olivacei*	Myoli.4.24.2006.6	Tyrannidae	*Mionectes olivaceus*	Panama	shady ravines with heavy thicket	Costa Rica to N Venezuela and S Peru
16	*Myrsidea chesseri*	Mysp.Crbar.8.16.2005.2	Pycnonotidae	*Criniger barbatus*	Ghana	understory and gallery forest	W Africa
17	*Myrsidea sp.*	Mysp.Rholi.4.24.2006.3	Tyrannidae	*Rhynchocyclus olivaceus*	Panama	lowland woodlands	C Panama to N Bolivia and Amazonia
18	*Myrsidea ledgeri*	Amsp.Phsoc.5.4.1999.6	Passeridae	*Philetairus socius*	South Africa	semi-arid savanna	South Africa
19	*Myrsidea sp.*	Mysp.Anvar.5.1.2006.4	Furnariidae	*Anabacerthia variegaticeps*	Panama	forest in lower highlands	S Mexico to N S. Am.
20	*Myrsidea fusca*	Myfus.4.26.2006.10	Thraupidae	*Ramphocelus passerinii*	Panama	shrubby areas, woodland borders	SE Mexico to W Panama
21	*Myrsidea laciniaesternata*	Mylac.4.19.1999.2	Thraupidae	*Habia sp.*	Mexico	evergreen and semideciduous forest	Mexico to Argentina and Colombia
22	*Myrsidea sp.*	Mysp.Eulan.5.1.2006.1	Thraupidae	*Euphonia laniirostris*	Panama	clearings, gardens, second growth	Costa Rica to Bolivia and Amazonia
23	*Myrsidea sp.*	Mysp.Tadow.4.26.2006.12	Thraupidae	*Tangara dowii*	Panama	forest and forest borders of highlands	Costa Rica and W Panama
24	*Myrsidea sp.*	Mysp.Chchr.5.1.2006.2	Thraupidae	*Chrysothlypis chrysomelas*	Panama	canopy and borders of humid forest	Costa Rica to E Panama
25	*Myrsidea sp.*	Mysp.Radim.4.24.2006.8	Thraupidae	*Ramphocelus dimidiatus*	Panama	scrub, clearings of lowlands	N S. Am.
26	*Myrsidea sp.*	Mysp.Cymor.2.8.1999.2	Corvidae	*Cyanocorax morio*	Mexico	humid to semiarid forest, sem-open areas	E Mexico to W Panama
27	*Myrsidea sp.*	Mysp.Thpun.4.24.2006.2	Thamnophilidae	*Thamnophilus punctatus*	Panama	lower growth, lowlands	Guatemala, Belize to Bolivia and S Brazil
28	*Myrsidea seminuda*	Mysem.5.1.2006.15	Thraupidae	*Thraupis palmarum*	Panama	shrubby areas, humid lowlands	S Honduras to Bolivia, Paraguay and S. Br
29	*Myrsidea sp.*	Mysp.Tugra.5.1.2006.14	Turdidae	*Turdus grayi*	Panama	woodland, clearings, arid regions	N Colombia, Mexico to Panama
30	*Myrsidea sp.*	Mysp.Pahom.4.24.2006.4	Cotingidae	*Pachyramphus homochrous*	Panama	canopy and borders, lowlands	C Panama to NW Venezuela and NW Peru
31	*Myrsidea eisentrauti*	Myeis.2.3.1999.6	Passeridae	*Sporopipes squamifrons*	South Africa	dry savanna, bushy desert fields	SW Africa
32	*Myrsidea masoni*	Mysp.Blcan.7.25.2005.7	Pycnonotidae	*Bleda canicapillus*	Ghana	understory and gallery forest	W Africa
33	*Myrsidea marksi*	Mysp.Phalb.8.16.2005.1	Pycnonotidae	*Phyllastrephus albigularis*	Ghana	understory and gallery forest	W Africa
34	*Myrsidea mccrackeni*	Mysp.Oxmad.8.16.2005.9	Sylviidae	*Oxylabes madagascariensis*	Madagascar	understory of humid evergreen forest	Madagascar
	Outgroup						
	Ricinus sp.	R.sp.C.parellinaAF385014	Cardinalidae	*Cyanocompsa parellina*			
	Dennyus hirundinis	D.hirundinisAF385013	Apodidae	*Apus apus*			

sequences for COI and EF1α. 12s gene sequences were aligned using Clustal X and then manually aligned with MacClade v4.05. All of the sequence data generated by this study have been submitted to Genbank (pending acceptance), and the 12s alignment was submitted to Treebase (pending acceptance).

Phylogenetic Analysis

Maximum parsimony heuristic searches were performed with 100 random addition sequence replicates (PAUP*, version 4.0b10; Swofford, 2002). Branch-swapping was by stepwise addition using TBR swapping algorithm. 1000 bootstrap replicates were performed with 10 random addition sequence replications.

I used the partition homogeneity test (ILD statistic, Farris et al. 1994, 1995) as implemented in PAUP* (version 4.0b10; Swofford 2002) to test for incongruence in the sequence data sets. For Brueelia we analyzed two data sets, one including only samples sequenced by me for COI, EF1α, and 12s, and another including COI and EF1α sequences from Johnson, Williams, et al. (2002). For the *Brueelia* data set including 12s, three different ILD tests were run, comparing all three genes, 12s to CO1 and 12s and C01 to EF1α. All parsimony uninformative characters were removed prior to the test.

I used Akaike Information Criterion in Modeltest 3.5 (Posada and Crandall 1998) to determine the best likelihood model for each data set. Maximum likelihood analyses were run using Garliv0.951 (Zwickl, 2006, unpublished Ph.D. dissertation; http://www.Zo.utexas.edu/faculty/antisense/Garli.html). I ran 5 independent runs and chose the best tree. 1000 bootstrap replicates were performed to assess statistical support for nodes in the likelihood tree.

Bayesian Inference analysis was performed using Mr. Bayes 3.1.1 (Ronquist and Huelsenbeck 2003). Mr. Modeltest (Nylander 2004) was used to determine the likelihood model for each of the seven data partitions. These partitions included 3 codon positions for each protein-coding gene and 1 partition for the non-coding 12s gene. We ran two analyses of 5,000,000 generations and 4 Markov chains with every 500th tree sampled. The first 500 trees were discarded as the burn-in and the consensus of the remaining trees was used. Neighbor-joining analyses were also performed on the *Brueelia* data set with a 16 parameter Log Det model to determine whether the complexity of the model of molecular evolution might affect the tree topology.

Biogeographic Analyses

MacClade (version 4.05; Maddison and Maddison, 1992) was used to map and reconstruct biogeographic distributions of the hosts onto the louse phylogenies. To test whether biogeography contained significant phylogenetic signal, I used Maddison and Slatkin's (1991) randomization procedure of 1,000 randomize biogeographic regions 1000 times on each of the louse phylogenies. These randomized character distributions were compared to the empirical character distributions mapped onto the *Brueelia* and *Myrsidea* louse trees to obtain a P-value for the test.

Results

Phylogenetic Analyses

Brueelia

Maximum parsimony, maximum likelihood and Bayesian analyses of the *Brueelia* data set with sequences from COI, EF1α, and 12s show that *Brueelia* from *Catharus* hosts are monophyletic. Clade 1 (Figure 1) is a well supported clade (Maximum parsimony (MP) = 100%, Maximum likelihood (ML) = 93%, and Bayesian posterior probability (B) = 100%) that includes all of the individuals from migratory *Catharus* hosts. Price et al. (2003) lists 3 species of *Brueelia* found on *Catharus* hosts. However, among the *Brueelia* that we sampled from *Catharus* species there is little to no genetic variation with only 0-0.55% uncorrected sequence divergence. These levels of nuclear and mitochondrial variation are consistent with all of these *Brueelia* collected from *Catharus* thrushes being a single biological species.

The well-supported clade 2 (Figure 1: MP, ML and B = 100%) includes a single louse from Slaty-backed Nightingale-thrush (*Catharus fuscator)*, a tropical resident *Catharus* thrush. This *Sturnidoecus* shows little genetic distinction from the *Sturnidoecus* species that inhabits Wood Thrush (*Hylocichla mustelina),* a close relative of *Catharus* (Winker and Rappole, 1988). These lice differ by only 0.28% uncorrected sequence divergence. Clade A (Figure 1) is dominated by lice from *Catharus* hosts. Two lice, from non-*Catharus* hosts come out between the *Catharus* clades. The louse, *Brueelia brunneinucha*, is from a Gray Catbird (*Dumetella carolinensis)* a Mimid that has similar habitat and range to the *Catharus* thrushes. The sister relationship of *B. brunneinucha* with *Brueelia* from migratory *Catharus* is not well supported by maximum parsimony (47%) or maximum likelihood (64%), but is well supported by Bayesian posterior probabilities (100%). These *Brueelia* differ by an average of 10.08% uncorrected sequence divergence. The other louse separating the two *Catharus* clades is from the Asian Fairy-bluebird (*Irena puella)*. This Asian species obviously does not share a range with any of the birds in the larger clade and yet this rather odd biogeographic placement is well-supported in Bayesian and maximum parsimony analyses (MP = 75% and B = 100%).

Clades 3 and 4 (Figure 1) also make up a larger, well-supported clade (MP, ML and B = 100%) with the lice from the Bobolink (*Dolichonyx oryzivorous)* and Brown Thrasher (*Toxostoma rufum).* Small birds such as sparrows and warblers dominate these clades. Clade 3 is very well supported by all analyses (MP, ML and B = 100%). It consists of a genetically indistinct *Brueelia* that is found on three different sparrow species, the White-crowned Sparrow (*Zonotrichia leucophrys leucophrys),* Dark-eyed Junco (*Junco hyemalis),* and White-throated Sparrow (*Zonotrichia albicollis)*. The uncorrected sequence divergence differs by an average of 0.19%. These three host species are closely related (Spicer and Dunipace, 2004) and they inhabit similar habitats and ranges, with the two sparrows being most similar. The *Brueelia* from the Swamp Sparrow (*Melospiza georgiana)* and the Ovenbird (*Seiurus aurocapillus)* make up clade 4, also strongly supported by all analyses (MP = 89%, ML = 95%, B = 100%). There are some genetic differences between these two lice, but not much, they likely constitute one species. The uncorrected sequence divergence of *Brueelia* from Swamp Sparrow and Ovenbird is only 0.69%. Clades 3 and 4 are well supported as sister clades (MP = 89%, ML = 95%, and B = 100%) and all share hosts with small body size,

Neotropical migration and some of the same habitat preferences. These have an average uncorrected sequence divergence differs of 6.67%.

I also analyzed a *Brueelia* data set that includes a number of additional taxa but only has DNA sequences from COI and EF1α (Figure 2) to help further elucidate some of the relationships among *Brueelia*. The *Catharus* louse clades appear as they did in Figure 1: two distinct clades, one of Brueelia inhabiting migratory *Catharus* and one for *Sturnidoecus* of the tropical *Catharus* together with the *Sturnidoecus* sp. from Wood Thrush. Clade 3 (Figure 2) includes a number of taxa present in Figure 1, plus 4 additional *Brueelia* from Asian hosts. *B. brunneinucha,* from the Gray Catbird, and the *Brueelia* from the Asian Fairy-bluebird (*Irena puella)* share similar relationships with the *Brueelia* of clade 1 as they did before, however now the *Brueelia* from the Asian Fairy-bluebird is joined by the well-supported clade (MP, ML and B = 100%) of genetically indistinct *Brueelia* from the four other Asian hosts. These four birds belong to four different families: Paridae, Dicruridae, Sittidae, and Muscicapidae. These four *Brueelia* have 0% uncorrected sequence divergence. This Asia clade is sister to the *Brueelia* from the Asian Fairy-bluebird (MP = 74%, ML = 96%, and B = 100%), however, the sister relationship of these 5 lice from Asian birds with respect to clade 3 is not strongly supported by maximum parsimony (49%) or maximum likelihood (55%) analyses, even though Bayesian posterior probabilities do support it (90%).

Brueelia from *Catharus* thrushes are monophyletic. Clade A (Figure 2) includes all lice from *Catharus* hosts, however, it also includes *Brueelia* from a number of non-*Catharus* hosts encompassing different sizes, biogeographies, and habitats. For example, the *Brueelia* from the *C. fuscator*, a tropical resident, is genetically indistinct (uncorrected sequence divergence differs by 0%) from the *Sturnidoecus* species from the Wood Thrush (clade 4). This clade is sister to clade 5 (Figure 2: MP, ML, and B = 100%), which includes 2 individual *B. laticeps* from the Black-billed Mountain-toucan (*Andigena nigrirostris)* and Emerald Toucanet (*Aulacorhynchus prasinus)*. Although there is strong support for clade 5, there is no support for this clade being sister to clade 4. Neither is there strong support for the placement of the *Brueelia* from the Mountain Barbet (*Megalaima monticola)* as sister to clades 4 and 5.

Clade 8 (Figure 2) consists of *Brueelia* from small Neotropical-nearctic migrants and White Woodpecker (*Melanerpes candidus)*. These relationships are similar to those shown in Figure 1. However, *Brueelia* of the House Finch (*Carpodacus mexicanus)* and the House Wren (*Troglodytes aedon)* have been added. *Brueelia anamariae*, from the House Wren, is well supported (MP = 94%, ML = 93%, and B = 99%) as sister to the rest of clade 7, and the uncorrected sequence divergence differs by an average of 3.75%. It is interesting to note that lice from the larger of these birds comprise clade 6, whereas the *Brueelia* from smaller-bodied birds comprise clade 7. The majority of the hosts in this clade are Neotropical-Nearctic migrants. However, a *Brueelia* from a Neotropical resident, the White Woodpecker, is basal to the rest of the group and this placement is fairly well supported (MP = 72%, ML = 94%, and B = 100%). Most of the hosts in this clade have similar habitat preferences and distributions, except for the White Woodpecker.

Two hosts that share similar habitat and range, as well as the same family, do not have closely related lice. *B. brunneinucha* from the Gray Catbird and *B. dorsale* from the Brown Thrasher come out in clades 3 and 9 respectively (Figure 2). These two *Brueelia* are only distantly related, which is surprising considering the close taxonomy and biogeography of their hosts.

In the maximum likelihood and Bayesian analyses the outgroups sometimes came out as sister to the louse from the Bar-bellied Cuckoo-shrike (*Coracina striata*).

Myrsidea

The phylogenetic analyses for *Myrsidea* shows relatively higher levels of genetic differentiation than that among taxa in the *Brueelia* tree (Figure 3). Clade 1 (MP = 100%, ML = 96%, and B = 100%) consists of three individuals of *Myrsidea incerta* collected from two different host species, Gray-cheeked Thrush (*Catharus minimus)* and Swainson's Thrush (*Catharus ustulatus).* Gray-cheeked and Swainson's Thrushes are not each other's closest relatives (Figure 4). Uncorrected sequence divergence between *M. incerta* differs by an average of 0.55%. Clade 2 (Figure 3: MP = 100%, ML = 98%, and B = 100%) is also of a single species, *Myrsidea pricei*, except these two individuals are from the same host species, the Hermit Thrush (*Catharus guttatus).* The uncorrected sequence divergence between these two individuals is 0.69%.

Clades 1 and 2 (Figure 3) are strongly supported. However, the placement of *Myrsidea* sp. from Ovenbird with respect to clades 1 and 2 is not strongly supported. *Myrsidea* from the One-colored Becard (*Pachyramphus homochrous)* is strongly supported as basal to clade 3 (MP = 73%, ML = 76%, and B = 100%), although this host is distantly related to the other hosts of clade 3 louse taxa. Furthermore, the One-colored Becard is a Neotropical resident and inhabits the canopy, whereas the other clade 3 hosts are most often found in the understory (uncorrected sequence divergence for the lice in clade 3 averaged 7.98%).

Unfortunately, we did not obtain *Myrsidea* from Veery (*Catharus fuscescens)*. There is no record of *Myrsidea* from Veery, so it is possible that this species does not have a *Myrsidea* louse (Price et al., 2003). The Myrsidea from the tropical *C. fuscator* is part of clade 6 (Figure 3) with a wide variety of *Myrsidea* from other hosts. None of these relationships are well- supported. However, the majority of hosts in this clade are from the Neotropics. Unlike the relationships that we see in the *Brueelia* tree, *Myrsidea* from the Black-headed Nightingale-thrush (*Catharus fuscator)* is not sister to the *Myrsidea* from Wood Thrush. The lice from Wood Thrush come out in the well-supported (MP = 100%, ML = 99%, and B = 100%) clade 4 (Figure 3) which is sister to the Crimson-backed Tanager (*Ramphocelus dimidiatus)*, a Central American Neotropical resident.

Biogeography seems to be an important factor in the phylogenetic relationships of these *Myrsidea*. Clade 7 (Figure 3) includes only hosts from the Neotropics, clade 9 includes two hosts from Madagascar, and clade 8 is mostly made up of hosts from Africa except for the Scaly-throated Foliage-gleaner (*Anabacerthia variegaticeps)* which is Neotropical.

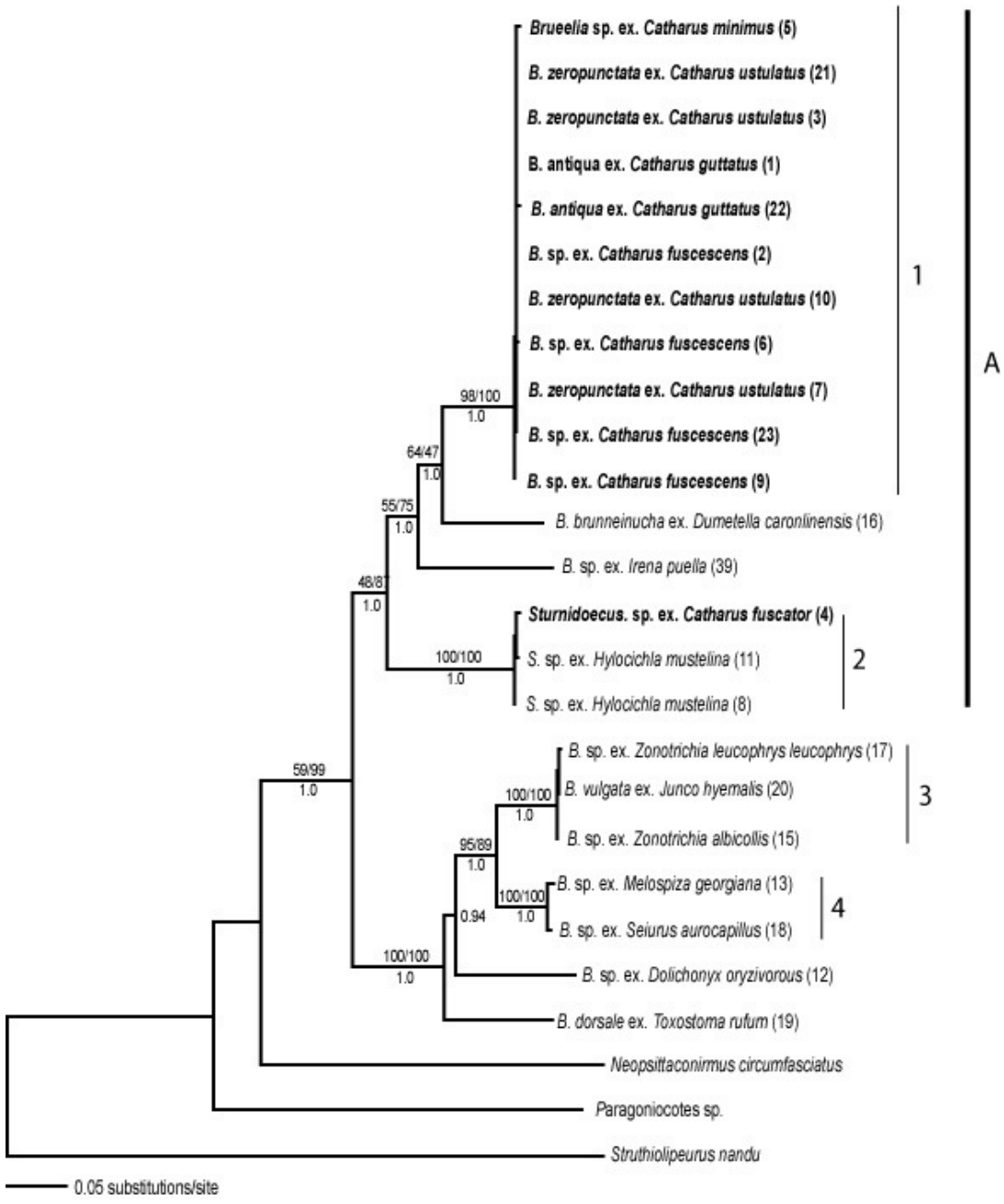

Figure 1: **Molecular phylogeny of the genus *Brueelia* based on 385 bp of CO1, 483 bp of 12s and 347 bp of EF1α.** Maximum likelihood values are above the node (<50% support of 1000 bootstrap replicates), maximum parsimony values are beside them (<50% 1000 bootstrap replicate support), and Bayesian posterior probabilities are below the node (consensus of 5,000,000 samples trees < 0.90). Bold taxa are parasites from *Catharus* hosts.

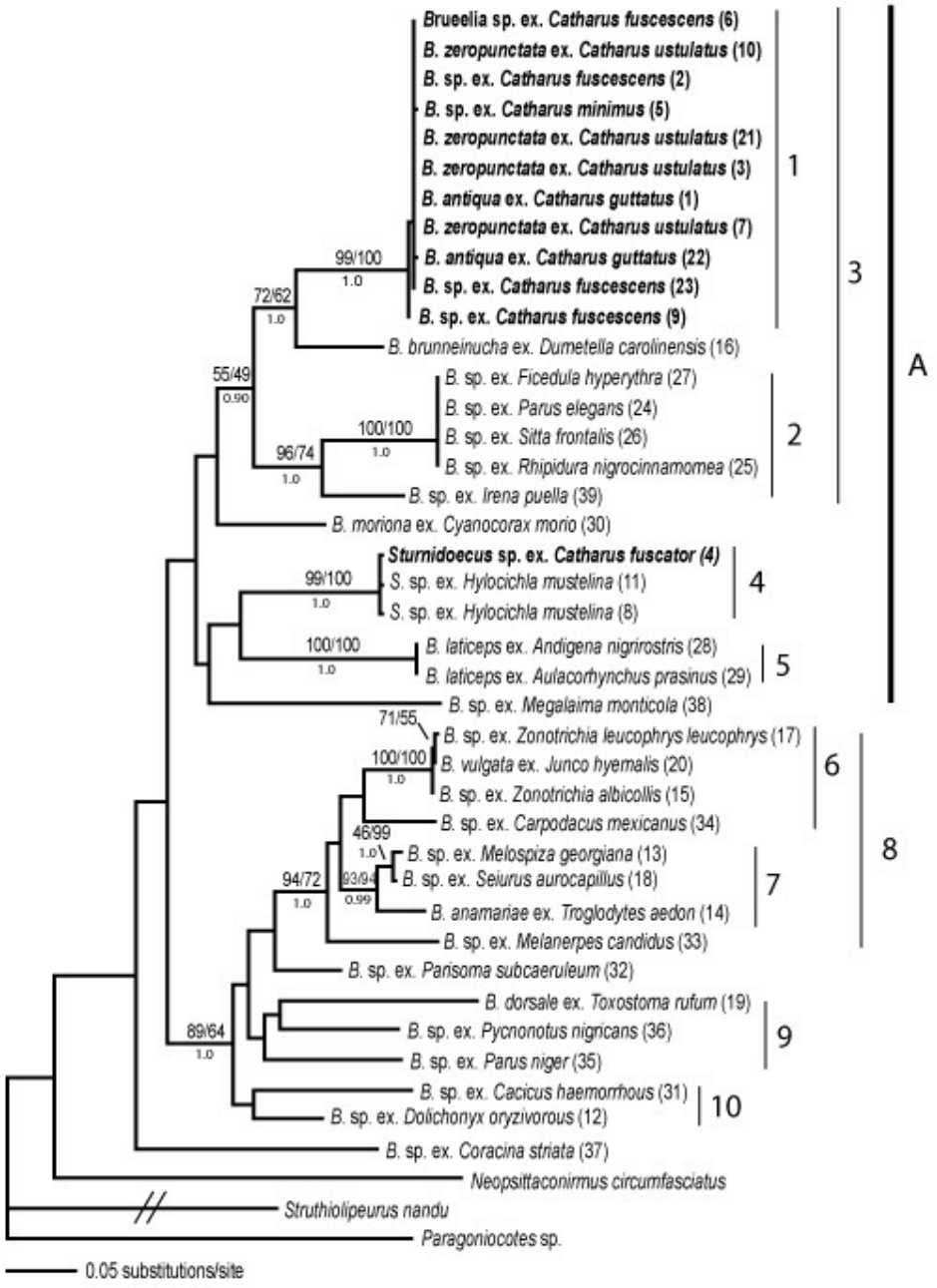

Figure 2: **Molecular phylogeny of the genus *Brueelia* based on 385 bp of CO1 and 347 bp of EF1α.** Maximum likelihood values are above the node (<50% support of 1000 bootstrap replicates), maximum parsimony values are beside them (<50% 1000 bootstrap replicate support), and Bayesian posterior probabilities are below the node (consensus of 5,000,000 samples trees < 0.90). The hash marks represent a shortening of the *Struthiolipeurus nandu* branch. Bold taxa are parasites from *Catharus* hosts.

Phylogenetic relationships within both louse groups are not congruent with the host thrush tree (Figure 4). If the trees were congruent, I would expect monophyletic groups of lice from Catharus thrushes, and I would expect the branching events of the parasite tree to mirror the branching events of the host tree. Instead, *Brueelia* from migratory *Catharus* thrushes form a genetically indistinct clade, whereas *Surnidoecus* from the tropical Slaty-backed Nightingale-thrush is indistinct from the sister group of *Catharus*, the Wood Thrush. *Myrsidea* from migratory *Catharus* form a number of distinct species; *Myrsidea incerta* and *Myrsidea pricei* have an average uncorrected sequence divergence of 6.86%. However, *Myrsidea incerta* is found on two distantly related *Catharus* thrushes. In the *Myrsidea* tree, lice from the Wood Thrush form a distinctly separate clade, but this clade (4: Figure 3), is not closely related to any of the lice from *Catharus* thrushes.

Geographic Analyses

Using the Maddison and Slatkin (Maddison and Maddison, 1992) test, I found that host biogeography mapped onto the louse topologies was significantly different than expected by random chance (*Brueelia* $P<0.001$, *Myrsidea* $P<0.000$). Therefore, biogeographic region has significant phylogenetic signal when mapped onto the *Brueelia* and *Myrsidea* phylogenies.

Discussion

Cospeciation

If *Brueelia* and *Myrsidea* were cospeciating with their *Catharus* thrush hosts, I would expect to see monophyletic groups of *Brueelia* and *Myrsidea* from *Catharus* and the parasite tree's branching events should mirror those of the host. However there is no genetic differentiation among *Brueelia* from *Catharus* hosts. The lice from migratory *Catharus* species all come out in an undifferentiated clade, which may suggest ongoing gene flow which causes the phenomenon of failure to speciate in parasites (Banks et al., 2006; Johnson, Williams, et al., 2002). Ischnoceran lice, in particular *Brueelia*, are able to attach to hippoboscid flies and hitch a ride to a new host (Kierans, 1975). This mode of dispersal may allow a single *Brueelia* species to move freely among individuals of all of the migratory *Catharus* species. Phoresis may also be the mechanism by which the tropical resident *C. fuscator* and migrant Wood Thrush share identical *Sturnidoecus*. *Sturnidoecus* is also well known for its phoretic relationship with hippoboscid flies (Kierans 1975). In this case, a North American Neotropical migrant might be picking up its *Sturnidoecus* louse from a tropical resident host. This is the first definitive demonstration of such a pattern for lice.

Myrsidea are unable to phorese on hippoboscid flies (Kierans, 1975). For the most part, *Myrsidea* differs from *Brueelia* in that distinct *Myrsidea* species inhabit the *Catharus* thrushes. However, these species do not match the phylogenetic history of *Catharus* thrushes. For example, Swainson's and Gray-cheeked thrushes, although not each other's closest relative (Winker and Pruett, 2006), share the same species of louse, *M. incerta*. These results suggest that *M. incerta* has failed to speciate on Swainson's and Gray-cheeked thrushes due to ongoing dispersal/gene flow between hosts. Swainson's and Gray-cheeked thrushes have overlapping wintering and breeding ranges, so dispersal between these hosts is possible. However, the mechanism by which they do this is unknown.

Neither is it known how the host-switch occurred between the *Myrsidea* from *Catharus* thrushes and the Ovenbird. The *Myrsidea* from Ovenbird comes out in the middle of the two *Myrsidea* species from *Catharus* thrushes. These hosts share similar habitat preferences and geographic distributions and therefore these hosts could potentially come into physical contact. The *Myrsidea* tree had longer branch lengths, which likely indicates less frequent host-switching. Since *Myrsidea* are unable to attach to hippoboscid flies, dispersal between species is less frequent.

Biogeography

Varying levels of host switching and gene flow, not cospeciation, may account for the patterns shown on the *Brueelia* and *Myrsidea* trees. Both trees show significant phylogenetic signal when biogeographic regions are mapped onto the louse phylogeny. There is some overlap in both the breeding range and the wintering range of the Neotropical migrant *Catharus* clade. This overlap may create enough opportunities for host-switching and gene flow to result in a single louse species infesting all of these hosts. The same is true for the sparrow and warbler lice clades (clades 6 and 7 in Figure 2) in the *Brueelia* tree and the Asian clade (clade 2 in Figure 2) that comes out between the two *Catharus* clades. However, if biogeography were the sole reason for the speciation patterns, the lice from Neotropical warblers and sparrows should be more closely related to lice from *Catharus*, and the Asian clade should not come out between the two *Catharus* clades. The two Mimidae species (Gray Catbird and Brown Thrasher) that share similar breeding and wintering ranges should also share a louse.

It is possible that the Wood Thrush picked up its *Sturnidoecus* louse when it was on its wintering grounds from the Neotropical residents there. Although other migrant *Catharus* species also inhabit the same wintering grounds as the Slaty-backed Nightingale-thrush. Why would the Wood Thrush pick up a tropical louse, while the other *Catharus* thrushes don't? It is possible that the Slaty-backed Nightingale-thrush and the Wood Thrush are close in size, whereas the other migratory *Catharus* thrushes are smaller, perhaps the Sturnidoecus louse is unable to hide from the preening bill on the migratory *Catharus* thrushes.

Biogeography explains the majority of the relationships in *Myrsidea*. All of the Myrsidea from Neotropical migrants sampled, except for the lice from the Wood Thrush, form a monophyletic clade. Also, the rest of the clades tend to exhibit a biogeographic pattern as well. This strong biogeographic signal suggests a more extensive taxon sampling is necessary in order to resolve these lice phylogenies.

Habitat

Louse speciation may be limited to hosts that occupy the same biogeographic regions and also use the same type of habitat. If two birds are in the same region but one is high up in the canopy of the forest and the other is in the understory, there may be less chance for lice to move from one host to another. Of the *Brueelia* from Neotropical migrants, the *Catharus* are more likely to be found in dense forest understory whereas a number of the sparrow migrants prefer grassy, open areas. This

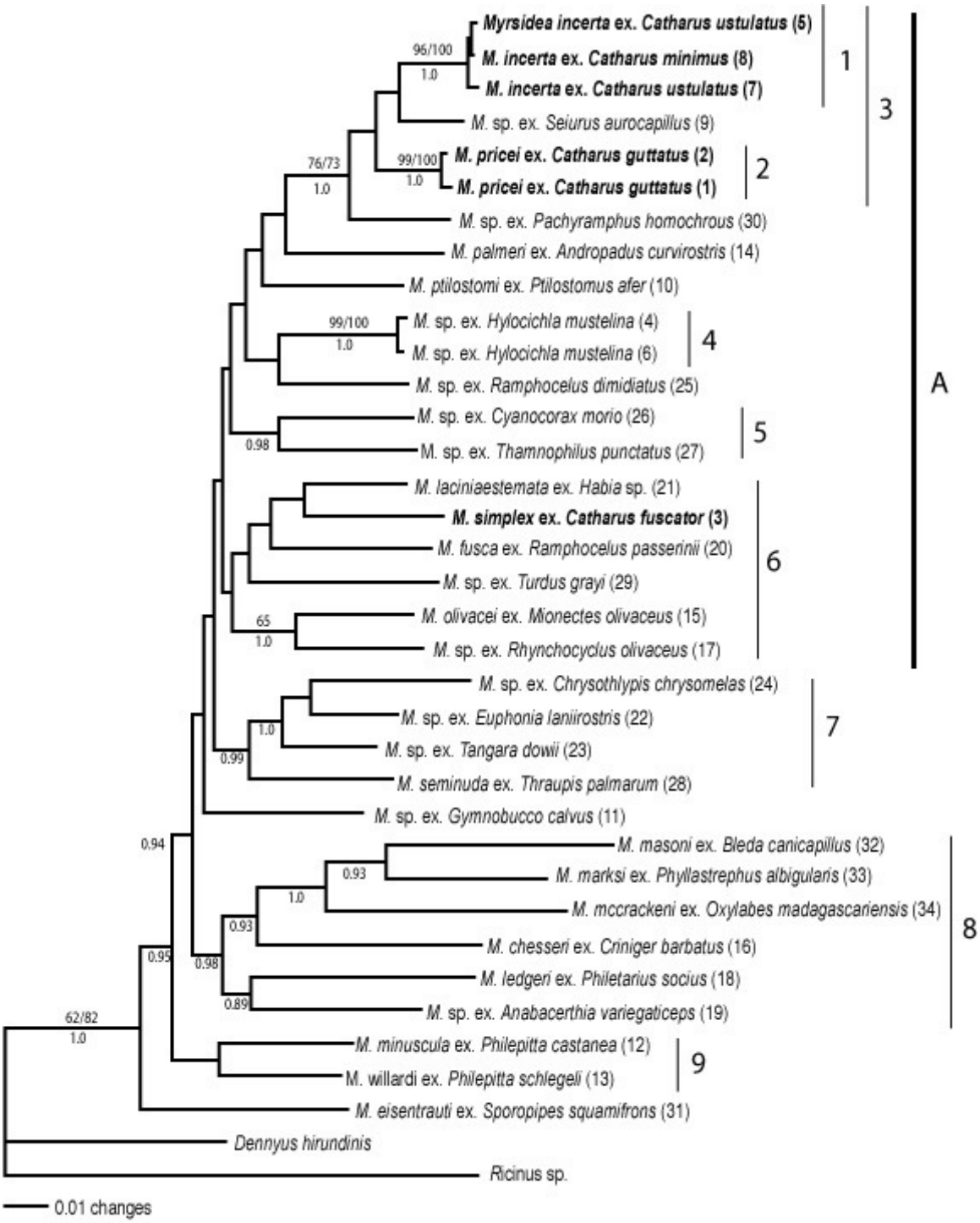

Figure 3: **Molecular phylogeny of the genus *Myrsidea* based on 379 bp of CO1 and 347 bp of EF1α.** Maximum likelihood values are above the node (<50% support of 1000 bootstrap replicates), maximum parsimony values are beside the maximum likelihood values (<50% 1000 bootstrap replicate support), and Bayesian posterior probabilities are at the below the node (consensus of 5,000,000 samples trees < 0.90). Bold taxa are lice from *Catharus* hosts.

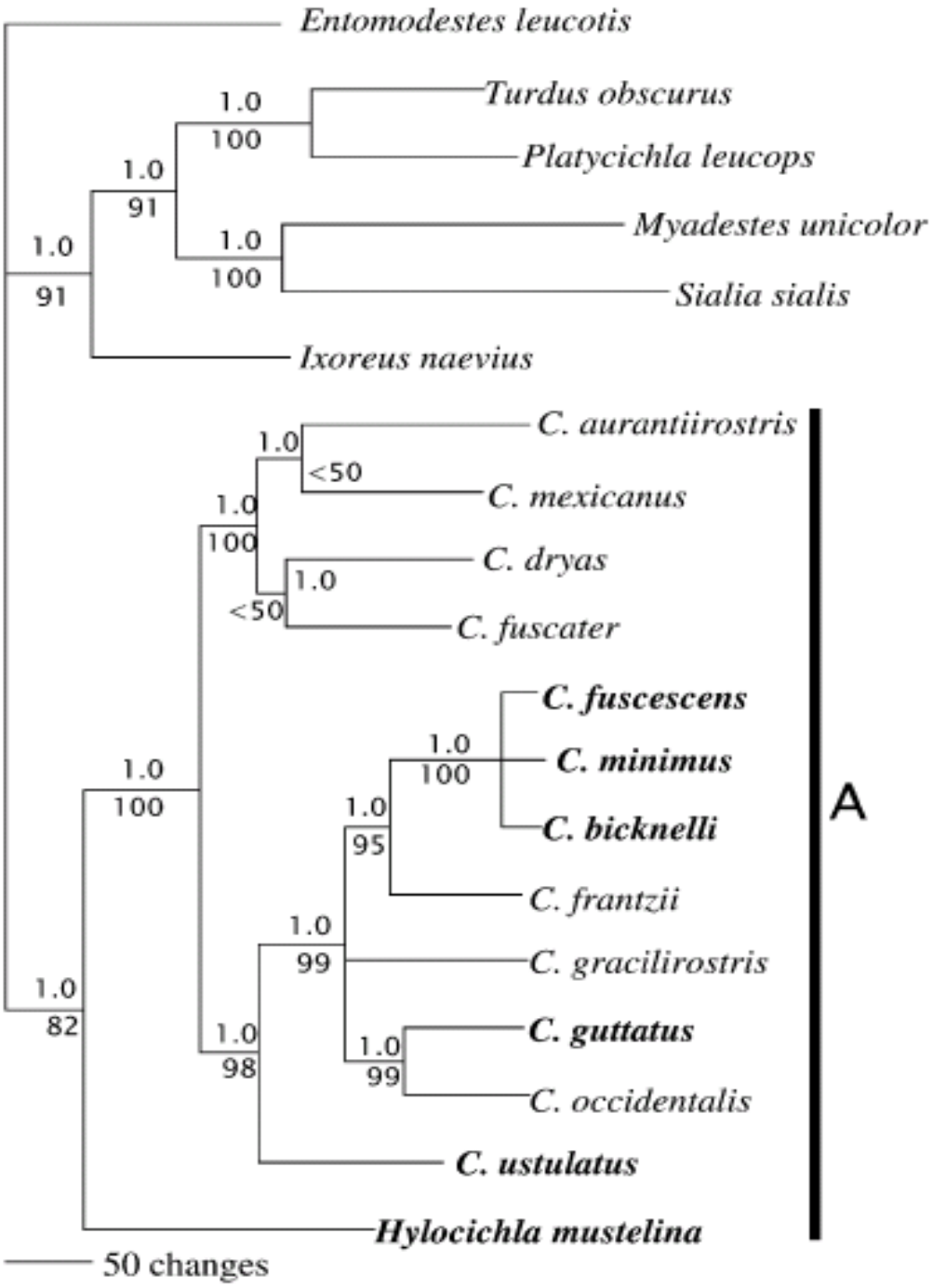

Figure 4: Phylogeny of the *Catharus* hosts from Winker and Pruett 2006, based on cytochrome *b* and ND2 genes and a ß-fibrinogen intron. The bold represents Neotropical migrants.

may explain why the lice from these two groups are only distantly related. Habitat may also explain the speciation pattern of the *Myrsidea* from Ovenbird. In the *Myrsidea* tree, the louse from Ovenbird is nested between the *Catharus* clades. However, this result might be confounded by the fact that there are no lice from sparrow species in the *Myrsidea* tree.

Habitat does not explain everything though, the *Brueelia* from the Ovenbird prefers the same type of habitat that the *Brueelia* from thrushes do and yet its louse is closely related to the sparrow lice, not the thrush lice. Considering that *Brueelia* are more easily transferred between hosts, it would suggest that *Brueelia* would match their host's habitat more closely than the less easily transferred *Myrsidea* would. It is possible that the *Brueelia* are being transferred to more hosts but they are unable to survive on the novel hosts, whereas the *Myrsidea* may be transferred less frequently but are more able to survive when they are transferred.

Host size

Biogeography and habitat may influence what hosts lice are able to get to, but one limiting factor of a successful host switch may be host size. Lice are adapted to the specific barb size of their hosts (Johnson et al., 2005; Tompkins and Clayton, 1999). Although larger hosts likely have larger barbs, it is not known if this is true for all birds. Lice may be able to transfer to a number of different hosts but are unable to hide from the host's defenses if the barbs of the new host are too big or small. Ultimately the determining factor of a successful host switch and therefore louse speciation may be host size.

Brueelia Paraphyly?

In the maximum likelihood and Bayesian analyses, the outgroups were coming out in the middle of the tree, sister to *B*. sp off of the Bar-bellied Cuckoo-shrike. I ran a neighbor-joining tree analysis and the outgroups did come out as an ingroup which supports long-branch length attraction as the explanation for why the outgroups get pulled in, because *B*. sp. off of the Bar-bellied Cuckoo-shrike has an especially long branch length. This is the Felsenstein concept. Over a long evolutionary time convergence tends to happen and with the long branch lengths, this can produce false affinity between long branches (Felsenstein, 1985). This concept may explain why the outgroups were appearing inside the ingroup.

Also, the model we used may not be complicated enough. Lice are AT rich (Simon et al., 1994) and we used the GTR model that assumes all changes are reversible with equal probabilities. It assumes that A to G and G to A are equally likely and occur at the same rate. When actually G to A is likely more frequent. Another explanation for the outgroups coming in is that *Brueelia* may not be monophyletic. It is possible that the group is paraphyletic and those outgroups belong there, however, the neighbor-joining analysis suggests that long-branch length attraction is the reason for the outgroups being pulled in.

The placement of the *Sturnidoecus* clade may also suggest that *Brueelia* is paraphyletic. *Sturnidoecus* comes out deep inside the *Brueelia* tree, as sister to *B. laticeps* from *Anigena nigrirostris* and *Aulacorhynchus prasinus* (clades 4 and 5, Fig. 2). However, this and unpublished data of Kevin P. Johnson's suggests a reclassification of *Sturnidoecus* may be necessary, and that *Sturnidoecus* should be considered a member of the genus *Brueelia*.

Conclusion

Neither *Brueelia* nor *Myrsidea* appear to have cospeciated with their *Catharus* hosts. For *Brueelia,* dispersal on Hippoboscid flies has led to a failure to speciate which resulted in a single species infesting all of the migratory *Catharus* thrushes. Although *Myrsidea* lice show greater genetic differentiation than do *Brueelia*, the phylogenetic relationships do not correspond with those of their hosts. In *Myrsidea,* the hosts seem to act like islands, allowing for the development of species. Host-switching events are likely not as common in *Myrsidea* as in *Brueelia*, but they do occasionally happen, which leads to unrelated hosts having closely related lice. It is also possible that the greater ease of transmission in *Brueelia* does not explain everything. Since *Myrsidea* interacts with the immune system, it is possible that they have fewer successful host transfers when they come into contact with a novel immune system (Moller and De Lope, 1999; Moller and Rozsa, 2005). Perhaps they are adapted to their host's immune system and are not generally able to survive a novel host's immune system. Although it is thought that lice are extremely likely to cospeciate with their hosts, this does not seem to be the case. Speciation patterns in lice seem more likely to correspond with their host's biogeography, habitat, or potentially, barb size. In the future more attention should be paid to these possible speciation patterns instead of just looking for cospeciation.

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