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# Independent origins of the feather lice (Insecta: *Degeeriella*) of raptors

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Although diurnal birds of prey have historically been placed in a single order due to a number of morphological characters, recent molecular phylogenies have suggested that this is a case of convergence rather than homology, with hawks (Accipitridae) and falcons (Falconidae) forming two distantly related groups within birds. The feather lice of birds have often been used as a model for comparing host and parasite phylogenies, and in some cases there is significant congruence between the two. Thus, studying the phylogeny of the lice of diurnal raptors may be of particular interest with respect to the independent evolution of hawks vs. falcons. Using one mitochondrial gene and three nuclear genes, we inferred a phylogeny for the feather louse genus *Degeeriella* (which are all obligate raptor ectoparasites) and related genera. This phylogeny indicated that *Degeeriella* is polyphyletic, with lice from falcons vs. hawks forming two distinct clades. Falcon lice were sister to lice from African woodpeckers, whereas *Capraiella*, a genus of lice from rollers lice, was embedded within *Degeeriella* from hawks. This phylogeny showed significant geographical structure, with host geography playing a larger role than host taxonomy in explaining louse phylogeny, particularly within clades of closely related lice. However, the louse phylogeny does reflect host phylogeny at a broad scale; for example, lice from the hawk genus *Accipiter* form a distinct clade. © 2015 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2015, **114**, 837–847.

ADDITIONAL KEYWORDS: Accipitriformes – birds – diurnal birds of prey – ectoparasites – Falconiformes – molecular phylogeny – Phthiraptera – systematics.

## INTRODUCTION

Insight into factors leading to the diversification of parasites can be gained from either comparing a parasite phylogeny directly with that of its hosts or by studying patterns of host association with respect to parasite phylogeny (Page, 2003; de Vienne *et al*., 2013). Several studies focusing on comparisons of host and parasite phylogenies (Johnson *et al*., 2002, 2003; Page *et al*., 2004; Weckstein, 2004; Banks, Palma & Paterson, 2006; Hughes *et al*., 2007), or on phylogenetic patterns of host specificity (Johnson, Malenke & Clayton, 2009; Johnson *et al*., 2011) and host association (Johnson *et al*., 2001), have involved feather lice. Feather lice (Insecta: Ischnocera: Philopteridae) are obligate ectoparasites of birds that complete their entire life cycle on their host. Transfer between host individuals typically requires direct contact, such as while rearing young or during copulation. Dispersal opportunities between species of hosts are generally rare. However, dispersal by attaching to winged hippoboscid flies (phoresy) has been documented for some groups of feather lice (Clay & Meinertzhagen, 1943; Keirans, 1975). Although phoresy potentially results in dispersal of lice to a novel species of host (Harbison & Clayton, 2011), survival might be low on these novel hosts, potentially because of differences in feather morphology, which result in lice being more susceptible to host-defense mechanisms such as preening (Clayton *et al*., 2003; Malenke, Johnson & Clayton, 2009).

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The generally low dispersal ability of feather lice, combined with reduced survival on foreign hosts, results in the phylogeny of these parasites often reflecting host relationships because of the process of cospeciation. However, the degree to which the phylogeny of lice matches that of their hosts varies from strong phylogenetic congruence (Clayton & Johnson, 2003; Hughes *et al*., 2007), to matching higher-level groups of birds and lice (Johnson *et al*., 2001), to no significant congruence between host and parasite phylogenies (Johnson *et al*., 2002; Weckstein, 2004; Banks *et al*., 2006). This diversity of patterns makes feather lice an important model system in studying the processes that influence codiversification of hosts and parasites. In general, there is considerable correspondence between the higher-level classification of birds (e.g. orders and families) and the generic host associations of feather lice (Price *et al*., 2003). However, because traditional louse classification was heavily influenced by host taxonomy, these looser relationships could be an artifact of taxonomic practice, rather than a reflection of actual relatedness (Johnson *et al*., 2002). In addition, several orders of birds have recently been shown to be paraphyletic (Hackett *et al*., 2008), which further compounds any evaluation of congruence assessed from classification alone.

Raptors (all diurnal birds of prey, including hawks, falcons, and eagles) have historically been placed in a single order. However, recent molecular phylogenies have suggested that the falcons (Falconidae) are distantly related to the other diurnal raptors (hawks, eagles, vultures, etc.), which are now placed together in a single group, Accipitriformes, to the exclusion of falcons (Hackett *et al*., 2008; Jetz *et al*., 2012). One genus of parasitic feather louse, *Degeeriella*, curiously occurs on both hawks and falcons, but not on other groups of birds (Price *et al*., 2003). However, morphological and molecular evidence has brought into question the monophyly of *Degeeriella*. Clay (1958) suggested that *Degeeriella fulva* (from hawks) and *Capraiella*, a genus of louse only recorded from rollers (Coraciidae, a family of birds unrelated to birds of prey), are closely related based on similarities in the male genitalia and head shape. Additionally, Dalgleish (1969) found evidence that *Degeeriella* from falcons are morphologically similar to some Old World *Picicola* of woodpeckers. A molecular phylogeny (Johnson *et al*., 2002) of the *Degeeriella* complex (as defined by Clay, 1958), which included only a single exemplar each of lice from falcons, hawks, and rollers, indicated some support for these relationships and polyphyly of *Degeeriella*. However, detailed assessment of this genus could not be made because of limited sampling.

Species delineation in *Degeeriella* is also potentially problematic. Currently, all *Degeeriella* from Falconidae [with the exception of *Degeeriella carruthi* from American Kestrel (*Falco sparverius*)] are currently placed in a single species, *Degeeriella rufa*. Similarly, *D. fulva* is recorded from a variety of hawk and eagle species (Price *et al*., 2003; Gonzalez-Acuña *et al*., 2008). Phoresy is well documented in *Degeeriella* (Keirans, 1975) and could result in a single parasite species found across a variety of hosts. However, studies of feather lice from pigeons and doves (Columbidae) have indicated that widespread taxa could in fact represent cryptic species, particularly in groups with a wide range of host sizes (Johnson *et al*., 2002; Malenke *et al*., 2009). Therefore, it is unknown if taxa currently recognized as widespread species of *Degeeriella* are truly a single species or represent distinct evolutionary lineages.

Using sequences from one mitochondrial and three nuclear genes, we reconstructed the phylogeny of the louse genus *Degeeriella* and relatives by sampling lice widely from many of the major groups of diurnal birds of prey along with *Capraiella* from rollers and *Picicola* from woodpeckers. We included raptor lice from most continents to evaluate the degree of biogeographical structure in parasite phylogeny. In addition, we included multiple representatives of some host genera to evaluate, in more detail, phylogenetic patterns of host association, with multiple samples from the same louse species in some cases.

## MATERIAL AND METHODS

### Specimen acquisition

Lice were collected from host birds in various ways, including ethyl acetate fumigation (Clayton, Gregory & Price, 1992), dust ruffling (Walther & Clayton, 1997), and manual searches of birds for lice from a variety of sources. A total of 58 specimens of *Degeeriella* from 37 host species were included, along with five *Capraiella* specimens from five host species (Table 1). *Degeeriella* were obtained from a wide variety of raptor groups, including falcons, soaring hawks, forest hawks, sea eagles, booted eagles, kites, and harriers, and *Capraiella* was sampled from both genera of rollers described. A single representative of *Acutifrons*, a morphologically similar genus recorded from caracaras (Falconidae), was also included. Additionally, other members of the *Degeeriella* complex (all from nonraptor hosts, including woodpeckers) included in the study by Johnson *et al*. (2002) were used as outgroups.

### Sequencing

Lice were collected and stored in 95% ethanol at –70 °C. The head and body were separated and placed

**Table 1.** Samples included in the study

| Louse species | Host species | Host order | Country | Extraction code | *COI* | *EF-1α* | *hyp* | *TMEDE6* |
|---|---|---|---|---|---|---|---|---|
| *Capraiella* sp. | *Coracias abysinicus* | Coraciiformes | Ghana | Cbsp.Coaby.9.6.2012.11 | pending | pending | pending | pending |
| *Capraiella* sp. | *Coracias caudata* | Coraciiformes | Malawi | Cbsp.Cocau.9.6.2012.3 | pending | pending | – | pending |
| *Capraiella* sp. | *Coracias spatula* | Coraciiformes | Malawi | Cbsp.Cospa.9.6.2012.4 | – | pending | pending | pending |
| *Capraiella* sp. | *Eurystomus orientalis* | Coraciiformes | Australia | Cbsp.Euori.9.6.2012.12 | pending | pending | pending | pending |
| *Capraiella* sp. | *Eurystomus gularis* | Coraciiformes | Ghana | Cbsp.Eugul.4.3.2000.5 | AF444852 | AF447190 | – | – |
| *Degeeriella carruthi* | *Falco sparverius* | Falconiformes | USA | Dgcar.Faspa.6.13.2012.6 | pending | pending | pending | pending |
| *Degeeriella carruthi* | *Falco sparverius* | Falconiformes | USA | Dgcar.9.8.1999.7 | AF444860 | AF447196 | pending | – |
| *Degeeriella frater* | *Accipiter tachiro* | Accipitriformes | Malawi | Dgsp.Actac.9.6.2012.2 | pending | pending | pending | pending |
| *Degeeirella frafer* | *Acciptier virgatus* | Accipitriformes | China | Dgsp.Acvir.11.2.2012.3 | pending | pending | pending | – |
| *Degeeriella fulva* | *Buteo augur* | Accipitriformes | Kenya | Dgsp.Buaug.5.24.2013.11 | pending | pending | – | pending |
| *Degeeriella fulva* | *Buteo jamaicensis* | Accipitriformes | USA | Dgsp.Bujam.6.4.2012.4 | pending | – | – | – |
| *Degeeriella fulva* | *Buteo jamaicensis* | Accipitriformes | Canada | Dgsp.Bujam.8.2.2013.1 | pending | – | – | – |
| *Degeeriella fulva* | *Buteo jamaicensis* | Accipitriformes | Canada | Dgsp.Bujam.8.2.2013.3 | pending | – | pending | – |
| *Degeeriella fulva* | *Buteo jamaicensis* | Accipitriformes | USA | Dgsp.Bujam.9.6.2012.6 | pending | pending | pending | pending |
| *Degeeriella fulva* | *Buteo lagopus* | Accipitriformes | Japan | Dgful.Bulag.12.3.2012.2 | pending | pending | pending | pending |
| *Degeeriella fulva* | *Buteo lagopus* | Accipitriformes | Canada | Dgsp.Bulag.8.19.2013.10 | pending | – | – | – |
| *Degeeriella fulva* | *Buteo regalis* | Accipitriformes | USA | Dgsp.Bureg.5.24.2013.10 | pending | pending | – | pending |
| *Degeeriella fulva* | *Buteo regalis* | Accipitriformes | USA | Dgful.1.15.2000.5 | AF444861 | AF447197 | pending | pending |
| *Degeeriella fusca* | *Circus assimilis* | Accipitriformes | Australia | Dgfus.Ciass.6.13.2012.2 | pending | pending | pending | pending |
| *Degeeriella fusca* | *Circus cyaneus* | Accipitriformes | Canada | Dgsp.Cicya.8.2.2013.8 | pending | – | – | – |
| *Degeeriella haydocki* | *Accipiter minullus* | Accipitriformes | Mozambique | Dgsp.Acmin.9.6.2012.5 | pending | pending | pending | – |
| *Degeeriella nisus* | *Accipiter nisus* | Accipitriformes | Sweden | Dgnis.Acnis.12.3.2012.6 | pending | pending | – | – |
| *Degeeriella nisus* | *Accipiter nisus* | Accipitriformes | Sweden | Dgnis.Acnis.12.3.2012.1 | pending | pending | pending | – |
| *Degeeriella nisus* | *Accipiter striatus* | Accipitriformes | USA | Dgnis.Acstr.6.4.2012.3 | pending | pending | pending | – |
| *Degeeriella quatei* | *Henicopernis longicauda* | Accipitriformes | Papua New Guinea | Dgqua.Helon.6.13.2012.1 | – | pending | – | pending |
| *Degeeriella regalis* | *Buteo galapagoensis* | Accipitriformes | Galapagos | Dgreg.Bugal.6.13.2012.5 | pending | pending | pending | – |
| *Degeeriella regalis* | *Buteo galapagoensis* | Accipitriformes | Galapagos | Dgsp.Bugal.5.24.2013.5 | – | pending | pending | pending |
| *Degeeriella regalis* | *Haliastur sphenurus* | Accipitriformes | Australia | Dgsp.Hasph.11.2.2012.4 | pending | pending | pending | pending |
| *Degeeriella rima* | *Kaupifalco monogrammicus* | Accipitriformes | Malawi | Dgsp.Kamon.9.6.2012.10 | pending | pending | pending | pending |
| *Degeeriella rufa* | *Falco berigora* | Falconiformes | Australia | Dgruf.Faber.6.4.2012.1 | pending | pending | pending | pending |
| *Degeeriella rufa* | *Falco cenchroides* | Falconiformes | Australia | Dgruf.Facen.6.4.2012.5 | – | pending | pending | pending |
| *Degeeriella rufa* | *Falco longipennis* | Falconiformes | Australia | Dgruf.Falon.6.4.2012.6 | pending | pending | pending | pending |
| *Degeeriella* sp. | *Accipiter cirrocephalus* | Accipitriformes | Australia | Dgsp.Accir.6.13.2012.7 | pending | pending | pending | pending |
| *Degeeriella* sp. | *Accipiter fasciatus* | Accipitriformes | Australia | Dgsp.Acfas.6.13.2012.3 | pending | – | pending | pending |
| *Degeeriella* sp. | *Accipiter francesii* | Accipitriformes | Madagascar | Dgsp.Acfra.6.4.2012.2 | pending | pending | pending | – |
| *Degeeriella* sp. | *Accipiter striatus* | Accipitriformes | Canada | Dgsp.Acstr.8.2.2013.11 | pending | – | pending | – |
| *Degeeriella* sp. | *Aquila morphnoides* | Accipitriformes | Australia | Dgsp.Himor.11.2.2012.2 | pending | – | – | – |
| *Degeeriella* sp. | *Aquila wahlbergi* | Accipitriformes | Malawi | Dgsp.Aqwah.9.6.2012.9 | pending | – | pending | – |
| *Degeeriella* sp. | *Buteo jamaicensis* | Accipitriformes | Canada | Dgful.Bujam.8.2.2013.6 | pending | – | – | – |
| *Degeeriella* sp. | *Buteo jamaicensis* | Accipitriformes | USA | Dgsp.Bujam.11.2.2012.5 | pending | – | – | pending |
| *Degeeriella* sp. | *Buteo magnirostris* | Accipitriformes | Peru | Dgsp.Bumag.1.31.2014.11 | pending | pending | – | pending |
| *Degeeriella* sp. | *Buteo platypterus* | Accipitriformes | Panama | Dgsp.Bupla.6.4.2012.8 | pending | pending | pending | pending |
| *Degeeriella* sp. | *Buteo swainsoni* | Accipitriformes | Canada | Dgsp.Buswa.1.31.2014.2 | pending | pending | – | pending |
| *Degeeriella* sp. | *Falco sparverius* | Falconiformes | Canada | Dgcar.Faspa.1.31.2014.1 | pending | pending | – | pending |
| *Degeeriella* sp. | *Falco sparverius* | Falconiformes | Canada | Dgsp.Faspa.2.21.2014.11 | pending | pending | pending | pending |
| *Degeeriella* sp. | *Falco sparverius* | Falconiformes | Canada | Dgsp.Faspa.2.21.2014.12 | pending | pending | pending | – |

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**Table 1.** *Continued*

| Louse species | Host species | Host order | Country | Extraction code | *COI* | *EF-1α* | *hyp* | *TMEDE6* |
|---|---|---|---|---|---|---|---|---|
| *Degeeriella* sp. | *Falco sparverius* | Falconiformes | Canada | Dgsp.Faspa.2.21.2014.13 | pending | pending | pending | – |
| *Degeeriella* sp. | *Falco sparverius* | Falconiformes | Canada | Dgsp.Faspa.2.21.2014.14 | pending | pending | pending | – |
| *Degeeriella* sp. | *Falco sparverius* | Falconiformes | Canada | Dgsp.Faspa.2.21.2014.15 | pending | pending | pending | – |
| *Degeeriella* sp. | *Falco sparverius* | Falconiformes | Canada | Dgsp.Faspa.2.21.2014.16 | pending | pending | pending | – |
| *Degeeriella* sp. | *Falco sparverius* | Falconiformes | Canada | Dgsp.Faspa.8.2.2013.10 | pending | – | pending | – |
| *Degeeriella* sp. | *Falco sparverius* | Falconiformes | Canada | Dgsp.Faspa.8.2.2013.16 | pending | – | – | – |
| *Degeeriella* sp. | *Haliaeetus leucocephalus* | Accipitriformes | Canada | Dgdis.Haleu.8.2.2013.5 | pending | – | pending | – |
| *Degeeriella* sp. | *Haliaeetus pelagicus* | Accipitriformes | Japan | Dgsp.Hapel.12.3.2012.5 | – | – | pending | – |
| *Degeeriella* sp. | *Haliastur indus* | Accipitriformes | Australia | Dgsp.Haind.6.13.2012.4 | pending | pending | pending | – |
| *Degeeriella* sp. | *Henicopernis longicauda* | Accipitriformes | Papua New Guinea | Dgsp.Helon.11.2.2012.1 | – | pending | pending | pending |
| *Degeeriella* sp. | *Ictinia mississippiensis* | Accipitriformes | USA | Dgsp.Icmis. 11.2.2012.6 | pending | pending | – | pending |
| *Degeeriella* sp. | *Ictinia mississippiensis* | Accipitriformes | USA | Dgsp. Icmis.6.4.2012.7 | pending | pending | – | pending |
| *Degeeriella* sp. | *Ictinia plumbea* | Accipitriformes | Brazil | Dgsp.Icplu.9.6.2012.8 | pending | pending | pending | – |
| *Degeeriella* sp. | *Leucopternis semiplumbeus* | Accipitriformes | Panama | Dgsp.Lesem.6.13.2012.8 | pending | pending | pending | pending |
| *Degeeriella* sp. | *Pseudastur albicollis* | Accipitriformes | Brazil | Dgsp.Lealb.9.6.2012.7 | pending | pending | pending | – |
| *Degeeriella vagans* | *Accipiter cooperi* | Accipitriformes | USA | Dgsp.Accoo.9.6.2012.1 | – | pending | pending | – |
| *Degeeriella vagans* | *Accipiter gentilis* | Accipitriformes | Sweden | Dgsp.Acgen.2.1.2013.1 | pending | pending | – | pending |
| Outgroup | | | | | | | | |
| *Acutifrons* sp. | *Caracara cheriway* | Accipitriformes | USA | Assp.Cache.5.24.2013.6 | pending | pending | pending | – |
| *Austrophilopterus pacificus* | *Andigena nigrirostris* | Piciformes | Peru | Appac.1.17.2000.8 | AF444846 | AF447184 | – | pending |
| *Austrophilopterus* sp. | *Selenidera gouldi* | Piciformes | Brazil | Apsp.Segou.1.17.2000.7 | AF444848 | AF447186 | – | pending |
| *Austrophilopterus* sp. | *Ramphastos brevis* | Piciformes | Ecuador | Apsp.Rabre.1.17.2000.6 | AF444847 | AF447185 | pending | pending |
| *Austrophilopterus subsimilis* | *Ramphastos sulfuratus* | Piciformes | Mexico | Ausub.1.27.1999.12 | AF444850 | AF447188 | pending | – |
| *Austrophilopterus torquatus* | *Pteroglossus torquatus* | Piciformes | Mexico | Ausp.Pttor. 1.27.1999.1 | AF444849 | AF447187 | pending | pending |
| *Buceromersonia* sp. | *Tockus erythrorhynchus* | Coraciiformes | Tanzania | Bmsp.Toery.5.24.2013.9 | pending | pending | – | pending |
| *Colinicola docophoroides* | *Callipepla californica* | Galliformes | USA | Cxdoc.1.15.2000.1 | AF444859 | AF38666 | pending | pending |
| *Cotingacola* sp. | *Querula purpurata* | Passeriformes | Brazil | Issp.Qupur.10.12.1999.12 | AF444863 | AF447198 | – | pending |
| *Cotingacola stotzi* | *Querula purpurata* | Passeriformes | Brazil | Cnsto.10.12.1999.11 | AF444854 | AF447192 | – | pending |
| *Cuclotogaster hopkinsi* | *Francolinus africanus* | Galliformes | South Africa | Cusp.Frafr.2.3.1999.11 | AF444858 | AF447195 | – | pending |
| *Cuculicola atopus* | *Piaya cayana* | Cuculiformes | Mexico | Cuato.1.27.1999.4 | AF444856 | AF447193 | – | – |
| *Cuculicola* sp. | *Chrysococcyx klaas* | Cuculiformes | Ghana | Cusp.Chkla.4.3.2000.10 | AF444857 | AF447194 | – | – |
| *Picicola capitatus* | *Dendropicos fuscescens* | Piciformes | South Africa | Picap.2.3.1999.10 | AF444866 | AF447201 | pending | pending |
| *Picicola porisma* | *Colaptes auratus* | Piciformes | USA | Pipor.10.17.2000.5 | AF444867 | AF447202 | pending | pending |
| *Picicola snodgrassi* | *Melanerpes carolinensis* | Piciformes | USA | Pisno.10.5.1999.8 | AF444868 | AF447203 | – | – |
| *Picicola* sp. | *Chelidoptera tenebrosa* | Piciformes | Brazil | Pisp.Chten.1.17.2000.12 | AF444869 | AF447204 | pending | pending |
| *Picicola* sp. | *Galb ula alb iros tris* | Piciformes | Brazil | Pisp.Gaalb.1.17.2000.10 | AF444870 | AF447205 | – | pending |
| *Picicola* sp. | *Monasa nigrifrons* | Piciformes | Bolivia | Pisp.Monig.1.17.2000.3 | AF444872 | AF447207 | pending | pending |
| *Picicola* sp. | *Nystalus chacuru* | Piciformes | Bolivia | Pisp.Nycha.1.17.2000.1 | AF444873 | AF447208 | pending | – |
| *Picicola* sp. | *Mesopicus pyrrhogaster* | Piciformes | Ghana | Pisp.Mepyr.4.11.2000.9 | AF444871 | AF447206 | – | – |
| *Rhynonirmus* sp. | *Scolopax bukidnonensis* | Charadriiformes | Philippines | Rhsp.Scsp.7.14.1999.9 | AF444875 | AF447210 | pending | pending |
| *Trogoninirmus* sp. | *Trogon melanocephalus* | Trogoniformes | Mexico | Trsp.Trmel.1.27.1999.3 | AF444876 | AF447211 | pending | – |

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together in digestion buffer. DNA was extracted from each specimen using a DNeasy Blood and Tissue Kit (Qiagen) following a modified version of the protocol for Total DNA from Animal Tissues. The modifications included lengthening the incubation period in step 2 to 36 h and decreasing the amount of Buffer AE in step 7 to 50 μL (which was repeated twice in different 1.5-mL collection tubes). The head and body were removed from the buffer and mounted on a microslide in balsam as a voucher.

After extraction, polymerase chain reaction (PCR) amplification was performed in 50-μL reaction volumes to amplify four genes: one mitochondrial protein-coding gene, cytochrome oxidase I (*COI*); and three nuclear protein-coding genes: elongation factor-1α (*EF-1α*), hypothetical protein EOG9XHC5 (*hyp*), and transmembrane emp24 domain-containing protein 6 precursor (*TMEDE6*). Primers L6625 and H7005 (Hafner *et al*., 1994) were used for *COI*, primers Ef1-For3 and Ef1-Cho10 (Danforth & Ji, 1998) were used for *EF-1α*, primers BR50-181L and BR50-621R (Sweet, Allen, & Johnson, 2014) were used for *hyp*, and primers BR69-190F and BR69-432R (Sweet *et al*., 2014) were used for *TMEDE6*. The PCR amplification conditions followed those of Sweet *et al*. (2014), with an annealing temperature of 46 °C (except for *EF-1α*, for which the annealing temperature was 50 °C). Sequencing reactions were performed using 1 μL of BigDye and were then submitted for sequencing on an ABI 3730xl capillary machine at the University of Illinois Keck Center for Comparative and Functional Genomics. Raw forward and reverse strands of each sequence were aligned and assembled in Sequencher 4.8 (minimum match = 60; minimum overlap = 20) and manually adjusted. Each gene was then assembled into a single contig and exported to seaview 4.3.0 as a FASTA file. The built-in MUSCLE aligner was used to produce multiple alignments with all alignment settings at default values, followed, when necessary, by manual adjustments by eye (Edgar, 2004; Gouy, Guindon & Gascuel, 2010).

Sequence data for one sample, *D. rufa*, from *Falco berigora*, was assembled from a paired-end Illumina run using the automated Target Restriction Assembly Method (aTRAM DOI: 10.5281/zenodo.10431) using sequences of each target gene from other falconid *Degeeriella* (J. M. Allen, D. L. Huang, Q. C. Cronk, K. P. Johnson, unpubl. data).

### Analysis

Each gene was first analyzed separately to ensure that gene trees were not in conflict (posterior probability greater than 0.95). This included selecting an evolutionary model for each gene using modelgenerator, with the model having the best Akaike information criterion score selected (Keane *et al*., 2006). GTR + I + G was selected for *COI*, HKY + G was selected for *EF-1α*, GTR + G was selected for *hyp*, and TrN + G was selected for *TMEDE6* (with HKY + G, which was the second-best model, used in programs in which TrN + G was not available). Gene trees were inferred using 40 million generation BEAST runs under the model selected by modelgenerator (Drummond & Rambaut, 2007). Excluding the placement of specimens collected from American Kestrel (*F. sparverius*), for which the *COI* gene tree conflicted with gene trees from nuclear genes, trees inferred from individual genes did not include any well-supported (posterior probability above 0.95) topological conflicts. Thus, gene sequences were concatenated for analysis. In the case of lice from American Kestrels, these formed a monophyletic clade when individual nuclear gene trees were inferred. This clade was well supported (posterior probability greater than 0.95) in *EF-1α* and *TMEDE6* gene trees, whereas the *hyp* gene tree had a posterior probability of 0.85 for this arrangement. However, the mitochondrial *COI* gene tree conflicted strongly with the nuclear gene trees. The *COI* gene supported two distinct clades (each with a posterior probability of 1.0) containing American Kestrel lice; one was composed solely of lice from this host species, whereas the other also contained lice from falcons other than American Kestrel.

In the combined analysis, each gene was treated as a separate partition to allow for different models to be used for each gene. Phylogenies based on all genes together were inferred using Bayesian methods [MrBayes: 20 million generations, nrun = 4, nchain = 4, sampling every 1000 generations, burn-in = 5000 samples (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003); and BEAST: 40 million generations, sampling every 1000 generations, burn-in = 10 000 samples] (Drummond & Rambaut, 2007); maximum likelihood (ML) (garli: 10 independent runs, default settings, automated stop criterion = 50 000) (Zwickl, 2006); and maximum parsimony (MP) (using PAUP*, 1000 random addition sequences with tree bisection and reconnection branch swapping) (Swofford, 2003). Posterior probabilities (using BEAST), parsimony bootstrap values (using PAUP*, 1000 replicates of 100 random addition sequences with maxtrees set at 100 because of computational constraints), and ML bootstrap values (using garli, 500 bootstap replicates on default settings with an automated stop criterion = 5000) were used to evaluate branch support (Swofford, 2003; Zwickl, 2006).

## RESULTS

The tree for *Degeeriella* and relatives, resulting from combined analyses of three nuclear and one

mitochondrial gene, was well resolved and generally highly supported. *Degeeriella* was not monophyletic, instead being separated into two well-supported clades that included other genera (Fig. 1). *Degeeriella* from members of the Falconidae formed a monophyletic group (MP bootstrap = 94; ML bootstrap = 99; posterior probability = 1.0) that was sister to some (but not all) representatives of the genus *Picicola*, a group of lice that parasitizes woodpeckers. This arrangement also results in *Picicola* being paraphyletic. All the *Degeeriella* from Accipitriformes (hawks, eagles, and their allies), together with the genus *Capraiella* from rollers (Coraciidae), formed a well-supported monophyletic group (MP bootstrap = 83; ML bootstrap = 98; posterior probability = 1.0). Within the *Degeeriella* complex recognized by Clay 1958 more broadly, the *Picicola* from African woodpeckers, *Capraiella*, *Acutifrons* (a genus of lice primarily from caracaras), and all *Degeeriella* comprised a well-supported monophyletic group (ML bootstrap = 92; posterior probability = 1.0).

Considering first the lice of the Falconidae, the sole representative of *Acutifrons*, a *Degeeriella*-like genus from caracaras (a group of species within Falconidae that are placed in a different subfamily from the majority of falcons) was recovered as sister to a clade comprising the *Degeeriella* from falcons + *Picicola* from African woodpeckers (MP bootstrap = 52; ML bootstrap = 96; posterior probability = 1.0). *Degeeriella rufa* and *D. carruthi* are the only two species of lice recorded from the diverse falcon genus *Falco*, although *D. rufa* is not monophyletic with respect to *D. carruthi*. Surprisingly, for the mitochondrial *COI* gene tree, two genetically distinct and distantly related *Degeeriella* were found on American Kestrels, which previously had been known to host only *D. carruthi*, and this result also appears in the combined analysis. Some specimens of lice from American Kestrels grouped with *D. rufa*, whereas others formed a distinct clade containing only lice from American Kestrels. This could explain Clay's (1958) observation that some specimens from American Kestrel have head morphology more similar to that of *D. rufa*. This species has been treated by some authorities as a subspecies of *D. rufa* (which has a high degree of morphological variation), although many (but not all) specimens of *D. carruthi* have different head morphology from *D. rufa* (Clay, 1958). However, because the nuclear gene trees strongly conflicted with this result, mitochondrial introgression could also explain these results. *COI* divergence ranged from 13% to 17% between the two clades of lice from American Kestrels, but was less than 3% among members of the same clade. The results from mitochondrial *COI* conflicted with all nuclear gene trees, which placed all lice from American Kestrel in a single clade, which was typically well supported. Although *Degeeriella* species have traditionally been defined based on host associations (and often specimen identification is based on the host species), there are instances where multiple *Degeeriella* species have been found on a single host species (Mey, 1997; Price *et al*., 2003). As raptors are sparsely sampled and lice identifications have often been based on host records rather than on morphological examination, it is possibly not uncommon for a bird species to host multiple *Degeeriella* species.

Among the *Degeeriella* of hawks (Accipitriformes), clades tended to be structured by both geography and host taxonomy. The earliest diverging clade in the group includes lice from a variety of kite and hawk species that are all Neotropical residents or migrants to the Neotropics. The genus *Capraiella*, from rollers, is then sister to the remaining *Degeeriella* from Accipitriformes (MP bootstrap = 93; ML bootstrap = 96; posterior probability = 0.99). Resolution among the other major lineages in this group is relatively poor. However, the *Degeeriella* of northern-hemisphere *Accipiter* and *Circus* form a group (MP bootstrap = 80; posterior probability = 0.99) as do the *Degeeriella* of southern-hemisphere *Accipiter* (MP bootstrap = 100; ML bootstrap = 100; posterior probability = 1.0).

In some cases lice collected from the same host species do not form monophyletic groups, although this could be an example of geographical substructure in the case of the two *D. fulva* specimens from Rough-legged Hawk (*Buteo lagopus*) because one host was sampled from North America and the other from Asia. Although both *D. fulva* and *Degeeriella regalis* have been recorded from Red-tailed Hawks (*Buteo jamaicensis*) (and a few other raptor species), all samples from Red-tailed Hawks had a *COI* pairwise distance of no greater than 1.3%. This low divergence suggests that we had only sampled one species (*D. fulva*) from Red-tailed Hawks, and this result was consistent with specimens for which morphological species determinations could be made.

In some of the cases in which lice from the same host species do not form a monophyletic group, lice from the same geographical region tend to be more closely related to each other, regardless of host taxonomy. For example, a clade of closely related lice from Red-tailed Hawk, Ferruginous Hawk (*Buteo regalis*), and Swainson's Hawk (*Buteo swainsoni*) from western North America are virtually identical in their *COI* sequences, whereas the *COI* sequence from a Red-tailed Hawk from eastern North America had a pairwise distance of 1.3% from the western North America specimens. Geographical structuring of the *Degeeriella* phylogeny also occurs for host species that are found throughout the Holarctic, such as the

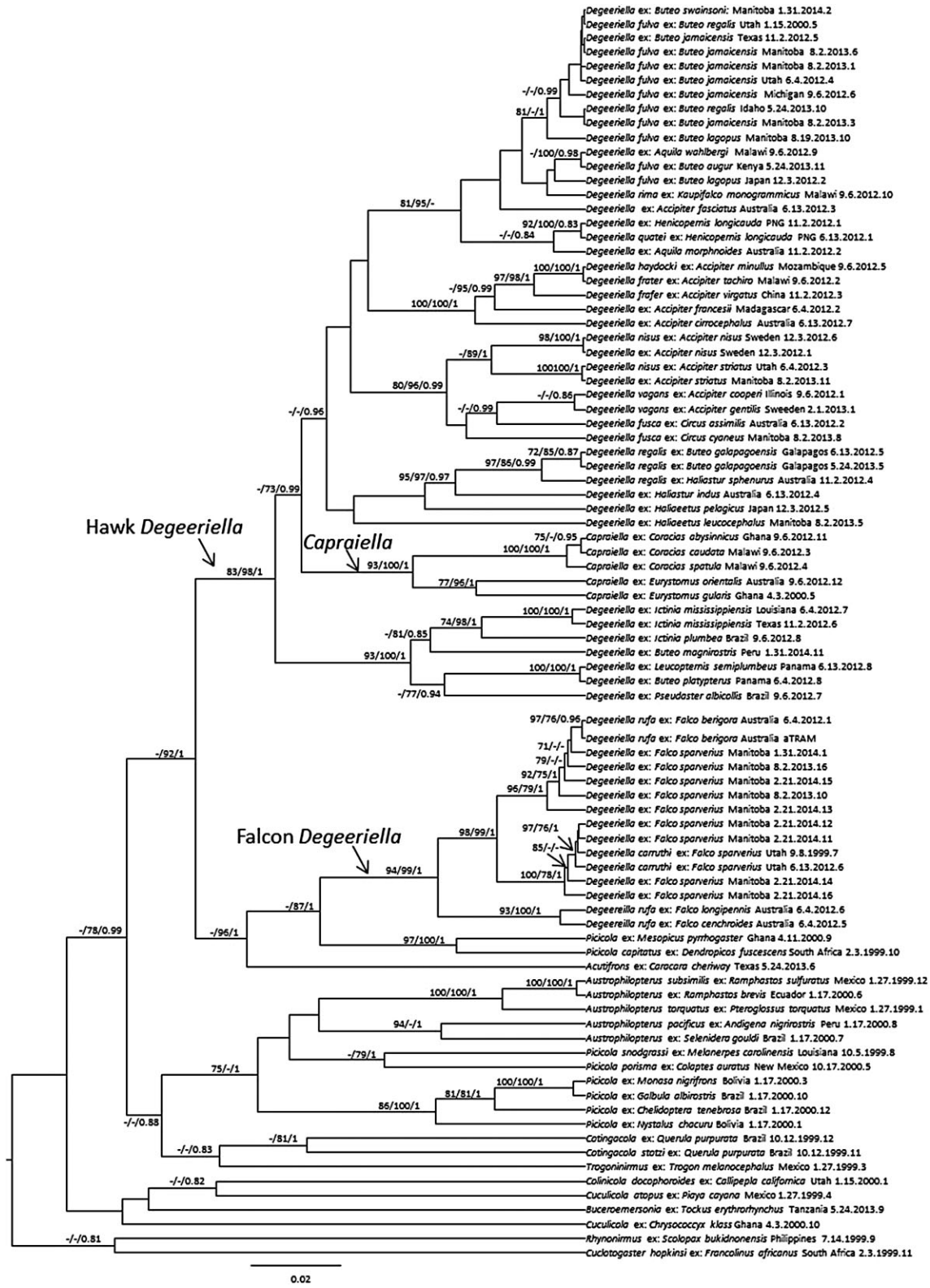


**Figure 1.** Phylogeny of *Degeeriella* and selected outgroups based on the results of the Bayesian analysis after 20 million generations. Numbers on branches denote MP bootstrap/ML bootstrap/posterior probability. The cut-off for MP and ML bootstraps is 70, and the cut-off for posterior probabilities was set at 0.80. Note that the hawk *Degeeriella* clade contains lice from a variety of accipitrid birds, including hawks, eagles, and kites, along with lice from rollers.

Rough-legged Hawk. Lice from Rough-legged Hawks in North America are in the North American clade previously mentioned, whereas those from Eurasia are in a distinct Old World clade. Phoresis on hippoboscid flies is known for *Degeeriella*, which could explain how birds in a given geographical region could share lice.

## DISCUSSION

A phylogeny based on one mitochondrial and three nuclear genes for the feather louse genus *Degeeriella* agrees with the assessment of relationships based on morphology by Dalgleish (1969) and Clay (1958), who suggested that the *Degeeriella* from falcons are closely related to *Picicola* from African woodpeckers, whereas the *Degeeriella* from hawks are more closely related to *Capraiella* from rollers. These results extend the conclusions of Johnson *et al*. (2002) by more densely sampling within *Degeeriella*, confirming the existence of only two distinct clades, but also that *Degeeriella*, as currently defined, is paraphyletic. With this denser taxon sample, we find that roller lice (*Capraiella*) are embedded within *Degeeriella* from hawks, although *Capraiella* does form a monophyletic group. Lice from the two genera of rollers, *Coracias* and *Eurystomus*, form two distinct subclades within *Capraiella*.

No prior molecular phylogenetic study has included *Acutifrons*, a louse genus found on caracaras. Here we find it to be sister to the clade comprising lice from African woodpeckers and falcons. Given that caracaras are the sister taxon of true falcons (Fuchs, Johnson & Mindell, 2012), one interpretation is that a host switch occurred from Falconidae to woodpeckers. However, additional taxon sampling is required to determine whether *Acutifrons* is monophyletic with respect to *Degeeriella*. Similarly, the genus *Capraiella* is placed within the hawk *Degeeriella* clade and the most-parsimonious explanation would be that host switch occurred from an accipitriform to a roller. However, further taxon sampling is again required to refine our understanding of the direction of the host switch. In both instances, a clade of lice from nonraptorial birds is embedded within a clade of raptorial birds. If a host switch by lice from predators to prey occurred, this would conflict with the hypothesis that lice would transfer from prey to predator as lice attempted to flee a dead host (Clay, 1949; Whiteman *et al*., 2004). Instead, the phylogenetic arrangement suggests that some other method of host switching could be responsible, such as phoresy. This interpretation, however, relies on the assumption of equally weighting host-switches from predators to prey, as from prey to predators. Another possibility is that lice switched from prey to raptors twice in each clade, although it is a less-parsimonious interpretation.

When possible, lice were identified to species. Some specimens could not be conclusively identified because they were nymphs or not the correct sex for species identification. With respect to previous taxonomic arrangements in *Degeeriella*, Clay (1958) divided members of *Degeeriella* into seven species groups, the most diverse being the *fulva* group. Our topology supports this group, with specimens of *D. fulva*, *Degeeriella rima*, *Degeeriella nisus*, *Degeeriella vagans*, *Degeeriella frater*, *Degeeriella haydocki*, and *Degeeriella fusca* forming a clade. Additionally, Elbel & Price (1973) described *Degeeriella quateri* and placed it within the *fulva* group. Our analysis also supports this placement. Clay treated *D. vagans*, *D. frater*, and *D. haydocki* as subspecies of *D. nisus*, all of which are included in our phylogeny. Although our topology places *D. haydocki* and *D. frater* as sister species, *D. nisus* and *D. vagans* are placed in a different clade (which also contains *D. fusca*). We also sampled multiple representatives of the *rufa* group and also found it to be well supported by our phylogeny. Testing the remaining species groups will require additional taxon sampling.

Interesting phylogenetic patterns of host association also emerge at lower taxonomic levels. The earliest diverging clade of *Degeeriella* from hawks includes lice from a wide range of hosts, including two species of *Ictinia* kites and three hawks. Although these hosts are not closely related, they are all residents of the Neotropics or are Neotropical migrants, and are similar in size. Other clades of *Degeeriella* occurring on hawks are also structured by both geography and body size. *Degeeriella* from large North American soaring hawks (including Red Tailed Hawk, Ferruginous Hawk, Swainson's Hawk, and the North American exemplar of Rough-legged Hawk) all form a single, well-supported clade, which is sister to a group of large African or Euro-African migrants, including the Old World exemplar of Rough-legged Hawk, Augur buzzard (*Buteo augur*), and Wahlberg's Eagle (*Aquila wahlbergi*) (although this group lacks support in analyses). Additionally, lice from five small (75–380 g) *Accipiter* species, from Africa, southern Asian, and Australia, form a well-supported clade. A correlated relationship between host and parasite body size (known as Harrison's rule) is well documented for a wide variety of feather lice (Clayton *et al*., 2003; Johnson, Bush & Clayton, 2005; Tryjanowski, Szczykutowicz & Adamski, 2007; Malenke *et al*., 2009; Yamagishi *et al*., 2014) and may explain some of these patterns of host association. A second clade of *Accipiter* lice includes hosts from the Holarctic region plus two species of *Circus*. Wink & Sauer-Gürth (2004) recovered a sister relationship between *Circus*

and *Accipiter*, which might explain the closely phylogenetic relationship of their lice. This division within the *Degeeriella* of *Accipiter* also reflects host relationships recovered by Breman *et al*. (2013), who placed all host species included in the African/Asian/Australian clade as sister to a group of all hosts from the Holarctic clade of *Accipiter* lice. Within the Holarctic clade, lice from Sharp-shinned Hawk (*Accipiter striatus*) and Eurasian Sparrowhawk (*Accipiter nisus*) (two specimens of each) were sister taxa congruent with the proposed close relationship between these host taxa (Wink & Sauer-Gürth, 2004; Breman *et al*., 2013). Lice from the Brown Goshawk (*Accipiter fasciatus*) was placed outside these clades and instead placed as the sister to the large hawk clade, although this placement was weakly supported. This Australian accipiter (weighing over 500 g), is much larger than the other accipiters sampled in this region. Further sampling of *Degeeriella* from *Accipiter* species in south-east Asia and Australia is required to help resolve these patterns.

When possible, we included multiple individuals of lice from a single host species. Although, in most instances, lice from the same host species formed monophyletic clades, there were several examples for which this was not the case. Most notable were lice from the Rough-legged Hawk. This species has a Holarctic distribution, and both an Old World sample and a New World sample were included in our study. The Old World specimen fell within the clade of lice from large hawks from the Old World, and the New World specimen fell within the clade of lice from large hawks in the New World (the pairwise distance for *COI* is 8.7%). These relationships suggest that host geography can be as important as host phylogeny in structuring louse phylogeny, at least at the fine scale. Johnson, Adams & Clayton (2001) found similar levels of *COI* species-level divergence within other ischnoceran lice. This pattern is also supported by the relationships between lice collected from the Red-tailed Hawk (*B. jamaicensis*), Swainson's Hawk (*B. swainsoni*), and Ferruginous Hawk (*B. regalis*) when looking only at *COI*. Lice from these species in flyways west of the Mississippi River are genetically nearly identical (pairwise distances for *COI* are all 0.0%), whilst a Red-tailed Hawk louse from east of the Mississippi is more divergent (the pairwise distance for *COI* is 1.3% from the other members of this clade). Further sampling of other large raptor species in this flyway are needed to determine if this is an example of flyway homogenization, in which birds in a given flyway share closely related lice. Some evidence of flyway homogenization was found for the lice of small sandpipers and stints, but not in lice of large sandpipers (Gustafsson & Olsson, 2012). Interestingly, they also found no evidence of flyway differentiation of lice, whereas we found that lice from Old and New World Rough-legged Hawks were genetically differentiated into geographically structured clades.

In another case, 11 lice from American Kestrel (from which only *D. carruthi* is recorded) were included in our study, two from the western USA (from the same host individual) and nine from central Canada (from three different individuals). The western US lice, along with half of the Canadian lice, formed a clade, whereas the remaining Canadian samples did not. These remaining Canadian samples were placed as more closely related to *Degeeriella* from *F. berigora*, but did not themselves form a clade. Additional taxon sampling from the host genus *Falco* is needed. This, along with the placement of lice from *Falco longipennis* and *Falco cenchroides* as distinct from lice from *F. berigora*, suggests that *D. rufa* might contain multiple cryptic species and American Kestrels may be host to more than one species of *Degeeriella*.

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