Tales of the Flying Earth: The effect of Host Flyways on the Phylogeny of Shorebird Lice (Phthiraptera: Ischnocera)

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The variation in biological communities leads to speciation, and there by evolution, which is the spice of life.

Lakshminarayana (1979)

To strive, to seek, to find, and not to yield.

Lord Tennyson (1842)

To my grandmothers, the great loves of my life

Dissertation abstract

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On the wings, bodies, and heads of most birds there are lice. These lice spend their whole lives on their host, with the exception of the few lice that get the opportunity to transfer from one host to another, typically when the hosts come into physical contact with each other. In shorebirds (Charadriiformes), such opportunities are unevenly distributed over the year. The hosts are spread out over vast areas in their Arctic breeding grounds during the Arctic summer, but form dense, multi-species flocks in the tropics and subtropics during the Arctic winter. During autumn and spring, when the hosts migrate between the Arctic to the tropics, they follow more or less well-defined routes, called flyways. In this thesis, the impact of this host migration pattern on the phylogeny of shorebird lice is evaluated. More specifically, two complementary hypotheses of pattern formation in the evolutionary history of shorebird lice, flyway homogenisation and flyway differentiation, are tested by phylogenetic reconstruction of the evolutionary history of two genera of lice (*Lunaceps* and *Carduiceps*) that parasitize the same group of sandpiper (Scolopacidae: Calidrinae) hosts. Flyway homogenisation is founded on the assumption that opportunities for lateral spread of lice between hosts of different species are prevalent in flyways, which will facilitate gene flow between louse populations on different host species, and prevent speciation of lice on host species that use the same stop-over points and wintering grounds. Over evolutionary time, this would cause a pattern of host species migrating along the same flyways having genetically similar or identical louse populations. Flyway differentiation is, conversely, the hypothesis that the division of a widely spread host species into discrete populations that each follow different flyways during migration will work as an isolating mechanism on the lice. If the generation time of the lice is significantly shorter than that of their hosts, this would result in a pattern where the same Holarctic-breeding host species is parasitized by genetically different louse populations in different parts of the world. Extrapolating from data published on other groups of lice, flyway homogenisation is expected to be more pronounced in wing lice (*Lunaceps*) than in body lice (*Carduiceps*) as these are topologically better placed on the host to take advantage of opportunities of lateral transfer to novel host species. Flyway differentiation is expected to be more pronounced in *Carduiceps* than in *Lunaceps*, as wing lice of vagrant hosts migrating along the “wrong” flyway would transfer to novel hosts more easily, and could prevent complete isolation between flyways. While no evidence is found in either genus for flyway differentiation, there is evidence for flyway homogenisation in *Lunaceps*, with three *Lunaceps* species occurring on multiple host species using the same flyways. Surprisingly, most *Carduiceps* collected across the world are genetically almost identical, and thus less isolated on their hosts than are *Lunaceps*. Both *Lunaceps* and *Carduiceps* show some partial evidence of a division between lice on New World hosts and those on Old World hosts. This division in echoed in a larger molecular study on the proposed louse family Rallicolidae, where several species group together according to host biogeography rather than host relationships, thus contradicting the so-called Fahrenholz’ rule that states that parasite phylogeny should come to mirror host phylogeny. In the same phylogeny, evidence is presented that the genus *Quadraceps*, widely distributed on most groups of shorebirds, is paraphyletic with regards to most other louse genera on shorebirds, and is in need of further study. Finally, the genus *Lunaceps* is revised morphologically. Six new species and one new subspecies are described, and all old species are re-described and illustrated, several for the first time. Five previously recognised species are placed as synonyms to other species, one species is transferred to the genus *Quadraceps*, one species is resurrected from synonymy, one species is considered a *nomen dubium* and three populations are placed as *incerta sedis*.

Keywords: **Phthiraptera, Lice, Ischnocera, Chewing lice, Charadriiformes, Shorebirds, Scolopacidae, Sandpipers, Flyways, Revision, *Lunaceps*, *Quadraceps*, *Carduiceps***

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Svensk sammanfattning

På vingarna, kroppen och huvudet på många fåglar finns det löss. Dessa löss tillbringar normalt hela sina liv på en och samma värdfågel, förutom de få löss som får tillfälle att förflytta sig till en annan värdindivid. Detta händer oftast bara då två fåglar kommer i fysisk kontakt med varandra. Hos vadarfåglar (Charadriiformes) är sådana tillfällen ojämt spridda över året. De häckar glest utspridda över stora områden kring Arktis under den nordliga sommaren, men bildar ofta stora täta flockar som kan innefatta flera olika fågelarter under övervintringen i tropikerna och subtropikerna under den nordliga vintern. Under vår och höst, när vadarfåglarna flyttar mellan Arktis och tropikerna, följer de speciella mer eller mindre väldefinierade flyttvägar, så kallade ”flyways” (flyttvägar).

I den här avhandlingen studeras till vilken grad dessa flyttmönster har påverkat fylogenin hos vadarfåglarnas löss. Mer specifikt undersöks två komplementära hypotetiska evolutionära mönster hos två släkten käklöss (*Lunaceps* och *Carduiceps*) som parasiterar samma grupp småvadare (Scolopacidae: Calidrinae) genom att rekonstruera deras respektive fylogenier.

”Flyway homogenisation” (”flyttvägslikriktning”) är en hypotes som baseras på antagandet att värdfåglarnas beteende under flyttning och övervintring ger tillräckligt med tillfällen för löss att sprida sig från en fågel till en annan för att tillåta genflöde mellan luspopulationer på olika värdarter. Detta medför att artbildning på de respektive värdarterna förhindras. Över evolutionär tid skulle detta ge ett mönster där värdarter som använder samma flyttvägar parasiteras av luspopulationer som är genetiskt väldigt lika eller identiska.

Hypotesen om ”flyway differentiation” (”flyttvägsåtskiljnad”) utgår däremot från att flera värdarter som häckar runt hela norra polcirkeln delas upp under flyttning och övervintring i flera diskreta flyttvägar, vilket antas fungera som en isolerande mekanism för deras respektive luspopulationer. Om lössens generationstid är väsentligt kortare än värdarnas resulterar det i ett mönster där samma värdart som häckar över hela Holarktis parasitiseras av genetiskt olika luspopulationer i olika delar av världen.

Baserat på data från andra lusgrupper antas flyttvägslikriktning vara mer tydligt hos vinglöss (i det här fallet *Lunaceps*) än hos kroppslöss (*Carduiceps*), eftersom de är bättre placerade, topologiskt, på värden för att kunna utnyttja tillfälliga fysiska kontakter mellan värdindivider, och därmed sprida sig till nya värdarter. Flyttvägsåtskiljnad förväntas vara mer uttryckt hos *Carduiceps* än hos *Lunaceps*, eftersom vinglöss på enstaka felflugna värdindivider som dyker upp i ”fel” flyttväg lättare skulle kunna sprida sig till nya värdar, och därmed förhindra total isolation mellan luspopulationer i olika delar av världen.

Inga belägg har framkommit för flyttvägsdifferentiering i någondera lussläkte, men belägg för åtminstone partiell flyttvägslikriktning påvisas hos *Lunaceps*, där tre olika arter återfinns hos mer än en värdart som flyttar längs samma flyttväg. De flesta *Carduiceps* över hela världen är överraskande nog i stort sett genetiskt identiska, och kan därmed sägas vara minder isolerade på deras respektive värdar än *Lunaceps* är.

För båda släktena finns belägg för en grundläggande uppdelning mellan löss från värdar som häckar i Gamla världen och de som häckar i Nya världen. Samma uppdelning återfinns i en större fylogeni över den tidigare föreslagna familjen Rallicolidae, i vilken flera arter grupperar sig efter värdarnas geografiska utbredning snarare än efter dessas inbördes släktskap. Detta motsäger den s.k. Fakrenholzska regeln, enligt vilken parasiters fylogeni är en spegelbild av värdarnas.

I samma stora fylogeni presenteras belägg för att lussläktet *Quadraceps*, som är vitt spridd på de flesta vadarfågelgrupper, är parafyletiskt med avseende på de flesta andra lussläkten på vadarfåglar. Hela Rallicolidae är i behov av mer arbete.

Slutligen revideras släktet *Lunaceps* morfologiskt. Sex nya arter och en underart beskrivs, och all gamla arter ombeskrivs och illustreras, vissa för första gången. Fem arter som tidigare accepterades som goda arter sänks till synonymer av andra arter, en art förflyttas till släktet *Quadraceps*, en återhämtas från en tidigare synonymisering, ett namn bedöms vara ett *nomen dubium* och tre populationer placeras som *incerta sedis*.

List of papers

This thesis is based on the following papers, which will be referred to in the introduction by their Roman numerals:

I. Flyway homogenisation or differentiation? Insights from the phylogeny of the sandpiper (Charadriiformes: Scolopacidae: Calidrinae) wing louse genus *Lunaceps* (Phthiraptera: Ischnocera).
International Journal for Parasitology 42 (2012), 93-102

II. The "Very Thankless Task": Revision of *Lunaceps* Clay and Meinertzhagen, 1939 (Phthiraptera, Ischnocera, Philopteridae), with description of six new species and one new subspecies[1]
Accepted by Zootaxa

III. Unexpected host distribution patterns of *Carduiceps* feather lice (Phthiraptera: Ischnocera): shorebird lice are not like dove lice
Submitted to Systematic Entomology

IV. Molecular phylogeny of the "Quadraceptinae" *sensu* Eichler (1963) (Phthiraptera: Ischnocera) with an assessment of the generic circumscription of the genus *Quadraceps* – zero, four, or 400 species?
Manuscript

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[1] Species descriptions in this thesis are not issued for permanent scientific record or purposes of zoological nomenclature, and are not regarded as published within the meaning of the International Code for Zoological Nomenclature (ICZN), Ed. 4, Article 8.2 and 8.3 (Anonymous, 2012).

It is doubtful if there is any species of bird in the world which is without at least one kind of feather louse. This pained the early entomologists, one of whom remarked that "even the gorgeous peacock is infested by one of extraordinary dimensions and singular form"; and Benjamin Franklin ruefully laments the choice of the bald eagle as the emblem of America: "as he is generally poor and often very lousy".

M. Rothschild and T. Clay, 1952

1. Introduction

Birds are fascinating animals, but even more fascinating than birds are the multitudes of parasites that live in or on their bodies. These parasites span several phyla of metazoa, and several orders of Arthropods, including various trematodes, cestodes and nematodes, several groups of ticks and mites (Acari), fleas (Siphonaptera) and parasitic flies (Hippoboscidae), as well as true lice (Phthiraptera), of which two suborders, the Amblycera and the Ischnocera (see more below), parasitize birds.

The Phthiraptera stands apart from most other parasites, in that, with a few notable exceptions, they entirely lack a free-living dispersal stage during which they can spread to new host individuals. While the Amblycera may sometimes leave dead hosts, and could at least theoretically spread to new hosts this way[2], the Ischnocera are more limited to their host, and typically die with it, being unable to survive long outside the host. A number of extinct lice, previously being hosted by now extinct birds, are known (Stork and Lyal, 1993; Mey, 1990, 2005), and the main focus of two of the four papers included in this thesis, the genus *Lunaceps*, may contain a further two, as well as at least one that may become extinct within the next 100 years (see Paper II).

Typically, the only opportunities for lice to leave one host and disperse to another are during the host's mating (Hillgarth, 1996) and in the host's nest, when migration between parents and chicks is possible (Clayton and Tompkins, 1994; Brooke, 2010). However, there are many important exceptions to this (see below).

This dependency on the host also extends to their choice of food. Essentially, lice are limited to what is on offer on their host, and a variety of strategies have evolved. Most commonly, lice will either scrape off and eat parts of the feathers (the Ischnocera) or eat skin flakes and drink blood (the Amblycera) (Crutchfield and Hixson, (1943). However, some groups have more specialized feeding

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[2] Bird banders sometimes come in contact with the Amblycera when they run down their hands. In my experience from the material collected during this thesis, this seems to be especially common in *Menacanthus* lice on swallows and martins (Passeriformes: Hirundinidae), for reasons unknown to me.

methods, such as the quill-inhabiting *Actornithophilus* (on shorebirds, Charadriiformes; Clay, 1962a; Price and Leibovitz, 1969) and *Somaphantus* (on wildfowl, Galliformes; Emerson, 1958), and the *Piagetiella* that live inside the throat pouches of pelicans and cormorants (Pelecaniformes; Eichler, 1950a; Price, 1970). Water is taken from the air with a special water-vapour uptake system (Rudolph, 1983).

Lice are distributed across all bird orders, with no species of bird being known to lack lice entirely. While some species of birds (*e.g.*, divers, Gaviiformes, and ostriches, Struthioniformes) are parasitized by only a single species of louse, others (notably tinamous, Tinamiformes, and wildfowl, Galliformes) may be hosts to ten species or more, with the record being the Little Tinamou *Crypturellus soui* with 23 known species in 11 genera (Price *et al.*, 2003a). More typically, a single bird species is parasitized by 3-5 species of lice.

However, not all individual birds are parasitized by all species of lice known from that species (see *e.g.*, Geist, 1935; Keirans, 1967; Clayton *et al.*, 1992). Typically, an individual of a bird species with five known species of lice is parasitized by one to three, but it is also very common, especially in songbirds (Passeriformes) for a host to have no lice at all (Gustafsson and Olsson, *in prep.*). As the tinamous have the greatest diversity of lice in general, it should come as no surprise that the largest number of louse species collected from the same host individual (9) is from a tinamou (Ward, 1957). Similarly, a bird infested with lice may have anywhere from one louse individual into the ten-thousands, in a domestic pigeon *Columba livia domestica* (*e.g.*, Ash, 1960; see Fig. 1).

Host specificity also varies between louse groups. Some louse genera are specific to a single bird order or family, whereas others can be found on several, with the record being the genus *Colpocephalum*, which can be found on 11 orders of bird. On the species level, some louse species are specific to a single host subspecies (such as some tinamou lice), whereas others are widely distributed on a number of hosts from different families. The most widely spread lice include *Menacanthus eurysternus* with 176 hosts from two different host orders, *Anatoecus dentatus* with 67, and *Laemobothrion maximum* with 50 (all data from Price *et al.*, 2003a)[3].

This thesis focuses on lice of shorebirds (Charadriiformes; Fig. 2).

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[3] Many of the louse species with wide host distributions have previously been divided into several species with narrower host distributions. Subsequent synonymisation of similar species had lead to some louse species having large host distributions. These synonymisations have sometimes included species which are poorly described, but which may have been recognisable as separate species if they had been described properly. Therefore, all these host attributions may change when these species are studied molecularly, and the presently accepted host distributions of a purportedly homogeneous species are tested with molecular data.

Fig. 1. Lice collected from the chest of a Great Cormorant *Phalacrocorax carbo* at Ottenby Bird Observatory, Sweden. The sample represents the amount of lice collected from the surface of the bird's body, over the area of the cotton bud (ca. 4x4 cm), by pressing the ethyl acetate drenched cotton bud onto the plumage of the bird, and then remove it. Some lice have been dislodged from the cotton bud to show the great amount of lice obtained from this small area. The total amount of lice on the bird was not counted.

Fig. 2. Small flock of mixed shorebirds (Charadriiformes) at wintering grounds, 80 Mile Beach, Australia. This flock includes Greater Sand Plover *Charadrius leschenaultii*, Lesser Sand Plover *Charadrius mongolus*, Oriental Plover *Charadrius veredus*, Red-capped Plover *Charadrius ruficapillus*, Terek Sandpiper *Xenus cinereus*, Curlew Sandpiper *Calidris ferruginea*, Red-necked Stint *Calidris ruficollis*, Little Tern *Sternula albifrons* (in the background).

When Giebel stated that his *Nirmus angulicollis*, from a petrel, found its nearest ally in *N. fenestratus* of the cuckoo, he wrote mischievous rubbish.
L. Harrison, 1916

2. Morphology and classification of the Phthiraptera

Despite being highly specialized for their parasitic lifestyle, lice are unmistakably insects. Three main body parts can be recognised: the head with eyes, antennae, and mouth; the thorax where the legs attach; and the abdomen, where the intestines and the genital elements lie (see Figs. 2-5). However, unlike free-living insects, they lack wings, and both the eyes and the antennae are often very small. For thorough introductions to louse morphology, see Clay (1951a) and Smith (2001).

From the anterior margin of the head to the posterior margin of the abdomen, lice are covered with bristles or setae. The number, distribution, and morphology [see Smith (2000) for setal types] of these are often very useful in determining species identity. Similarly, the shape and extent of tergites, sternites and pleurites on the abdomen, and the various thickenings (carinae) and weakenings (sutures) of the head are commonly important for identification to genus or species level.

Lice vary in size, from less than a millimetre (in the wildfowl louse genus *Goniocotes*; see *e.g.*, Ansari, 1955a; Lonc *et al.*, 1992) to over a centimetre (in the bird of prey louse *Laemobothrion*; see Nelson and Price, 1965) (Rothschild and Clay, 1952), and females are generally larger than males (Tryjanowski *et al.*, 2007). While most lice are brown-beige-yellow, there are some instances where the colour of the louse matches that of its host, such as the white *Quadraceps* species of terns and gulls (Timmermann, 1949). It has been suggested (Eichler, 1948; Rothschild and Clay, 1952) that this has to do with camouflage to escape host preening.

2.1 Classification of the Phthiraptera

The true lice are divided into four suborders[4] (Fig. 7), of which only two can be found on birds. The Anoplura are blood-sucking lice endemic to mammals, and include both the Human Head Louse, *Pediculus humanus*, and the Crab

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[4] A taxonomic term that occurs frequently throughout the louse literature is “Mallophaga”, a group that traditionally contained the suborders Ischnocera, Amblycera, and Rhynchophthirina, excluding the sucking lice Anoplura. This grouping is paraphyletic and artificial, and is therefore not widely used today. Nevertheless, the image that these three suborders group together is persuasive, and the most recent checklist of chewing lice (Price *et al.*, 2003a) excludes the Anoplura.

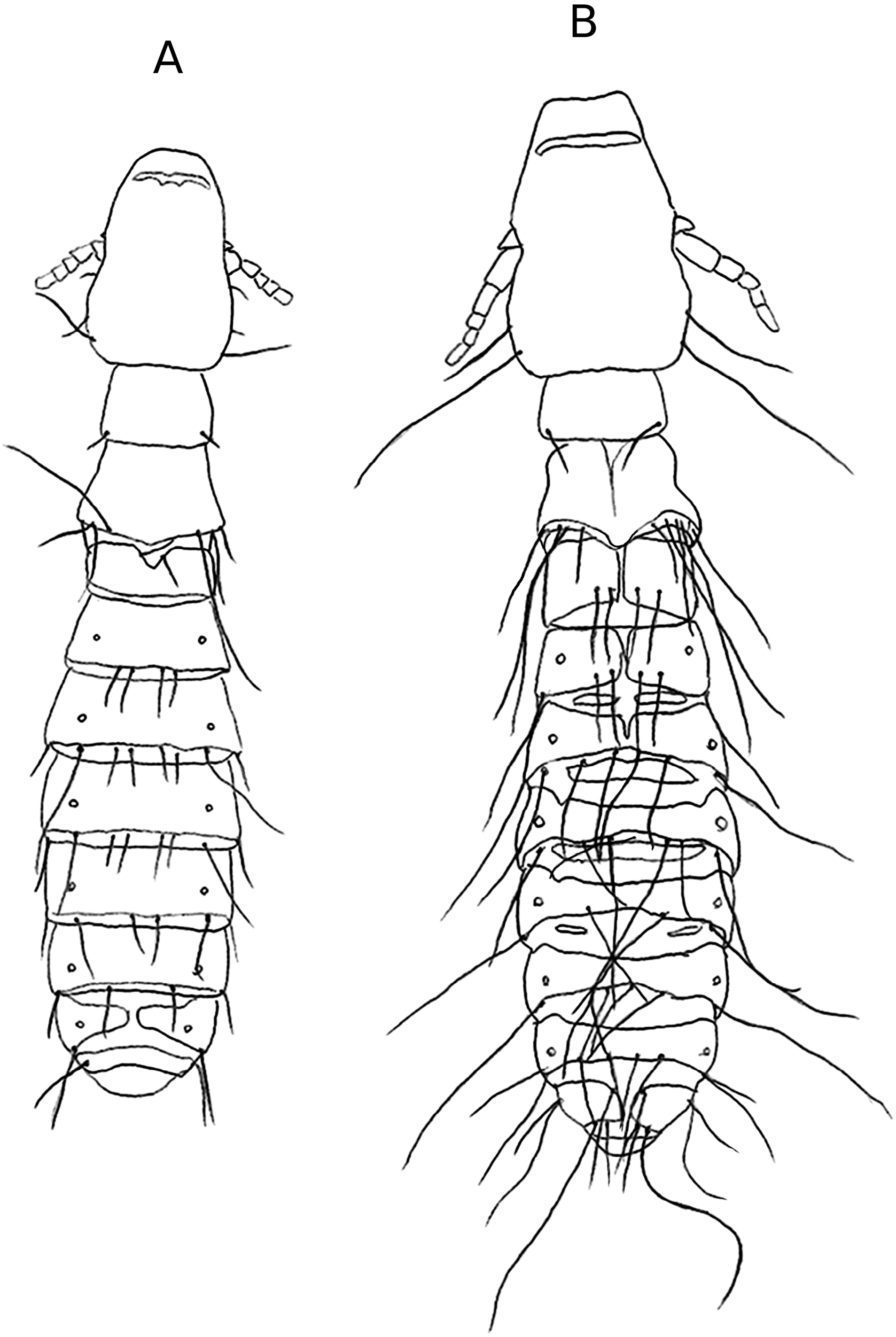

Fig. 3. Outlines of A) *Lunaceps drosti ex Calidris canutus canutus* and B) *Rhynonirmus scolopacis ex Gallinago Gallinago*. Both drawings are of male specimens. Legs and small setae, as well as all internal details, have been removed for clarity. Note the superficial similarity of the preantennal area. These two genera are the only ones parasitic on shorebirds that include species with a transverse preantennal suture. However, as can be seen in Paper IV, they are not closely related, with *Lunaceps* being nested within the great *Quadraceps*-clade, and *Rhynonirmus* being placed together with *Degeeriella*. Eichler (1963) placed *Lunaceps* in Rallicolidae and *Rhynonirmus* in Lipeuridae.

Louse, *Pthirius pubis*. Closely related to this group (*e.g*., Johnson *et al*., 2004) are the Rhynchophthirina, found on elephants and some African pigs. More distantly, and sister to them both, are the Ischnocera, which includes the by far greatest radiation of lice, with approximately 2700 of the 4500 known lice (Price *et al*., 2003a), found mainly on birds, but the family Trichodectidae also on mammals. Lastly, there is the suborder Amblycera, which is also distributed across the two host classes (Aves and Mammalia). This thesis will focus almost exclusively on the Ischnocera.

The Ischnocera are common to all groups of birds, and in most cases, a single species of bird will host more than one species from more than one genus, beside one or more Amblycera (Price *et al*., 2003a). While not the rule, it is not uncommon to find more than one species of louse on a single host individual. Perhaps because of this, there has been a trend over evolutionary history for different lineages of lice coexisting on the same host species to diversify into specializing on different niches on the hosts, and even relatively closely related lice can look quite different.

These various niches are typically correlated with a specific set of feathers on the bird, which are often supposed to have been largely constant over evolutionary time. Perhaps for this reason, distantly related groups of lice living in the same niche on different groups of bird have come to resemble each other greatly. This has lead to a wide-spread taxonomic and systematic confusion that has only recently, with the advent of molecular and analytical methods, started to become clearer, only to reveal a whole new layer of intricate puzzles.

These "niche-determined" morphological forms have no formal taxonomic significance, and each contain several distantly related genera of lice. Despite this, they are often useful for discussion on distribution patterns, and have been given informal names that are used commonly throughout the Phthirapteran literature. The most commonly recognized forms of Ischnoceran lice are (Clay, 1949a; Rothschild and Clay, 1952):

The "wing louse" type is elongated with narrow head and abdomen. This slenderness allows them to escape preening by inserting themselves between the barbs of the feathers, or sometimes along the rachis. Representatives of the wing louse type include *Brueelia* (on songbirds), *Anaticola* (on ducks and allies, Anseriformes), and, most importantly for this thesis, *Lunaceps* (on sandpipers, curlews and godwits, Charadriiformes: Scolopacidae) and some *Quadraceps* (most shorebirds) (Fig. 3, 4).

The "head louse" type is characterized by a wide, often roughly triangular head and a stout, often almost circular, abdomen. These lice avoid being detached by the host by sitting on the head, which is inaccessible to the host's beak. Genera such as *Philopterus* (on songbirds, Passeriformes) and *Saemundssonia* (primarily on shorebirds, Charadriiformes) belong in this group (Fig. 5).

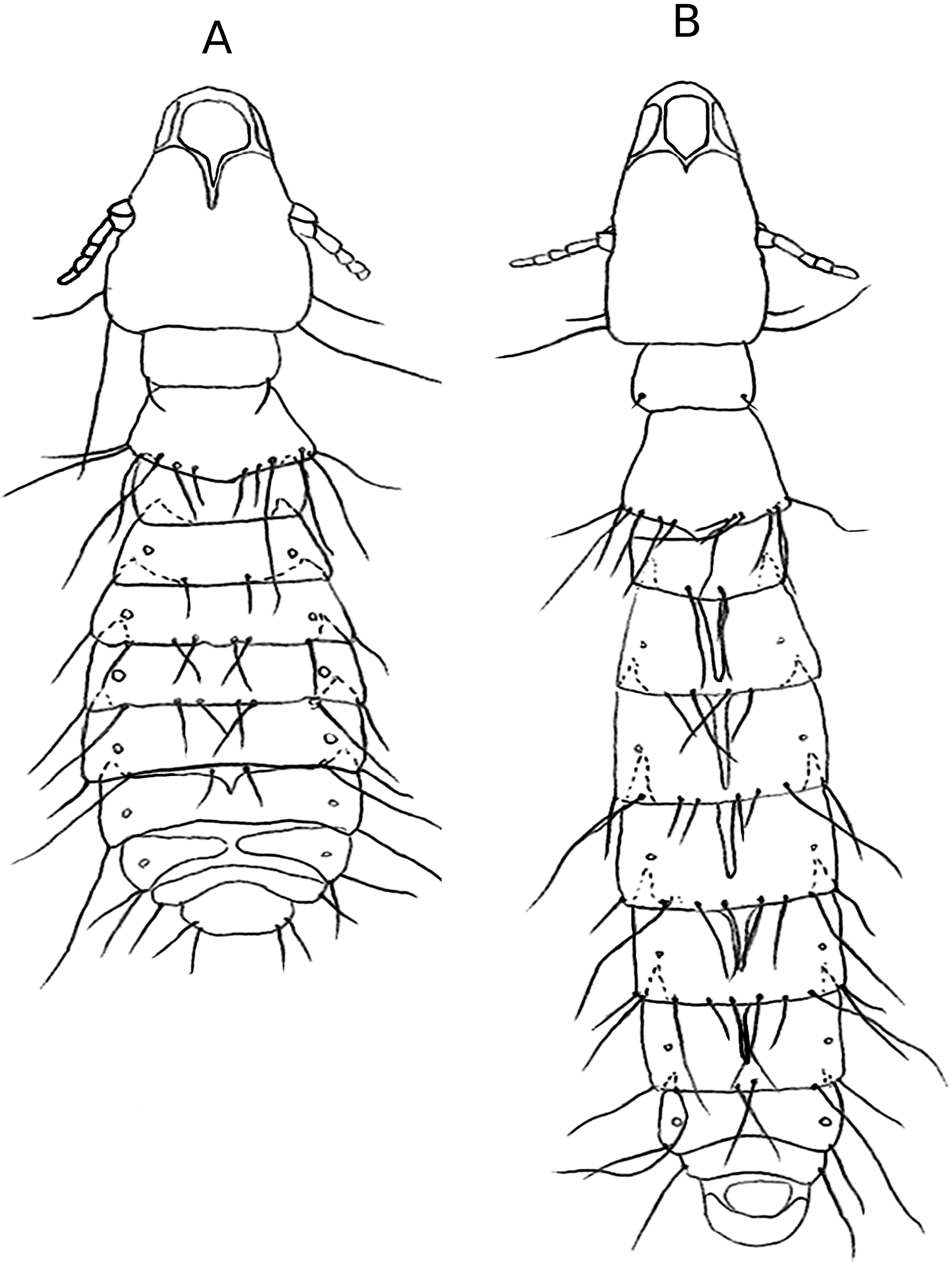

Fig. 4. Outlines of A) *Quadraceps ravus ex Actitis hypoleucos* and B) *Quadraceps fissus ex Charadrius semipalmatus*. Both drawings are of male specimens. Legs and smaller setae, as well as all internal details, have been removed for clarity. These two species are comparatively closely related (Paper IV).

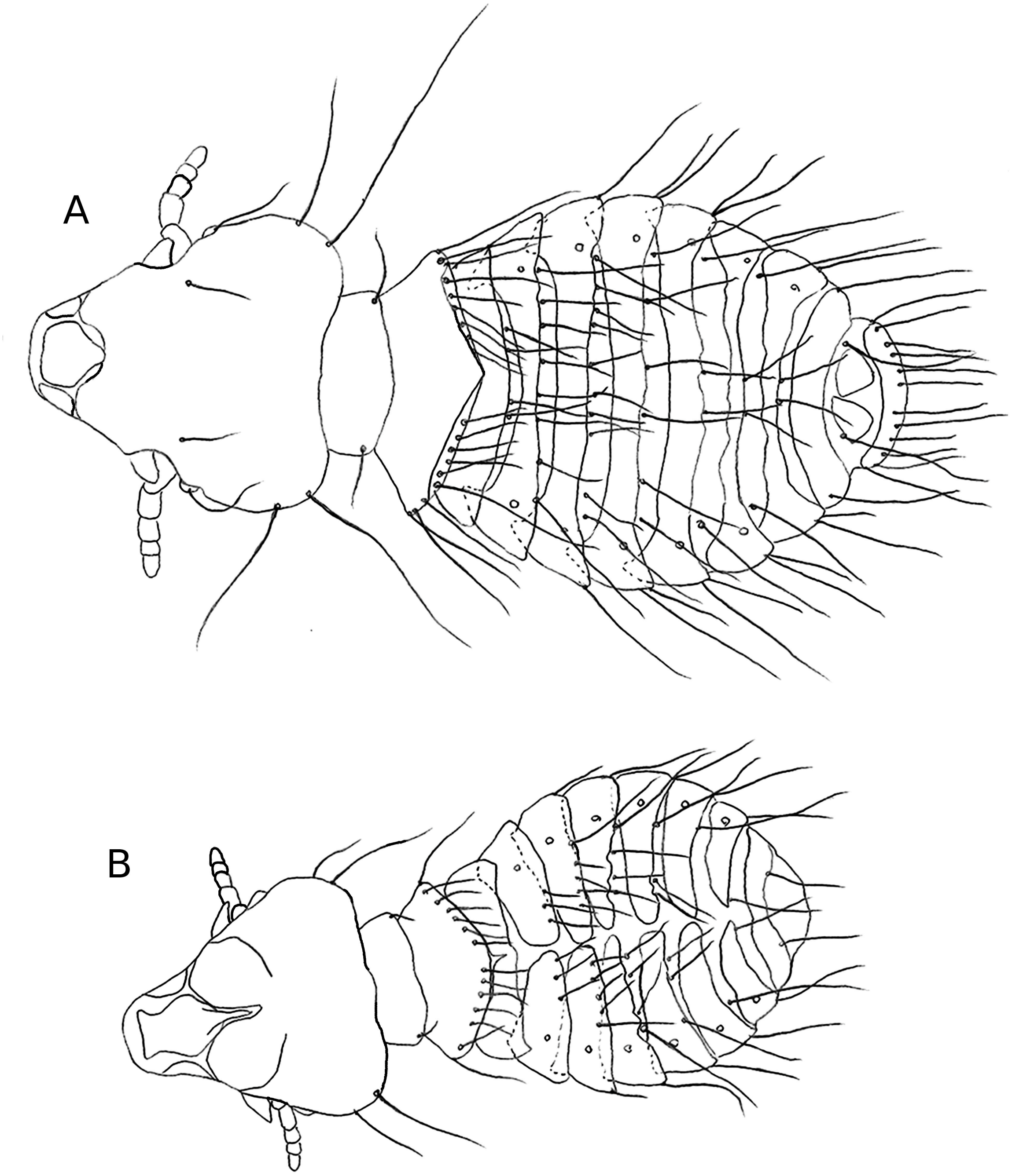

Fig. 5. Outlines of A) *Cummingsiella ovalis ex Numenius arquata* and B) *Saemundssonia sternae ex Sterna hirundo*. Both drawings are of male specimens. Legs and smaller setae, as well as all internal details, have been removed for clarity. Both these genera contain lice with broad, rounded abdomens and more or less triangular heads. Note the distinctive posterior extension of the dorsa anterior plate in *Saemundssonia*, characteristic of the genus.

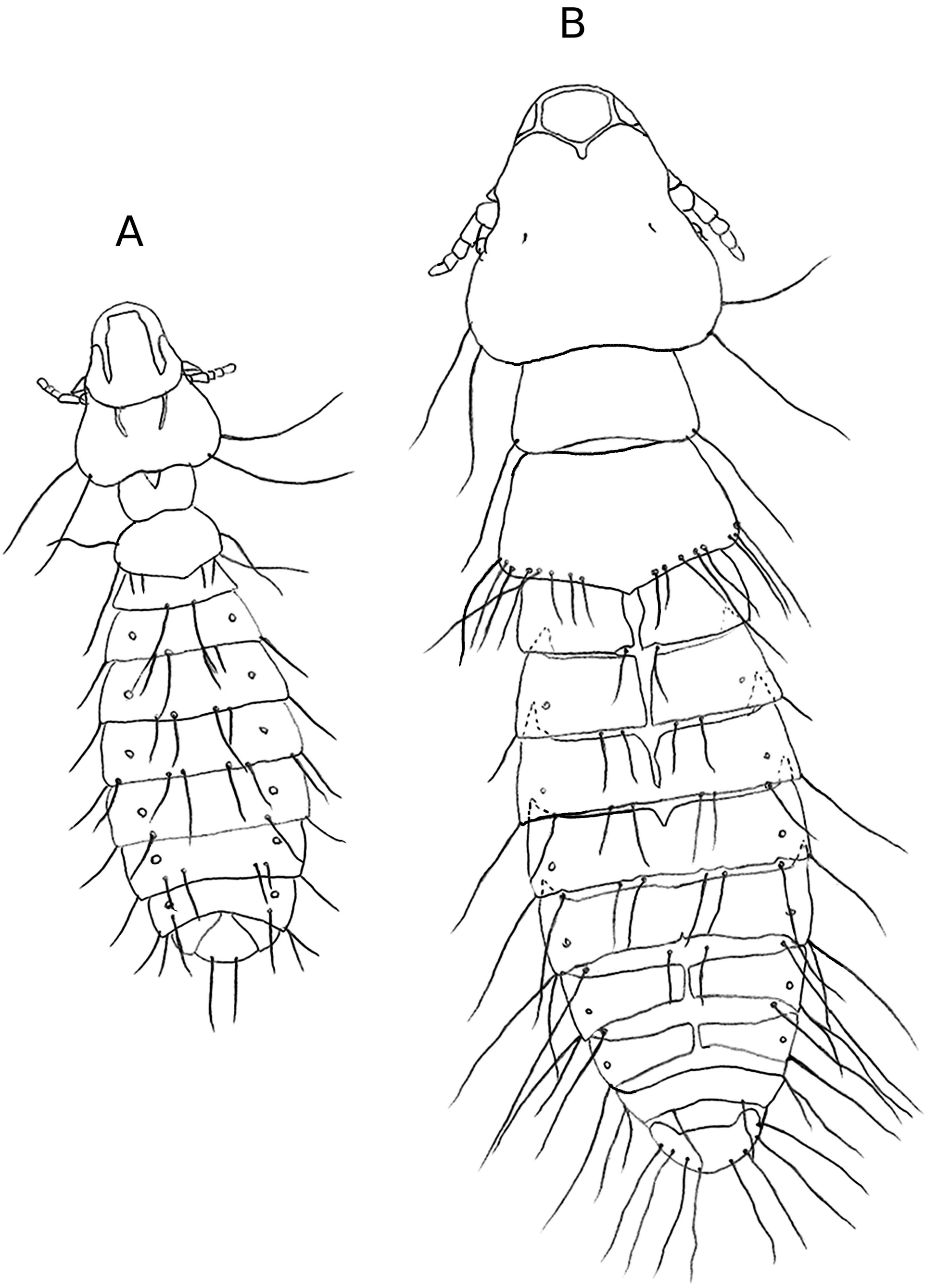

Fig. 6. Outlines of male A) *Carduiceps zonarius ex Calidris canutus rogersi* and B) *Cirrophthirius recurvirostrae ex Recurvirostra avosetta*. Both drawings are of male specimens. Legs and smaller setae, as well as all internal details, have been removed for clarity. Characteristic for *Carduiceps* is the complex preantennal area and structural features of the lateral sides of the abdomen, neither of which have been adequately illustrated here. *Cirrophthirius* is characterized, among other things, by the chaetotaxy of the female abdomen.

The "body louse" type, which is similar to the head lice in that they are stocky with a broad abdomen, but the head is often bell-shaped. These escape preening by escaping into the downy basal parts of the feathers where they are relatively safe. This group contains genera such as *Goniodes* (on wildfowl, Galliformes) and *Physconelloides* (on pigeons and doves, Columbiformes). Some *Quadraceps* (most shorebirds) belong in this group (Fig. 4), as do *Carduiceps* (Scolopacid shorebirds; Fig. 6a).

Not all louse genera can be placed in any of these three categories, and not all groups of birds have lice belonging to all three groups. The Amblycera have no such commonly accepted "niche-categories", apart from those that live inside feather shafts. Amblyceran lice are more agile that ischnoceran lice, and escape preening by running away on the skin of the host.

Apart from the family Goniodidae [parasitic on wildfowl (Galliformes) and pigeons (Columbiformes)] and perhaps the Heptapsogastridae [parasitic on the South American tinamous (Tinamiformes) and Seriemas (Gruiformes: Cariamidae)], no consensus exists on the division of the Ischnocera into families, and most genera are placed in the large family Philopteridae (Price *et al.*, 2003a; Fig. 7). Eichler (1963) proposed an extensive classification of the Ischnocera, but provided little in the way of motivation for these groupings. More recent work (Cruickshank *et al.*, 2001) has shown that many of Eichler's (1963) proposed families are probably monophyletic units that may be accepted as families, but the relationships between these groups are not fully resolved, and many large-scale phylogenies (see below) offer too little resolution at deeper levels for any definite conclusions to be drawn.

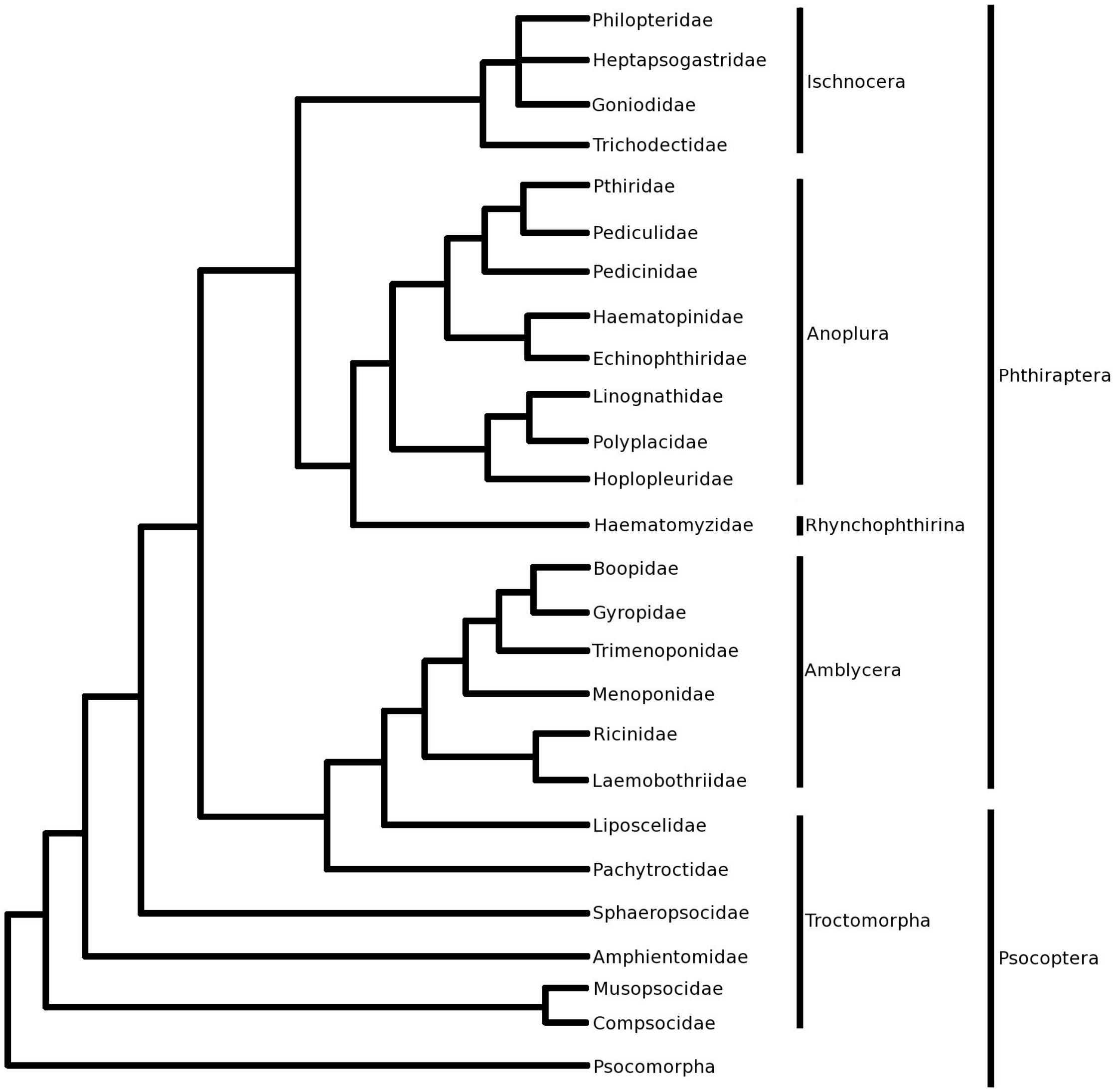

Fig. 7. Speculative family-level phylogeny of the Phthiraptera, based on Johnson *et al.* (2004; Fig. 1), Yoshizawa and Johnson (2010; Fig. 1), Smith *et al.* (2011; Fig. 1), although neither of these trees exhibits all relationships presented here. Several families of Phthiraptera, particularly of the Anoplura not included in any of the three analyses. The phylogeny of the Ischnocera with the broadest taxon sampling to date (Cruickshank *et al.*, 2001) is too poorly resolved to be included here. Both Phthiraptera and Psocoptera are reciprocally paraphyletic. Most louse genera mentioned in this thesis are members of Philopteridae, however the Amblyceran louse genera parasitizing shorebirds are all members of Menoponidae.

It was not until I had begun the writing of this paper that I realized how numerous are the permissible meanings of the word "relationship".
G. H. E. Hopkins, 1949a

3. Coevolution and bird-louse interactions

One of the central questions of louse research is, "How do the parasites interact with their hosts?" or, more importantly, "How have the parasites interacted with their hosts over evolutionary time?" These are general questions of wide scope, encompassing everything from the actual effect of a louse infestation on an individual host, to the greater themes of host-parasite coevolution and cospeciation.

That the lice have a direct effect on their individual hosts can hardly be doubted. Metabolic rate of hosts has been shown to increase as an effect of lice eating their feathers (Booth *et al*., 1993), and may increase feather fragility (Kose and Möller, 1999; Kose *et al*., 1999). They influence host life expectancy (Brown *et al*., 1995; Clayton *et al*., 1999), flight performance (Barbosa *et al*., 2002), and have been associated with or implicated in a variety of host afflictions, including wet-feather disease (Humphreys, 1975), ulcers in throat pouches (Wobeser *et al*., 1974; Kuiken *et al*., 1999; Dik, 2006), and adventitious moult (Taylor, 1981).

Simultaneously, the hosts have evolved multiple methods for getting rid of lice. The most well-known and obvious methods are perhaps preening and scratching (Cotgreave and Clayton, 1994). The importance of preening cannot be overstated, and the relationship between bill morphology and louse load has been intensely studied (Brown, 1972; Clayton, 1991; Clayton and Cotgreave, 1994; Clayton and Walther, 2001; Moyer *et al*., 2002a; Clayton *et al*., 2005; Chen *et al*., 2011). High louse loads on individual birds is often connected to bill deformities (*e.g*., Worth, 1940; Ash, 1960; Ledger, 1970).

However, birds also employ other, perhaps less obvious, methods such as sunning (Blem and Blem, 1993; Moyer and Wagenbach, 1999)[5], bathing in

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[5] "Sunning" refers to birds sitting in sunny spots, spreading wings and tail in order to raise the temperature of the feathers, which supposedly kills off lice. When in Tanzania in 2011, I observed the African Openbill *Anastomus lamelligerus* behave in a similar manner several times. The storks would fold their wings in a funnel-like shape in front of them, and direct the opening of this funnel towards the sun. They would stand like that for several minutes, and then viciously preen their wings and chest, before resuming the position. A stork observed in Msasani Bay, Dar es Salaam, repeated this behaviour for almost 40 minutes. Most of the observations of this sunning behaviour took place around noon, but the actual effect of this behaviour on the lice could not be studied.

alkaline water (Meinertzhagen, 1950), and "anting" (reviewed by *e.g.*, Groskin, 1950; Dater, 1953; Whittaker, 1957; Potter, 1970), whereby ants, pieces of fruit (Laskey, 1948; Clayton and Vernon, 1993) or other materials (Miller, 1952; Nice, 1955; Dubois, 1969) are rubbed or placed in the plumage. The world's only toxic birds, the Pitohuis *Pitohui spp.*, may have evolved the neurotoxin present in their skin and feathers as a defence against lice (Dumbacher, 1999). It has been suggested that living in areas of low humidity may decrease ectoparasitic pressure (Moyer *et al.*, 2002b), as lice are unable to use their water-vapour uptake system at low ambient humidity (Rudolph, 1983), but this was not confirmed by Carrillo *et al.* (2007).

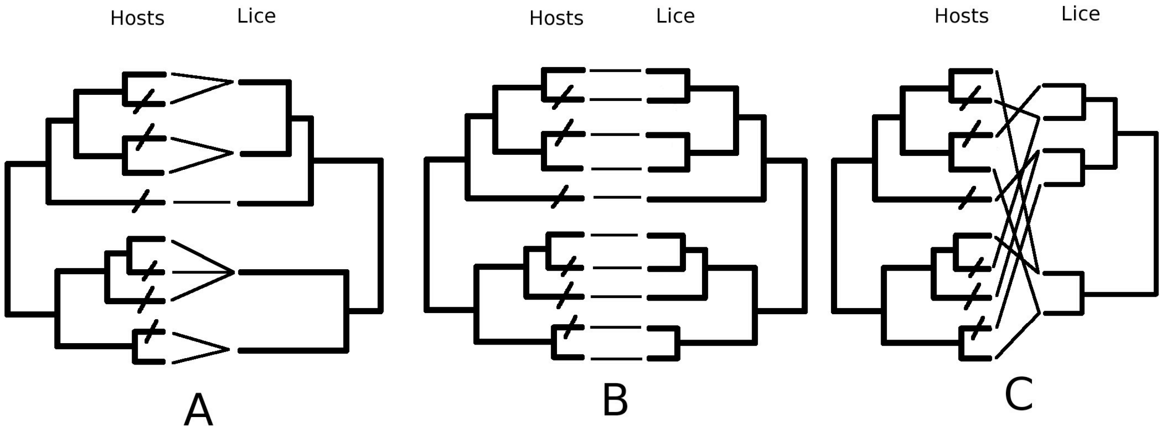

Fig. 8. Some abstractions of patterns of louse-host relationships. A) Kellogg's view (here anachronistically interpreted phylogenetically). Closely related host species occurring in two different geographical areas (such as North America and Europe) have the same species of lice, which colonized a common ancestor of the hosts. Kellogg believed that speciation in the lice lagged behind the speciation of the hosts, causing a specific pattern which can be used as evidence for host relationships. B) Eichler's view, following Fahrenholz' rule (here interpreted phylogenetically). Isolation of host populations into discrete units, separated geographically, initiates a speciation process in their lice. Over time, the relationships of the lice corresponds to those of their hosts (*i.e.* "louse phylogeny mirrors host phylogeny"). Again, patterns deduced from louse relationships can be applied directly to host relationships, and, it was argued, may even be more conclusive than characters of the hosts themselves, as these can often be "obscured". C) A biogeographical pattern. The distribution of lice is dominated by the biogeography of the hosts, such that hosts that occur in the same geographical region have closely related lice, regardless of whether the hosts themselves are closely related.

3.1 Fahrenholz' rule and the species concept in louse systematics

Differences in bill morphology, feather structure, and utilization of other louse defences can be expected to vary between host species. As lice lack a free-living dispersal stage, but are generally limited to periods of direct contact between two hosts, either horizontally during mating (Hillgarth, 1996) or vertically between parents and nestlings (Clayton and Tompkins, 1994; Lee and Clayton, 1995; Brooke, 2010), to transfer to new or novel host individuals, they can be expected to adapt to the specific host species they are on.

However, the fidelity of a louse lineage to a host lineage has been a matter of some controversy during the 20th century. Many experts believed there was a strong correlation between the relationships among the hosts and the relationships among the lice, in that the relationships of the hosts and the relationships of the parasites should mirror each other[6]. Kellogg (1914) wrote:

> “[T]he host distribution of these wingless permanent ectoparasites is governed more by the genetic relationships of the hosts than by their geographic range, or by any other ecological conditions”

Eichler (1941, 1942) encoded this in Fahrenholz’ rule[7], which states:

> “Among numerous (mainly permanent) parasites, the historical development and splitting of the hosts is paralleled by a corresponding development and splitting of the parasites. Therefore, the resulting phylogenetic relationships of the parasites can be used to draw conclusions about the (often obscured) phylogenetic relationships of the hosts.” (Translated by Klassen, 1992).[8]

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[6] The following historical perspective was previously reviewed by Klassen (1992) and Choudhury *et al.* (2002). Klassen (1992) puts the start of coevolutionary thought with von Ihering (1891, 1902), but Hopkins (1951) somewhat unconvincingly pushes its roots back to Jardine (1841). It is doubtful if Jardine’s remark (“One more remarkable analogy we would notice, and one perhaps by which it has not yet struck ornithologists to trace the alliance between the various groups [of birds]”), made before Darwin’s (1859) *Origin of Species*, can in any way be said to be connected to the origin of the concept of coevolution.

[7] On the dispute for the true name of this rule, see Choudhury *et al.* (2002). I can here add only that Kellogg (1913) quite explicitly state that “With the splitting up of the ancient host species […] there has been no equivalent evolutionary divergence of the isolated groups of individuals of the parasite species” (p. 157), elaborated slightly on the following page. I interpret this as meaning that Kellogg did *not* envision anything similar to Fahrenholz’ rule, which is the conclusion Choudhury *et al.* (2002) also reached.

[8] “Bei zahlreichen (vorwiegend ständigen) Parasiten ist mit der historischen Entwicklung und Aufspaltung der Wirte gleichlaufend auch eine entsprechende Entwicklung und Aufspaltung der Parasiten einhergegangen. Aus den sich ergebenden verwandschaftlichen Beziehungen der Parasiten lassen sich deshalb Rückschlüsse ziehen auf die (oft verdeckten) Verwandtschaftsverhältnisse der Wirte”[8] Later, he defined it more succinctly, and not as categorically: “In groups of permanent parasites the classification of the parasites *usually* corresponds directly with the natural relationships of the hosts.” (Eichler, 1948; my emphasis). Lakshinarayana (1977) reformulates this rule to “the ancestors of extant parasites must have been parasites of the ancestors of extant hosts”. This interpretation is not entirely analogous with Eichler’s formulation, in that it does not assume that there is a “splitting off” of louse taxa connected to the “splitting off” of host taxa. Lakshinarayana’s interpretation is wider than Eichler’s, as it includes also cases where the radiation of a group of birds has *not* resulted in the radiation of its parasites.

This hypothesis relies heavily on the absence of transfer between a louse species' regular host and any host individuals not belonging to the same species. "Straggling" is assumed to be of little or no evolutionary importance, and direct contact between hosts is (implicitly) assumed to be the only mode of dispersal. Whether or not this is true was largely unknown at the time.

Fahrenholz' rule (Fig. 8) was very important in development of Phthirapteran taxonomy during the 20th century, especially in Eastern Europe, and could sometimes be taken to extremes[9], as in Zlotorzyckas's (1970) division of duck lice into separate subspecies for every host species despite small morphological differences. On the species level, the strict application of this rule meant that lice taken from a novel host was assumed to be a new species, sometimes almost without reference to morphology, size, or comparisons with other species (*e.g.*, the description of *Lunaceps parabolicus* by Eichler [in Niethammer], 1953a; see Paper II). In fact, Eichler (1941) stated that (my translation and emphasis):

> "[It is] methodologically more appropriate to say that "we cannot yet tell apart the parasites from these two different hosts" than to say that "this parasite occurs on both these hosts." [Footnote in original: "Verified cases where one and the same form of Mallophaga habitually occurs on different host forms or very different host genera **are almost entirely unknown**"] [10]

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[9] In the interest of fairness, it should be pointed out that not even Eichler saw a dogmatic application of Fahrenholz' rule as desirable in all cases: "This working hypothesis [that host relationships should weigh heavily in dividing taxa into species] should not, on the other hand, by exaggerated, so that closely related lineages that live on different hosts are treated as different [species] at any cost, even when painstaking examinations of two series cannot reveal any comprehensible morphological differences [between them]." ("Andererseits darf man diese Arbeitshypothese doch nicht so übertreiben, dass man von nahe verwandten, aber verschiedenen Wirten stammende Herkünfte um jeden Preis als verschiedenen betrachten will, auch wenn sich bei sorgfältigster Untersuchung zweier Serien keine fassbaren morphologicshen Unterschiede erkennen lassen." (Eichler, 1980; my translation).

[10] "[Es ist] methodologisch richtiger, davon zu sprechen, dass "wir die Parasiten von diesen beiden verschiedenen Wirten bisher noch nicht unterschieden können", als dass "dieser Parasit bei diesen beiden verschiedenen Wirten vorkomme". [Footnotein original: "Sicher nachgeprüfte Fälle des regelmässigen Vorkommen eiener und derselben Mallophagenform auf verschiedenen Wirtsformen oder gar verschiedenen Wirtsgattungen **kennen wir fast überhaubt keine**."] (My emphasis). Eichler (1967) echoed the same sentiment: "Where a pronounced host specificity exists, we must expect infraspecific divisions as the hosts differentiates. Therefore [we] must warn against maintaining that two ostensibly similar lineages from different hosts are identical, until a very thorough analysis has been performed" (my translation of: "Wo eine ausgeprägte Wirtspecificität besteht, ist mit wirtlicher Differenzierung im infraspezifischen Bereich zu rehcnen. Deshalb muss dann davor gewarnt waren, zwei augenscheinlich gleiche Herkünfte von verschiedenen Wirtsarten für identisch zu halten, bevor nicht eine sehr eingehende Analyse vorgenommen wurde."

That is, the occurrence of the same louse species on two different hosts is *a priori* more likely to be due to faulty taxonomy[11] where the characters to tell the two louse populations apart are simply not know yet, than to be an example of a louse with two natural hosts. This may seem like a good principle, but has the disadvantage that it makes the classification and systematics entirely arbitrary. Any two populations can always be claimed to be differentiated on a taxonomically relevant level by characters that are unknown at the time. Adding new data to show that the two populations are identical is meaningless, as the difference can always be claimed to lie in another, still unknown, set of characters.

The value of host relationships in the louse systematics of Eichler and other proponents of Fahrenholz' rule was believed to be paramount, and the analogy of free-living animals was often used:

> "There is also reason to accept a difference between forms by their occurrence on different hosts, similar to [how we treat] the distribution of a free-living animal species on different continents. Timmerman has therefore (recently) also revaluated the host criterion in this direction somewhat, and I am of the opinion that the greatest value should be placed on this criterion. (Eichler, 1980)[12]

3.2 The genus concept in louse systematics

Application of Fahrenholz's rule on the genus level was equally contentious. Louse genera were split according to host relationships both in cases where the original genus was morphologically homogeneous, and when it was morphologically heterogeneous. The former case could result in genera that were indistinguishable unless the host species was known. In the latter case, lice that are not closely related could be grouped together because they lived on

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[11] Eichler (1941) especially criticizes the "Kellogg school" for being "lumpers", and "habitually putting closely related forms of lice in the same species" ("Kellogg und seine Schule […] haben deshalb regelmässig nahe verwandte Mallophagenformen in eine Art zusammengeworfen"). Eichler (1973) later echoed these sentiments, but with Hopkins and Clay as recipients of mild criticism: "Hier ist Mayr offenbar der alten Klassifikation von Hopkins und Clay zum Opfer gefallen, die in ihrem Katalog alle mehr oder weniger nahe verwandte Mallophagengattungen in Grossgattungen vereinigten." ["Here Mayr has apparently fallen victim to the old classification of Hopkins and Clay [1952], who in their catalogue combine all more or less closely related genera of Mallophaga in large genera." (my translation).]

[12] My translation of: "Es besteht also ebenso Veranlassung, eine Verschiedenheit der Formen beim Vorliegen verschiedene Wirte anzunehmen, wie etwa bei der Verbreitung eine freilebenden Tierart auf verschiedene Kontinenten. Timmermann hat deshalb auch (neulich) das Kriterium des Wirtes in dieser Richtung wieder etwas aufgewertet, und ich selbst bin der Meinung, dass man auf dieses Kriterium grössten Wert legen sollt." The "Kriterium" he speaks of is "Wirte als Kriterium für der Trennung zweier Formen" (= Host as the criterion for the division of two forms" (Eichler, 1980).

closely related hosts, even if this was due to multiple colonisations of those hosts.

Zlotorzycka (1964a) argues in favour of this approach, and against the "lumping method". Her method for genus delimitation was based firstly on whether any "distinct new characters of taxonomical value that are absent in the species typical of the primary genus" could be found on a species, and if this is the case, she considered "the taxonomical position of the host of the primary genus and that of the genus or genera newly established". However, in 1971 (Eichler and Zlotorzycka, 1971) the distribution has started to gain ascendancy over morphology:

> "For delimitation of genera, morphologically delimitable groups of species with a clearly defined distribution should be separated as genera even in those cases where the morphological borders to neighbouring genera are not so clear."[13]

Species that occur on the same host species, referred to as synhospital species (Eichler, 1966)[14], presented a problem for the adherents of Fahrenholz' rule, especially when these were placed in the same genus. If "the historical development and splitting of the hosts is paralleled by a corresponding development and splitting of the parasites" (Eichler, 1942; translation by Klassen, 1992), then the verified occurrence of two species of lice of the same genus on the same host requires that either the hosts or the lice are "incorrectly" split into species. But when two species of lice of the same genus were found on the same host individual, it is clear that the classification of the hosts cannot be wrong, and the classification of the lice must be changed. Perhaps nowhere has this view of louse taxonomy been expressed more succinctly than by Eichler (1971) (my emphasis):

> "The chicken louse *Eomenacanthus cornutus* (Schömmer, 1913) *sensu* Hohorst 1940 **can not remain** in the same genus with *Eomenacanthus stramineus* (Nitzsch in Giebel, 1874b). Therefore the new genus *Gallacanthus* nov. gen. is erected for *cornutus*."[15]

Synhospital species of the same genus are relatively common in the Shorebirds, with multiple *Quadraceps*-species occurring on avocets, some gulls, some terns, some oystercatchers, and some plovers (Price *et al.*, 2003a). Zlotorzycka (1967)

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[13] "Für die Gattungsabgrenzung sollte gelten, dass morphologisch abgrenzbare Gruppen von Arten mit klar umgrenzter Verbreitung auch dann als Gattungen unterscheiden werden sollten, wenn die Grenze zu Nachbargattungen morphologisch nicht scharf ist."

[14] The same condition was called "synoxenia" by Wenzel *et al.* (1966) (Ref: Nelson, 1972).

[15] "Die Hühnerfederlingsart *Eomenacanthus cornutus* (Schömmer, 1913) sensu Hohorst 1940 **kann nicht** mit *Eomenacanthus stramineus* (Nitzsch in Giebel, 1874b) in der gleichen gattung **verbleiben**, weshalb für sie die neue Gattung *Gallacanthus* nov. gen. errichtet wird." (My emphasis; English translation also in original)

argued that synhospital species “can be recognized as [different] genera”[16], and erected the genus *Chadraceps* and the subgenus *Laminonirmus* on this basis. Both are now considered synonymous with *Quadraceps* (Price *et al.*, 2003a; however see Paper IV).

This view of the relationship between lice and the hosts was understandable in a period where morphology and the judgment of a small number of experts, often with different opinions on how to draw limits between species, were the only criteria to assign any taxonomic rank. Even at the time, strict application of Fahrenholz’ rule was criticized by some authors:

> “Thus, genera are now being erected for groups of species morphologically indistinguishable from the remaining species in the genus merely because they parasitize a distinct group of hosts.” (Clay, 1951a)

> “We are confident that certain authors, noting (for instance) the occurrence of a *Cuclotogaster* on a member of the Musophagidae, would give the species generic rank on any character, however trivial, that would serve to distinguish it from its congeners, but such a procedure would not only be completely unjustified but would hinder our search for knowledge by obscuring the extremely interesting fact that this genus, so characteristic of the Galliformes, also occurs on Musophagidae.” (Hopkins and Clay, 1952). [17]

These authors thus represented a more or less opposite point of view, compared to the adherents of Fahrenholz’ rule, and argued rather for a system of classification where morphology was given primacy over host relationships:

> “We would certainly be inclined to give greater weight to an apparently trivial difference found in a group of species confined to one group of hosts than if it occurred in species distributed sporadically over various groups of hosts, but we think it essential that the primary considerations should be morphological and that distribution should only be used for purposes of confirmation.” (Hopkins and Clay, 1952)

> “Where a genus is found on more than one host order […] the species found on each host order cannot be segregated into genera unless there is a morphological basis for this. […] However, unless there is good evidence to the contrary, genera must be based on morphological criteria and not on hypothetical speculations of their evolution based on distribution.” (Clay, 1951a)

> “Their [Eichler and Zlotorzycka] hypothesis leads to the conclusion that the classification of Mallophaga is based more on the classification of the host than upon its own merits. According to their hypothesis the inclusion of two previously recognised host species as

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[16] “Diese Mallophagen, welche deutliche Spezifität zeigen, kann man als Gattungen anerkennen”

[17] As far as I can tell, Hopkins and Clay (1952) were too cynic here, and no one has ever proposed a split of *Cuclotogaster* based on host relationships. The species in question, however, is listed as “? host” by Price *et al.* (2003a) and is not listed under the Musophagidae.

> conspecific or the division of one species into two or more separate species would automatically synonymize or erect species of lice." (Nelson, 1972)

Hopkins and Clay (1952) believed that groups of lice that form a continuum across one or several host groups should not be subdivided into smaller genera based on host associations.

> "Others […] consider that the absence of any sharp distinction between what we would often agree to be two natural groups is a fatal bar to their acceptance as genera." (Hopkins and Clay, 1952)

The absence of such distinctions might, for instance, mean that a new species from a previously unsampled host could be impossible to place. Clay (1951a) pointed to the disadvantages of the "splitting school":

> "This erection of genera for polytypic or superspecies merely burdens the memory with names which give no clue to relationships, in many cases makes it impossible to place a species if only one sex is known, and probably means the future erection of further monotypic genera for the inclusion of new species. "

Further, it was believed in the early 20th century, that louse evolution was slower than that of their hosts:

> "At the same time one must admit that the belief that the differentiation of species of Mallophaga has lagged behind that of their hosts is probably correct, and that, on any conception of the nature of a species which we can at present envisage, there will still remain, after our most detailed works on systematics, a residuum of species which definitely occur normally on more than one host." (Hopkins, 1939)

This view contrasts with Eichler's concept of more or less a one-to-one relationship between host species and louse species, which essentially forces speciation of lice to be simultaneous with speciation in the hosts.

During much of the 20th century, a state of "tug-of-war" can be said to have existed between on the one hand those authors who applied Fahrenholz' rule more strictly (*e.g.*, Eichler, 1959), and those who did not automatically accept a new species or genus solely on the basis of host affinities. Most of the genera and species deemed to be inseparable from older species and genera by Hopkins and Clay (1952, 1953, 1955) were established by a small number of authors who belonged to the former school of thought, and only 55% of the species described by Eichler were considered valid species by Price *et al.* (2003a).[18]

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[18] When Clay (1974) wrote, on the morphological continuum in *Ardeicola*, that it "diff[ered] only specifically on different hosts, even the extreme splitters having been unable to make any generic divisions", she no doubt referred to Eichler and the other strict adherents to Fahrenholz' rule. Predictably, Eichler (1982) split the genera *Cicardeicola* and *Threskardeicola* from *Ardeicola*, relying not on a thorough study of the taxa involved, but on

3.3 Applying louse data to host systematics

Notwithstanding their philosophical differences, both schools of thought agreed on one important implication of Fahrenholz' rule. If there is strict cospeciation between the lice and their hosts, distribution and relationships of the lice could be treated as any other character of the hosts, and be used to elucidate the relationships between the hosts [Kellogg and Kuwana, 1902; Kellogg, 1913; Harrison, 1914; Hopkins, 1942, 1949b; Eichler, 1948; Clay, 1951b; however Harrison (1915) and Clay (1946, 1965) had some reservations[19]]. In fact, it was argued, if the morphology or behaviour of the hosts has evolved to obscure relationships between them, the distribution and relationship of their lice might be preferable to morphological characters of the host when trying to reconstruct the hosts' evolutionary history (Hopkins, 1942, 1949b; Eichler, 1948).

However, even so, these same authors did recognise that there may be other factors contributing to the distribution of lice, so that the correspondence between the respective evolutionary histories of the hosts and the parasites need not always be perfect. For instance, Hopkins (1949b) suggested that lice "characteristic of the game-birds" on the Turacos (Musophagidae) had resulted from shared dust baths. This, and similar lines of reasoning, lead Hopkins (1942) to formulate the following general rule of thumb [This approach was adopted also by Eichler (1948)]:

> "My own rule in the matter is to regard one correspondence with reserve, two as establishing a strong probability, and three as a certainty".[20]

A classical example of the hypothesis that louse relationships can predict host relationships is the flamingos, Phoenicopteridae, a group of birds which long was of uncertain phylogenetic position. Two main schools of thought existed, divided on whether or not the flamingos were modified storks (Ciconiiformes) or modified ducks (Anseriformes). This example was taken up by Eichler (1942)[21], who argued that three of the four genera of lice on flamingos also

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the species group descriptions of Kumar and Tandan (1971) and Tandan (1976), a common methodology for Eichler, and one condemned by Hopkins and Clay (1953).

[19] See also the comments by Tandan and Hajela (1962) on Eichler's (1959) "*Abumarkub koenigi"* and the latter's long discussion on the phylogenetic affinities of its purported host, *Balaeniceps rex*. Tandan and Hajela (1962) showed that this was not the true host of this louse species, and concluded: "Without contributing to the knowledge of the bird lice, *Abumarkub koenigi* Eichler is liable to cause damage to the status of the Mallophaga [as a clue to bird relationships among ornithologists]".

[20] Lakshminarayana (1970, 1977) calls this "Hopkins' Principle".

[21] The correspondence between the lice of ducks and those of flamingos was made progressively obscured by the erection of a number of genera based on host associations (*Anseriphilus, Ewingella, Flamingobius, Scalarisoma*) throughout the 20th century, which curiously meant that when Eichler (1973) reformulated the comparison between the two louse

parasitize ducks, whereas the fourth can be found on both ducks and storks (see Price *et al*., 2003a). Both Hopkins (1942) and Eichler (1942, 1948) therefore drew the conclusion that flamingos are indeed modified ducks. Clay (1962b, 1974) allowed for the possibility that ancient transfer between an "Anseriform stock" to the ancestor of the flamingos is an alternative explanation, in agreement with von Kéler (1957a, b). As molecular (van Tuinen *et al*., 2001; Chubb, 2004) and morphological (Mayr, 2004) studies revealed that the flamingos may be closely related to grebes (Podicipediformes), interest in its lice was renewed, with Johnson *et al*. (2006) showing that the louse genus *Anaticola* (common to flamingos and ducks) and the louse genus *Aquanirmus* (endemic to grebes) were sister taxa.

Other examples of cases where the systematics of the parasites have been thought to shed some light on the systematics of their hosts can be found throughout the 20th century (*e.g*., Harrison, 1915; Clay, 1948, 1951c; Timmermann, 1952a, b, 1957a; Mey, 1999). However, more recent work have revealed that historical interactions between host and parasite lineages are seldom so clear-cut as Fahrenholz' rule and Hopkins' rule of thumb would suggest, but are often complicated and obscured by known or unknown processes.

3.4 Molecular work: testing Fahrenholz' rule

Molecular studies of lice have had many different themes, ranging from its relationships with other groups of insects (Yoshizawa and Johnson, 2003; Murrell and Barker, 2005) to host-parasite coevolution (*e.g*., Weckstein, 2004; Banks *et al*., 2006; Hughes *et al*., 2007), to population biology (Gómez-Díaz *et al*., 2007; Toon and Hughes, 2008).

It now seems clear that the Phthiraptera are nested within the Psocoptera (Lyal, 1985; Yoshizawa and Johnson, 2003; Fig. 7), and that the two are likely reciprocally paraphyletic, with the Amblycera being more closely related to the Psocopteran families Liposcelidae and Pachytroctidae than to other Phthiraptera (Johnson *et al*., 2004; Murrell and Barker, 2005; Yoshizawa and Johnson, 2010; Fig. 7). This suggests that parasitism of lice on both birds and mammals has developed at least twice. The split between lice and Liposcelidae has tentatively been placed between 100-145 million years ago (Grimaldi and Engel, 2006)[22], and Smith *et al.* (2011) have shown that the radiation of the major groups of lice began already before the Cretaceous-Palaeogene boundary, 65 million years ago.

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faunas, the connection between the two is not as apparent as it was when Hopkins made in 30 years earlier. None of these genera are accepted by Price *et al.* (2003a).

[22] Grimaldi and Engel (2006) treats the Phthiraptera as a monophyletic taxon in their tree, and it is unclear whether their tentative dating would represent the split between Ischnocera+Anoplura+Rhynchophthirina and Liposcelidae+Amblycera, or between Liposcelidae and Amblycera.

Relationships within Ischnocera, which is the most widely studied suborder of Phthiraptera and the focus of this thesis, are not always clear[23]. While the suborder itself appears to be monophyletic (*e.g.*, Johnson and Whiting, 2002; Barker *et al.*, 2003), different sets of data produce contrasting, and sometimes conflicting, phylogenies (Smith *et al.*, 2004). Cruickshank *et al.* (2001) recovered many of the ischnoceran families and subfamilies proposed by Eichler (1963), however while several of these groups may be monophyletic (*e.g.*, Goniodidae; Johnson *et al.*, 2001a; Johnson *et al.*, 2011), the relationships between them are still obscure. The elevated rate of mitochondrial evolution in lice (Page *et al.*, 1998; Johnson *et al.*, 2003a) has been proposed as a reason for the difficulty in getting support for any deeper groupings within the Ischnocera (Johnson *et al.*, 2011)[24].

On a still lower taxonomic level, several studies have revealed that relationships between lice and their hosts are complicated. While some groups of lice seem to have evolutionary histories that at least approximate that of their hosts (*e.g*.. Hafner and Nadler, 1988; Paterson *et al.*, 2000; Page *et al.*, 2004; Hughes *et al.*, 2007), and thereby would lend some support to the validity of Fahrenholz' rule, other groups largely lack such co-evolutionary patterns.

Instead, patterns corresponding better to the biogeography of the hosts than to the hosts' phylogenetic relationships have often been found, and genetically similar or identical lice inhabiting sympatric, but not necessarily closely related, hosts have been found in the genera *Brueelia* (songbird lice; Johnson *et al.*, 2002a; Bueter *et al.*, 2009), *Austrophilopterus* (toucan lice; Weckstein, 2004) and *Austrogoniodes* (penguin lice; Banks *et al.*, 2006), and influences from host biogeography on a broader scale have been found in *Penenirmus* (from woodpeckers and allies; Johnson *et al.*, 2001b), the *Degeeriella* complex (on a variety of hosts; Johnson *et al.*, 2002b), *Coloceras, Physconelloides* and

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[23] Only one phylogeny so far has focused exclusively on and included a broad range of the Amblycera (Marshall, 2003), and this study is based on morphological data. Page *et al.* (1998) constructed a molecular phylogeny of the genus *Dennyus*, and several studies have included some Amblycera (*e.g.*, Cruickshank *et al.*, 2001; Johnson *et al.*, 2003a), however the relationships within the Amblycera are far from well known.

[24] It should perhaps be mentioned that there are several peculiar aspects of louse mitochondria. The structure of the mitochondrial 12S sequence is highly variable between groups of lice, and therefore hard to align unambiguously in a data set containing widely separated louse taxa (Page *et al.*, 2002). The order of genes and other regions on the mitochondria is also dramatically rearranged compared to the otherwise very conservative order found throughout the insects (Shao *et al.*, 2001a, b; Covarcin *et al.*, 2006; Cameron *et al.*, 2007, 2011), and even within the Phthiraptera there is a great deal of variation of gene order (Cameron *et al.*, 2011). Lastly, and perhaps most interestingly, the mitochondrial DNA of lice are often divided into several smaller "minicircles", which collectively contain all the "standard" mitochondrial genes, but where no single minicircle has a complete set (Shao *et al.*, 2009; Cameron *et al.*, 2011). It is perhaps too early to speculate on what effects these peculiarities may have had on Phthirapteran evolution (though see Cameron *et al.*, 2007).

Campanulotes (from doves and pigeons; Johnson *et al.*, 2011) and in *Myrsidea* (songbird lice; Bueter *et al.*, 2009).

Another theme of the molecular work on co-evolution between lice and their hosts is the difference within the same set of hosts between different "kinds" of lice. The genetic population structure of body louse genus *Physconelloides* on New World pigeon and dove hosts has been found to be more pronounced than in the wing louse genus *Columbicola* on the same set of hosts (Johnson *et al.*, 2002c; Clayton and Johnson, 2003). Different genera showing different patterns of speciation and coevolution with their hosts has also been found in Passerines (Bueter *et al.*, 2009) and seabirds (Page *et al.*, 2004).

These differences between different louse groups on the same set of hosts are expected, as niche specialization into, *e.g.* ,"head lice", "body lice" and "wing lice" would likely provide different morphological groups of lice with different opportunities for dispersal to novel hosts. It is easy to hypothesise, for instance, that wing lice, already being present on the wings of birds, would be more prone to lateral spread in host species which form communal roosts, where the wings of different hosts, or even different host species, may occasionally come in contact. The same communal roosts may not be as conducive to dispersal for head lice, if these truly do not leave their niche, as the birds' heads are less likely to come in contact. However, as we shall see below, even less intuitive methods of louse dispersal are known to occur, which may further differentiate the capabilities and rates of spread to novel hosts of different groups of lice.

At the same time, morphological data has been found to be at odds with genetic data (*e.g.*, Smith *et al.*, 2004; Banks *et al.*, 2006; but see Johnson *et al.*, 2007, 2011), and cryptic speciation has been detected in several groups of lice (*e.g.*, Malenke *et al.*, 2009; Paper I, II). Part of this discrepancy is the residue of a century of unintentional obscuring of louse relationships by the strict application of Fahrenholz' rule (*e.g.*. Zlotorzycka, 1967)[25], resulting in a taxonomy and systematics that does not always accurately reflect these relationships. However, part of it must also be blamed on the wide-spread convergent evolution towards similar body shapes among lice (Smith, 2001; Smith *et al.*, 2004).

In short, the application of molecular methods to louse systematics has highlighted how complicated and convoluted the relationships between lice can

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[25] "Es war nötig, diese Taxa zu errichten, denn diese morphologisch ungleichförmige Mallophagengruppe, welche man zu *Quadraceps s. l.* rechnet, kommt vor allem auf zahlreichen Familien der Charadriiformes vor, sowie auf einigen Vetretern aus den Gruiformes und den Gressores." ("It was necessary to erect these taxa, as the morphologically heterogeneous louse group that is placed in *Quadraceps s. l.* is found mainly on numerous families of Charadriiformes, as well as on a few representatives of the Gruiformes and the Gressores [= Ciconiiformes]"; my translation. "These taxa" refer to a large number of genera, most of which are today counted as junior synonyms to *Quadraceps*, erected throughout the 20th century for *Quadraceps* species parasitizing different families of the Charadriiformes.

be, and how little we actually know. Several seemingly well-established genera have been found to be paraphyletic (Johnson *et al.*, 2002b; Johnson *et al.*, 2011), and the answer to the question, “What is the evolutionary history of this group of lice and their hosts?” cannot be standardized.

3.5 Other known and proposed patterns of louse-bird relationships

Fahrenholz’ rule has been central to most of the research on bird-louse relationships during the 20th and early 21st centuries, whether the researcher believed it accurately represents evolutionary history or not. However, other proposed rules have never, or only belatedly, become the subject of study.

Eichler (1942) formulated Szidat’s rule, which states that:

> “The trend towards higher development among the hosts tends to rub off on their (mainly permanent) parasites such that, within comparatively large [taxonomic] units, host taxa with a relatively low level of organization (primitive hosts) harbour parasites with relatively low level of organization (primitive parasites).”[26]
> (Translation modified after Klassen, 1992)

This rule may seem hard to test or defend, as no extant organism is more primitive than any other, and the objective division of extant hosts and lice into “primitive” and “not primitive” would be impossible[27]. The rule could be reformulated into the more testable “ groups of hosts that have been isolated from their closest relatives for a long time are parasitized by a limited number of ‘kinds’ of lice”. “Kinds” may here refer to suborders, families, or any other group of taxa above the genus level. If, for instance, parasitism on birds by the ancestors of Ischnocera developed on the ancestor of all Neognathes (most modern birds) only after these divided from the Palaeognathes (Ratites and Tinamous), then we would expect Ischnocera to exist only on Neognathes, unless there has been a secondary dispersal to Palaeognathes. Acquisition of a group of lice in the ancestor of a group of birds would then be analogous to a synapomorphy for that group (Harrison, 1915, argues briefly along these lines). This assumes that the “primitive” condition of the ancestor of modern birds is one of no parasitic lice, and that parasitism by lice has occurred several times during evolutionary history. As the Phthiraptera are nested within the non-parasitic Psocoptera, and paraphyletic with regards to the non-parasitic

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[26] “Die Neigung zur Höherentwicklung der Wirte färbt vielfach ab auf deren (vorwiegend ständige) Parasiten, so dass innerhalb vergleichbarer grosser Einheiten den Wirtsgruppen mit relativ niederer Organisationshöhe (primitive Wirte) auch mit relativ niederer Organisationshöhe (primitive Parasiten) zu eigen sind.”

[27] Szidat’s rule was applied by Zlotorzycka (1963a) on the *Falcolipeurus* of New World vultures. The hosts, she claimed, are “the phylogenetically oldest group of Falconiformes”, and their *Falcolipeurus* are also “more primitive”. She therefore established the genus *Trollipeurus* for the *Falcolipeurus* species on New World vultures, based mainly on differences of proportions. *Trollipeurus* was not rcognised by Price *et al.* (2003a).

Liposcelidae (Johnson *et al.*, 2004; Murrell and Barker, 2005; Yoshizawa and Johnson, 2010), these two assumptions seem to be carried out. However, the distribution of Amblycera and Ischnoceran lice on the prospective candidates for "primitiveness", the Palaeognathes, does not support this interpretation of Szidat's rule (Price *et al.*, 2003a). Furthermore, as the fossil record of lice is virtually non-existent (Dalgliesh *et al.*, 2006), it is impossible to rule out that the absence of a group of lice on a given bird may be secondary (Hopkins, 1942, 1943).

More support could, perhaps, be found for Eichler's rule:

> "Among systematic categories of equal rank, those taxa exhibiting a rich [diverse] branching pattern also possess a larger diversity of the (mainly permanent) parasite fauna than those with fewer branches." (Modified after Klassen, 1992)[28]

This rule, elaborated by Eichler (1942), is perhaps intuitive, at least from a Fahrenholzian perspective. If lice diversify to the same degree as their hosts, then a very diverse group of hosts should be parasitized by a similarly diverse group of lice. Taking the current taxonomy and systematics of lice as an approximation of louse diversity, this correlation is perhaps valid in some cases. Many bird orders with few members are parasitized by a very limited number of louse genera (Price *et al.*, 2003a)[29], but there are examples of larger orders that collectively are hosts to few genera of lice[30], as well as small orders that collectively are hosts to many genera of lice [31]. The largest bird order, Passeriformes, encompassing roughly half of the bird species of the world, are collectively parasitized by 17 genera of lice (Price *et al.*, 2003a), however several of these genera have previously been divided into smaller units (*e.g.*, Zlotorzycka, 1964b), and Mey (2004) have established additional genera derived from *Philopterus*, suggesting that the current taxonomy of several of the

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[28] "Unter in sich gleichwertigen grösseren systematischen Einheiten von Wirten haben diejenigen Gruppen, welche eine reiche Gliederung aufweisen, auch eine grössere Mannigfaltigkeit des (vorwiegend ständigen) Parasitenbestandes als diejenigen mit geringer Gliederung." (Eichler, 1942). Note that Eichler called this the "Entfaltungsregel" ("Divergence rule") or the "III. parasitogenetische Korrelationsregel" ("Third rule of parasitigeneic correlation"; Fahrenholz' rule is the first and Szidat's rule the second). The first mention of this rule as Eichler's rule is by Hopkins, in a note appended to Eichler (1948).

[29] Some examples: Apterygiformes (1/2), Casuariformes (2/2), Coliiformes (2/2), Gaviiformes (1/1), Podicipediformes (6/2), Rheiformes (1/2), Sphenisciformes (6/2), Struthioniformes (1/1). The first number is the number of birds genera in the order [data from Clements' Checklist, v. 6.6 (available from http://www.birds.cornell.edu/clementschecklist/], and the second number is the number of louse genera parasitizing members of that order (data from Price *et al.*, 2003a).

[30] For instance the Strigiformes [208/4, of which one (*Laemobothrion*) is known from a single host species (Price *et al.*, 2003a) Three of these genera are distributed on birds of other orders.]

[31] For instance the Tinamiformes (8/20) and Opisthocomiformes (1/6).

presently accepted louse genera on passerines may be divisible into smaller units. No phylogenies with extensive sampling of *Philopterus*, *Penenirmus* and *Brueelia* from across the Passeriformes have yet been published. Vas *et al.* (2011, 2012) tested Eichler's rule for genera of lice on families of birds and mammals, and found a strong positive correlation between species richness of host families and the generic richness of their lice[32].

Several other rules still await a more thorough discussion and testing, including Timmermann's rule (that "hosts that are unusual or differ from the norm in their morphology or their behaviour are often parasitized by correspondingly aberrant parasites", my translation[33]), Janiszewska's rule (that "[h]osts belonging to rather common species have often a much more diversified parasitic fauna than species of absolute greater rarity"[34]), and Zlotorzycka's rule (that "within a given group of birds, genera of large birds are parasitized by several different louse genera, or rather the lice have radiated more on genera of large birds, apparently corresponding to the greater number of empty ecological niches here [on large birds]"[35]. Zlotorzycka's rule was tested by Clayton and Walther (2001), who found no such correlation. Lastly, what may be called "Hopkin's rule" (Eichler, 1948) states that birds with few genera or species of lice also tend to have very low abundances and prevalence of the few lice they have[36]. Clayton and Walther (2001) found evidence in favour of this rule in a study of Neotropical birds, however Møller and Rózsa (2005) suggested that this correlation was valid only for Amblyceran lice.

A great number of correlations between louse abundance, prevalence or species-richness and features of the host's ecology have been proposed. Geist (1935) compared prevalence data for several orders of birds to see if gregariousness, body size, or an aquatic lifestyle was correlated to high louse prevalence. Although his comparison is crude, he found that the "humidity factor is not as important as generally considered", but that "the gregarious

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[32] Interestingly, the taxonomic richness of Amblyceran lice and that of Ischnoceran lice are positively correlated (Vas *et al*., 2011), even discounting any effects of Eichler's rule.

[33] "ungewöhnliche, in Baueigentümlichkeiten oder Verhaltensweisen von der Norm abweichende Wirte oft von entsprechend aberranten Schmarotzern parasitiert werden" (From Eichler, 1973).

[34] Translation in original, taken from Eichler (1973), who unfortunately provides no reference for this rule.

[35] My translation of "Innerhalb einer bestimmten Vogelgruppe sind besonders grosse Vogelgattungen von mehrerlei verschiedenen Mallophagengattungen besiedelt bzw. die Mallophagen haben sich auf grösseren Vogelgattungen starker entfaltet, offensichtlich entsprechend den hier in stärkerem Masse zur Verfügung stehenden ökologische Nischen." (Eichler, 1973.)

[36] "The paucity of genera and species of Mallophaga on a given group of birds is commonly accompanied by a low incidence of infestation and by light infestations. He [Hopkins] has examined numbers of wild bustards and in his experience they are rarely infested with Mallophaga and the number of lice on infested individuals is always low" (Eichler, 1948)

habit" and large host size was connected to high louse prevalence. Ansari (1948) claimed that land birds had more lice than water birds, and that smaller birds had more lice than larger birds. In Wheeler and Threlfall's (1986) data set, the arboreal passerines had fewer lice than the ground-feeding species. Felso and Rozsa (2006) showed that diving birds are parasitized by fewer louse genera than non-diving birds. Birds with larger bodies tend to have more lice (Rózsa, 1997; Clayton and Walther, 2001), as one might predict.

More widely studied are the fluctuations of louse populations over the year, and the data from these studies are often indicative of the dependence of the lice on their hosts. Lice would be expected to increase in abundance before the host's breeding season to increase the chances of successful colonization of the chicks, but they would not be expected to lay eggs near the time where birds molt, as the eggs are attached to the feathers and would be lost when the feather is lost. Both these patterns have been demonstrated, with louse population increases coinciding with host breeding periods across a large range of birds (Woodman and Dicke, 1954; Ash, 1960; Foster, 1969; Eveleigh and Threlfall, 1976; Chandra *et al.*, 1990; Clark *et al.,* 1994; Saxena *et al.*, 2007; Singh *et al.*, 2009), and louse nymphs are dominant on host nestlings (Eveleigh and Threlfall 1976), however there may be a geographical factor to this as well (Martin *et al.*, 2007). While the number of hatched lice do not decrease during the host's molt (Moyer *et al.*, 2002c), no eggs are laid during this period (Foster, 1969).

The impact of host coloniality on louse populations has been evaluated from several angles. Colonially breeding hosts have been show to more frequently be parasitized by lice than solitarily breeding hosts (Rózsa *et al.*, 1996; Whiteman and Parker, 2004; but see Poiani, 1992). However, louse populations on colonial hosts are less aggregated[37] than louse populations on solitary hosts, and colonial hosts do not have greater abundances of lice than solitary hosts (Rózsa *et al.*, 1996). Conversely, territorial birds, which are often more solitary, have been shown to have more aggregated louse populations (Szczykutowicz *et al*, 2006).

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[37] A highly aggregated louse population is one in which a few host individuals are parasitized by large louse populations, whereas most host individuals have few or no lice. In a less aggregated louse population, the total "meta-population" of lice is more evenly distributed on the host individuals.

The essence of the species is thus the reproductive isolation in the sense that (expressed vulgarly) the members of a specific species keep to themselves
W. Eichler, 1980 (my translation)

4. Host biogeography and the Phthiraptera

The geographical distribution of a louse species can be said to be limited by the combined geographical distribution of all the hosts on which it occurs. However, not all populations or individuals of a given host species are parasitized by all (or any) species of lice known from the host species, and the actual geographic spread of a louse species may often be considerably smaller than that of the sum of its hosts. Clay (1949a) lists several such examples. For instance, birds introduced to New Zealand often lack one or more species of lice known from their native range (Paterson *et al.*, 1999). Similarly, Starlings *Sturnus vulgaris* in North America lack the louse species *Sturnidoecus sturni* (Boyd, 1951). Ward (1958) suggested that the absence of the genera *Lipeurus* and *Cuclotogaster* in the New World has a similar explanation, although farther removed in time. Paterson and Gray (1999) named this phenomenon “missing the boat”, which is a form of founder effect.

Absence of a species or group of lice from potential hosts in a geographical area, if not due to insufficient sampling, leads to interesting questions regarding ancient distributions of hosts and lice. However, absence of a louse taxon is typically easier to explain than an unexpected presence, as an absence would be the result of either local extinction [Ward’s (1958) third scenario; “secondary absence” (Clay, 1976)], a “missing the boat” scenario [Ward’s (1958) second scenario, called the “filtering effect”; “primary absence” (Clay, 1976)], or by a later colonisation or evolution of a louse lineage on only part of a host lineage [Ward’s (1958) first scenario]. An unexpected presence, if not an artefact of collection, challenges Fahrenholz’s rule, and is likely to give deeper insights into how and when lice can spread to new hosts.

4.1 How lice disperse to new hosts

As previously mentioned, the most common way for lice to disperse to new hosts, whether of the same species or not, is likely through direct contact between two birds. While direct contact between two birds of the same species can occur under a number of circumstances depending on the species of bird, two major themes may be seen. Firstly, lice can spread from one bird to another when these mate (Hillgarth, 1996)[38]. Secondly, lice can spread from parents to chicks in the nest (Clayton and Tompkins, 1994; Lee and Clayton, 1995, Brooke, 2010). If lice were limited to these two modes of dispersal, Fahrenholz' rule could reasonably be said to be valid. However, as detailed above, this is not always the case, and some of the reasons for the disparity between the louse phylogeny and that of their hosts are known.

Already in the early 20th century it was known that some lice could "hitch-hike" from one host to another by attaching to Hippoboscid flies, a phenomenon known as phoresy (reviewed by Clay and Meinertzhagen, 1943, and Keirans, 1975). By phoresy, lice could easily disperse between hosts, and thus escape the limitations imposed by the lack of a free-living dispersal stage. It is still unclear how important phoresy has been in the evolution of lice, but it could be an explanation for the existence of genetically identical *Brueelia* lice, a genus commonly found engaging in phoresy (Keirans, 1975), on passerines from four different families in the Philippines, as well as the general mismatch between the phylogeny of *Brueelia* species and that of their hosts (Johnson *et al.*, 2002a). Interestingly, Harbison *et al.* (2008, 2009) found that wing lice would engage in phoresy more often than body lice, which correspond well to their lesser degree of host specificity, however it is unclear if this is the only explanation for this discrepancy.

As opportunities for transmission between hosts is often rare in nature, lice could be expected to use any opportunity of contact between host individuals, whether of the same species or not, to disperse. A range of other opportunities for transmission to novel hosts has been suggested, including sequentially shared nest holes (Harrison, 1915; Johnson *et al.*, 2002a; Weckstein, 2004), communal sand or dust baths (Hoyle, 1938; Hopkins, 1949b; Price *et al.*, 2003a), kleptoparasitic behaviour of the hosts (Hopkins, 1942), host courtship feeding (Lindholm *et al.*, 1998), host grouping at caterpillar outbreaks (Brooke and Nakamura, 1998), shared nesting islands (Banks *et al.*, 2006), and straggling from prey to host (Whiteman *et al.*, 2004). Communal roosts, common in many bird groups[39], may be very important (Kellogg, 1898), as evidenced by the fact that social birds more often have lice than more solitary relatives (Rózsa *et al.*, 1996; Whiteman and Parker, 2004; but see Poiani, 1992). A fascinating account of water-walking by *Trinoton* lice of ducks was given by Stone (1967). As ducks are often gregarious, form multi-species flocks, and can migrate over large distances and from fresh water to sea water, it should be no surprise that most ducks of the world are considered to hosts the same species, *Trinoton*

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[38] It follows, as Kellogg (1898) suggests, that a host-specific louse on a species of bird that at least occasionally hybridizes with another species of bird could easily become established on both host species. Nelson (1972) give some specific examples.

[39] This is presumably what is meant by "hiding together" (Harrison, 1915) and "huddling together" (Ansari, 1948).

querquedulae[40] (Price *et al*., 2003a). Finally, continued gene flow between two allopatric host species may be facilitated through a third species, sympatric with both (Johnson *et al*., 2003b), provided opportunities for dispersal exist.

4.2 Limitations to dispersal: Harrison's rule

However, there also appears to be limits to how a louse species can spread. For instance, the nestlings of the brood-parasites would provide regular opportunities for the establishment of the lice of its brood hosts on the Cuckoo. While nestlings of brood parasites regularly have brood host-specific lice (Brooke and Nakamura, 1998; Lindholm *et al*., 1998), these are not found in adult *Cuculus canorus* (Brooke and Nakamura, 1998), and only rarely in *Chrysococcyx caprius* (Lindholm *et al*., 1998). In brood-parasitic indigobirds, there is little overlap between the lice of indigobirds and the lice of their Estrildidae hosts (Balakrishnan and Sorenson, 2007), but lice on fledgling Brown-headed Cowbirds *Molothrus ater* can at least sometimes be used to establish the brood host (Hahn *et al*., 2000).

The rarity of persistence of brood host specific lice on adult brood parasites could be explained by their degree of relationship. If the majority of the populations of brood host specific lice never live on brood parasites, they would be unlikely to adapt to circumstances on the brood parasites. Occasional individuals of brood host specific lice that occur on brood parasites would therefore be unprepared for any specific defence mechanism the novel host may have, and could therefore be out-competed by brood parasite specific lice. In general, we would expect brood host specific lice to adapt more easily to brood parasites that are closely related to the brood hosts than to those that are distantly related, as conditions on closely related birds are more likely to be similar than conditions on distantly related birds. This prediction seems to explain the rarity of brood host specific lice on *Cuculus canorus*, but not why the lice of estrildids so rarely occur on indigobirds, with which they are closely related (Sorenson and Payne, 2001).

One factor that seems to be limiting dispersal of lice even between closely related host species is host size, a trend first noted by Harrison (1915):

> "[I]n general, when a genus is well distributed over a considerable number of nearly related hosts, the size of the parasite is roughly proportional to the size of the host."

This trend has been named Harrison's rule (Eichler, 1963), and seems to be generally valid in direct host-to-parasite comparisons (*e.g*., Clay, 1951b; Kirk, 1991; Johnson *et al*., 2005; Paper II). Transfer experiments, where lice from one host has been transferred to another host of the same or different size, has been

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[40] It should be noted, however, that no genetic study has so far been performed of the genus *Trinoton*, and the true picture may be quite different.

made on swifts (Apodiformes; Tompkins and Clayton, 1999) and doves (Bush and Clayton, 2006), and these seem to support Harrison's rule. Pigeon lice of the genus *Columbicola*, for instance, could not survive for long on hosts that were either substantially larger or substantially smaller than the "donor" host, but could survive on novel hosts that were of the same size. Bush and Clayton (2006) noted that survival on smaller hosts than the typical host species was increased when preening was obstructed, suggesting that host defences is what is disabling dispersal. On larger hosts, the impairing of preening had no effect, so preening is not the only factor influencing the survivability on a novel host.

Tompkins and Clayton (1999) suggested that feather barb size might be an influencing factor, in parallel with the significant correlation between hair width and head morphology in gopher lice (Reed *et al.*, 2000a, b; Morand *et al.*, 2000). However, pigeon lice do not seem to experience any difficulties in remaining on feathers of different sizes (Bush *et al.*, 2006), and the true answer is probably more complex. Clay (1951b) briefly discusses the effect other morphological characters of feathers that may have influenced the evolution of lice.

4.3 Lice distributed on sympatric hosts

Dispersal routes that are independent of host genealogy, such as phoresy, all have the potential to disrupt the Fahrenholzian relationship between host and louse phylogenies, and it is interesting to note that in many cases where a species of louse has been found to inhabit several more or less distantly related hosts, an ecological explanation can often be suggested.

For instance, toucans sequentially share nets holes, and host species that occur in the same area, and therefore could potentially use the same holes, have the same species of lice (Johnson *et al.*, 2002a; Weckstein, 2004). This suggests that other hosts that may use the same nest holes may also have the same lice in other cases (Hopkins, 1939), and appears to be the case with the owl louse genus *Strigiphilus* (Clayton, 1990). Valera *et al.* (2003) found no exchange between Bee-eaters *Merops apiaster* and Rock Sparrows *Petronia petronia* in mixed breeding sites, however these hosts are very distantly related. Mixed breeding sites may also explain the distribution of the same species of lice on *Uria lomvia* and *U. aalge* (Eveleigh and Threlfall, 1976), some penguin lice (Banks *et al.*, 2006), as well as the lice of trogons, barbets, and some passerines on the Philippines (Johnson *et al.*, 2002a).

These cases suggest that, if a dispersal-prone host is able to pick up local lice when sharing breeding sites in a new area with less dispersal-prone birds, the world population of the dispersal-prone host species may collectively be parasitized by a large amount of louse species, none of which overlap geographically. The owl *Bubo virginianus* and its three species of *Strigiphilus*, two of which are found on other owl hosts with overlapping geographical distribution, may be an example of this pattern (Clayton, 1990).

Perhaps parallel to this pattern is the distribution of *Aquanirmus* lice on grebes (Podicipediformes). Two of the grebe species that are distributed across the Northern Hemisphere have lice belonging to different species groups on each side of the Atlantic (Edwards, 1965; Clay, 1976). European populations of *Tachybaptus ruficollis* and *Podiceps auratus* have lice more closely related to those of *Podiceps cristatus*, an exclusively Old World host species, than to the lice on populations of the same hosts in North America. These latter populations, in turn, belong to the same species group as those of *Podiceps dominicus*, an exclusively New World host species. While grebes are not hole-nesters, they can often be found inhabiting the same lakes (pers. obs.).

A similar type of geographical distribution is that discussed by Clay (1964). Two species of gannet (*Sula sula* and *Sula leucogaster*; Pelecaniformes) are distributed across the tropic seas. In the Indo-Pacific, both hosts are parasitized by the louse species *Pectinopygus annulatus*, but the Indo-Pacific populations of *Sula sula* are also hosts to *Pectinopygus sulae*. In the Atlantic, both these louse species are replaced by *Pectinopygus garbei*, which occurs on both host species. This suggests that *P. garbei* has a geographical distribution that at least today is independent of the geographical distribution of any one single extant host species.

Together, these examples show that biogeography and other ecological features of a host can and does influence distribution of its lice independently of the host phylogeny. A last example of this is Timmermann's (1971) claim that the Lapwing *Vanellus vanellus* has become host of *Quadraceps* and *Saemundssonia* lice more closely related to those of other wader species inhabiting the more arctic areas where it now lives, than with the other more tropical species of lapwing. As can be seen in Paper IV, there is some evidence that this is true, as *Quadraceps junecus* is indeed more closely related to *Quadraceps charadrii* and *Quadraceps hospes* (from the Arctic-breeding *Pluvialis apricaria* and *Pluvialis squatarola*, respectively) than to *Quadraceps renschi* (from the Australia-breeding *Vanellus miles*), however the data set included only these two lapwings so no definite conclusions can be drawn.

> **The inscrutability of this group of birds is made even more painful by their enormous aesthetic appeal.**
> *J. Connor, 1988*

5. The Shorebirds (Charadriiformes)

5.1 Classification of the Shorebirds

The shorebirds (Charadriiformes) is a truly global bird order, occurring from the high Arctic (gulls, Laridae; terns, Sternidae) to the Antarctic (sheathbills, Chionidae; skuas; Stercorariidae), from the seashore (*e.g.*, many sandpipers, Scolopacidae; many plovers, Charadriidae) to high into the mountains (Ibisbill, Ibidorhynchidae; seedsnipes, Thinocoridae), and includes birds that are almost exclusively marine (auks, Alcidae) as well as bird that live on steppes and savannahs (buttonquails, Turnicidae; coursers, Glareolidae). This diversity in habitat choice, lifestyle and distribution is unparalleled among bird orders. However, despite their morphological and behavioural heterogeneity, the shorebirds form a monophyletic group of birds (Faine and Houde, 2004, 2007; Ericson *et al*, 2006; Hackett *et al.*, 2008; Pásko *et al.*, 2011), with no close living relatives (Hackett *et al.*, 2008).

Charadriiformes is divided into three suborders, the Lari, the Scolopaci, and the Charadrii (Ericson *et al.*, 2003; Paton *et al.*, 2003; Thomas *et al.*, 2004a, b; Paton and Baker, 2006; Fain and Houde, 2007; Ödeen *et al.*, 2010), each of which contain a variety of smaller groups, and "typical" shorebirds – characterised by long bills and legs – can be found in all three groups (Fig. 9).

The Scolopaci (Fig. 10), which has been the main interest for this study, contains several familiar groups of shorebirds, such as the curlews (genus *Numenius*), the redshanks and allies (genus *Tringa*), the snipes and woodcocks (genera *Gallinago*, *Scolopax*) and the sandpipers (subfamily Calidrinae). It is divided basally (Ericson *et al.*, 2003; Paton *et al.*, 2003; Thomas *et al.*, 2004b; Fain and Houde, 2007; Gibson, 2010) into a tropical group [the Australian plains-wanderer (Pedionomidae), the Andean seedsnipes (Thinocoridae), and the pantropical painted-snipes (Rostratulidae) and jacanas (Jacanidae)] and a larger group (Scolopacidae) whose main breeding distribution is the Arctic and temperate regions of North America and Eurasia (Message and Taylor, 2005). Within this latter family, the sandpipers and allies (Calidrinae) is the most species-rich group (Message and Taylor, 2005).

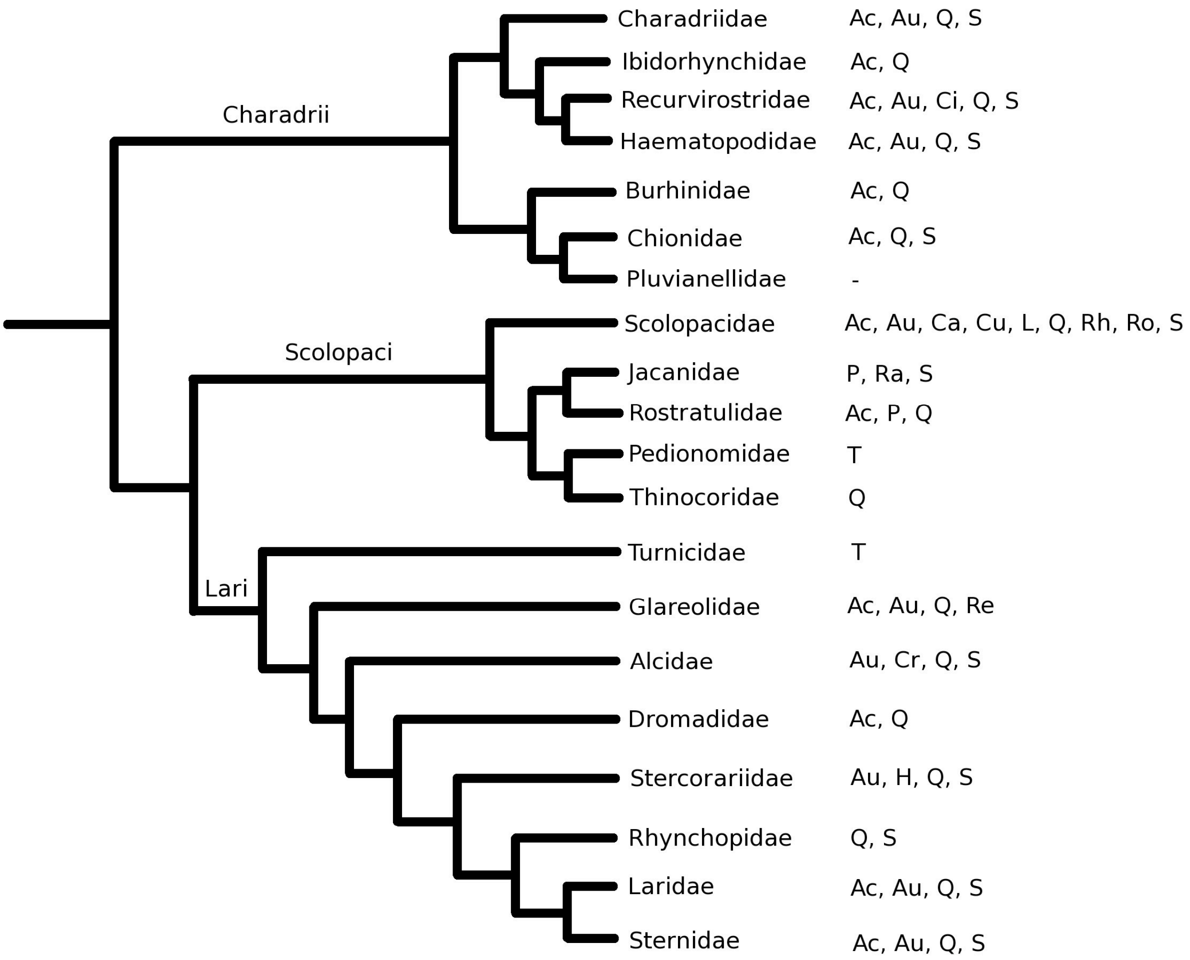

Fig. 9. Schematic phylogeny of the Charadriiformes, redrawn after Thomas *et al.* (2004a). Turnicidae and Ibidorhynchidae placed according to Baker *et al.* (2007) and Pereira and Baker (2010), respectively. Distribution of louse genera on the different families of Charadriiformes are listed on the right. Abbreviations used: Ac = *Actornithophilus*; Au = *Austromenopon*; Ca = *Carduiceps*; Ci = *Cirrophthirius*; Cr = *Craspedonirmus*; Cu = *Cummingsiella*; H = *Haffneria*; L = *Lunaceps*; P = *Pseudomenopon*; Q = *Quadraceps*; Ra = *Rallicola*; Rh = *Rhynonirmus*; Ro = *Rotundiceps*; S = *Saemundssonia*; T = *Turnicola*. Distribution data from Price *et al.* (2003). No lice are known from the Pluvianellidae. *Turnicola sp.* was reported from *Pedionomus torquatus* by Mey and Christidis (1997).

The Calidrinae, or sandpipers and stints (hereafter: sandpipers; Fig. 11), is a relatively homogeneous group, containing 26 species. The subfamily has traditionally been divided into several genera, but recent evidence indicate that these are all nested within the large genus *Calidris* (Borowik and McLennan, 1999; Gibson, 2010), and do not represent natural divisions of the sandpipers.

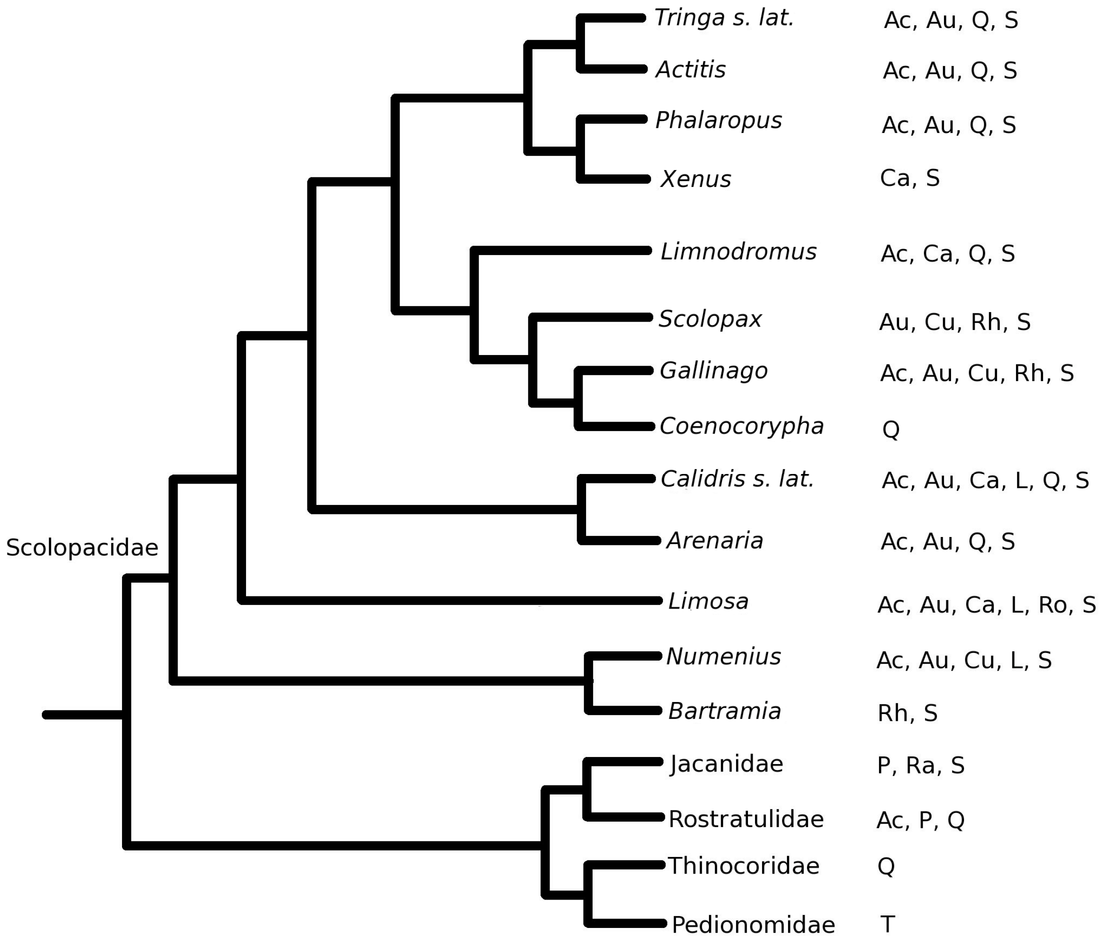

Fig. 10. Schematic phylogeny of the Scolopacidae, redrawn after Gibson (2010). Distribution of louse genera on the different taxa of Scolopacidae are listed on the right. Abbreviations used: Ac = *Actornithophilus*; Au = *Austromenopon*; Ca = *Carduiceps*; Cu = *Cummingsiella*; L = *Lunaceps*; P = *Pseudomenopon*; Q = *Quadraceps*; Ra = *Rallicola*; Rh = *Rhynonirmus*; S = *Saemundssonia*; T = *Turnicola*. Distribution data from Price *et al.* (2003).

5.2 The migration behaviour of Shorebirds

The Scolopacidae, and especially the Calidrinae, epitomizes a tendency found throughout all parts of the Charadriiformes of the Northern Hemisphere in that while the breeding localities are in the high Arctic or temperate zones, they spend the Arctic winters on the shores of Africa, Australasia, and South America[41] (*e.g.*, Wymenga *et al.*, 1990; Wilson and Barter, 1998; Message and

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[41] Within the Calidrinae, this is not true for the Purple Sandpiper *Calidris maritima* and the Rock Sandpiper *Calidris ptilocnemis*, both of which winter only slightly south of their breeding grounds. Purple sandpiper, for instance, breed in the mountains of Northern Scandinavia, but winters along the West Coast of Norway and Sweden (Svensson *et al.*, 1999). Some other sandpipers winter in smaller numbers in the Northern Hemisphare, but the majority migrate further south.

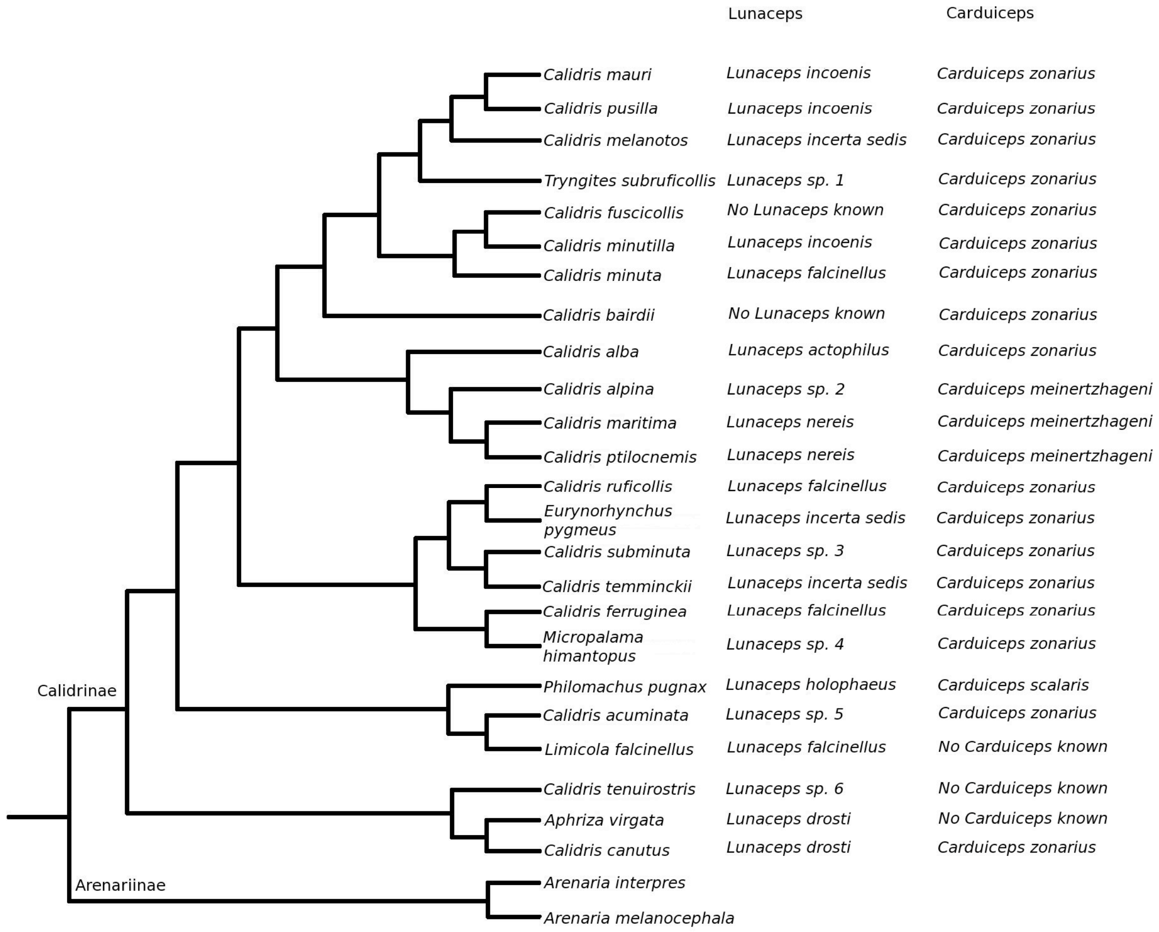

Fig. 11. Schematic phylogeny of the Calidrinae, redrawn after Gibson (2010), with distribution of *Lunaceps* species after Paper IV and distribution of *Carduiceps* after Price *et al.* (2003a). To avoid inadvertently publishing new names, some species are referred to by numbers. These species will be described in the published version of Paper II.

Taylor, 2005; Tjørve and Tjørve, 2007; Lopes *et al.*, 2008). Migration between the two regions often follow the coastlines of North America and Eurasia[42] in specific patterns, termed flyways (Fig. 12). Within each flyway, stop-over localities can often be quite set (Wilson and Barter, 1998), and several Scolopacids are vulnerable to environmental change and human development of coastal wetlands (Wilson and Barter, 1998; Bird *et al.*, 2010). However, flyways are believed to have changed over time (Wenink *et al.*, 1996; Kraaijeveld and Nieboer, 2000; Buehler *et al.*, 2006; Rönkä *et al.*, 2008) when habitats and coastlines were changed by recurring glaciations and fluctuating sea levels, affecting both breeding areas and locations of suitable stop-over areas during migration.

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[42] But see Gill *et al.* (2005, 2009) for an example of a bird that does not follow coastlines.

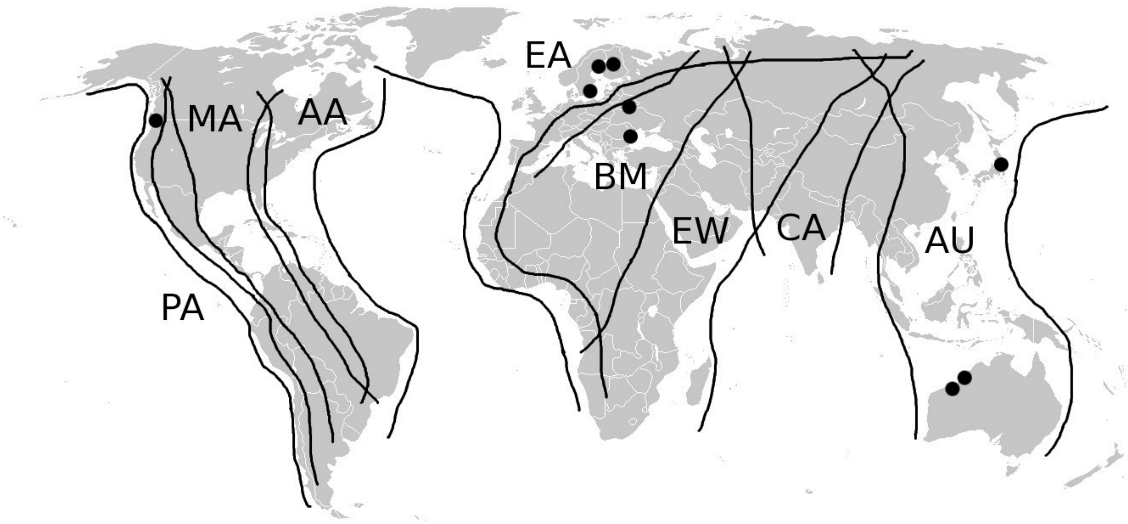

Figure 12. Simplified illustration of some flyways used by migrating shorebirds. Flyway names are abbreviated as follows: AA = Atlantic Americas; AU = East Asian/Australasian; BM = Black Sea/Mediterranean; CA = Central Asian; EA = East Atlantic; EW = East Africa West Asia; MA = Mississippi Americas; PA = Pacific Americas. Several species of shorebirds use more than one flyway, and species breeding in the same region may chose different flyways. Black dots denote collection localities for shorebird lice used in this thesis: Vancouver (Canada), Ottenby and Umeå (Sweden), Oulu (Finland), Turov (Belarus), Danube Delta (Romania), Tori-no-Umi (Japan), and Broome and 80 Mile Beach (Australia).

Another prominent feature of shorebirds, also driven to its extreme in the Scolopacids, is gregariousness. Although great assemblages of shorebird can be found on breeding grounds (*e.g.*, gull or auk colonies), the largest groups are typically found in the wintering quarters, where thousands of individuals can share a beach or lagoon, in enormous flocks. Very often, these flocks contain several species (Fig. 2), and even representatives from all three of the shorebird suborders[43].

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[43] While collecting material for this thesis in Australia, I had the opportunity to witness some of these gigantic flocks first-hand on 80 Mile Beach, south of Broome. Within a fairly small area, it was not unusual to spot all, or a subset of, the following species during a single day: Great Knot *Calidris tenuirostris*, Red Knot *Calidris canutus*, Curlew Sandpiper *Calidris ferruginea*, Sanderling *Calidris alba*, Sharp-tailed Sandpiper *Calidris acuminata*, Red-necked Stint *Calidris ruficollis*, Grey-tailed Tattler *Heteroscelis brevipes*, Marsh Sandpiper *Tringa stagnatilis*, Greenshank *Tringa nebularia*, Whimbrel *Numenius phaeopus*, Far Eastern Curlew *Numenius madagascariensis*, Bar-tailed Godwit *Limosa lapponica*, Black-tailed Godwit *Limosa limosa* (all Scolopaci), Red-capped Plover *Charadrius ruficapillus*, Lesser Sand Plover *Charadrius mongolus*, Greater Sand Plover *Charadrius leschenaultii*, Oriental Plover *Charadrius veredus* (all Charadrii), Silver Gull *Chroicocephalus novaehollandiae*, Gull-billed Tern *Gelochelidon nilotica*, Sandwich Tern *Thalasseus sandvicensis*, Greater Crested Tern *Thalasseus bergii*, Lesser Crested Tern *Thalasseus bengalensis*, Arctic Tern *Sterna paradisaea*, and Little Tern *Sternula albiforns* (all Lari). These commonly mixed freely, and subgroups behaved as single, mixed, flocks, rather than multiple, species-specific, flocks. Some of these species can be seen in Fig. 2.

Together, these two features of the shorebird hosts could plausibly be conducive to transfer of ectoparasites between host individuals, host species, and even hosts groups of higher taxonomic level.

> **No group of insects has suffered so much at the hands of authors who were ignorant of, or careless about, the Rules of Nomenclature as have Mallophaga.**
> *T. Clay and G. H. E. Hopkins, 1950*

6. The lice of Shorebirds

This section is intended to give a short overview of the genera of lice discussed in this thesis, as well as a short history of their taxonomy and their present status.

6.1 The Rallicolidae Eichler, 1959 and the Quadraceptinae Eichler, 1963

The family Rallicolidae was first mentioned by Eichler (1959), and *Quadraceps* "and others" were included in it from the beginning. However, specific morphological or other criteria for the establishment of this family are not given in Eichler's 1959 paper, nor in his large summary of louse systematics (Eichler, 1963). The family "is hard to place," Eichler (1963) claims, "as the Rallicolinae seems to be related to the Brueeliinae [which he placed in Philopteridae] through *Furnaricola*"[44].

Rallicolidae was proposed to encompass most of the ischnoceran lice on shorebirds (see below) and rails (*Rallicola, Incidifrons*), as well as certain other genera from other host orders (*e.g*.., *Mulcticola, Alcedoffula, Galliphilopterus*) (Fig. 13). Rallicolidae was not found to be monophyletic by Cruickshank *et al.* (2001), with *Mulcticola* being sister group to *Ardeicola* or alone, and the genus *Rallicola* split in two clades. Within their main Rallicolidae clade, *Saemundssonia* and *Quadraceps* were sister groups, with a *Rallicola* as their closest relative. *Quadraceps* and *Saemundssonia* were also recovered as sister by Johnson *et al.* (2002a), Yoshizawa and Johnson (2003), Smith *et al.* (2004; in at least some data sets), but not in the morphological data set of Smith (2001). However, in most cases, very few species of any Rallicolid genus were included.

Johnson *et al.* (2003a) also included three other Rallicolid genera (*Mulcticola, Incidifrons, Rallicola, Cirrophthirius*) and Rallicolidae is supported in this analysis, however *Quadraceps* and *Rallicola* are both paraphyletic, and *Saemundssonia* and the larger group of *Quadraceps* are not sister groups. *Mulcticola* is placed within a clade of *Philopterus*, and *Rallicola* from *Centropus* (Cuculiformes) is sister to *Furnaricola* from Passerines.

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[44] My translation of "Die Plazierung dieser Familie [Rallicolidae] ist dadurch schwierig, dass die Rallicolinae über Furnaricola [sic!] den Brueliinae [sic!] verwandt zu sein scheinen." (spelling of Brueeliinae and lack of italics for *Furnaricola* as in original). *Furnaricola* is treated as a synonym of *Rallicola* by Hopkins and Clay (1952) and Price *et al.* (2003a).

Rallicola has not been thoroughly revised since Clay (1953), although subgroups, delimited by host associations, were revised by Emerson (1955) and Price and Clayton (1993, 1994).

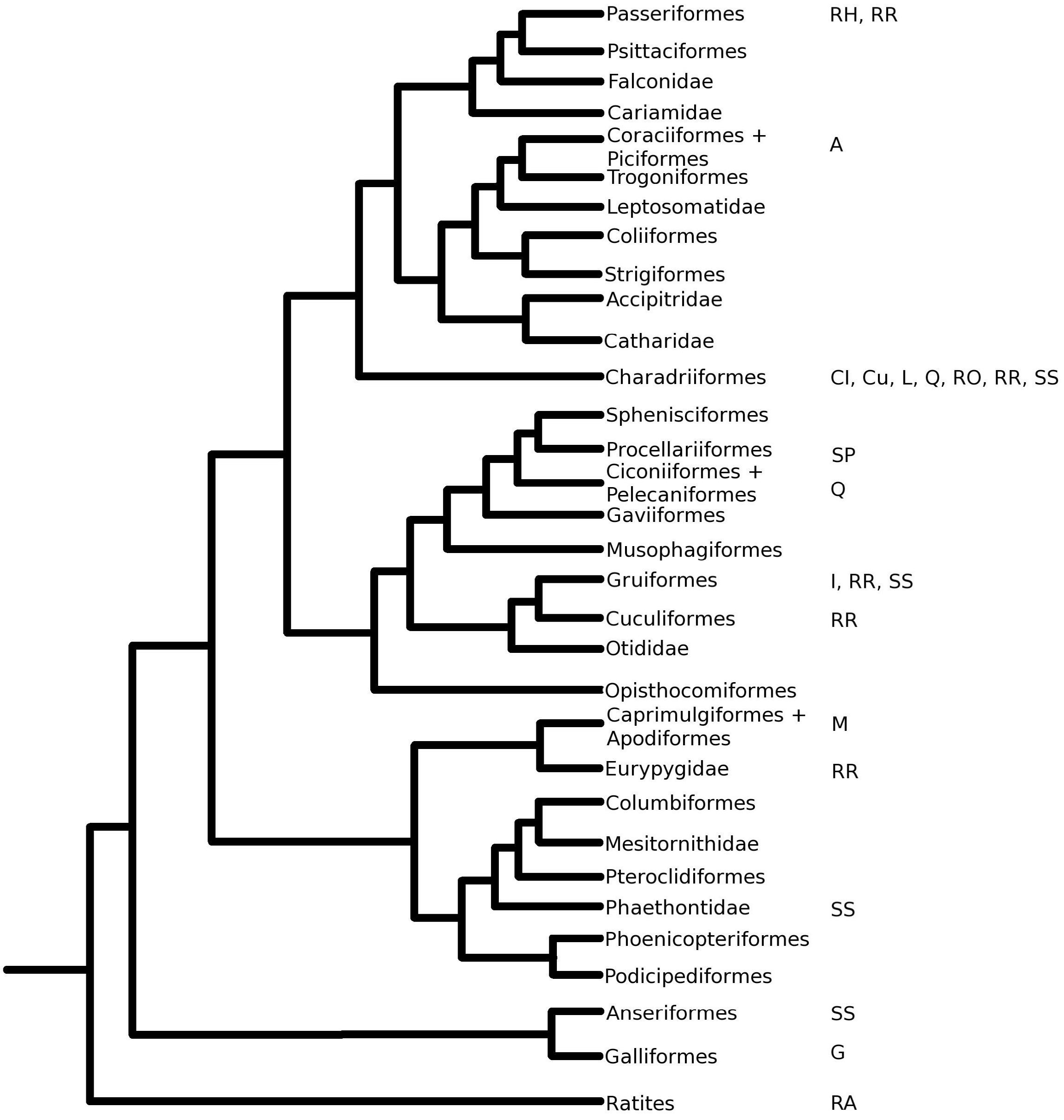

Fig. 13. Schematic phylogeny of birds (Aves), redrawn after Hackett *et al.* (2008). Distribution of louse genera placed in Rallicolidae by Eichler (1963) are listed on the right. Abbreviations used: A = *Alcedoffula*; CI = *Cirrophthirius*; CU = *Cummingsiella*; G = *Galliphilopterus*; I = *Incidifrons*; L = *Lunaceps*; M = *Mulcticola*; Q = *Quadraceps*; RA = *Rallicola (Aptericola)*; RH = *Rallicola (Huiacola)*; RO = *Rotundiceps*; RR = *Rallicola (Rallicola)*; SP = *Saemundssonia (Puffinoecus)*; SS = *Saemundssonia (Saemundssonia)*. Distribution data from Price *et al.* (2003). Note that in the phylogeny of Hackett *et al.* (2008), Ciconiiformes, Caprimulgiformes, Pelecaniformes, Coraciiformes, and Gruiformes are all paraphyletic.

6.2 Quadraceps *Clay and Meinertzhagen, 1939*

Quadraceps (Fig. 4A, B) was erected by Clay and Meinertzhagen (1939), and includes the majority of the Charadriiform lice. The genus is very heterogeneous, however, and has been split up into smaller units by some authorities (*e.g.*, Eichler, 1944; Timmermann, 1953a; Eichler and Zlotorzycka, 1964; Zlotorzycka, 1967). Conversely, Timmermann (1972, 1974) argued that all these forms, including the genus *Cummingsiella*, could not be separated morphologically, and should be included in the genus *Cummingsiella*, which has priority (Ewing, 1930). This was followed – to my knowledge – only by Eveleigh and Amano (1977). Most of the smaller genera, but not *Cummingsiella*, are included in *Quadraceps* by Price *et al.* (2003a).

Apart from some groups within the Scolopacidae, *Quadraceps* can be found on almost all families and species of shorebirds (Price *et al.*, 2003a). In a small number of cases there are more than one species of *Quadraceps* on the same host species. For instance, I have found both *Quadraceps fissus* and *Quadraceps hiaticulae* on the same individual Ringer Plover *Charadrius hiaticula*. One species, *Quadraceps umbrinus*, occurs on a host that is not within the Charadriiformes, namely the Hammerkop *Scopus umbretta* (Fig. 13). This species is nevertheless nested well inside *Quadraceps* (Paper IV).

For morphology of *Quadraceps*, see Timmermann (1957b) and Figure X. No thorough revision of the genus has been made since Zlotorzycka (1967), and it is unclear what the relationships between the different *Quadraceps* species are. Partial revisions, delimited after host group, were made by Eichler (1951), Timmermann (1952a-c, 1953a, b, 1954a, 1974), and Hopkins and Timmermann (1954).

6.3 Lunaceps *Clay and Meinertzhagen, 1939*

Lunaceps (Fig. 3A) was erected by Clay and Meinertzhagen (1939) and includes a small number of lice, most of which have a narrow suture which runs across the dorsal preantennal area, entirely or partially separating the dorsal anterior plate from the main plate of the head. The shape of this dorsal anterior plate is semicircular, and the name probably derives from its moon-like shape.

The genus occurs exclusively on some groups of Scolopacids (Fig. 10), but no two host groups (sandpipers, curlews, godwits) together form a monophyletic group to the exclusion of the rest of Scolopacidae, suggesting that host-switching has occurred frequently in this genus.

Lunaceps was revised by Timmermann (1954b) and in Paper II.

6.4 Saemundssonia *Timmermann, 1935*

Saemundssonia (Fig. 5B) was split from *Philopterus* by Timmermann (1935) on the basis of the morphology of the male genitalia. Another notable morphological character combining the genus is the “conspicuous darkly pigmented medioposterior process" of the dorsal anterior plate (Price *et al.*, 2003b). The genus contains head lice from shorebirds, cranes (Gruiformes), some seabirds (Procellariiformes), tropicbirds (Pelecaniformes, *Phaethon*), and the Pink-eared Duck *Malacorhynchus membranaceus*. *Saemundssonia* on seabirds are referred to the subgenus *Puffinoecus* (Price *et al.*, 2003a) (Fig. 13). The monophyly of *Saemundssonia* has never been tested molecularly, and although Paper IV contains some *Saemundssonia*, the majority of them are from shorebirds, and thus Paper IV does not test whether the species from cranes and the Pink-eared Duck are truly *Saemundssonia*.

The most recent complete revision of *Saemundssonia* is that of Eichler (1950b), however partial revisions have been made for the species occurring on gulls (Timmermann, 1951a), terns (Clay, 1949b; Ward, 1955), some Scolopacidae and Charadriidae (Timmermann, 1969; Martens, 1974), skuas (Palma, 2000) and auks (Price *et al.*, 2003b).

6.5 Carduiceps *Clay and Meinertzhagen, 1939*

Carduiceps (Fig. 6A) was described by Clay and Meinertzhagen (1939), and contains almost exclusively lice from the Calidrinae and the genus *Limosa* (Price *et al.*, 2003a). It is distinguished from *Quadraceps* by the shape of the preantennal suture, with two posterior-pointing extensions, and by the "tiger-stripes" of the abdomen, formed by thickenings of the pleurites (Timmermann, 1954c).

Carduiceps was placed by Eichler (1963) in the family Esthiopteridae, and is the only representative of this proposed group on Shorebirds. Inasmuch as any conclusions can be drawn from the known host distributions, *Carduiceps* appears to parasitize almost only hosts that are not parasitized by *Quadraceps* (Fig. 10). *Xenus cinereus* is the only Tringinae host to be parasitized by a *Carduiceps*, and no *Quadraceps* are known from this host. However, *Philomachus pugnax* is parasitized by species from both genera (although to my knowledge, *Quadraceps lahorensis* has been reported only by Ansari, 1955b).

Timmermann (1954c) has performed the only revision of this small genus.

6.6 Other Ischnoceran genera of lice on Shorebirds

Several smaller genera seem to replace *Quadraceps* on especially hosts of the family Scolopacidae. Apart from *Lunaceps* and *Carduiceps,* these include *Cummingsiella* (Ewing, 1930; on *Gallinago*, *Scolopax*, *Numenius*; Fig. 5A) and *Rotundiceps* (Edwards, 1952; on *Limosa*; not illustrated), both placed in Quadraceptinae by Eichler (1963), and *Rhynonirmus* (Thompson, 1935; on *Bartramia, Gallinago*, *Scolopax*; Fig. 3B), which he placed in Lipeuridae.

Outside the Scolopacidae, the genus *Cirrophthirius* (Timmermann, 1953a[45]; in Quadraceptinae; not illustrated) parasitizes avocets (Recurvirostridae). Some auks (Alcidae) are parasitized by the genus *Craspedonirmus* (Thompson, 1940; in Esthiopteridae; not illustrated), otherwise mainly found on loons (Gaviiformes) (Price *et al*., 2003a), and the skuas (Stercorariidae) are parasitized by the genus *Haffneria* (Timmermann, 1966; referable, by implication, to Eichler's Pseudonirmidae; not illustrated) most closely related to seabird lice (Procellariiformes; Page *et al*., 2004). The Jacanas (Jacanidae) are parasitized by *Rallicola* (Johnston and Harrison, 1911; not illustrated), otherwise found on *e.g*., rails (Rallidae; see Harrison, 1915; Clay, 1953). The distribution of the different louse genera on shorebirds is summarized in Fig. 9 and 10.

Assuming Eichler's (1963) classification is correct, this implies four separate groups of ischnoceran lice on Shorebirds (Rallicolidae, Esthiopteridae, Lipeuridae, and Pseudonirmidae), which suggests four separate colonization events. *Haffneria* is closely related to lice on Seabirds (Page *et al*., 2004), and its hosts, the skuas, are kleptoparasites that may steal food from Seabirds, suggesting a possible route for dispersal between the two host groups.

Most of these genera have never been revised, and typically contain very few species (Price *et al*., 2003a).

6.7 Amblyceran lice of Shorebirds

The Amblycera of Shorebirds belong mainly to two distantly related genera (Marshall, 2003): *Austromenopon* Bedford, 1939, and *Actornithophilus* Ferris, 1916. Both of these genera can be found on most Charadriiform families (Price et al., 2003a) (Fig. 8), and *Austromenopon* is also found on tropicbirds (Phaethon), many Seabirds (Procellariiformes) and the Hammerkop (*Scopus umbretta*; Ciconiiformes) (Fig. 13). *Actornithophilus* is the only genus of lice that is widely spread within the Charadriiformes, but does not occur on any hosts outside this order (Fig. 13).

Austromenopon is a skin-surface louse genus, whereas *Actornithophilus* lives inside feather shafts. This may be the reason why *Actornithophilus* is not collected as often as *Austromenopon* (Gustafsson and Olsson, *in prep*.). The two genera are well separated morphologically (see Clay, 1969; Price *et al*., 2003a; Marshall, 2003). Interestingly, both these genera have been reported from bird eggs (Thompson, 1936, 1957; Eichler, 1953b; Rankin, 1982), which, if not a coincidence, is a testimony to the greater mobility and increased tendency to leave the host in the Amblycera.

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[45] Eichler (1952) named the same species *Rhombiceps*, however it was the opinion of Hopkins and Clay (1953) that this genus was never actually described, and therefore a *nomen nudum*. Price *et al*. (2003a) follow Hopkins and Clay's (1953) decision to synonymise the two, with *Cirrophthirius* being given priority.

No complete revision of *Austromenopon* has been made, however Timmermann (1954d) reviewed the genus briefly, and the species on Seabirds have been revised by Timmermann (1963) and Price and Clay (1972). Clay (1959) provided a key to the species on shorebirds.

Timmermann (1954e) provided a key and review of the species-groups of *Actornithophilus*, and Clay (1962a) provided a key to the genus, however no more recent revision exists. Zlotorzycka (1963b) separated the species on gulls into the genus *Larithophilus*, however this genus was not recognised by Price *et al*. (2003a).

Two other Amblyceran genera have been reported from Shorebirds. *Pseudomenopon* Mjöberg, 1910, is found on Jacanas (Jacanidae) and Painted-snipes (Rostratulidae), and *Rediella* Hopkins, 1948, has been collected from one species of Pratincole (Glareolidae) (Price *et al*., 2003a). *Rediella* is unique to the Charadriiformes, whereas *Pseudomenopon* also occur on many rails (Gruiformes: Rallidae) and grebes (Podicipediformes) (Price *et al*., 2003a) (Figs. 8, 13).

A name as *Saemundssonia scolopacis-phaeopodis scolopacis-phaeopodis scolopacis-phaeopodis* (Schranck) to denote the population on the whimbrel is of course a nomenclatorial monster.
G. Timmermann, 1951b

7. Aims of this thesis

Already Hopkins (1939) suggested that straggling might occur naturally between shorebirds in dense flocks:

> Furthermore, many birds are apt to roost in company, especially on migration, while the habits of many sea-birds of breeding in the closest proximity with other species, and that of many waders and water-birds of feeding in close company, are well known. All these causes may give rise to casual natural straggling, though it is probable that unless the two host-species are very closely related, the lice so transferred will have but a very short period of survival on their new and unfamiliar host.

Although Hopkins' (1939) prediction was unknown to me when I started working with lice, the main aim of this thesis is to test whether the behavioural features associated with migration had any effects on the distribution and evolution of lice on shorebirds? More specifically, I want to test two patterns of louse distribution hypothesized from the ecological features of the hosts, and the known patterns of louse dispersal.

7.1 Flyway homogenization

The first pattern (Fig. 14) I have termed "Flyway homogenization" (Paper I), which rests on the assumption that the dense flocks of sandpipers that occur on migration and wintering would offer excellent opportunities for lice to disperse between different hosts. As these flocks typically contain more than one species of sandpiper, there may also be opportunities for lice to disperse between hosts of different species. Further, as many of these sandpiper species have non-overlapping breeding areas, or show much lower densities on breeding grounds, dispersal of lice on wintering grounds and migration stop-over points may essentially overshadow any distribution patterns based on host breeding biogeography. Instead, if this scenario is true, we should see a pattern where all sandpipers migrating along the same flyway would have the same species of lice.

Flyway homogenisation is expected to be more common in wing lice (*Lunaceps*) than in body lice (*Carduiceps*). This is both because wing lice may be topologically better placed on the host to to take advantage of opportunities of lateral transfer to novel host species, and because wing lice on other host groups are known to use non-contact methods of dispersal, such as phoresy

(Harbison *et al.*, 2008, 2009). This may be the reason why in pigeons, wing louse populations are less geographically structured than body louse populations (Johnson *et al.*, 2002a; Clayton and Johnson, 2003).

To simplify matters, the impact of the low amount of vagrant sandpipers that migrate along the "wrong" flyway is assumed to be negligible, although it should be noted that such individuals occur regularly.

I test this hypothesis by examining two genera of lice more or less specific to sandpipers, *Lunaceps* and *Carduiceps*, and analyse to what extent lice collected along the same flyways differ. This hypothesis was tested in Paper I and Paper III.

7.2 Flyway differentiation

At the same time, I hypothesized that another pattern could appear (Fig. 15). Several of the sandpiper species migrate along more than one flyway, with different breeding populations wintering in different areas of the world. In a few cases, these populations have been given subspecific status (Dickinson, 2003; Message and Taylor, 2005). For instance, the subspecies of Red Knot *Calidris canutus* migrating past Sweden and wintering in West Africa is *C. canutus canutus*, whereas the subspecies migrating past Japan and wintering in Australia are *C. canutus rogersi* and *C. canutus piersmai* (Buehler *et al.*, 2006). The breeding areas of these three subspecies are also distinct (Buehler *et al.*, 2006).

If these populations breed in different areas, migrate along different flyways, and winter in different areas, this could act as an isolating mechanism for their lice, and different subspecies of the hosts may have genetically different populations of lice, even if the morphology may lag behind. By comparison, different subspecies of tinamous often have different species of lice (Price *et al.*, 2003a).

Flyway differentiation is predicted to be more common in body lice (*Carduiceps*) than in wing lice (*Lunaceps*). Body lice are less favourably placed on the host to be able to take advantage of opportunities of lateral transfer outside of the breeding or nesting season, and are also known to be indifferent to opportunities of phoresy in experimental settings (Harbison *et al.*, 2008, 2009).

I test this hypothesis by analysing the same set of data as above, looking for evidence that different populations of the same host species carry different clades of lice, and whether these are sufficiently different to warrant species status or not. This hypothesis was tested in parallel to the first hypothesis, in Papers I and III.

7.3 Morphological revision of Lunaceps

In addition to the testing of the two hypotheses above, a morphological revision of the genus *Lunaceps* was also carried out, in order to ascertain whether the species limits recovered in Paper I corresponded to morphological differences or not. Previously existing species descriptions of *Lunaceps* lice are almost

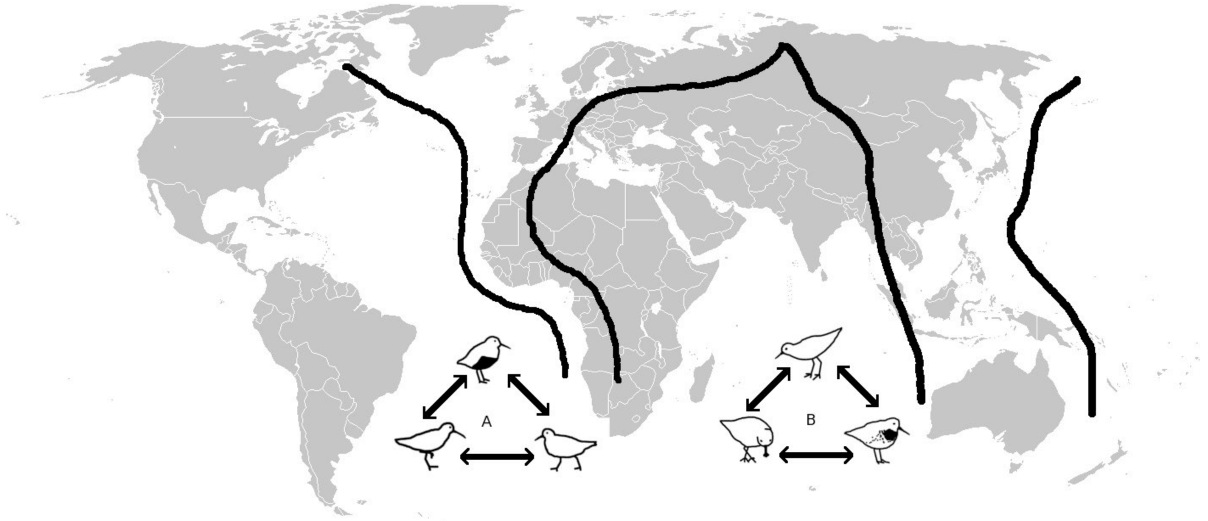


Fig. 14. Under the hypothesis of flyway homogenisation, gene flow would exist between louse populations parasitic on different host species migrating along the same flyway. Over time, this would homogenise the louse populations of all potential host species along that flyway. A) East Atlantic Flyway, with Dunlin *Calidris alpina*, Curlew Sandpiper *Calidris ferruginea* and Red Knot *Calidris canutus*. B) East Asian/Australasian Flyway, with Sharp-tailed Sandpiper *Calidris acuminata*, Spoon-billed Sandpiper *Eurynorhynchus pygmeus* and Great Knot *Calidris tenuirostris*.

invariably very hard to use, including both the description of the genus (Clay and Meinertzhagen, 1939) and the last revision of the genus (Timmermann, 1954a). This revision constitutes Paper II.

7.4 The phylogeny of the Quadraceptinae

The view of Quadraceptine systematics is particularly illustrative of the divided views on louse systematics of the 20th century described above. Many previous authors have believed *Quadraceps* to be a morphologically heterogeneous genus, and have subdivided it into smaller units (Eichler, 1940, 1943, 1944, 1949, 1954, 1982; Timmermann, 1950, 1953a, 1954f; Eichler and Zlotorzycka, 1964; Zlotorzycka, 1967). The genera *Lunaceps, Cummingsiella*, *Rotundiceps*, and *Cirrophthirius* were recognised as valid by Price *et al.* (2003), whereas most of the other proposed Quadraceptine louse genera on shorebirds were not. Both *Cummingsiella, Rotundiceps*, and *Lunaceps* occur mainly on hosts that are not parasitized by *Quadraceps*, but these hosts are closely related to host species that are parasitized by *Quadraceps*.

This anomalous distribution pattern could be the result of several different processes. The smaller genera could represent an older lineage of Quadraceptine lice which was previously more widely distributed on shorebirds, but which has now largely been out-competed by *Quadraceps*. Alternatively, *Quadraceps* could have parasitized these hosts (or their ancestors) but become extinct, and the smaller genera could subsequently have established populations on their

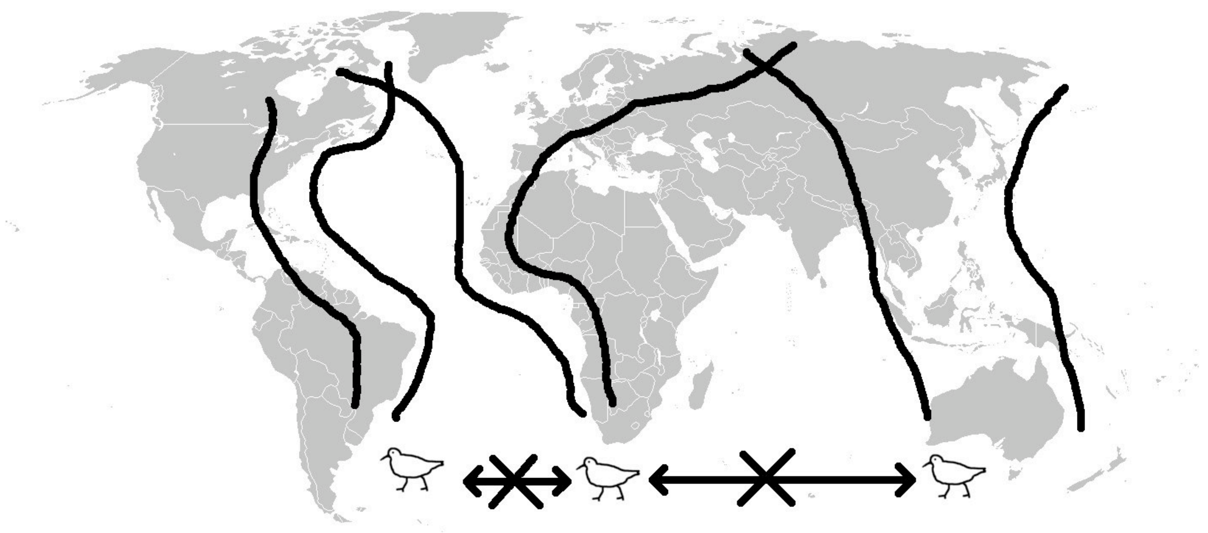


Fig. 15. Under the hypothesis of flyway differentiation, gene flow would not exist between louse populations parasitic on different populations the same host species that migrates along different flyways. Over time, this would differentiate the louse populations on the same host species so that host populations using different flyways would have different species of lice. For example, the louse populations of three populations of Red Knot *Calidris canutus* migrating along the Atlantic Americas, East Atlantic, and East Asian/Australasian flyways would be isolated from each other, and over time form three different species. Globally, the Red Knot would be parasitized by as many different louse species of a given genus as there are isolated flyways.

present hosts in the absence of *Quadraceps*. It is also possible that the present taxonomy of the group simply does not reflect the relationships within the Quadraceptinae, and that *Quadraceps* as circumscribed today is paraphyletic with regards to these, and other, genera.

Lastly, most of the genera Eichler (1963) assigned to Quadraceptinae have one thing in common, namely that the majority of their species are distributed within the Charadriiformes or the Rallidae (Gruiformes). However, there are a few exceptions, which would be hard to explain both from a Fahrenholzian perspective of them being inherited from common ancestors, and from a host-switching perspective, as these birds would rarely if ever come in contact with each other (Fig. 13). Paper IV tests the monophyly of Quadraceptinae *sensu* Eichler (1963), and the position of *Lunaceps* within the Quadraceptinae.

7.5 The Swedish Taxonomy Initiative

A separate part of my studies has been devoted to a survey of the lice on birds in Northern Europe, sponsored by the Swedish Taxonomy Initiative. This survey remains incomplete for many groups of birds, and no results of this survey have yet been published. However, a list of the Phthiraptera known from the Nordic countries is attached as Appendix I to this thesis. This list is based both on material collected during my studies and a literature survey. The list should not be seen as complete, even for already published material, as for instance little data for Denmark has been available to me.

> **Making satisfactory mounts of lice in Canada balsam is a very simple process, though it is certainly more tedious than making useless ones.**
> *G. H. E. Hopkins, 1949a*

8. Methods of collection and analysis

8.1 Collection

The basis of this thesis was a collection of lice taken from a variety of bird hosts on three continents: Eurasia (Sweden, Finland, Romania, Belarus, Japan), Australia, and North America (Canada, USA).

Birds were caught by a number of methods, including mist nets, cannon nets, whosh nets, wilster nets, hand nets, noose mats, Heligoland-type traps, Ottenby type walk-in traps, duck traps, floating duck nets, or removing nestlings from the nests by hand (Fig. 16). Apart from some collection in the Gothenburg area (Sweden), all bird capture was carried out during regular or project-based bird banding activities, and in cooperation with bird banders. Birds were identified, measured and banded before they were searched for parasites. Handling by banders before fumigation may reduce the amount of lice on a bird (Vas and Fuisz, 2011), however many banders have though that the risk of accidentally releasing a bird before it has been banded has been too high. Fumigating birds after they have been banded, measured, and handled by banders has therefore generally been the only workflow possible.

While large birds (roughly > Domestic pigeon *Columba livia*) were searched manually and lice picked off with a forceps, most birds were fumigated (Fig. 17). A cloth collar was fastened around the neck of the bird, and the bird's body was lowered into a glass jar. Ethyl acetate was used as a fumigant. This chemical was found to be less efficient than chloroform and carbon dioxide by Visnak and Dumbacher (1999), but is less dangerous and less cumbersome to travel with, easier to order abroad, and safer for both the bird and the researcher. Fumigation continued for 10-20 minutes, roughly corresponding to the size of the bird. Birds that became drowsy or injured during fumigation were released immediately. Some birds managed to pull their heads into the fumigation chamber, and these birds were held under observation, if possible, and then released without further fumigation. All fumigation chambers were placed in good ventilation when possible for the duration of fumigation.

All birds were released after fumigation, and lice were collected from the fumigation chamber by a cotton bud or a forceps. When collecting indoors (Ottenby, Furenko, Fukushimagata) birds were ruffled over a white surface before release, and lice were collected by forceps. When collecting outdoors (all other localities) this was typically impossible, and not attempted. Lice were stored in 95% alcohol, if possible in a fridge or freezer, however when collection circumstances did not permit this, they were kept at ambient temperature.

8.2 Data analysis

This thesis consists of studies that rely on both molecular and morphological evidence. For the morphological studies, resulting in Paper II, I relied heavily on a large number of microscopy slides borrowed from museums across the world (see Paper III for a detailed list). These were studied by light microscopy, measured, and redescribed, with line drawings. These redescriptions supplement the description of six new species and one new subspecies, and were necessary as none of the previous descriptions of any *Lunaceps* species was very satisfactory. While some morphological data was collected in a matrix form for ease of comparison, no cladistic study of this data was performed.

The morphological revision of *Lunaceps* was augmented by a molecular study. Lice selected for molecular studies were cut apart between the prothorax and pterothorax, and DNA was extracted, amplified, and sequenced. Details of these procedures, as well as details about data analysis can be found in Papers I, III, and IV, and will not be reiterated here. Exoskeletons were retrieved after DNA extraction, and mounted in Canada balsam on microscopy slides. These mounts serve as vouchers for the published DNA sequences, and have been or will be deposited at the Göteborg Natural History Museum (Gothenburg, Sweden; GNM), the Swedish Museum of Natural History (Stockholm, Sweden; SMNH), or the Yamashina Institute for Ornithology (Abiko, Japan; YIO).

Fig. 16. Bird catching by various methods. A) Francois Lemoine inspecting a mist net at Furen-Ko Bird Observatory, Japan. The birds – in this case Reed Bunting *Emberiza schoeniclus*, Long-tailed Rosefinch *Uragus sibiricus* and some unidentifiable species – fly against the thin nets, fall into pockets formed by the net, and entangle themselves. They are then extracted with utmost care. B) Mist nets at Furenko Bird Observatory, Japan, arranged in long series between a bicycle path and an area of bamboo and bushes. This setup is about 800 metres long. After extraction, the birds are placed in the white cloth bags before being banded. C) A duck trap at Ume Delta Bird Observatory, Sweden. Ducks swim into this passive trap, but cannot easily get out due to the funnel-like construction of the entrances. Food is provided inside. At Ottenby Bird Observatory, the duck catching capability of the trap is enhanced by the presence of domesticated ducks permanently on the inside of the trap. D) A wilster-net at Ume Delta Bird Observatory, Sweden. The large net lies flat on the ground, until birds – often lured there by a combination of bird calls and plastic lures – are landing in front of the net. The net is then pulled manually over them, which requires exact timing. E) The Heligoland traps of Ottenby Bird Observatory, Sweden, flanking the banding station. Birds are flushed into these funnel-like traps by yelling and clapping by the bird banders, and collected in a small box.

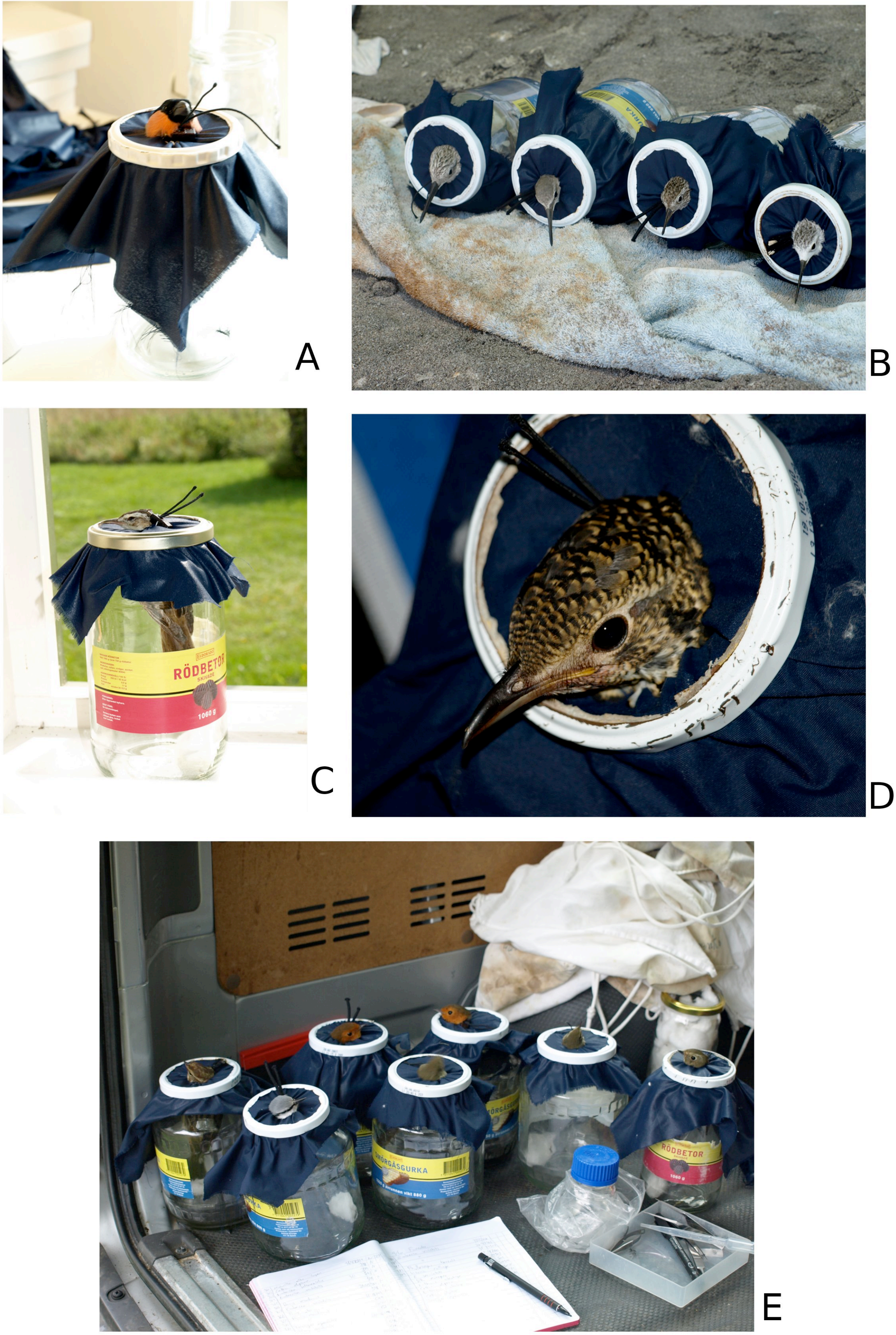
A

B

C

D

E


A
B
C
RÖDBETOR
1060 g
D
SMÖRGÅSGURKA
RÖDBETOR
E

Three loci were used in the phylogeny reconstructions: COI, 12S and 16S[46]. In addition, four nuclear[47] and one mitochondrial[48] primer sets were tried, but without any success, for *Lunaceps* and *Carduiceps*. For most of the *Quadraceps* species included in Paper IV, only COI sequences were obtained, but primers for 12S, 16S, cytochrome *b*, and opsin have worked for some species, and there is a potential to expand the data set of Paper IV using these and other primer sets.

A total of three phylogenetic and two other statistical methods were used to analyse the data sets of this thesis. For phylogeny reconstruction, I used Bayesian Inference in MrBayes (Huelsenbeck and Ronquist, 2001, 2005), Parsimony Bootstrap in PAUP* (Swofford, 2002), and Maximum Likelihood in PhyML (Guindon and Cascuel, 2003; Guindon *et al.*, 2010). These three methods estimate phylogenies based on different assumptions and algorithms, and each have different strengths. In addition, for Paper I, two non-phylogenetic analyses were used: *s* of Slatkin and Maddison (Maddison and Slatkin, 1991) and the Genealogical Sorting Index (Cummings *et al.*, 2008). Details of settings for these programs can be found in Papers I, III, and IV, and will not be reiterated here.

Fig.17. Examples of the simple fumigation chambers used to collect samples for this thesis. A) Bullfinch *Pyrrhula pyrrhula* hanging from its neck in fumigation chamber at Ottenby Bird Observatory, Sweden. B) Sedge Warbler *Acrocephalus schoenbaenus* being fumigated at Ottenby Bird Observatory, Sweden. C) Several birds can be fumigated at the same time. Here (from left to right), Great Knot *Calidris tenuirostris*, Wandering Tattler *Heteroscelis brevipes*, Sharp-tailed Sandpiper *Calidris acuminata*, Marsh Sandpiper *Tringa stagnatilis* are fumigated simultaneously at 80 Mile Beach, Australia. D) Close-up on head of White's Thrush *Zoothera dauma* to show how cloth is fastened to fumigation chamber. E) Approaching the upper limit of birds that can be fumigated at the same time, Furen-ko Bird Observatory, Hokkaido, Japan (from left to right): Reed Bunting *Emberiza schoeniclus*, Nuthatch *Sitta europaea*, Japanese Robin *Erithacus akahige*, unknown passerine, Japanese Robin, Arctic Warbler *Phylloscopus borealis*, Red-flanked Bluetail *Tarsiger cyanurus*.

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[46] Primers used: L6625 and H7005 (COI; Hafner *et al.*, 1994), 12SAI and 12SBI (12S; Simon *et al.*, 1994), 16SAR and 16SBR (16S; Simon *et al.*, 1994).

[47] The examined primer sets were: EF1-For3 and EF1-Cho10 (Elongation Factor 1a; Danforth and Ji, 1998), LWRhF and LWRhR (opsin; Mardulyn and Cameron, 1991), F6999, F7081, and R7495 (ND5; Yoshizawa, 2004), and LepWG1 and LepWG2a (*wingless*; Brower and DeSalle, 1998).

[48] CYB146L and CYB825H (Gómez-Díaz *et al.*, 2007).

> **In the progress of this work, however, the author has had to contend with repeated rebukes from his friends for entering upon the illustration of a tribe of insects whose very name was sufficient to create feelings of disgust.**
>
> *H. Denny, 1842*

9. Results – Phylogeny and biogeography of shorebird lice

9.1 Phylogeny of shorebird lice

The ischnoceran lice of shorebirds do not form a monophyletic group. Instead, as shown in Paper IV, at least three groups of lice parasitize shorebirds. The majority are within Eichler's (1963) Rallicolidae, but *Carduiceps* and *Rhynonirmus* (placed in Esthiopteridae and Lipeuridae, respectively, by Eichler) are only distantly related. The genera *Turnicola, Craspedonirmus* and *Haffneria*, which were not included in any analysis, were all placed in different families by Eichler (1963).

Eichler's (1963) Rallicolidae appears to form a monophyletic group in Paper IV, but the relationship between its two proposed subfamilies (Rallicolinae and Quadraceptinae) differs between analyses. The phylogeny of Paper IV is based only on the mitochondrial COI, and support values are low for most groupings across the three analyses. Any discussion on the relationships of the taxa studied must therefore be speculative, and the phylogeny is presented here mainly to identify areas of future research into interesting and problematic areas. In the most resolved analysis (Maximum Likelihood), Quadraceptinae is monophyletic, but nested within Rallicolinae. In the Bayesian inference analysis, Quadraceptinae and Rallicolinae are sister groups. In both cases, *Rallicola sp. ex Aramides cajanea* is placed within Quadraceptinae, as a sister to *Incidifrons*. The lack of any deeper structure in the Bootstrap analysis precludes any analysis of the validity of the two subfamilies. *Rallicola* was under-sampled in this thesis, and it is likely that a broader sampling of the genus may resolve the relationships between Rallicolinae and Quadraceptinae.

Quadraceps is the most widely sampled genus in Paper IV, and both the Maximum Likelihood and the Bayesian Inference analyses suggest that it may be paraphyletic. Assuming that the scattered clades of *Quadraceps* would not form a monophyletic group in a better resolved analysis, the genera *Lunaceps*, *Saemundssonia*, *Cummingsiella*, and *Incidifrons* may need to be included in *Quadraceps* in order to retain all the species currently placed in *Quadraceps* in the genus. This would have the unfortunate consequence that several easily identified genera well established in the literature would have to be synonymised with *Incidifrons*, which has priority (Ewing, 1929).

Supposing the topology of the phylogeny presented in Paper IV remains essentially the same in a more robust analysis, including more taxa and more genes, this suggests that an alternative to lumping together most of Quadraceptinae into *Incidifrons* may be to divide *Quadraceps* into smaller genera, and resurrect many of the genera listed as synonyms to *Quadraceps* by Price *et al.* (2003a). The proposed genera *Koeniginirmus* (Eichler, 1940), *Oedicnemiceps* (Eichler, 1943), *Glareolites* (Eichler, 1944), *Mjoeberginirmus* (Eichler, 1944), *Haematophagus* (Timmermann, 1950), *Proneptis* (Timmermann, 1953a), *Cistellatrix* (Timmermann, 953a), and *Chadraceps* (Zlotorzycka, 1967) can all be recognised as distinct clades in the phylogeny of Paper IV.

In Paper I, which focuses on a smaller group, but is based on a more comprehensive selection of molecular loci and a higher number of individuals per taxon than Paper IV, *Lunaceps* is monophyletic and nested within a paraphyletic *Quadraceps*. There is little correspondence between the phylogeny of the hosts of *Lunaceps* (see *e.g.*, Gibson, 2010) and that of *Lunaceps*. Instead, a number of single-host *Lunaceps* species are mixed with others that span several host species. In general, *Lunaceps* on smaller Calidrinae hosts are distributed over several hosts in the same geographical region (New World or Old World), whereas *Lunaceps* on larger Calidrinae hosts are all single-host species. The three sampled *Lunaceps* from *Numenius* species are almost genetically identical.

The *Carduiceps* phylogeny of Paper III corresponds very well to the relationships established by Timmermann (1954c) and the taxonomy adopted by Price *et al* (2003a). One species, *Carduiceps zonarius*, completely dominates the phylogeny, being found on all sampled host species except three. These three are all hosts to a single species of *Carduiceps* each. *Carduiceps* is tentatively placed in Eichler's (1963) Esthiopteridae in Paper III. It forms a clade together with *Columbicola* in the Bayesian Inference analysis of the most extensive data set, but this relationship may be spurious and based on the small number of taxa sampled. The relationship with *Columbicola* has never been suggested before. *Columbicola* has been extensively studied molecularly (Clayton and Johnson, 2003; Clayton *et al.*, 2003; Johnson *et al.*, 2002c, 2003b, 2007; Malenke *et al.*, 2009), however no *Carduiceps* sequences have ever been published prior to this study, and *Carduiceps* has never been included in any phylogenetic study.

9.2 Biogeography of shorebird lice

I hypothesized that shorebird lice would largely follow two different, but complementary, biogeographical patterns due to host migration ecology.

Firstly, the mixed flock behaviour of shorebirds was expected to give ample opportunity for lice to spread laterally to all potential host species along a given flyway, absent other limiting factors such as size. This would suggest that lice on all potential host species that migrate along a given flyway may be genetically the same, as gene flow between populations on different host species would be allowed. I called this hypothetical pattern “flyway homogenisation”.

Secondly, the usually very strict adherence of a host population to a single flyway was expected to isolate their louse populations, so that populations of the same host species migrating along different flyways would have different species of lice. This hypothetical pattern is called “flyway differentiation”.

These two hypothesized patterns could enhance each other, but either of them could exist independent of the other. The extremes are shown in Table 1.

I tested these two hypotheses by sampling and sequencing two genera of shorebird lice, *Lunaceps* and *Carduiceps*. I further hypothesized that flyway differentiation would be more common in the body louse genus *Carduiceps*, as body lice have been found to be less prone to dispersal using non-contact methods, such as phoresy (Johnson *et al.*, 2002c; Clayton and Johnson, 2003; Harbison *et al.*, 2008, 2009). For the same reason, flyway homogenisation should be more common in the wing louse genus *Lunaceps* than in *Carduiceps*.

However, while there are some examples of homogenisation in *Lunaceps* (Paper I), only two of the clades with material from more than one species are limited to a single flyway. The most widely distributed *Lunaceps* species, *Lunaceps falcinellus* (Clade I in Paper I) is found across two flyways, and does not occur on all species migrating along either flyway. There is also no support for flyway differentiation in *Lunaceps*, as all hosts sampled from more than one flyway had the same species of lice throughout their range. However, as there is a split between the lice of Nearctic breeders and those of Palaearctic breeders, flyway differentiation may exist within the host species that have a Holarctic sistribution, such as *Calidris canutus* or *Calidris alpina*. This could not be determined, as neither of these host species were sampled in North America.

Carduiceps most closely resembles scenario III in Table 1, in that most host species are parasitized by the same louse species, *Carduiceps zonarius*. There is a slight, generally unsupported, split between material of this species from North America and that from Eurasia, but the division is not complete. The only other species sampled from more than one flyway was *Carduiceps meinertzhageni* from *Calidris alpina*, which shows no evidence of flyway differentiation. *Calidris alpina* and *Philomachus pugnax* are the only two Calidrine hosts sampled that were not parasitized by *Carduiceps zonarius*, however the reason for this is unknown.

The same divide between North American and Eurasian lice is found also in Paper IV, where both *Quadraceps* species on *Charadrius hiaticula* and *Charadrius semipalmatus* are genetically different. Similarly, the Old World samples of *Quadraceps semifissus* and *Quadraceps hemichrous* are closely related, even though the host of *Q. semifissus* is more closely related to the host of *Quadraceps zephyra*.

	Flyway homogenisation present	**Flyway homogenisation absent**
Flyway differentiation present	All birds migrating along a given flyway have the same species of lice. However, host species that migrate along multiple flyways, have different species of lice along different flyways. Gene flow is present between louse populations on all potential hosts migrating along a given flyway, but not between flyways. The total number of lice in the genus is equal to the number of flyways.	Birds migrating along the same flyway have different lice, and populations of the same host species migrating along different flyways have different species of lice. Gene flow is absent between all louse populations on all potential host species. The total number of lice in the genus on a given host species is equal to the number of flyways it migrates along, and the total number of lice in the genus is equal to the sum of all such numbers for the host group concerned.
Flyway differentiation absent	All birds have the same species of lice, regardless of which flyway they migrate along. Gene flow is present between louse populations on host species migrating along a given flyway, but not between louse populations on populations of the same host species migrating along different flyways. The total number of species in the genus is one.	Other mechanisms that structure louse populations are active, making it impossible to predict the number of louse species in a genus, and between which louse populations gene flow can exist, without knowledge of these mechanisms.

Table 1. Extreme scenarios of flyway differentiation and flyway homogenisation for a given louse genus. The first three examples assume no other structuring mechanism, such as Harrison's rule, is operating on the louse populations, or that the effect of such mechanisms is negligible.

One of the great problems in the present study has been to keep the work down to a reasonable length.
J. A. Ledger, 1980

10. Conclusions and future perspectives

As is often the case, the actual distribution patterns of lice are more complex than predicted by theory. Neither Fahrenholz' rule, nor the flyway-based hypothesis of flyway homogenisation and flyway differentiation (hereafter: flyway hypotheses) presented in this thesis can adequately predict phylogenetic relationships between shorebird lice.

Like Fahrenholz' rule, the flyway hypotheses can be used as a null hypothesis for predicting the phylogenetic relationships between lice on migrating birds that follow set flyways and form large mixed flocks. If the phylogenetic patterns of a group of lice are similar to what would be expected from the flyway hypotheses, this implies that a specific set of assumptions holds true for the group of lice studied. Some of these assumptions are summarized in Section 7 and Table 1. Others include the assumption that no other structuring mechanisms, such as Harrison's rule, have had any great impact on the phylogenetic history of the lice in question. As gene flow between louse populations on host populations migrating along different flyways need to be low or nonexistent for flyway differentiation to occur, it is also assumed that phoresy and other dispersal mechanisms have no or little impact. There are no documented cases of phoresy involving shorebird lice (Keirans, 1975), but this mechanism cannot be ruled out for all groups of lice on birds that migrate along flyways.

10.1 The flyway hypotheses tested

The flyway hypotheses of this thesis predicted that the wing louse genus *Lunaceps* would be subject to both flyway differentiation and flyway homogenisation. The wing lice are suitably placed topologically to take advantage of opportunities for lateral transfer to novel hosts in dense, mixed flocks at stop-over and wintering grounds. Therefore, unless there are other barriers for lateral spread, there should be a constant gene flow between *Lunaceps* populations on different hosts along the same flyway, and speciation on the different host species should not occur. Similarly, with little contact between populations of the same host species migrating along different flyways and wintering in different areas, there should be little gene flow between *Lunaceps* on the same host species migrating along different flyways. We would expect these two mechanisms to give rise to a pattern where one or a few

Lunaceps species are present along a given flyway, but differ from the *Lunaceps* species found along another flyway, even if the hosts migrating along these two flyways were the same. Size-dependent mechanisms, such as Harrison's rule, suggests that there may still be some leeway for multiple species of *Lunaceps* along the same flyway, but on hosts of roughly the same size, one species should be predominating.

The body louse genus *Carduiceps* is not expected to be influenced by flyway homogenisation, as they are topologically less suitably positioned to take advantage of opportunities for lateral spread in dense, mixed flocks of hosts. However, flyway differentiation would still be expected, as the host populations of different flyways are not expected to meet often enough to permit a steady gene flow between *Carduiceps* populations on the same host species migrating along different flyways. The flyway hypotheses thus predicts that in *Carduiceps*, we should see several species on host species migrating along the same flyway, but these *Carduiceps* species should be different from those occurring on the same host species migrating along another flyway.

Neither of these hypotheses are supported by our data. There are some tendencies of flyway homogenisation in *Lunaceps*, in that several smaller sandpipers and stints share genetically identical *Lunaceps* populations. All *Lunaceps* material sampled from the Pacific Americas flyway is genetically identical, but the material sampled from the two Old World flyways is not as homogeneous. Instead, both Old World flyways sampled contain both *Lunaceps* species that occur on several host species, and *Lunaceps* species that occur on a single host species. Flyway homogenisation is therefore not complete. In all cases where *Lunaceps* were sampled from the same host species along more than one flyway, they were genetically identical, even when the host species were divided into different subspecies along different flyways. Only *Lunaceps* from *Calidris alpina ssp.* differed slightly between flyways, but this difference had no support in any analysis.

However, the phylogeny of *Lunaceps* does not fit very well to the predictions of Fahrenholz' rule either. Direct comparisons between the *Lunaceps* phylogeny in Paper I and the Calidrinae phylogeny of Gibson (2010) reveals that there is little correspondence, and no host groupings of any of the *Lunaceps* clades containing material from more than one host are monophyletic. The Slatkin and Maddison test performed on this material rejected the host phylogeny-based model of *Lunaceps* evolution, but could not reject either of the flyway-based models.

The body louse genus *Carduiceps* fits the predictions of Fahrenholz' rule and the flyway hypotheses even worse. Virtually all *Carduiceps* sampled falls into the same clade, which spans ten host species and all three sampled flyways. There is a slight division of *Carduiceps zonarius* into one Old World clade and one New World clade, but this division is not complete, and is never well supported by any locus analyzed. The only other *Carduiceps* species sampled over more than one flyway is genetically identical across its range.

One particularly interesting finding of this thesis is that the phylogenies of *Lunaceps* and *Carduiceps* show opposite patterns compared to those of pigeon lice (Johnson *et al.*, 2002c; Clayton and Johnson, 2003) where body lice show more phylogenetic structure than wing lice. This suggests that patterns found in the lice of one group of birds need not necessarily apply to all groups of birds, and many mechanisms of dispersal and successful colonisation likely remain to be discovered.

10.2 Extension of the flyway hypotheses to other louse ecotypes

These flyway studies were limited to three genera of lice, *Lunaceps* and *Carduiceps*, and most of the *Quadraceps* species were not sampled from more than one flyway. Those that were indicate a similar division into one group from New World hosts and one that is homogeneous across the Old World (*e.g.*, *Quadraceps fissus, Quadraceps hiaticulae*), and several species included in Paper IV are genetically identical across large distances within the Old World (*Quadraceps obscurus, Saemundssonia lari, Quadraceps punctatus*).

Other studies comparing different louse genera on the same set of hosts have included the same two ecotypes as I included here: body lice and wing lice. An extension of these comparisons to other groups of lice is needed, to study what factors may structure the distribution of head lice or amblyceran lice. In the Calidrinae, these categories would be represented by *Saemundssonia*, and *Actornithophilus* and *Austromenopon*, respectively.

Flyway hypotheses-based predictions of the head louse genus *Saemundssonia* are difficult. One the one hand, they would be even worse situated, topologically, than *Carduiceps* to be able to take advantage of opportunities for lateral spread between hosts in mixed flocks, as the heads of the birds would possibly never come into contact with each other. On the other hand, shorebirds usually put their heads under their wings while resting. This would bring their *Saemundssonia* lice into a better position to exploit any body contact between different host species, especially as shore birds often rest at high tide, when lack of dry ground may force them into closer proximity than usual. No *Saemundssonia* have been found outside the host's heads in the birds sampled for this study, and the capabilities of *Saemundssonia* species to move around on the body of their hosts is unknown.

In the current taxonomy (Price *et al.*, 2003a), all *Saemundssonia* on sandpipers are placed in the same two species, *Saemundssonia tringae* and *Saemundssonia platygaster*. These species are widely spread, occurring on *Tringa, Phalaropus, Arenaria, Charadrius, Vanellus* and *Jacana*, although these species limits have never been tested molecularly. If the current taxonomy is correct, this would speak in favour for an enhanced capability to disperse, compared to, *e.g.*, *Lunaceps* and *Carduiceps* which both have more limited distributions. Wherein this greater capability for dispersal lies is presently unknown.

For the Amblyceran genus *Austromenopon*, common on all shorebirds, predictions of the flyway hypotheses are clearer. *Austromenopon* is expected to be widely distributed across sandpiper hosts, as it is a highly mobile genus, which readily climbs onto banders' hands (pers. obs.). Most *Austromenopon* species are distributed over large numbers of closely related hosts (Price *et al.*, 2003a)[49], but few are actually known from Calidrine hosts, and only two of these hosts are parasitized by the same *Austromenopon* species under the current taxonomy (Price *et al.*, 2003a). Nevertheless, the flyway hypotheses would predict *Austromenopon* to be affected by flyway homogenisation, but not necessarily by flyway differentiation. Small amounts of sandpipers occur outside the flyway those populations normally migrate along yearly[50]. The high mobility of *Austromenopon* lice makes it likelier that these sporadic visits of novel sandpipers to a given flyway would be enough to keep up a gene flow between populations in different parts of the world.

Actornithophilus is a shaft-dwelling louse, and may therefore be limited in its capabilities for dispersal, depending on how much of their life is spent inside the quills, if there is a seasonal fluctuation in when they inhabit quills, and how easily they can leave the feather shafts. These are factors that are presently unknown, but *Actornithophilus* were found more often, and in greater numbers, in the wintering grounds of Australia than closer to the breeding areas in Sweden when I collected material for this thesis (data not shown). This may indicate that there is a dispersal mechanism in action during wintering that is absent during earlier parts of migration. Most *Actornithophilus* known from sandpipers are considered to belong to the same species in the current taxonomy (Price *et al.*, 2003a), and this is the prevailing pattern among other groups of shorebirds[51].

10.3 Extending the flyway hypotheses to other host groups

While flyway homogenisation largely depends on there being opportunities for lateral spread between host species migrating along different flyways at least at

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[49] *Calidris alpina* is host to *Austromenopon alpinum*, *Calidris canutus* to *Austromenopon lutescens*, *Calidris maritima* to *Austromenopon erilis*, and *Philomachus pugnax* to *Austromenoponlutescens*. No *Austromenopon* are known from any other Calidrinae species.

[50] As an example, the *Lunaceps* from *Tryngites subruficollis* used in this thesis were collected from a *Tryngites subruficollis* captured at Öland, eastern Sweden. This locality is in the East Atlantic Flyway, but the host normally migrates along the Mississippi American or Pacific Americas flyways.

[51] For example, *Actornithophilus grandiceps* is found on seven species of *Haematopus*, *Actornithophilus hoplopteri* on 12 species of *Vanellus*, *Actornithophilus ochraceus* on 19 *Charadrius* and allies, *Actornithophilus piceus lari* on 31 Laridae, and *Actornithophilus piceus piceus* on 23 Sternidae (Price *et al.*, 2003a).

some point during the migration cycle, flyway differentiation does not require this. Instead, for flyway differentiation it is only necessary that a host metapopulation uses more than one flyway during migration, and that occurrences outside the normal flyway for a given populations are rare enough for gene flow between louse populations to be very low, or non-existent. Conditions like these are present throughout the Charadriiformes, but also in several other groups of birds.

Within the Charadriiformes, other groups of Scolopacids, such as *Tringa, Numenius, Limosa, Limnodromus,* and *Phalaropus* are all suitable candidates for testing the flyway hypotheses. Outside Scolopacidae, *Charadrius* and *Pluvialis* are perhaps the most suitable candidates for further study, as they both occur in mixed flocks with other shorebirds. *Quadraceps* from some of these genera were included in Paper IV. The most persistent pattern in shorebird lice seems to be the division between Old World and New World species, but the latter were under-sampled in this thesis, precluding any appreciation of how common this division is.

Most gulls are parasitized by *Quadraceps punctatus* or *Quadraceps ornatus, Actornithophilus piceus lari, Austromenopon transversum* and *Saemundssonia lari*. Under the current taxonomy, these species have global ranges (Price *et al.*, 2003a). Gulls, like many smaller shorebirds, are highly gregarious, and often form mixed-species flocks that may be very dense. The opportunities for lateral spread from one host species to another are often abundant, and judging from current taxonomy and the genetic similarity between some of the species included in Paper IV, it appears that these opportunities are real, and that there is, or at least has been, gene flow between louse populations on different gull species.

The flyway hypotheses can be applied also to non-Charadriiform birds, as long as they conform to the necessary behaviour patterns. Several groups of birds migrate along flyways, and have populations that are divided into different flyways and wintering grounds. Ducks (Anseriformes), many birds of prey (Falconiformes), cranes (Gruiformes) and many passerines (Passeriformes) are all good examples.

Under the current taxonomy (Price *et al.*, 2003a), ducks around the world are almost all hosts to the same set of lice: *Anatoecus dentatus, Anatoecus icterodes, Anaticola crassicornis, Holomenopon leucoxanthum, Holomenopon clypeilargum,* and *Trinoton querquedulae*. Ducks can be intensely gregarious, and form enormous mixed-species flocks outside breeding season. Stone (1967) discovered that one of these louse species, *Trinoton querquedulae*, can walk on water and does so in the direction of any disturbance of the water surface (such as a duck), while other genera of lice may preferentially spread by more conventional methods. None of the lice on ducks have been thoroughly studied genetically, with a broad sampling of material from across the world and across host species.

10.4 Revision of Rallicolidae

There is a need for a thorough revision of the genera of Rallicolidae. While *Saemundssonia* and *Lunaceps* both appear to be monophyletic, *Quadraceps* and *Rallicola* seem not to be. While the paraphyly of *Rallicola* may be an artefact of the low amount of sampled species, the paraphyly of *Quadraceps* is more extensive, and was found both in a limited data set (Paper I) and in a larger one (Paper IV).

Most genera placed in Eichler's (1963) Rallicola have not been thoroughly revised for a long time. *Quadraceps* and *Cirrophthirius* were last revised by Zlotorzycka (1967), *Rallicola* by Clay (1953), *Saemundssonia* by Eichler (1950c), *Alcedoffula* by Tendeiro (1967), and apart from Paper II, *Lunaceps* was last revised by Timmermann (1954b). Smaller parts, often delimited by host association rather than by morphology, of many of these genera have been revised since (see Section 6, above). Since their respective last thorough revisions, at least 14 *Quadraceps* names, 67 *Rallicola* names, 62 *Saemundssonia* names, and one *Alcedoffula* name have been published (Price *et al.*, 2003a). *Mulcticola, Cummingsiella, Galliphilopterus,* and *Incidifrons* have never been revised.

A complete revision of all genera included by Eichler (1963) in Rallicolidae is therefore sorely needed. The aims of such a revision would be manifold.

The division between Rallicolinae and Quadraceptinae is not supported by the Maximum Likelihood analysis in Paper IV, but is supported by the Bayesian Inference analysis of the same data set. In both analyses, *Rallicola* is paraphyletic, with *Rallicola sp. ex Aramides cajanea* being placed as sister to *Incidifrons transpositus ex Fulica americana*, and with both of these placed as more closely related to *Quadraceps s. str.* than to the other *Rallicola*. The large spread of *Rallicola* across several host orders (Fig. 13) has previously prompted its division into different genera (see Eichler, 1963, for a list), most of which are not recognised today (Price *et al.*, 2003a). What is the relationship between Quadraceptinae and Rallicolinae, and how are Rallicolinae and *Rallicola* structured?

As shown tentatively in Paper IV, *Quadraceps* is also divided into several clades, interspersed in the Maximum Likelihood and Bayesian Inference phylogenies with clades containing other genus level taxa, such as *Lunaceps* and *Saemundssonia*. Many of these *Quadraceps* clades correspond roughly to previously proposed genera that have been synonymised with *Quadraceps*, including *Haematophagus, Chadraceps* and *Koeniginirmus*. *Quadraceps s. str.* appears to form a very small clade, containing only three, maybe four, species. What are the relationships between *Quadraceps* and the other shorebird louse genera? What taxonomic system would be most useful to both reflect these relationships and provide nomenclatorial stability to the group? Should *Quadraceps* be divided into several smaller genera, or should *Saemundssonia*, *Lunaceps* and the other closely related genera be included in an expanded *Quadraceps* (which would then perhaps be called *Incidifrons*)?

The genus *Mulcticola* forms a sister group to all other Quadraceptinae in the Bayesian Inference phylogeny of Paper IV, and to all the other Quadraceptinae except *Cirrophthirius* in the Maximum Likelihood phylogeny. This genus is not found on shorebirds, but on nightjars (Caprimulgiformes), but few Quadraceptinae from non-Charadriiform hosts were included in Paper IV, so it is difficult to judge if this is spurious. *Mulcticola* has been placed outside the Rallicolidae in a previous phylogeny (Cruickshank *et al.*, 2001). What are the true relationships between these genera – *Mulcticola, Galliphilopterus, Alcedoffula* – and the rest of Rallicolidae? Are these genera monophyletic, and can they be placed, as Eichler (1963) did, inside Quadraceptinae, or would another higher categorization of the genera of Rallicolidae be more illustrative of evolutionary relationships?

Paper II is a revision of the genus *Lunaceps*, and revealed several undescribed species and sometimes complicated host-parasite relationships, with some species being distributed across several hosts, and others being more restricted. Some species – such as *Lunaceps nereis* and *Lunaceps rileyi* – are very distinct, whereas others – *Lunaceps falcinellus, Lunaceps superciliosus* and *Lunaceps incoenis* – are virtually identical, and can often be told apart only in larger series. Does this imply that there is a similar hidden diversity among the other Rallicolid genera? In Paper IV, both *Quadraceps fissus* and *Quadraceps hiaticulae* are divided into two clades according to host relationships, suggesting that a larger sample of Quadraceptinae taxa may reveal similar examples. However, *Quadraceps anagrapsus*, *Quadraceps alcae, Quadraceps punctatus* and *Quadraceps obscurus* are genetically identical across multiple hosts, and it therefore cannot be assumed that any *Quadraceps* species occurring on more than one host must conceal a genetic diversity.

These are some of the many questions that could be answered only by a comprehensive revision of the Rallicolidae. However, a revision of Rallicolidae could also be instrumental in understanding the evolutionary history of lice in general. Representatives of the Rallicolidae parasitize many of the major groups of birds, and *Rallicola* alone is distributed across four of the five major clades of birds (Fig. 13). Collectively, the hosts of the rallicolid lice span the globe from the auks and sandpipers of the Arctic to the sheathbills and skuas of the Antarctic, including both highly migratory species and ones that are sedentary throughout the year. The hosts inhabit most kinds of habitats in the world, from the wide oceans to the high mountains, and exhibit all degrees of gregariousness, both within and between species. The Rallicolidae and their hosts offer opportunities to study almost every imaginable scenario for louse transmission and dispersal, and could provide an often easily accessible framework for asking questions about the historical development of the louse distribution patterns and communities we see today.

10.5 Molecules and morphology

A revision of the Rallicolidae would need to take into account both molecular and morphological methods. A drawback in all three molecular data sets studied in this thesis is that none of them include any data from nuclear genes. For *Lunaceps* and *Carduiceps*, I tried four sets of nuclear primers that have previously been used for estimating louse phylogenies, but all failed to amplify any products (see section 8.2 above). At least one primer set (*wingless*) appears to work for *Quadraceps*, and the mitochondrial cytochrome *b*, COI, 12S, and 16S primers work as well. This means that the data set of Paper IV could be expanded into a multi-gene data set using already developed primer sets. More nuclear genes would be desirable, however, and new primer sets may have to be developed for the nuclear regions of *Lunaceps* and *Carduiceps*.

The data sets compiled for this thesis have been analysed by two common phylogenetic methods: Bayesian Inference and Parsimony Bootstrap (the Rallicolidae COI data set also by Maximum Likelihood). While these methods are widely used across all animal taxa, there is a set of phylogenetic methods including tree comparisons that are of particular use to host-parasite research. Co-evolutionary analyses focus especially on the relationship between two sets of taxa, believed to have shared a parallel evolutionary history due to (at least) one set's dependence on the other set. The two data sets are compared statistically and points of parallel bifurcations are identified. Several programs to compare phylogenetic trees exist, such as TreeMap (Page, 1994; Charleston, 1998), TreeFitter (Ronquist, 1995), and ParaFit (Legendre *et al.*, 2002). These have previously been used to study co-evolution between lice and hosts in passerines (Johnson *et al.*, 2002a), penguins (Banks *et al.*, 2006), cormorants (Hughes *et al.,* 2007), and seabirds (Page *et al.*, 2004; Hammer *et al.*, 2010)

This thesis did not contain any co-evolutionary analyses of any data set, as no complete data set of the host species of *Lunaceps* or *Carduiceps* have been published[52]. There are published phylogenies and data sets for several other groups of Rallicolidae hosts, such as auks (Alcidae; Friesen *et al.*, 1996; Moum *et al.*, 2002; Pereira and Baker, 2008; Humphries and Winker, 2010), gulls (Laridae; Crochet *et al.*, 2000; Crochet *et al.*, 2002; Pons *et al.*, 2005), jacanas (Jacanidae; Whittingham *et al.*, 2000), plovers (*Charadrius*; Joseph *et al.*, 1999), shanks and allies (*Tringa* and allies; Pereira and Baker, 2005), terns (Sternidae;

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[52] Gibson (2010) is used as a reference to the phylogeny of Scolopacidae and Calidrinae throughout this thesis. However, while the phylogeny is available online, it is from a M.Sc. thesis at the University of Toronto, and the data set it is based on has not been published. Thomas *et al.* (2004a) has also been used as a reference for host phylogeny several times, but this is a super-tree based on a number of other published phylogenies. There is therefore no data set comparable to those compiled for the louse phylogenies behind the tree of Thomas *et al.* (2004a). The data set of Borowik and McLennan (1999), including most relevant taxa, appears to be unavailable on GenBank.

Bridge *et al*., 2005), skuas (Stercorariidae; Cohen *et al*., 1997; Ritz *et al*., 2008), nightjars and allies (Caprimulgiformes; Larsen *et al*., 2007; Han *et al*., 2010), cranes and allies (Gruiformes; Fain *et al*., 2007), kingfishers (Moyle, 2006), and the ovenbird-woodcreeper assemblage" (Furnariidae-Dendrocolaptinae; Fjeldså *et al*., 2005; Irestedt *et al*., 2004, 2006). Several large-scale phylogenies spanning the whole Charadriiformes are also available (Ericson *et al*., 2003; Paton *et al*., 2003; Thomas *et al*., 2004b; Paton and Baker, 2006; Baker *et al*., 2007; Fain and Houde, 2007; Hackett *et al*., 2008; Ödeen *et al*., 2010). These, and other data sets, are ready for comparison with louse data sets with material collected from these hosts

However, morphological data and a traditional morphological revision of each of the genera in Rallicolidae also have natural parts in any future work on the group. Above all, this is important for identification purposes, and for placement of taxa that cannot be examined molecularly, such as extinct species and species that are hard to collect, either due to the scarcity of its host, or because of scarcity of the species itself. While, ideally, a molecular revision of the Rallicolidae should include all known taxa, this may be impractical for taxa that live in remote places, have small, sparse populations, or are hard to catch for practical reasons. A comprehensive morphological revision, tied to robust estimations of phylogeny, may therefore be vital in the classification of all known Rallicolidae taxa.

Morphological work on the Rallicolidae will also have practical aspects for the end users of biodiversity information. Reliable, robust keys to all taxa will aid in identification of species for amateurs and others who do not have the ability to determine collected specimens by molecular methods. The revision of *Lunaceps* I did during this thesis revealed a previously unappreciated diversity within the genus, and preliminary studies of the *Quadraceps* material I have collected suggests that more detailed investigations into morphological variation and character evolution of the group will be exceedingly rewarding, both on a personal level and on a professional level. Tracking character evolution and relating similar morphological traits of various groups of lice to their evolutionary history can only be made once these morphological traits are well known. Many distantly related groups of lice are superficially similar (Smith, 2001; Smith *et al*., 2004), and convergent or parallel evolution appears to be common. Examinations of nymphal series may reveal vital clues to appropriate genus limits (Mey, 2004), and may shed light on the developmental pathways that underlie superficially similar morphologies in distantly related taxa.

In short, while a molecular phylogeny may be preferable for a variety of reasons, a morphological re-examination of Rallicolidae may be as important in order to understand, and above all use, phylogenetic data.

10.6 Summary

As is detailed above, this thesis has only begun to scratch the surface of the complex evolutionary histories and dispersal mechanisms of Rallicolid lice. Many species of Rallicolidae doubtlessly remain to be discovered, and the phylogenetic structure, evolutionary history, historical relationships, and dispersal events and capabilities of most of the taxa in Rallicolidae are still poorly known. The variety in ecologies and behaviour patterns of the hosts of the Rallicolidae offer almost limitless opportunities for hypothesis testing regarding louse dispersal and speciation patterns. Well-resolved and extensive phylogenies of many of the host groups are already available, and only a lack of molecular data on such groups as *Quadraceps*, *Mulcticola, Alcedoffula* and *Rallicola* prevents this data source from being utilized.

I have in this thesis presented and tested atwo new null hypotheses of phylogenetic relationships between lice parasitic on birds following set migration routes and forming large, mixed-species flocks during migration and wintering.

The first hypothesis, called flyway homogenisation, assumes that opportunities for lateral transfer of lice to novel hosts are much more prevalent during the migration and wintering on the host than during the hosts' breeding season. All other things being equal, there should be gene flow between louse populations on different host species during migration and wintering, and the lice on a set of hosts that follow the same flyway should form a homogeneous population. This should appear in phylogenetic analyses as all louse material collected from a given flyway being genetically similar or identical, regardless of what host it is collected from.

The second hypothesis, called flyway differentiation, assumes that the divisions of populations of the same host species into different flyways will act as an isolating mechanism for their lice. In many cases, the hosts themselves are divided into different subspecies along different flyways, and this should be reflected in their lice as well. In phylogenetic analyses, this should appear as the same host species – whether divided into different subspecies along different flyways or not – being parasitized by genetically different lice along different flyways.

These two proposed mechanisms could act independent of each other, but do not contradict each other, and both could hold true at the same time for a given set of hosts and lice. As wing lice are more prone to lateral dispersal using non-contact methods, wing lice are more likely to show evidence of flyway homogenisation, whereas body lice are more likely to show evidence of flyway differentiation.

Testing these hypotheses on two genera of shorebird lice, the wing ouse genus *Lunaceps* and the body louse genus *Carduiceps*, I find that neither of the expected patterns dominate in either genus. Some species of *Lunaceps* show evidence of flyway homogenisation, but these species do not occur on all potential hosts along the flyways they were collected from, and in one case (*Lunaceps* clade 1 in Paper I, Fig. 1) the same *Lunaceps* species occurs on multiple host species migrating along two different flyways.

In both genera, there is some indication of incipient flyway differentiation, as Old World and New World material are divided into different clades on host sets that migrate along flyways in both parts of the world (*Lunaceps* clade 8 in Paper I, Fig. 2; *Carduiceps zonarius* in Paper III, Fig. 2), but there is no support for these divisions, and in *Carduiceps* the pattern is not consistent. A similar divide between Old World and New World taxa is seen in *Quadraceps sl. lat.* (paper IV).

As the phylogenetic tests of two genera of shorebird lice (*Lunaceps* and *Carduiceps*) from the same set of hosts (mainly the Calidrinae) show patterns that contrast with those expected from the flyway hypotheses, there is reason to assume that host flyways are not the only factor in the hosts that structure the phylogenetic relationships between their lice. Other factors may include host size, host phylogeny, and host microhabitat choice on wintering grounds.

11. Abstracts of included papers

Paper I.

Flyway homogenisation or differentiation? Insights from the phylogeny of the sandpiper (Charadriiformes: Scolopacidae: Calidrinae) wing louse genus *Lunaceps* (Phthiraptera: Ischnocera).

International Journal for Parasitology 42 (2012), 93-102

The wing louse genus *Lunaceps* Clay & Meinertzhagen, 1939, is the most speciose chewing louse (Phthiraptera) genus inhabiting sandpipers (Charadriiformes: Calidrinae) and is known from almost all sandpiper species. The hosts follow specific flyways from the Arctic breeding grounds to the wintering locations in the Southern hemisphere, and often form large mixed-species flocks during migration and wintering. We estimate a phylogeny of *Lunaceps* based on three mitochondrial loci, supporting monophyly of the genus but revealing extensive paraphyly at the species level. We also evaluate the relative importance of flyway differentiation (same host species has different lice along different flyways) and flyway homogenisation (different host species have the same lice along the same flyway). We find that while the *Lunaceps* lice of smaller sandpipers and stints show some evidence of flyway homogenization, those of larger sandpipers do not. No investigated host species migrating along more than one flyway shows any evidence of flyway differentiation. The host-parasite associations within *Lunaceps* are in no case monophyletic, rejecting strict cospeciation.

Paper II.

The “Very Thankless Task”: Revision of *Lunaceps* Clay and Meinertzhagen, 1939 (Phthiraptera, Ischnocera, Philopteridae), with description of six new species and one new subspecies

Accepted by Zootaxa

The louse genus *Lunaceps* Clay and Meinertzhagen, 1939, parasitic on shorebirds (Charadriiformes: Scolopacidae) is revised. Six new species and one new subspecies of *Lunaceps* Clay and Meinertzhagen, 1939 parasitic on shorebirds (Charadriiformes, Scolopacidae) are described. They are *L. enigmaticus* sp. nov. from Stilt Sandpiper *Micropalama himantopus* (Bonaparte, 1826), *L. kukri* sp. nov. from Long-billed Curlew *Numenius americanus* Bechstein, 1812, *L. mintoni* sp. nov. from Great Knot *Calidris tenuirostris* (Horsfield, 1821), *L. rothkoi* sp. nov. from Buff-breasted Sandpiper *Tryngites subruficollis* (Vieillot, 1819), *L. schismatus* sp. nov. from Dunlin *Calidris alpina* (Linnaeus, 1758), *L. superciliosus* from Sharp-tailed Sandpiper *Calidris acuminata* (Horsfield, 1821) and Long-toed Stint *Calidris subminuta* (Middendorff, 1853), and *L. numenii madagascariensis* ssp. nov. from Far

Eastern Curlew *Numenius madagascariensis* (Linnaeus, 1766). Furthermore, the species *L. cabanisi* Timmermann, 1954, and *L. pusillus* are placed as new junior synonyms of *L. incoenis* (Kellogg and Chapman, 1899); the species *L. haematopi* Timmermann, 1954, *L. oliveri* Timmermann, 1954, and *L. husainii* Ansari, 1956, are placed as new junior synonyms of *L. numenii numenii* (Denny, 1842), *L. numenii phaeopi* (Denny, 1842), and *L. falcinellus* Timmermann, 1954, respectively, and the subspecies *L. holophaeus timmermanni* Bechet, 1968, is regarded as a new junior synonym of *L. falcinellus* Timmermann, 1954. *Lunaceps limosella limosa* Bechet, 1968, which was previously considered a junior synonym of *L limosella* Timmermann, 1954, is resurrected as a valid species. *Lunaceps wilsoni* Carriker, 1956, is considered a *nomen dubium*, and *L. parabolicus* Eichler (in Niethammer), 1953, is removed to the genus *Quadraceps* Clay and Meinertzhagen, 1939 as *Quadraceps parabolicus comb. nov.*, although its status in *Quadraceps* needs further attention. All species and subspecies of *Lunaceps* are illustrated and redescribed, and a key is provided for their identification. Three populations, from which only poor or limited data are available, are placed as *incerta sedis*.

Paper III.

Unexpected host distribution patterns of *Carduiceps* feather lice (Phthiraptera: Ischnocera): shorebird lice are not like dove lice

Submitted to Systematic Entomology

The body louse genus *Carduiceps* Clay & Meinertzhagen, 1939 (Phthiraptera: Ischnocera: Philopteridae) is widely spread on sandpipers and stints (Aves: Charadriiformes: Scolopacidae: Calidrinae), and known from almost all species. The current taxonomy includes three species on the Calidrinae (*Carduiceps meinertzhageni, Carduiceps scalaris, Carduiceps zonarius*) and four on other hosts. We estimate a phylogeny of four of the seven species of *Carduiceps* (the three mentioned above and *Carduiceps fulvofasciatus*) from 13 of the 29 hosts based on three mitochondrial loci, and evaluate the relative importance of flyway differentiation (same host species has different lice along different flyways) and flyway homogenisation (different host species have the same lice along the same flyway). We find no evidence for either process. Instead, the present, morphology-based, taxonomy of the genus corresponds exactly to the genetic-based, with all four species monophyletic. The distribution patterns suggest that interspecific competition may be responsible for upholding the mutually exclusive host specificity of *Car. meinertzhageni* and *Car. zonarius*. *Car. zonarius* is found both to inhabit a wider range of hosts than wing lice of the genus *Lunaceps* occurring on the same group of birds, and to occur on *Calidris* sandpipers of all sizes, both of which is unexpected for a body louse. We also include several other genera of feather lice of the proposed family

Esthiopteridae, and find *Carduiceps* to be isolated within this family. Relationships between other genera in Esthiopteridae remain obscure.

Paper IV.

Molecular phylogeny of the "Quadraceptinae" *sensu* Eichler (1963) (Phthiraptera: Ischnocera) with an assessment of the generic circumscription of the genus *Quadraceps* – zero, four, or 400 species?
Manuscript

Often based primarily on host relationships, the louse genus *Quadraceps* (Phthiraptera: Ischnocera) has been divided into numerous smaller genera during the 20th century, most of which have more recently been synonymised with *Quadraceps*. However, the dominating pattern of louse-host relationships within the Shorebirds (Charadriiformes) is one where a particular host is either parasitized by *Quadraceps* or by another, often superficially similar, genus, such as *Lunaceps* or *Cummingsiella*. This suggests that *Quadraceps* may be an artificial taxon, resulting from the retaining in the genus of all those species not distinct enough to warrant their own. A previous study (Gustafsson and Olsson, 2012 International Journal for Parasitology, 43, 93-102) suggested that *Quadraceps* may not be monophyletic unless both *Saemundssonia*, *Lunaceps*, and *Cummingsiella* are included. We performed a preliminary one-gene test of this hypothesis, using a vast range of taxa from shorebirds. Due to the small data set, no conclusions can be drawn, however the results of this analysis suggest that *Quadraceps* may, indeed, be paraphyletic, and would require the inclusion of almost all other recognised genera of the Quadraceptinae in order to be monophyletic.

Acknowledgements

Work

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As may be inferred from the sheer length of this introduction, as well as the many travels I have been on over the last few years, I have given considerably liberty by my supervisor, Urban. Although it has sometimes been frustrating not to have a louse expert as a supervisor, and having to mail other people or just try to figure out answers from the literature, this has been more than compensated for by having all my own proposals for collection trips, studies, and so on almost invariably being approved of immediately and enthusiastically, together with suggestions on whom to contact, how to proceed and much more. It seems that, to Urban, everything is possible and worthwhile, it is just a matter of time and work.

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Family

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But as blood is thicker even than *Kaiserschmarrn*, so is Jönköping closer to Gothenburg than is Wien, and it is to my wonderful family I have turned for relaxation, comfort, support, encouragement and all forms of joy throughout my time as a PhD student. From my father Roland driving me to Ottenby in his spare time to my mother Kristina grudgingly accepting the cats in her house, from my sister Hannah giving me and my brother free hands in the officiating at her wedding to Joel, to my brother Henrik taking me to watch a Christmas concert with console game music, my immediate family has indulged their oldest son and elder brother incessantly, and, I can hope, they have felt that I have reciprocated. From bricks of such clay are built the best of relationships, and if there is a limit to the mutual love between me and my family, no telescope built by mankind has hitherto been able to find it. To my father, my mother, my sister, my brother, my brother-in-law, my grandfather, and the newest member of the family, Theo, I give my thanks and my unding love.

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Let me end by also thanking the creatures that have changed my life the most, and that only in the last year: the cats Prim and Gauss. I end with a quote I hope you will carry with you throughout this dissertation, as well as the rest of your life:

I urge you to please notice when you are happy, and exclaim or murmur or think at some point, “If this is not nice, I don’t know what is.”

K. Vonnegut (2003)

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Appendix I. Phthiraptera of the Nordic Countries

The following is not intended to be an exhaustive list, as there are few data sources available for several regions (especially Norway and Denmark), but to be a summary of the distribution data I have come across during my PhD. Individual data sources for all distribution records are not quoted, but a complete list of the literature used can be found at the end of this section.

Swedish records include those collected during this PhD (marked in bold), however some of this material has been sent to experts around the world for use upcoming revisions, and the names may change. The Swedish records also include data from the collection at the Natural History Museum, Stockholm, which I looked at in 2008. Much of this material is still unidentified, and the identity of the hosts of many of the unidentified lice are either missing or given in an archaic taxonomy, making it hard to identify. No doubt this collection contains several species not listed here.

For Finnish records, I have relied entirely on Eichler and Hackman (1973), who summarized all known data of Ischnocera and Amblycera for Finland. No similar list exists for mainland Norway and Denmark, to my knowledge, and Icelandic data has been compiled by a number of sources. Data for Svalbard, Jan Mayen and Bear Island were compiled when writing a chapter on the Phthiraptera of Svalbard for an upcoming project, and the references used are detailed below. For the Faroe Islands, I used Palma and Jensen's (2005) list. Other records were obtained from locality lists of revisions or descriptions, however no thorough search for such records have been made, and there will undoubtedly be additional data concealed in this type of texts

Of the regions surveyed, Finland and Iceland appear to be well studied, as do the Faroe Islands, Svalbard, Jan Mayen, and Bear Island, and there is perhaps little hope of finding additional species of Phthiraptera in any region, apart from species on occasional guests. As no comprehensive list of the Phthiraptera of Denmark and Norway has been found, it is unknown how true this statement is for these countries. If the list below is at all representative of what is known from these two countries, the vast majority of potential species would seem to remain to be discovered there. For the Swedish list, I would estimate that at least two thirds of the species of lice that could potentially be found here have still not been recorded. Only two bird species have had all the lice known from them collected in Sweden, *Caprimulgus europeus* and *Phalacrocorax carbo*. For all other bird species recorded in Sweden, species of lice remain to be recorded. The list of bird hosts with no lice recorded from Sweden includes several common species, such as *Bucephala clangula*, *Columba oenas*, and *Fulica atra*, but the main bulk of potential records are within the Passeriformes.

To avoid inadvertently publishing any new names in this list, two species of *Lunaceps* are listed as "*Lunaceps sp*.". These will be described in the published version of Paper II.

Table 1. The Phthiraptera of the Nordic Countries. Abbreviations used: BJO = Bear Island; DEN = Denmark; FAR = Faroe Islands; FIN = Finland; ICE = Iceland; JAN = Jan Mayen; NOR = Norway; SVA = Svalbard; SWE = Sweden. Data sources are listed at the end of the table. Taxa collected in this study bolded. Unidentified taxa generally not included.

Louse taxon	*Host taxon*	*Known distribution*
Anoplura		
Antarctophthirius		
Antarctophthirius trichechi	*Odobenus rosmarus*	SVA, SWE?
Cervophthirius		
Cervophthirius tarandi	*Rangifer tarandus*	SWE

Echinophthirius		
Echinophthirius horridus	*Phoca* spp.	NOR, SVA, SWE
Enderleiniellus		
Enderleiniellus nitzschi	*Sciurus vulgaris*	DEN, NOR, SWE
Haematopinus		
Haematopinus aperis	*Sus scrofa*	SWE
Haematopinus asini	*Equus caballus*	SWE
Haematopinus eurysternus	*Bos taurus*	SWE
Haematopinus suis	*Sus scrofa*	SWE
Haemodipsus		
Haemodipsus leporis	*Lepus timidus*	NOR
Haemodipsus lyriocephalus	*Lepus timidus*	DEN, FIN, NOR, SWE
Haemodipsus ventricosus	*Oryctolagus cuniculus*	SWE
Hoplopleura		
Hoplopleura acanthopus	Microtinae spp.	DEN, FIN, NOR, SWE
Linognathus		
Linognathus setosus	*Canis familiaris*	DEN, FIN, NOR, SWE
Linognathus stenopsis	*Capra hircus*	SWE
Linognathus vituli	*Bos taurus*	SWE
Neohaematopinus		
Neohaematopinus sciuri	*Sciurus vulgaris*	DEN, NOR
Pediculus		
Pediculus humanus	*Homo sapiens*	DEN, FIN, ICE, NOR, SWE
Polyplax		
Polyplax borealis	*Evotomys rufocanus?*	NOR
Polyplax serrata	*Mus spp.*	DEN, NOR, SWE
Polyplax spinigera	*Arvicola terrestris*	SWE
Polyplax spinulosa	Muridae spp.	DEN, SWE
Pthirius		
Pthirius pubis	*Homo sapiens*	DEN, FIN, ICE, NOR, SWE
Schizophthirius		
Schizophthirius sicistae	*Sicista subtilis*	NOR
Solenopotes		
Solenopotes capillatus	*Bos taurus*	FIN, NOR, SWE

Amblycera

Actornithophilus		
Actornithophilus bicolor	*Arenaria interpres*	FAR, FIN, ICE, SVA
Actornithophilus flumineus	*Actitis hypoleucus*	FIN
Actornithophilus gracilis	*Vanellus vanellus*	FAR, FIN, ICE, SWE
Actornithophilus grandiceps	*Haematopus ostralegus*	FAR, ICE, SWE
Actornithophilus multisetosus	*Lymnocryptes minima*	FAR, FIN, SWE
Actornithophilus ochraceus	*Charadrius* spp.	FAR, FIN
Actornithophilus paludosus	*Tringa nebularia*	FIN
Actornithophilus patellatus	*Numenius arquata*	FAR, FIN
Actornithophilus pediculoides	*Arenaria interpres*	FIN, SWE

Actornithophilus piceus	*Larus* spp.	FIN
Actornithophilus pustulosus	*Philomachus pugnax*	FIN, SWE
Actornithophilus spinulosus	*Limosa limosa*	ICE
Actornithophilus totani	*Tringa* spp.	FAR, FIN, SWE
Actornithophilus umbrinus	*Calidris* spp.	FAR, FIN, SVA, SWE
Actornithophilus uniseriatus	*Recurvirostra avosetta*	SWE
Amyrsidea		
Amyrsidea lagopi	*Lagopus* spp.	FIN, NOR
Amyrsidea minuta	*Pavo cristatus*	SWE
Amyrsidea perdicis	*Perdix perdix*	SWE
Ancistrona		
Ancistrona vagelli	*Fulmarus glacialis*	FAR, SVA
Austromenopon		
Austromenopon aegialitidis	*Charadrius* spp.	SWE
Austromenopon alpinum	*Calidris alpina* ssp.	FIN, SWE
Austromenopon atrofulvum	Sternidae spp.	FIN, SWE
Austromenopon brevifimbriatum	*Fulmarus glacialis*	FAR, ICE, SVA
Austromenopon corporosum	*Phalaropus fulicarius*	SVA
Austromenopon crocatum	*Numenius arquata*	FIN
Austromenopon decorosum	*Tringa* spp.	FAR, SWE
Austromenopon erilis	*Calidris maritima*	FAR
Austromenopon fuscofasciatum	Stercorariidae spp.	FAR, FIN, SVA
Austromenopon haematopi	*Haematopus ostralegus*	FAR, FIN
Austromenopon hystriculum	*Actitis hypoleucos*	SWE
Austromenopon lutescens	*Philomachus pugnax*	FAR, FIN, ICE, SVA, SWE
Austromenopon micrandrum	*Recurvirostra avosetta*	SWE
Austromenopon nigropleurum	Alcidae spp.	BJO, FAR, FIN, ICE, JAN, SVA, SWE
Austromenopon paululum	*Puffinus* spp.	FAR
Austromenopon pelagicum	*Hydrobates pelagicus*	FAR
Austromenopon phaeopodis	*Numenius phaeopus*	FAR, FIN, ICE
Austromenopon spenceri	*Phalarpus lobatus*	FIN
Austromenopon squatarolae	*Pluvialis squatarola*	FAR, SWE
Austromenopon transversum	*Larus* spp.	FAR, FIN, SWE
Austromenopon uriae	*Uria lomvia*	SVA
Ciconiphilus		
Ciconiphilus decimfasciatus	Ardeidae spp.	FAR, ICE, SWE
Ciconiphilus pectiniventris	*Anser, Branta* spp.	FAR
Ciconiphilus quadripustulatus	*Ciconia* spp.	SWE
Colpocephalum		
Colpocephalum apivorus	*Pernis apivorus*	FAR, SWE
Colpocephalum flavescens	*Haliaeetus albicilla*	FIN, SWE
Colpocephalum fregili	*Corvus* spp.	FAR, FIN, ICE, SWE
Colpocephalum impressum	*Aquila chrysaetos*	FIN
Colpocephalum inaequale	*Dryocopus martius*	FIN, SWE
Colpocephalum nanum	*Accipiter, Buteo* spp.	FIN, SWE
Colpocephalum turbinatum	Falconiformes spp., *Columba livia domestica*	SWE

Colpocephalum zebra	*Ciconia ciconia*	SWE
Colpocephalum zerafae	*Falco peregrinus*	SWE
Cuculiphilus		
Cuculiphilus fasciatus	*Cuculus canorus*	FIN, SWE
Dennyus		
Dennyus hirundinis	*Apus apus*	FAR, FIN, SWE
Eidmanniella		
Eidmanniella pellucida	*Phalacrocorax* spp.	FAR, SWE
Eidmanniella pustulosa	*Morus bassana*	FAR, ICE
Gruimenopon		
Gruimenopon canadense	*Grus grus*	FAR
Gruimenopon longum	*Grus grus*	FAR, FIN
Heleonomus		
Heleonomus macilentus	*Grus grus*	FAR, FIN
Hohorstiella		
Hohorstiella lata	*Columba livia*	FIN
Holomenopon		
Holomenopon brevithoracicum	*Cygnus cygnus*	ICE
Holomenopon leucoxanthum	Anatidae spp.	FAR, FIN, SWE
Holomenopon loomisi	*Melanitta fusca* *Somateria mollissima*	FAR
Holomenopon setigerum	*Anas* spp.	FIN
Holomenopon tadornae	*Tadorna tadorna*	SWE
Holomenopon transvaalense	*Anas platyrhynchos*	FIN
Kurodaia		
Kurodaia cryptostigmatia	Strigidae spp.	FIN, SWE
Kurodaia flammei	*Asio flammeus*	FIN
Kurodaia fulvofasciata	*Buteo buteo*	SWE
Kurodaia haliaeeti	*Pandion haliaetus*	FAR, FIN, SWE
Laemobothrion		
Laemobothrion atrum	*Fulica atra*	FAR
Laemobothrion maximum	*Haliaeetus albicilla*	FIN
Laemobothrion tinnunculi	*Falco* spp.	FIN, SWE
Menacanthus		
Menacanthus agilis	*Phylloscopus spp.*	FAR, FIN
Menacanthus alaudae	*Alauda arvensis*	BJO, FIN, ICE, SWE
Menacanthus camelinus	*Lanius collurio*	FIN, SWE
Menacanthus curuccae	*Sylvia* spp.	FAR, FIN, SWE
Menacanthus eisenachensis	*Acrocephalus scirpaceus*	FAR
Menacanthus eurysternus	Passeriformes spp.	BJO, FAR, FIN, SWE
Menacanthus exilis	*Oenanthe oenanthe*	FIN
Menacanthus gonophaeus	*Corvus* spp.	FAR, FIN, SWE
Menacanthus pallidulus	*Gallus gallus*	FIN, SWE
Menacanthus pici	Picidae spp.	FAR, FIN, SWE
Menacanthus pusillus	Motacillidae spp.	FAR, FIN, SWE
Menacanthus sinuatus	Paridae spp.	FAR, FIN, SWE
Menacanthus stramineus	*Gallus gallus*	FAR, FIN, ICE, NOR, SWE
Menacanthus tenuifrons	*Troglodytes troglodytes*	FAR

Menopon		
Menopon gallinae	*Gallus gallus*	FAR, FIN, ICE, NOR, SWE
Menopon pallens	*Perdix perdix*	FIN, ICE
Myrsidea		
Myrsidea anaspila	*Corvus corax*	FIN, ICE
Myrsidea anathorax	*Corvus monedula*	FAR, FIN, SWE
Myrsidea balati	*Passer montanus*	SWE
Myrsidea brunnea	*Nucifraga caryocatactes*	FIN
Myrsidea cornicis	*Corvus corone*	FAR, FIN, SWE
Myrsidea cucullaris	*Sturnus vulgaris*	FIN, SWE
Myrsidea indivisa	*Garrulus glandarius*	FIN, SWE
Myrsidea isostoma	*Corvus frugilegus*	FAR
Myrsidea latifrons	*Riparia riparia*	FIN, SWE
Myrsidea picae	*Pica pica*	FIN, SWE
Myrsidea quadrifasciata	*Passer domesticus*	SWE
Myrsidea quadrimaculata	*Loxia curvirostra*	FAR
Myrsidea rustica	*Hirundo rustica*	FAR, SWE
Myrsidea serini	*Carduelis chloris*	SWE
Myrsidea troglodyti	*Troglodytes troglodytes*	FAR
Nosopon		
Nosopon clayae	*Pernis apivorus*	SWE
Nosopon lucidum	*Falco columbarius*	FAR, SWE
Pseudomenopon		
Pseudomenopon dolium	*Podiceps* spp.	FIN, SWE
Pseudomenopon pilosum	*Fulica atra*, *Gallinula chloropus*	FAR, FIN, SWE
Pseudomenopon scopulacorne	*Rallus aquaticus*	FAR
Ricinus		
Ricinus elongatus	Passeriformes spp.	FAR, FIN, SWE
Ricinus frenatus	*Regulus regulus*	FAR
Ricinus fringillae	Passeriformes spp.	FAR, FIN, SWE
Ricinus rubeculae	*Erithacus rubecula*	FAR
Ricinus thoracicus	*Plectrophenax nivalis*	FAR
Trinoton		
Trinoton anserinum	*Anser, Cygnus* spp.	FAR, FIN, ICE, SVA, SWE
Trinoton querquedulae	Anatidae spp.	FAR, FIN, NOR, SWE

Ischnocera

Anaticola		
Anaticola anseris	*Anser, Branta* spp.	FAR, FIN, ICE, SVA, SWE
Anaticola branderi	*Clangula hyemalis*	FAR, FIN
Anaticola crassicornis	*Anas* spp.	FAR, FIN, ICE, NOR, SWE
Anaticola mergiserrati	Aythyinae spp.	FAR, FIN, SVA, SWE
Anaticola rheinwaldi	*Branta bernicla*	FAR, FIN, SWE
Anaticola tadornae	*Tadorna tadorna*	FIN, SWE

Anatoecus		
Anatoecus cygni	*Cygnus* spp.	FAR, FIN, SWE
Anatoecus dentatus/icterodes	Anatidae spp.	FAR, FIN, ICE, SVA, SWE
Anatoecus penicillatus	*Cygnus olor*	SWE
Aquanirmus		
Aquanirmus bucomfishi	*Podiceps auritus*	FAR
Aqanirmus podicepis	*Podiceps cristatus*	FIN
Ardeicola		
Ardeicola ardeae	*Ardea cinerea*	SWE
Ardeicola ciconiae	*Ciconia ciconia*	FIN
Ardeicola exilis	*Geronticus eremita*	SWE
Ardeicola expallidus	*Egretta garzetta*	FAR
Austrogoniodes		
Austrogoniodes demersus	*Spehnicus demersus*	SWE
Brueelia		
Brueelia antimarginalis	*Turdus pilaris*	FIN
Brueelia argula	*Corvus corax*	FIN
Brueelia biocellata	*Pica pica*	FIN, SWE
Brueelia blagovescenskyi	*Emberiza schoeniclus*	SWE
Brueelia brachythorax	*Plectrophenax nivalis*	JAN, SVA
Brueelia breueri	*Carduelis chloris*	FIN
Brueelia chrysomystris	*Carduelis spinus*	FAR
Brueelia corydalla	*Anthus pratensis*	ICE
Brueelia cruciata	*Lanius collurio*	FIN
Brueelia curuccae	*Sylvia curruca*	SWE
Brueelia cyclothorax	*Passer domesticus*	FAR
Brueelia domestica	*Hirundo rustica*	FAR
Brueelia ferianci	*Anthus trivialis*	SWE
Brueelia glandarii	*Garrulus glandarius*	FIN
Brueelia gracilis	*Delichon urbica*	FAR, FIN, SWE
Brueelia iliaci	*Turdus iliacus*	FAR, SWE
Brueelia kluzi	*Fringilla coelebs*	FIN
Brueelia limbata	*Loxia curvirostra*	FAR, FIN, SWE
Brueelia marginata	*Turdus pilaris*	FAR, FIN, SWE
Brueelia merulensis	*Turdus merula*	FAR, FIN
Brueelia munda	*Oriolus oriolus*	FAR, FIN
Brueelia nebulosa	*Sturnus vulgaris*	FAR, FIN, SWE
Brueelia olivacea	*Nucifraga caryocatactes*	FIN
Brueelia paratricapillae	*Sylvia atricapilla*	FAR
Brueelia perforata	*Corvus frugilegus*	FIN
Brueelia propinqua	*Loxia pytyopsittacus*	FIN
Brueelia pyrrhularum	*Pyrrhula pyrrhula*	FIN, SWE
Brueelia rosickyi	*Sylvia nisoria*	SWE
Brueelia sibirica	*Carduelis flammea*	FAR
Brueelia straminea	*Dendrocopos major*	FIN
Brueelia tenuis	*Riparia riparia*	FIN
Brueelia tristis	*Erithacus rubecula*	FAR
Brueelia turdinulae	*Turdus philomelos*	FAR
Brueelia uncinosa	*Corvus corone*	FIN, SWE

Brueelia varia	*Corvus monedula*	FAR, FIN
Brueelia viscivori	*Turdus viscivorus*	FIN
Bovicola		
Bovicola equi	*Equus caballus*	ICE
Bovicola ovis	*Ovis aries*	ICE
Campanulotes		
Campanulotes bidentatus	*Columba palumbus*	FAR, FIN
Campanulotes compar	*Columba livia*	FAR, FIN, SWE
Campanulotes drosti	*Columba oenas*	FIN
Capraiella		
Capraiella subcuspidata	*Coracias garrulus*	FIN
Carduiceps		
Carduiceps meinertzhageni	*Calidris* spp.	FAR, FIN, SVA, SWE
Carduiceps scalaris	*Philomachus pugnax*	FIN, SWE
Carduiceps zonarius	*Calidris* spp.	BJO, FAR, FIN, ICE, SVA, SWE
Chelopistes		
Chelopistes meleagridis	*Meleagris gallopavo*	FIN, NOR, SWE
Cirrophthirius		
Cirrophthirius recurvirostrae	*Recurvirostra avosetta*	SWE
Coloceras		
Coloceras chinense	*Streptopelia decaocto*	FAR
Coloceras damicorne	*Columba* spp.	FAR, FIN
Columbicola		
Columbicola bacillus	*Streptopelia decaocto*	FAR, FIN, SWE
Columbicola claviformis	*Columba palumbus*	FAR, FIN, SWE
Columbicola columbae	*Columba livia*	FAR, FIN, NOR, SWE
Craspedonirmus		
Craspedonirmus colymbinus	*Gavia* spp.	FAR, FIN, ICE, SWE
Craspedonirmus immer	*Gavia immer*	FAR
Craspedorrhynchus		
Craspedorrhynchus aquilinus	*Aquila chrysaetos*	FIN, SWE
Craspedorrhynchus dilatatus	*Buteo lagopus*	FIN, SWE
Craspedorrhynchus haematopus	*Accipiter gentilis*	FIN, SWE
Craspedorrhynchus melittoscopus	*Pernis apivorus*	FAR, FIN, SWE
Craspedorrhynchus nisi	*Accipiter nisus*	FIN, SWE
Craspedorrhynchus platystomus	*Buteo buteo*	FIN, SWE
Craspedorrhynchus spathulatus	*Milvus milvus*	SWE
Cuclotogaster		
Cuclotogaster heterogrammicus	*Perdix perdix*	SWE
Cuclotogaster heterographus	*Gallus gallus*	NOR, SWE
Cuculicola		
Cuculicola latirostris	*Cuculus canorus*	FIN, SWE
Cuculoecus		
Cuculoecus latifrons	*Cuculus canorus*	FIN, SWE
Cummingsiella		
Cummingsiella ambigua	*Gallinago gallinago*	FAR
Cummingsiella aurea	*Scolopax rustica*	FIN

Cummingsiella ovalis	*Numeniu arquata*	FAR, FIN, SWE
Degeeriella		
Degeeriella aquilarum	*Aquila chrysaetos*	FIN
Degeeriella discocephalus	*Haliaeetos albicilla*	FIN, ICE, SWE
Degeeriella fulva	Falconiformes spp.	FAR, FIN, SWE
Degeeriella nisus	*Accipiter nisus*	FAR, FIN, SWE
Degeeriella phlyctophagus	*Pernis apivorus*	FIN, SWE
Degeeriella regalis	*Milvus* spp.	SWE
Degeeriella rufa	*Falco* spp.	FAR, FIN, ICE, SWE
Degeeriella vagans	*Accipiter gentilis*	FIN, SWE
Esthiopterum		
Esthiopterum gruis	*Grus grus*	FAR, FIN, SWE
Falcolipeurus		
Falcolipeurus sulcifrons	*Haliaeetos albicilla*	FIN
Falcolipeurus suturalis	*Aquila chrysaetos*	SWE
Fulicoffula		
Fulicoffula lurida	*Fulica atra*	FAR, FIN
Fulicoffula rallina	*Rallus aquaticus*	FAR
Fulicoffula stammeri	*Porzana porzana*	FIN
Goniocotes		
Goniocotes gallinae	*Gallus gallus*	FAR, FIN, NOR
Goniocotes microthorax	*Perdix perdis*	FIN
Goniocotes rotundiceps	*Syrmaticus reevesi*	SWE
Goniodes		
Goniodes bituberculatus	*Tetrao urogallus*	FIN, SWE
Goniodes colchici	*Phasianus colchicus*	SWE
Goniodes dispar	*Perdix perdix*	FIN, SWE
Goniodes dissimilis	*Gallus gallus*	FIN
Goniodes gigas	*Gallus gallus*	NOR
Goniodes lagopi	*Lagopus* spp.	FIN, ICE, NOR, SVA, SWE
Goniodes pavonis	*Pavo cristatus*	FIN, SWE
Goniodes tetraonis	*Tetrao tetrix*	FIN, NOR, SWE
Haffneria		
Haffneria grandis	Stercorariidae spp.	FAR, FIN
Halipeurus		
Halipeurus diversus	*Puffinus spp.*	FAR
Halipeurus gravis	*Puffinus gravis*	FAR
Halipeurus pelagicus	Hydrobatinae spp.	FAR, NOR
Incidifrons		
Incidifrons fulicae	*Fulica atra*	FAR, FIN, SWE
Lagopoecus		
Lagopoecus affinis	*Lagopus* spp.	FIN, ICE, NOR, SVA, SWE
Lagopoecus colchicus	*Phasianus colchicus*	SWE
Lagopoecus lyrururs	*Tetrao tetrix*	FIN, SWE
Lagopoecus pallidovittatus	*Tetrao urogallus*	FIN, SWE
Lagopoecus tetrastei	*Bonasa bonasia*	FIN, SWE
Lipeurus		
Lipeurus caponis	*Gallus gallus*	FIN, NOR, SWE

Lunaceps		
Lunaceps actophilus	*Calidris alba*	FAR, FIN, SWE
Lunaceps drosti	*Calidris canutus*	FAR, FIN, SWE
Lunaceps falcinellus	Calidrinae spp.	FIN, SWE
Lunaceps holophaeus	*Philomachus pugnax*	FIN, SWE
Lunaceps limosella	*Limosa lapponica*	FIN
Lunaceps nereis	*Calidris maritima*	FAR, ICE, SVA
Lunaceps numenii numenii	*Numenius arquata*	FAR, FIN
Lunaceps numenii phaeopi	*Numenius phaeopus*	FAR, FIN, ICE, SVA, SWE
Lunaceps sp.	*Tryngites subruficollis*	SWE
Lunaceps sp.	*Calidris alpina* ssp.	FAR, FIN, ICE, JAN, SVA, SWE
Mulcticola		
Mulcticola hypoleucus	*Caprimulgus europeus*	FIN, SWE
Naubates		
Naubates harrisoni	*Puffinus griseus*	FAR
Neophilopterus		
Neophilopterus incompletus	*Ciconia ciconia*	SWE
Neophilopterus tricolor	*Ciconia nigra*	FIN
Ornithobius		
Ornithobius bucephalus	*Cygnus olor*	ICE, SWE
Ornithobius cygni	*Cygnus cygnus*	FAR, FIN
Ornithobius hexopthalmus	*Branta leucopsis*	FAR, FIN, SVA, SWE
Oxylipeurus		
Oxylipeurus minor	*Tetrao tetrix*	FIN
Oxylipeurus tetraonis	*Tetrao urogallus*	FIN, SWE
Paraclisis		
Paraclisis diomedeae	*Diomedea melanophris*	FAR
Pectinpygus		
Pectinopygus bassani	*Morus bassana*	FAR, FIN, ICE, SWE
Pectinopygus brevicornis	*Phalacrocorax aristotelis*	FAR
Pectinopygus gyricornis	*Phalacrocorax carbo*	FAR, FIN, ICE, SWE
Penenirmus		
Penenirmus affectator	*Sylvia borin*	SWE
Penenirmus albiventris	*Troglodytes troglodytes*	FAR, FIN, ICE, SWE
Penenirmus arcticus	*Picoides tridactylus*	FIN
Penenirmus auritus	Picidae spp.	FAR, FIN, SWE
Penenirmus heteroscelis	*Dryocopus martius*	SWE
Penenirmus pari	Paridae spp.	FAR, FIN
Penenirmus phylloscopis	*Phylloscopus trochilus*	SWE
Penenirmus pici	Picidae spp.	SWE
Penenirmus rarus	*Phylloscopus collybita*	FAR, SWE
Penenirmus serrilimbus	*Jynx torquilla*	FAR, FIN, SWE
Penenirmus speciosus	*Sylvia curruca*	FAR
Perineus		
Perineus nigrolimbatus	*Fulmarus glacialis*	FAR, ICE, SVA
Philopterus		
Philopterus atratus	*Corvus frugilegus*	FAR, FIN, SWE

Philopterus bischoffi	*Turdus pilaris*	FIN, SWE
Philopterus capillatus	*Ficedula hypoleuca*	FIN
Philopterus cincli	*Cinclus cinclus*	FIN
Philopterus citrinellae	*Carduelis chloris* *Emberiza citrinella*	FIN, SWE
Philopterus coarctatus	*Lanius* spp.	FIN, SWE
Philopterus corvi	*Corvus corax*	FAR, FIN, ICE, SWE
Philopterus crassipes	*Nucifraga caryocatactes*	FIN
Philopterus curvirostrae	*Loxia curvirostra*	FAR, FIN, SWE
Philopterus desertus	*Muscicapa striata*	FIN, SWE
Philopterus erythrini	*Carpodacus erythrinus*	FAR
Philopterus excisus	*Delichon urbica*	FAR, FIN, SWE
Philopterus fortunatus	*Fringilla coelebs*	FIN, SWE
Philopterus fringillae	*Passer domesticus*	FIN. ICE
Philopterus garrulae	*Bombycilla garrulus*	FAR
Philopterus garruli	*Garrulus glandarius*	FIN, SWE
Philopterus guttatus	*Corvus monedula*	FAR, FIN
Philopterus hamatus	*Plectrophenax nivalis*	BJO, FAR, FIN, ICE
Philopterus hansmuenchi	*Loxia leucoptera*	FIN, SWE
Philopterus hanzaki	*Anthus petrosus*	SWE
Philopterus kelikovae	*Eremophila alpestris*	BJO
Philopterus linariae	*Carduelis flammea*	FAR, FIN, SWE
Philopterus lineatus	*Certhia familiaris*	FIN
Philopterus markevichi	*Ficedula parva*	SWE
Philopterus microsomaticus	*Hirundo rustica*	FIN, SWE
Philopterus modularis	*Prunella modularis*	FIN
Philopterus montani	*Passer montanus*	SWE
Philopterus nativus	*Turdus torquatus*	FIN
Philopterus ocellatus	*Corvus corone*	FAR, FIN, ICE
Philopterus oenanthe	*Oenanthe oenanthe*	ICE, SVA
Philopterus pallescens	*Parus* spp.	FIN
Philopterus passerinus	*Motacilla alba*	FIN, SWE
Philopterus pavidus	*Motacilla flava*	SWE
Philopterus phylloscopi	*Phylloscopus trochilus*	SWE
Philopterus picae	*Pica pica*	FIN, SWE
Philopterus rapax	*Fringilla montifringilla*	FAR, FIN, SWE
Philopterus reguli	*Regulus regulus*	FAR, FIN, SWE
Philopterus residuus	*Emberiza schoeniclus*	BJO, FIN, SWE
Philopterus rubeculae	*Erithacus rubecula*	FIN
Philopterus stadleri	*Alauda arvensis*	FIN
Philopterus timmermanni	*Turdus iliaci*	FAR, FIN; ICE
Philopterus troglodyti	*Troglodytes troglodytes*	SWE
Philopterus turdi	*Turdus* spp.	FAR. FIN, SWE
Philopterus vernus	*Turdus viscivorus*	FIN, SWE
Picicola		
Picicola candidus	*Picus viridis*	FIN, SWE
Quadraceps s. lat.		
Quadraceps aethereus	*Alel alle*	SVA
Quadraceps alcae	Alcidae spp.	FAR, FIN, ICE, SWE
Quadraceps auratus	*Haematopus ostralegus*	FAR, ICE, SWE

Quadraceps bicuspis	*Charadrius dubius*	FIN
Quadraceps charadrii	*Pluvialis apricaria*	FAR, FIN, ICE, SWE
Quadraceps connexus	*Phalaropus lobatus*	FIN
Quadraceps decipiens	*Recurvirostra avosetta*	SWE
Quadraceps eugrammicus	*Larus minutus*	FIN
Quadraceps fissus	*Charadrius hiaticula*	FAR, FIN, ICE, JAN, SWE
Quadraceps furvus	*Tringa erythropus*	FIN, ICE
Quadraceps helgovauki	*Fratercula arctica*	FAR
Quadraceps hiaticulae	*Charadrius hiaticula*	FAR, FIN, ICE, SVA, SWE
Quadraceps hospes	*Pluvialis squatarola*	FIN, SWE
Quadraceps houri	*Sterna paradisaea*	FAR, SWE
Quadraceps junceus	*Vanellus vanellus*	FAR, FIN, SWE
Quadraceps klatti	*Alle alle*	FAR, FIN, SVA
Quadraceps lahorensis	*Philomachus pugnax*	FIN
Quadraceps latus	*Cursorius cursor*	SWE
Quadraceps longicollis	*Thalasseus sandvicensis*	FIN, SWE
Quadraceps normifer	*Stercorarius parasiticus*	FAR, FIN, ICE, SVA, SWE
Quadraceps nycthemerus	*Sternula albifrons*	SWE
Quadraceps obliquus	*Uria* spp.	FAR, SVA, SWE
Quadraceps obscurus	*Tringa glareola*	SWE
Quadraceps obtusus	*Tringa totanus*	BJO, FAR, FIN, SWE
Quadraceps ochropi	*Tringa ochropus*	FIN
Quadraceps ornatus **ssp.**	Laridae spp.	FAR, FIN, ICE, SVA, SWE
Quadraceps parvopallidus	*Stercorarius longicauda*	FAR
Quadraceps phaeonotus	*Chlidonias niger*	SWE
Quadraceps phalaropi	*Phalaropus fulicarius*	SVA
Quadraceps punctatus **ssp.**	Laridae spp.	FAR, FIN, SWE
Quadraceps punctifer	*Eudromias morinellus*	FIN
Quadraceps ravus	*Actitis hypoleucos*	FIN, SWE
Quadraceps sellatus	*Sterna hirundo*	FIN, ICE, SWE
Quadraceps semifissus	*Recurvirostra avosetta*	SWE
Quadraceps similis	*Tringa nebulosa*	FIN, SWE
Quadraceps stellaepolaris	*Stercorarius pomarinus*	FAR, FIN
Quadraceps strepsilaris	*Arenaria interpres*	BJO, FAR, FIN, ICE, SWE
Rallicola		
Rallicola cuspidatus	*Rallus aquaticus*	FAR
Rallicola fulicae	*Fulica atra*	FAR, FIN
Rallicola minutus	*Gallinula chloropus*	FAR
Rallicola mystax	*Porzana porzana*	FIN
Rhynonirmus		
Rhynonirmus helvolus	*Scolopax rusticola*	FIN
Rhynonirmus scolopacis	*Gallinago gallinago*	FAR, FIN, SWE
Saemundssonia		
Saemundssonia calva	*Uria* spp.	FAR, ICE, SVA,

		SWE
Saemundssonia celidoxa	*Alca torda*	FAR, FIN, ICE
Saemundssonia cephalus	*Stercorarius parasiticus*	FAR, FIN, ICE, SVA, SWE
Saemundssonia clayae	*Scolopax rusticola*	FIN, SWE
Saemundssonia conica spp.	*Pluvialis* spp.	FAR, FIN, ICE, SWE
Saemundssonia euryrhyncha	Stercorariidae spp.	FAR, FIN, ICE
Saemundssonia fraterculae	*Fratercula arctica*	FAR, FIN, ICE
Saemundssonia grylle	*Cepphus grylle*	FAR, FIN, ICE, SVA
Saemundssonia haematopi	*Haematopus ostralegus*	FAR, FIN, ICE, SWE
Saemundssonia incisa	*Oceanodroma leucorhoa*	FAR, ICE
Saemundssonia inexpectata	*Stercorarius longicauda*	FAR, SVA
Saemundssonia integer	*Grus grus*	FIN, SWE
Saemundssonia lari **ssp**.	Laridae spp.	FAR, FIN, ICE, SVA, SWE
Saemundssonia laticaudata	*Thalasseus sandvicensis*	SWE
Saemundssonia limosae	*Limosa lapponica*	FIN, SWE
Saemundssonia lobaticeps	*Chlidonias nigra*	SWE
Saemundssonia lockleyi	*Sterna paradisaea*	FAR, NOR, SVA, SWE
Saemundssonia melanocephalus	*Sternula albifrons*	FIN, ICE, SWE
Saemundssonia merguli	*Alle alle*	FAR, FIN, ICE, SVA
Saemundssonia occidentalis	*Fulmarus glacialis*	FAR, ICE, SVA
Saemundssonia peusi	*Puffinus griseus*	FAR
Saemundssonia platygaster ssp.	Scolopacidae spp.	FIN, ICE, SWE
Saemundssonia scolopacisphaeopodis ssp.	*Numenius* spp.	FAR, FIN, ICE, SVA
Saemundssonia sternae	*Sterna hirundo*	FIN, ICE, SWE
Saemundssonia thalassidromae	*Hydrobates pelagicus*	FAR
Saemundssonia tringae	Calidrinae spp.	BJO, FAR, FIN, ICE, SVA, SWE
Strigiphilus		
Strigiphilus barbatus	*Asio otus*	SWE
Strigiphilus ceblebrachys	*Bubo scandiaca*	FAR, FIN, NOR, SVA, SWE
Strigiphilus crenulatus	*Surnia ulula*	FIN, SWE
Strigiphilus cursor	*Asio flammeus*	FAR, FIN, SWE
Strigiphilus goniodicerus	*Bubo bubo*	SWE
Strigiphilus heterocerus	*Strix uralensis*	FIN, SWE
Strigiphilus pallidus	*Aegolius funereus*	FIN, NOR, SWE
Strigiphilus portigi	*Strix aluco*	FIN, SWE
Strigiphilus remotus	*Strix nebulosa*	SWE
Strigiphilus rostratus	*Tyto alba*	FIN, SWE
Strigiphilus splendens	*Glaucidium passerinum*	FIN
Strigiphilus strigis	*Bubo bubo*	DEN, FIN, SWE
Sturnidoecus		
Sturnidoecus sturni	*Sturnus vulgaris*	FAR, FIN, SWE
Sturnidoecus carpodaci	*Carpodacus erythrinus*	SWE
Traveculus		
Trabeculus aviator	*Puffinus puffinus*	FAR

Trabeculus hexakon	*Puffinus* spp.	FAR
Upupicola		
Upupicola upupae	*Upupa epops*	FAR

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