



# Unlocking the black box of feather louse diversity: A molecular phylogeny of the hyper-diverse genus *Brueelia* <sup>☆</sup>



Sarah E. Bush <sup>a,\*</sup>, Jason D. Weckstein <sup>b,1</sup>, Daniel R. Gustafsson <sup>a</sup>, Julie Allen <sup>c</sup>, Emily DiBlasi <sup>a</sup>, Scott M. Shreve <sup>c,2</sup>, Rachel Boldt <sup>c</sup>, Heather R. Skeen <sup>b,3</sup>, Kevin P. Johnson <sup>c</sup>

<sup>a</sup> Department of Biology, University of Utah, 257 South 1400 East, Salt Lake City, UT 84112, USA

<sup>b</sup> Field Museum of Natural History, Science and Education, Integrative Research Center, 1400 S. Lake Shore Drive, Chicago, IL 60605, USA

<sup>c</sup> Illinois Natural History Survey, University of Illinois, 1816 South Oak Street, Champaign, IL 61820, USA

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## ABSTRACT

Songbirds host one of the largest, and most poorly understood, groups of lice: the *Brueelia*-complex. The *Brueelia*-complex contains nearly one-tenth of all known louse species (Phthiraptera), and the genus *Brueelia* has over 300 species. To date, revisions have been confounded by extreme morphological variation, convergent evolution, and periodic movement of lice between unrelated hosts. Here we use Bayesian inference based on mitochondrial (COI) and nuclear (EF-1 $\alpha$ ) gene fragments to analyze the phylogenetic relationships among 333 individuals within the *Brueelia*-complex. We show that the genus *Brueelia*, as it is currently recognized, is paraphyletic. Many well-supported and morphologically unified clades within our phylogenetic reconstruction of *Brueelia* were previously described as genera. These genera should be recognized, and the erection of several new genera should be explored. We show that four distinct ecomorphs have evolved repeatedly within the *Brueelia*-complex, mirroring the evolutionary history of feather-lice across the entire order. We show that lice in the *Brueelia*-complex, with some notable exceptions, are extremely host specific and that the host family associations and geographic distributions of these lice are significantly correlated with our understanding of their phylogenetic history. Several ecological phenomena, including phoresis, may be responsible for the macroevolutionary patterns in this diverse group.

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*"Taxonomist's nightmare... evolutionist's delight"*  
[MacIntyre (1967), after A.J. Cain]

## 1. Introduction

In 2012 a British birder was the first person to see 9000 different species of birds (McCarthy, 2012). This impressive tally is roughly 85–90% of all known bird species. Although a few new species of birds are being discovered and described each year

(Sangster and Luksenburg, 2015), it is estimated that over 95% of all bird species have already been described (Mayr, 1982). In short, birds are among the best known groups of organisms on the planet. Despite this knowledge, however, birds represent many additional layers of undiscovered diversity. Each bird species harbors a complex community of parasites and other symbionts, many of which are undescribed and understudied.

Songbirds (Passeriformes), the largest order of birds, are host to one of the largest, and most poorly understood groups of feather lice. The genus *Brueelia* Kéler 1936 has over 300 described species (Price et al., 2003; Cicchino, 2004; Rékási and Saxena, 2005; Valim and Palma, 2006, 2015; Cicchino and González-Acuña, 2008, 2009; Sychra et al., 2009, 2010a, 2010b; Valim and Weckstein, 2011; Najer et al., 2012a, 2012b, 2012c; Mey and Barker, 2014; Najer et al., 2014; Valim and Silveira, 2014), and thousands of slides with specimens of unidentified and undescribed species of *Brueelia* line the drawers of museum collections around the world.

Lice in the genus *Brueelia* are incredibly diverse. They vary enormously in body shape: from short, round, "head" louse ecomorphs, to long, thin, "wing" louse ecomorphs (Johnson et al., 2012). They

<sup>☆</sup> This paper was edited by the Associate Editor S.L. Cameron.

\* Corresponding author.

E-mail address: [bush@biology.utah.edu](mailto:bush@biology.utah.edu) (S.E. Bush).

<sup>1</sup> Current address: Department of Ornithology and Department of Biodiversity, Earth, and Environmental Sciences, Academy of Natural Sciences of Drexel University, 1900 Benjamin Franklin Parkway, Philadelphia, PA 19103, USA.

<sup>2</sup> Current address: Division of Mathematics and Natural Sciences, Brescia University, Owensboro, KY 42301, USA.

<sup>3</sup> Current address: Biology Department, Loyola University Chicago, Chicago, IL 60660, USA.

vary in color from light to dark (Bush et al., 2010), and in pigmentation patterns from simple to complex. Indeed, the morphological diversity within *Brueelia* echoes the diversity among all feather lice in the order Phthiraptera. A thorough understanding of the macroevolutionary patterns within *Brueelia* promises to illuminate the ecological and evolutionary forces influencing diversity among lice in general. However, this tantalizing diversity is a quintessential example of a “taxonomist’s nightmare... evolutionist’s delight” (MacIntyre, 1967). Convergent evolution of similar morphological characteristics is known to occur among lice (Johnson et al., 2012), which suggests that taxonomy based solely on morphological characters may obscure our understanding of the phylogenetic relationships within this group.

Lice in the genus *Brueelia* are also perplexing from another perspective. Among the groups of lice studied thus far, host specificity tends to correlate with cospeciation (Clayton et al., 2004). Lice on gophers are extremely host specific, and show among the strongest patterns of cospeciation in any system. Similarly, body lice on doves are quite host specific, and show a significant degree of cospeciation with their hosts, whereas wing lice on the same hosts are less host specific and show significantly less cospeciation than body lice (Clayton and Johnson, 2003; Clayton et al., 2004). *Brueelia* are considered to be highly host specific, with over 85% of described species recorded from just a single host species (Price et al., 2003). Despite this apparent high degree of host specificity, however, a preliminary cophylogenetic analysis did not support a hypothesis of cospeciation (Johnson et al., 2002a).

There are at least two plausible explanations for this pattern. First, while specificity is a necessary condition for cospeciation, it is not a sufficient condition. For example, herbivorous beetles in the genus *Belpharida* are specific to particular host plants (*Bursera*), yet the beetle phylogeny is not congruent with the phylogeny of the host plants (Becerra, 1997). This is, in part, because these insects are relatively mobile organisms and can move between different host plants. In contrast, most lice are relatively immobile, only moving between hosts during periods of direct contact (Clayton et al., in press). *Brueelia* species, however, are known to hitch rides on hippoboscids flies (Fig. 1). This phoretic behavior may provide these lice with opportunities to switch to and adapt to new host species. If phoresis between host species is rare, and gene flow is limited, then lice may specialize and become quite specific on the “new” host species. Thus, rare phoretic events over macroevolutionary time could simultaneously support high levels of host specificity while disrupting patterns of cospeciation at a coarse macroevolutionary time-scale.

Alternatively, the apparent host specificity of lice in the *Brueelia* complex may be a taxonomic artifact. Early louse taxonomists tended to describe new species on the basis of host associations, rather than on the basis of the lice themselves. This unfortunate practice has required synonymization of nearly 2000 species and subspecies of chewing lice in comparison to only 4464 valid species and subspecies (Price et al., 2003). Indeed, initial molecular studies of lice in this genus indicate that a single species of *Brueelia* can infest multiple host species across several distantly related host families (Johnson et al., 2002a). A comprehensive taxonomic revision, independent of louse morphology, and host associations, is needed to identify the ecological and evolutionary drivers of diversity in this group.

Here we provide a molecular based phylogenetic reconstruction for lice in the genus *Brueelia* and related lice in the genera *Bizarri-frons*, *Buerelius*, *Meropoecus*, *Motmotnirmus*, and *Sturnidoecus*, which are core members of the “*Brueelia* complex” (Clay and Tandan, 1967; Ledger, 1980; Valim and Palma, 2012, 2015). These genera are primarily found on songbirds (Passeriformes), although a few species are known to occur on Coraciiformes (bee-eaters), Piciformes (woodpeckers, barbets, and toucans), Trogoniformes

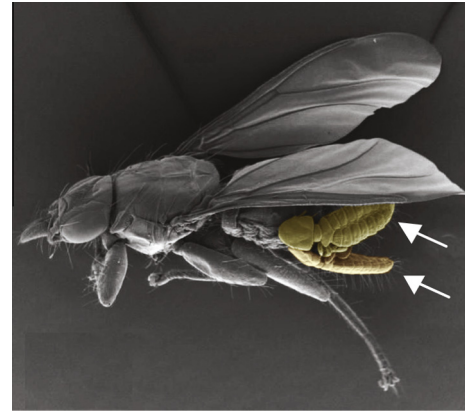


Fig. 1. Phoretic *Brueelia* sp. (arrows) hitching a ride on a hippoboscid fly. Fly collected from a blackbird *Turdus merula*. False-color SEM (SEM by V.S. Smith).

(trogons), and Cuculiformes (couas). Our sampling includes lice from all of these host groups. We use DNA sequences of nuclear (EF-1 $\alpha$ ) and mitochondrial (COI) genes to provide a phylogenetic reconstruction of a worldwide sampling of over 300 specimens of lice from the *Brueelia*-complex and related genera (Johnson et al., 2002a). This is the largest phylogenetic reconstruction for any group in the order Phthiraptera. We discuss these results in the context of prior generic classifications and recommend that several previously recognized genera be considered valid. We also discuss emerging patterns of host specificity, biogeography, morphology, and behavior that are intimated by our new understanding of the phylogenetic relationships of these feather lice.

## 2. Materials and methods

### 2.1. Sampling

We sampled a total of 333 louse specimens belonging to the *Brueelia*-complex (see Table 1 in Bush et al., in press). These lice were sampled from 250 bird species belonging to 66 bird families and five orders (Passeriformes, Coraciiformes, Cuculiformes, Piciformes, and Trogoniformes). Sampled lice include 38 known species and 211 lice that represent either new species of lice or new host associations. These samples were collected from 23 countries and all continents except Antarctica. An additional 30 outgroup taxa for rooting the phylogeny were selected to represent nested sister taxonomic relationships within the family Philopteriidae (Cruickshank et al., 2001; Johnson et al., 2001a; Smith et al., 2011). These 30 louse outgroup species were from 27 host species, in 17 host families, collected from 9 countries.

Lice were collected either from euthanized bird specimens using ethyl acetate fumigation or from live birds dusted with pyrethrum powder (Clayton and Drown, 2001; Bueter et al., 2009). Care was taken to make sure that individual hosts were kept separate at all times and to clean all working surfaces between fumigation. Lice were collected by the authors and colleagues during field-work conducted over several decades and were stored in vials of 95% ethanol, usually in ultracold (−80 °C) freezers.

### 2.2. DNA extraction, amplification and alignment

DNA was extracted from lice using either the Qiagen DNeasy micro-kit (Valencia, California, USA) following the manufacturer’s protocol as described by Valim and Weckstein (2011), or the Qiagen DNeasy tissue kit (Valencia, California, USA) following the manufacturer’s protocol as described by Johnson et al. (2001b).

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