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COMPARATIVE PHYLOGENETIC HISTORIES OF TWO LOUSE GENERA FOUND ON *CATHARUS* THRUSHES AND OTHER BIRDS

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ABSTRACT: The louse genera *Brueelia* (Ischnocera) and *Myrsidea* (Amblycera) are broadly codistributed on songbirds (Passeriformes), but differ in a variety of life history characteristics. We used mitochondrial and nuclear DNA sequences to assess levels of genetic divergence and reconstruct phylogenies of these 2 genera, focusing especially on *Catharus* thrushes in North America. We then qualitatively compared the phylogenies and levels of divergence within these 2 genera of codistributed parasites. Neither *Brueelia* nor *Myrsidea* appears to cospeciate with *Catharus* thrushes or passerine birds in general. The *Myrsidea* phylogeny exhibits significant levels of biogeographic structure, whereas the *Brueelia* phylogeny does not. *Myrsidea* and *Brueelia* also differ in their levels of intra-generic genetic divergence, with *Myrsidea* showing higher levels of genetic divergence and host specificity than *Brueelia*. Our genetic data support traditional morphology-based taxonomy in several instances in which the same species of *Brueelia* has been reported on multiple host taxa, e.g., all migrant *Catharus* spp. carry *B. antiqua*, with little haplotype divergence. *Myrsidea* found on each *Catharus* sp. are in general genetically distinct, except for *M. incerta*, which parasitizes both *Catharus ustulatus* and *Catharus minimus*. The strong biogeographic signal in the *Myrsidea* phylogeny and higher relative levels of host specificity of *Myrsidea* spp. suggest that infrequent host-switching, followed by speciation, is shaping the evolutionary history of this group. In contrast, the relatively lower host specificity of *Brueelia* spp. suggests that host-switching, combined with more frequent ongoing dispersal, has been more important in the evolutionary history of *Brueelia*.

Comparative phylogenetic studies of co-occurring parasite groups are particularly effective for understanding the relationship between specific life history characteristics and patterns of coevolutionary history (Johnson and Clayton, 2003a). Different types of parasites vary in their degree of host specificity, ability to disperse to other host species, and ability to survive on multiple host species. If replicate co-occurring groups of parasites exhibit different coevolutionary histories, one can ask whether features of the parasite's biology correlate with these differences in the degree of congruence between host and parasite phylogenies (Page et al., 1996). This method is particularly powerful when replicate parasite lineages exhibit varying life-history characteristics.

Avian chewing lice (Phthiraptera) are ideally suited for comparative phylogenetic studies, in part because they are permanent ectoparasites (Clayton, 1991). Bird species typically host multiple chewing louse taxa, each of which has unique life history characteristics. Furthermore, co-occurring louse taxa often include species from 2 different suborders, i.e., Amblycera and Ischnocera. Several studies have compared patterns of phylogenetic history among replicate groups of codistributed ischnoceran chewing louse genera (Johnson, Williams, et al., 2002; Clayton, Al-Tamimi, and Johnson, 2003; Clayton, Bush et al., 2003; Clayton and Johnson, 2003; Johnson and Clayton, 2003a; Clayton et al., 2004; Johnson and Clayton, 2004), and these studies have correlated life history differences between the parasites with differences in cophylogenetic history. Except for a recent comparative phylogeography study of 3 parasite species found on the Galapagos hawk (*Buteo galapagoensis*; Whiteman et al., 2007), little work has been done comparing the evolutionary histories of codistributed ischnoceran and amblyceran taxa. Amblycera and Ischnocera exhibit marked differences in ecology, behavior, and morphology (Marshall, 1981) and provide ideal replicates of parasite evolutionary history on a single host group.

Members of the suborders Ischnocera and Amblycera also differ in their dispersal abilities. On average, ischnoceran lice have relatively short legs, are highly sedentary (Marshall, 1981), and will not usually abandon their host, even if it dies (Keirans, 1975; Marshall, 1981). Amblyceran lice are generally more agile, with long, well-developed legs, and will abandon a dead host in search of a new one (Keirans, 1975; Marshall, 1981; Johnson and Clayton, 2003b). Although ischnoceran lice do not readily disperse under their own power, they are known to disperse by ''hitchhiking,'' also known as phoresis, on parasitic hippoboscid flies (Diptera: Hippoboscidae) (Askew, 1971; Marshall, 1981; Harbison et al., 2008). Along with physical contact between hosts, ''hitchhiking'' may play an important role in the transfer of lice between individuals of the same host species, or even between different host species (Corbet, 1956; Harbison et al., 2008). Amblyceran lice are almost never found in phoretic association with hippoboscid flies (Kierans, 1975). Therefore, phoresy likely plays a role only in the dispersal of ischnoceran, and not amblyceran lice (Marshall, 1981).

Johnson et al. (2002) constructed a phylogeny of the ischnoceran genus *Brueelia* and found little concordance between this phylogeny and published host phylogenies. They suggested that this result implicated phoretic dispersal as playing a major role in breaking down levels of cospeciation between species of *Brueelia* and their hosts. Johnson et al. (2002) also stated that comparisons of phylogenies of non-phoretic amblyceran lice from passerines, e.g., *Myrsidea* spp., might provide insights into whether the lack of cospeciation between *Brueelia* spp. and their passerine hosts is due to high levels of phoretic dispersal or is a pattern general to all passerine louse phylogenies.

In the present study, we used mitochondrial and nuclear DNA sequences to assess levels of genetic divergence and reconstruct phylogenies of *Brueelia* (Ischnocera) and *Myrsidea* (Amblycera), 2 genera of avian chewing lice that are codistributed on passeriform birds, but which differ in a variety of life history characteristics. In addition to differences in dispersal abilities,

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Brueelia spp. and *Myrsidea* spp. also differ in their food preferences, which may be linked to patterns of host specificity. Species of *Myrsidea* feed on host body fluids and blood, which means that they may interact closely with the host's immune system (Marshall, 1981). In contrast, species of *Brueelia* feed only on feather barbs, which are relatively inert protein structures. Therefore, it is possible that *Myrsidea* spp. have fewer successful host transfers when they come into contact with a novel immune system (Möller and De Lope, 1999; Möller and Rozsa, 2005). Given the higher transmission abilities of *Brueelia* and the interaction of *Myrsidea* with its host's immune system through blood feeding, we predicted that levels of dispersal should be higher and levels of host specificity should be lower for *Brueelia* compared with *Myrsidea*. Thus, we qualitatively compared the phylogenies and levels of divergence within these 2 genera of codistributed parasites to examine how differences in their life history characteristics are related to differences in their phylogenetic histories. In particular, we concentrated our sampling on species of *Myrsidea* and *Brueelia* from *Catharus* thrushes, which include 5 species of common North American migrant passerine birds. Multiple data sets document that *Catharus* thrushes are a monophyletic group (Outlaw et al., 2003; Winker and Pruett, 2006). Therefore, we chose to use this monophyletic group of hosts to explore patterns of speciation in their associated chewing lice. Keeping in mind the noted differences in transmission abilities and food preferences, we examined genetic divergences and phylogenetic relationships within *Brueelia* and *Myrsidea* to assess species limits, evolutionary history, and patterns of host specificity with respect to what is known about the hosts' phylogenetic history. We also qualitatively compared broad patterns in the phylogenies of *Brueelia* and *Myrsidea* from a variety of other host groups.

MATERIALS AND METHODS

Specimen collection

Birds were captured in Shaw Woods at the Skokie River Nature Preserve in Lake Forest, Illinois (42°15′37.2″N, 87°51′34″W), as part of the Shaw Woods Avian Monitoring Project (SWAMP; Gordon et al., 2002). Twelve standard mist nets (35 mm mesh and 12 m in length) were set up in brush-cleared lanes. The nets were open from 5:00 to 10:00, 27 days from May 1–31, 2006. Captured birds were removed from the nets and placed in clean cloth bags for transport to the banding station. The cloth bags were used only once per day and were then turned inside out and washed and dried prior to use the next day. The 5 focal migrant thrush (Passeriformes: Turdidae) species of our study, i.e., *Hylocichla mustelina*, *C. minimus*, *C. ustulatus*, *C. fuscescens*, and *C. guttatus*, were banded with permanent, aluminum leg bands from the U.S. Federal Bird Banding Laboratory, dusted with pyrethrum flea powder (Hartz, Secaucus, New Jersey), which was then rubbed into their feathers for approximately 5 min, and then ruffled following the procedure of Walther and Clayton (1997) and Clayton and Drown (2001). We placed the lice into labeled vials of 95% ethanol, which we stored frozen at −80 C prior to DNA extraction. We also collected lice from window-killed thrushes and other Nearctic-Neotropical migrant specimens, salvaged by the Field Museum of Natural History in downtown Chicago, Illinois. Each of these bird specimens was isolated for 10–15 min in a new zip lock bag containing a cotton ball saturated with a drop of ethyl acetate to kill the lice. After fumigation, the specimen's feathers were rigorously ruffled over a clean piece of white paper until no more lice fell off of the bird. These lice were picked up with a paint brush, placed in a vial of 95% ethanol, and stored frozen at −80 C. The paper and brush were carefully kept clean to eliminate the possibility of cross-contamination between birds. Salvaged host specimens were then prepared as vouchers and deposited in the Field Museum's bird collection.

Louse identification was made using the Price et al. (2003) chewing louse checklist and the taxonomic descriptions cited within. We amplified and sequenced DNA for 24 *Brueelia* chewing lice, including 13 individuals from 5 *Catharus* thrush species and 11 other *Brueelia* chewing lice from a range of other host species. We also included previously published COI and EF-1α sequences from 15 *Brueelia* spp. analyzed by Johnson et al. (2002), increasing our total *Brueelia* sample to 39 specimens (See Table I for GenBank accession numbers and voucher data). Outgroup (ischnoceran) taxa for the *Brueelia* phylogeny included *Neopsittaconirmus*, *Paragoniocotes*, and *Struthiolipeurus* (See Table I for GenBank accession numbers; Johnson et al., 2001, 2003; Smith et al., 2004). We also amplified and sequenced DNA from 34 *Myrsidea* chewing lice, including 6 individuals from 4 *Catharus* host species and 28 from a range of other hosts (see Table II for GenBank accession numbers). Outgroup (amblyceran) taxa for the *Myrsidea* phylogeny included *Ricinus* and *Dennyus* (See Table II for GenBank accession numbers; Johnson and Whiting, 2002).

DNA amplification and sequencing

To extract DNA from each louse, we placed it in a clean dish of fresh absolute ethanol under a dissection scope and plucked the head from the body using a set of sterilized forceps. The head and body were then placed into a 1.5-ml tube, which was left open until the ethanol dried. We used the Qiagen Dneasy micro-kit or tissue kit (Valencia, California), following the manufacturer's protocols, to extract genomic DNA. We retained the head and body of each specimen as a morphological voucher and mounted them on a microslide. These voucher louse specimens were deposited in either The Field Museum or Illinois Natural History Survey insect collections.

We amplified 379–385 base pairs (bp) of the mitochondrial cytochrome *c* oxidase subunit I (COI) gene with primers L6625 and H7005 (Hafner et al., 1994), and 347 bp of the nuclear elongation factor 1-α (EF-1α) gene with primers EF1-For3 and EF1-Cho10 (Danforth and Ji, 1998) using the thermalcycling regime published by Weckstein (2004). Most polymerase chain reaction (PCR) products were amplified using Taq Gold (AmpliTaq Gold; Perkin-Elmer Corporation, Foster City, California) and, for EF-1α amplifications, we added 2.5 μl of bovine serum albumin to each 25-μl reaction. For a few problematic samples, we used Taq beads (Promega, Madison, Wisconsin) to amplify EF-1α. PCR products were purified with either Exonuclease and Shrimp Alkaline Phosphatase enzymatic reactions (United States Biochemical, Cleveland, Ohio) or by cutting bands from a low melt agarose gel and digesting them with gelase (Epicentre Technologies, Madison, Wisconsin).

We cycle sequenced 1 μl of purified PCR product with 1 μl of ABI Big Dye kit (version 3.2, Applied Biosystems, Foster City, California) and 0.6 μl of 10 μM primer, and ran these sequenced products on an ABI Prism 3730 automated DNA sequencer (Perkin-Elmer Applied Biosystems). Sequencher (version 4.5, Genecodes Co., Ann Arbor, Michigan) was used to reconcile double-stranded sequences and to align the protein coding genes, COI and EF-1α, by eye.

Phylogenetic analysis

We used PAUP* to perform maximum parsimony (MP) heuristic searches with 100 random addition sequence replicates, TBR branch swapping, and stepwise addition (version 4.0b10; Swofford, 2002); 1,000 bootstrap replicates were performed, with 10 random additions per replicate. We used the partition homogeneity test (ILD statistic, Farris et al., 1994, 1995) as implemented in PAUP* (version 4.0b10; Swofford, 2002) to test for incongruence between COI and EF-1α sequence data partitions for both louse genera. All parsimony uninformative characters were removed from the data sets prior to the test.

For maximum likelihood (ML) analyses we used Garliv0.951 (Zwickl, 2006; http://www.zo.utexas.edu/faculty/antisense/garli/Garli.html), which estimates model parameters that best fit the data during the analysis. We ran 5 independent Garli replicates, each with a different starting point, and considered the tree with the best likelihood score the best phylogenetic hypothesis. We also performed 1,000 bootstrap replicates to assess statistical support for nodes in the phylogeny.

Bayesian inference (BI) analysis was performed using MrBayes 3.1.1 (Ronquist and Huelsenbeck, 2003). For the BI analysis, we implemented a mixed model approach to account for differences in evolutionary model parameters between data partitions (Nylander et al., 2004). We divided each

TABLE I. Voucher numbers, localities, host associations, and collecting locality information for all *Brueelia* louse specimens used in this study.

#	Louse species	Voucher number	Host family	Host species	Locality	GenBank Accession Numbers
1	*Brueelia antiqua*	Bran.6.13.2006.1	Turdidae	*Catharus guttatus*	Illinois	FJ171221, FJ171244
2	*Brueelia antiqua*	Brsp.Cafu.6.13.2006.2	Turdidae	*Catharus fuscescens*	Bolivia	FJ171227, FJ171250
3	*Brueelia antiqua*	Brze.6.13.2006.3	Turdidae	*Catharus ustulatus*	Panama	FJ171238, FJ171262
4	*Brueelia concavus*	Brsp.Cafr.6.13.2006.4	Turdidae	*Catharus fuscater*	Panama	FJ171225, FJ171248
5	*Brueelia antiqua*	Brsp.Cami.6.13.2006.12	Turdidae	*Catharus minimus*	Illinois	FJ175385, FJ171253
6	*Brueelia antiqua*	Brsp.Cafu.6.13.2006.6	Turdidae	*Catharus fuscescens*	Illinois	FJ171228, FJ171251
7	*Brueelia antiqua*	Brze.6.13.2006.7	Turdidae	*Catharus ustulatus*	Illinois	FJ171239, FJ171263
8	*Brueelia concavus*	Stsp.Hymu.6.13.2006.8	Turdidae	*Hylocichla mustelina*	Illinois	FJ171242, FJ171266
9	*Brueelia antiqua*	Brsp.Cafu.6.13.2006.9	Turdidae	*Catharus fuscescens*	Illinois	FJ171226, FJ171249
10	*Brueelia antiqua*	Brze.6.13.2006.10	Turdidae	*Catharus ustulatus*	Illinois	FJ171237, FJ171261
11	*Brueelia concavus*	Stsp.Hymu.6.13.2006.11	Turdidae	*Hylocichla mustelina*	Illinois	FJ171241, FJ171265
12	*Brueelia* sp.	Brsp.Door.6.13.2006.13	Emberizidae	*Dolichonyx oryzivorous*	Illinois	FJ171230, FJ171254
13	*Brueelia* sp.	Brsp.Mege.6.27.2006.17	Emberizidae	*Melospiza georgiana*	Illinois	FJ171232, FJ171256
14	*Brueelia anamariae*	Bana.6.27.2006.18	Troglodytidae	*Troglodytes aedon*	Illinois	FJ171220, FJ171243
15	*Brueelia vulgata*	Brsp.Zoal.6.27.2006.19	Emberizidae	*Zonotrichia albicollis*	Illinois	FJ171234, FJ171258
16	*Brueelia brunneinucha*	Brbr.6.27.2006.20	Mimidae	*Dumetella carolinensis*	Illinois	FJ171223, FJ171246
17	*Brueelia vulgata*	Brsp.Zole.6.27.2006.21	Emberizidae	*Zonotrichia l. leucophrys*	Illinois	FJ171235, FJ171259
18	*Brueelia* sp.	Brsp.Seau.6.27.2006.22	Parulidae	*Seiurus aurocapillus*	Illinois	FJ171233, FJ171257
19	*Brueelia dorsale*	Brdo.6.27.2006.24	Mimidae	*Toxostoma rufum*	Illinois	FJ171224, FJ171247
20	*Brueelia vulgata*	Brvu.6.27.2006.28	Emberizidae	*Junco hyemalis*	Illinois	FJ171236, FJ171260
21	*Brueelia antiqua*	Brze.6.27.2006.29	Turdidae	*Catharus ustulatus*	Illinois	FJ171240, FJ171264
22	*Brueelia antiqua*	Bran.6.27.2006.30	Turdidae	*Catharus guttatus*	Illinois	FJ171222, FJ171245
23	*Brueelia antiqua*	Brsp.Cafu.6.27.2006.31	Turdidae	*Catharus fuscescens*	Illinois	FJ171229, FJ171252
24	*Brueelia* sp.*	Brsp.Paele.7.14.1999.3	Paridae	*Parus elegans*	Philippines	AY149382, AY149412
25	*Brueelia* sp.*	Brsp.Rhnig.7.14.1999.11	Rhipiduridae	*Rhipidura nigrocinnamomea*	Philippines	AY149384, AY149414
26	*Brueelia* sp.*	Brsp.Sifro.7.14.1999.1	Sittidae	*Sitta frontalis*	Philippines	AY149383, AY149413
27	*Brueelia* sp.*	Brsp.Fihyp.7.14.1999.2	Muscicapidae	*Ficedula hyperythra*	Philippines	AY149410, AY149411
28	*Brueelia laticeps**	Brlat.1.17.2000.14	Ramphastidae	*Andigena nigrirostris*	Peru	AY149398, AY149428
29	*Brueelia laticeps**	Brlat.1.17.2000.15	Ramphastidae	*Aulacorhynchus prasinus*	Peru	AY149399, AY149429
30	*Brueelia moriona**	Brmor.4.7.1999.8	Corvidae	*Cyanocorax morio*	Mexico	AY149400, AY149430
31	*Brueelia* sp.*	Brsp.Cahae.10.12.1999.9	Icteridae	*Cacicus haemorrhous*	Brazil	AY149393, AY149423
32	*Brueelia* sp.*	Brsp.Pasub.2.3.1999.5	Cisticolidae	*Parisoma subcaeruleum*	South Africa	AY149396, AY149426
33	*Brueelia* sp.*	Brsp.Mecan.1.15.2000.12	Picidae	*Melanerpes candidus*	Bolivia	AY149395, AY149425
34	*Brueelia* sp.*	Brsp.Camex.2.1.2000.8	Fringillidae	*Carpodacus mexicanus*	Utah	AY149394, AY149424
35	*Brueelia* sp.*	Brsp.Panig.1.12.1999.11	Paridae	*Parus niger*	South Africa	AY149391, AY149421
36	*Brueelia* sp.*	Brsp.Pynig.1.12.1999.8	Pycnonotidae	*Pycnonotus nigricans*	South Africa	AY149397, AY149427
37	*Brueelia* sp.*	Brsp.Costr.7.14.1999.10	Campephagidae	*Coracina striata*	Philippines	AY149390, AY149420
38	*Brueelia* sp.*	Brsp.Memon.10.5.1999.10	Megalaimidae	*Megalaima monticola*	Malaysia: Sabah	AY149388, AY149418
39	*Brueelia* sp.	Brsp.Irpu.6.27.2006.23	Irenidae	*Irena puella*	Malaysia: Sabah	FJ171231, FJ171255
	Outgroup					
	Paragoniocotes sp.	PaspArast.2.10.1999.7	Psittacidae	*Aratinga astec*	Mexico	AF348870, AY314839
	Neopsittaconirmus circumfasciatus	Nscir.11.22.2001.12	Psittacidae	*Platycercus elegans*	Australia	AY314819, AY314838
	Struthiolipeurus nandu	Slnan.2.4.2002.4	Rheidae	*Rhea americana*	captive	AF545768, AF320360

* Indicates *Brueelia* specimens with COI and EF-1α sequences previously published by Johnson, Adams et al. (2002).

of the protein coding sequences into 3 partitions according to codon position. Therefore, we had 6 partitions for both the *Myrsidea* and *Brueelia* data sets. We used Mr. Modeltest (Nylander, 2004) to determine the appropriate likelihood model for each of these data set partitions. We ran 2 analyses of 5,000,000 generations and 4 Markov chains, with every 500th tree sampled. The first 500 trees were discarded as the burn-in, and the consensus of the remaining trees was used.

Biogeographic analyses

We used MacClade (version 4.05; Maddison and Maddison, 1992) to map and reconstruct the biogeographic region where each louse was collected onto both the *Myrsidea* phylogeny and the *Brueelia* phylogeny. The geographic areas for the *Myrsidea* data set included Europe, Africa, the Neotropics, North America, and Madagascar; the *Brueelia* data set included Asia, Africa, the Neotropics, North America, and Australia. To test whether biogeography contained significant phylogenetic signal, we used Maddison and Slatkin's (1991) randomization procedure to randomize these biogeographic regions 1,000 times on each of the louse phylogenies. We pruned both the *Myrsidea* and *Brueelia* phylogenies to include only 1 exemplar per louse species, because including multiple exemplars per louse taxon would bias the test toward rejecting the null hypothesis (Weckstein, 2004). We compared the randomized character distributions generated by the Maddison and Slatkin (1991) procedure with the empirical character distributions mapped onto the *Brueelia* and *Myrsidea* louse trees to obtain a *P* value for the test.

TABLE II. Voucher numbers, localities, host associations, and collecting locality information for all Myrsidea louse specimens used in this study.

#	Louse species	Voucher number	Host family	Host species	Locality	GenBank Accession Numbers
1	*Myrsidea pricei*	Mypr.6.14.2006.1	Turdidae	*Catharus guttatus*	Illinois	FJ171277, FJ171303
2	*Myrsidea pricei*	Mypr.6.14.2006.2	Turdidae	*Catharus guttatus*	Illinois	FJ171273, FJ171299
3	*Myrsidea simplex*	Mysi.6.14.2006.3	Turdidae	*Catharus fuscater*	Panama	FJ171276, FJ171302
4	*Myrsidea* sp.	Mysp.Hymu.6.14.2006.4	Turdidae	*Hylocichla mustelina*	Illinois	FJ171284, FJ171311
5	*Myrsidea incerta*	Myin.6.14.2006.5	Turdidae	*Catharus ustulatus*	Illinois	FJ171268, FJ171294
6	*Myrsidea* sp.	Mysp.Hymu.6.14.2006.6	Turdidae	*Hylocichla mustelina*	Illinois	FJ171285, FJ171312
7	*Myrsidea incerta*	Myin.6.14.2006.7	Turdidae	*Catharus ustulatus*	Illinois	FJ171269, FJ171295
8	*Myrsidea incerta*	Myin.6.14.2006.8	Turdidae	*Catharus minimus*	Illinois	FJ171270, FJ171296
9	*Myrsidea* sp.	Mysp.Seau.6.14.2006.10	Parulidae	*Seiurus aurocapillus*	Illinois	FJ171289, FJ171318
10	*Myrsidea ptilostomi*	Mypt.6.14.2006.12	Corvidae	*Ptilostomus afer*	Ghana	FJ171274, FJ171300
11	*Myrsidea* sp.	Mysp.Gybu.6.14.2006.13	Lybiidae	*Gymnobucco calvus*	Ghana	FJ171283, FJ171310
12	*Myrsidea minuscula*	Mymin.7.25.2005.9	Philepittidae	*Philepitta castanea*	Madagascar	FJ171271, FJ171297
13	*Myrsidea willardi*	Mywil.7.25.2005.10	Philepittidae	*Philepitta schlegeli*	Madagascar	FJ171292, FJ171322
14	*Myrsidea palmeri*	Mysp.Ancur.8.16.2005.5	Pycnonotidae	*Andropadus curvirostris*	Ghana	DQ366673, FJ171304
15	*Myrsidea olivacei*	Myoli.4.24.2006.6	Tyrannidae	*Mionectes olivaceus*	Panama	FJ171272, FJ171298
16	*Myrsidea chesseri*	Mysp.Crbar.8.16.2005.2	Pycnonotidae	*Criniger barbatus*	Ghana	DQ366672, FJ171308
17	*Myrsidea* sp.	Mysp.Rholi.4.24.2006.3	Tyrannidae	*Rhynchocyclus olivaceus*	Panama	FJ171288, FJ171317
18	*Myrsidea ledgeri*	Amsp. Phsoc.5.4.1999.6	Passeridae	*Philetairus socius*	South Africa	AF545733, AF320429
19	*Myrsidea* sp.	Mysp.Anvar.5.1.2006.4	Furnariidae	*Anabacerthia variegaticeps*	Panama	FJ171278, FJ171305
20	*Myrsidea fusca*	Myfus.4.26.2006.10	Thraupidae	*Ramphocelus passerinii*	Panama	FJ171267, FJ171293
21	*Myrsidea laciniaesternata*	Mylac.4.19.1999.2	Thraupidae	*Habia* sp.	Mexico	AF545732, AF545793
22	*Myrsidea* sp.	Mysp.Eulan.5.1.2006.1	Thraupidae	*Euphonia laniirostris*	Panama	FJ171282, FJ171309
23	*Myrsidea* sp.	Mysp.Tadow.4.26.2006.12	Thraupidae	*Tangara dowii*	Panama	FJ171290, FJ171319
24	*Myrsidea* sp.	Mysp.Chchr.5.1.2006.2	Thraupidae	*Chrysothlypis chrysomelas*	Panama	FJ171280, FJ171307
25	*Myrsidea* sp.	Mysp.Radim.4.24.2006.8	Thraupidae	*Ramphocelus dimidiatus*	Panama	FJ171287, FJ171316
26	*Myrsidea* sp.	Mysp.Cymor.2.8.1999.2	Corvidae	*Cyanocorax morio*	Mexico	FJ171281, AF320431
27	*Myrsidea* sp.	Mysp.Thpun.4.24.2006.2	Thamnophilidae	*Thamnophilus punctatus*	Panama	EU650229, FJ171320
28	*Myrsidea seminuda*	Mysem.5.1.2006.15	Thraupidae	*Thraupis palmarum*	Panama	FJ171275, FJ171301
29	*Myrsidea* sp.	Mysp.Tugra.5.1.2006.14	Turdidae	*Turdus grayi*	Panama	FJ171291, FJ171321
30	*Myrsidea* sp.	Mysp.Pahom.4.24.2006.4	Cotingidae	*Pachyramphus homochrous*	Panama	FJ171286, FJ171314
31	*Myrsidea eisentrauti*	Myeis.2.3.1999.6	Passeridae	*Sporopipes squamifrons*	South Africa	AF545731, AF320428
32	*Myrsidea masoni*	Mysp.Blcan.7.25.2005.7	Pycnonotidae	*Bleda canicapilla*	Ghana	FJ171279, FJ171306
33	*Myrsidea marksi*	Mysp.Phalb.8.16.2005.1	Pycnonotidae	*Phyllastrephus albigularis*	Ghana	DQ366669, FJ171315
34	*Myrsidea mccrackeni*	Mysp.Oxmad.8.16.2005.9	Sylviidae	*Oxylabes madagascariensis*	Madagascar	DQ860183, FJ171313
	Outgroup					
	Ricinus sp.	Risp.Cypar.2.6.1999.4	Cardinalidae	*Cyanocompsa parellina*	Mexico	AF385014, AF385033
	Dennyus hirundinis	Dehir.9.26.1997.6	Apodidae	*Apus apus*	United Kingdom	AF385013, AF385032

RESULTS

The partition homogeneity test between the COI and EF-1α partitions did not show significant conflict for the *Brueelia* ($P = 1.00$) or *Myrsidea* ($P = 0.889$) data sets. Therefore, we combined these 2 gene partitions for both of the louse data sets. The *Brueelia* data set included an aligned matrix of 733 bp of DNA sequence for 42 taxa (3 outgroup, 39 ingroup) and provided 288 variable characters, of which 212 were parsimony informative. For *Myrsidea*, we analyzed a single aligned matrix of 726 bp of DNA sequences for 36 taxa (2 outgroups, 34 ingroup), providing a total of 303 variable characters, of which 238 were parsimony informative.

Among *Brueelia* ingroup taxa, uncorrected sequence divergence ranged from 0.0% to 14.7% for both genes combined, from 0.0% to 22.9% for COI, and from 0.0% to 7.6% for EF-1α. Among *Myrsidea* ingroup taxa, uncorrected divergences were comparatively higher and ranged from 0.28% to 18.1% for all genes, from 0.0% to 26.7% for COI, and from 0.0% to 11.8% for EF-1α.

As noted by Johnson et al. (2002), we found 2 indel events in COI, including a 3 bp deletion of the 23rd codon position and a 6 bp insertion at the 91st and 92nd codon positions in *Brueelia*. We coded these sites as missing in our analysis (following Johnson et al., 2002). None of the EF-1α data or *Myrsidea* COI data contained indels.

Phylogenetic analyses

Brueelia species:: MP, ML, and BI analyses of the *Brueelia* data strongly support 2 distinct clades of *Brueelia* from *Catharus* thrush hosts that are not sister groups (Fig. 1). The first included *Brueelia* inhabiting migratory *Catharus* (*B. antiqua*) and the second included *Brueelia* from the tropical *Catharus* (*B. concavus*), together with those of wood thrush (*Hylochichla mustelina*). The monophyly of *Brueelia* from migratory *Catha-*

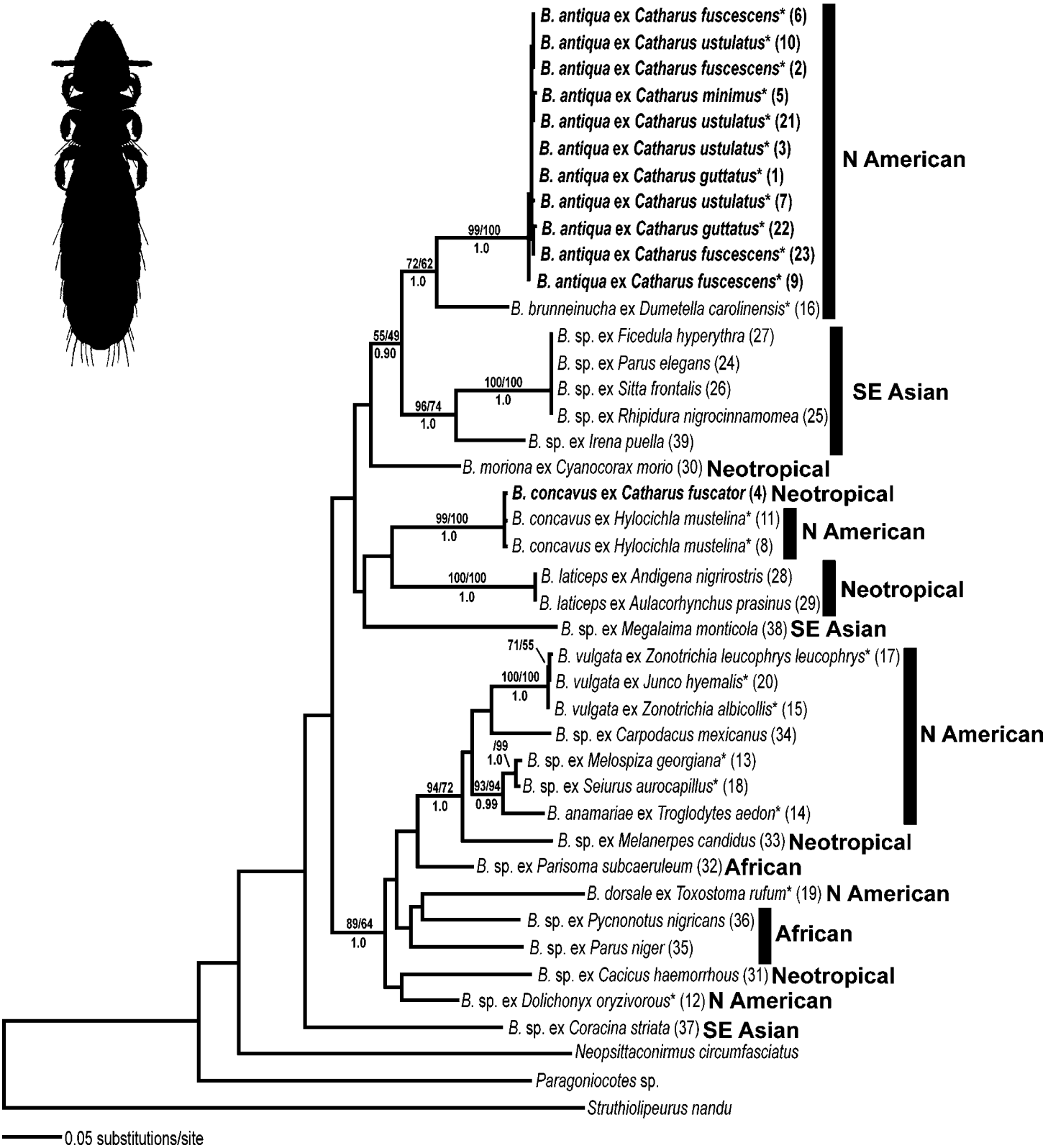

FIGURE 1. ML tree topology (−ln L = 5480.12041) including MP and ML bootstrap values for 1,000 replicates and BI posterior probabilities (consensus of 5,000,000 sample trees) for species of *Brueelia* based on 385 bp of COI and 347 bp of EF-1α sequence data. ML/MP bootstrap values are above the node and BI posterior probabilities are below the node. Only bootstrap values >50% and posterior probabilities >90% are shown. Bold taxa are *Brueelia* chewing lice collected from *Catharus* thrush hosts. Numbers in parentheses next to host name refer to numbers and voucher information listed in Table I. Host labels with an asterisk indicate that the host is a partial or long distance Nearctic migrant. Those without an asterisk are tropical residents.

rus hosts is strongly supported by bootstrapping (MP = 100%, ML = 99%) and BI posterior probability (100%). Although Price et al. (2003) list 2 species of *Brueelia* found on migratory *Catharus* hosts, our specimens sampled from migratory *Catharus* spp. show little to no genetic differentiation, with 0%–1.05% uncorrected mitochondrial COI sequence divergence between haplotypes.

Brueelia brunneinucha, from gray catbird (Mimidae: *Dumetella carolinensis*), which has a similar habitat and geographic range to the *Catharus* thrushes, is relatively well supported by bootstrapping (MP = 62%, ML = 72%) and BI posterior probabilities (100%) as the sister to *B. antiqua* from migratory *Catharus* (Fig. 1). *Brueelia brunneinucha* differs from *B. antiqua* by an average of 8.49% uncorrected COI sequence divergence. The other well-supported clade (Fig. 1; MP = 100%, ML = 99%, and BI = 100%) of *Brueelia* from *Catharus* thrushes includes *Brueelia* from *Catharus fuscater*, a tropical resident *Catharus* thrush. This *Brueelia* shows little genetic distinction from the *Brueelia* sp. collected from wood thrush (*Hylocichla mustelina*), a close relative of *Catharus* (Winker and Rappole, 1988; Winker and Pruett, 2006). These lice differ by only 0.53% uncorrected COI sequence divergence. This *B. concavus* clade is sister to *Brueelia laticeps* from black-billed mountain toucan (*Andigena nigrirostris*) and emerald toucanet (*Aulacorhynchus prasinus*). However, there is little statistical support for this sister relationship.

Brueelia from various small-bodied Neotropical-Nearctic migrants from 4 avian families (Emberizidae, Fringillidae, Parulidae, and Troglodytidae) and white woodpecker (*Melanerpes candidus*) also form a strongly supported clade (MP = 94%, ML = 72%, and BI = 100%; Fig. 1). Within this clade, *Brueelia* from the swamp sparrow (Emberizidae: *Melospiza georgiana*) and ovenbird (Parulidae: *Seiurus aurocapillus*) are relatively well supported as sisters by most analyses (MP = 99%, BI = 100%) and, at 1% uncorrected COI sequence divergence, are only slightly more genetically divergent than other within-clade comparisons. Therefore, these 2 lice parasitizing genetically distant hosts from different avian families likely constitute a single species. *Brueelia anamariae*, from the house wren (Troglodytidae: *Troglodytes aedon*), is well supported (MP = 94%, ML = 93%, and BI = 99%) as sister to *Brueelia* sp. from the swamp sparrow and ovenbird. These 3 louse taxa have an average uncorrected COI sequence divergence of 4.79% from their sister clade, which includes 3 *Brueelia vulgata* from the dark-eyed junco (Emberizidae: *Junco hyemalis*), white-throated sparrow (Emberizidae: *Zonotrichia albicollis*), and white-crowned sparrow (Emberizidae: *Zonotrichia leucophrys*) and *Brueelia* sp. from the house finch (Fringillidae: *Carpodacus mexicanus*). The house finch, dark-eyed junco, and white-crowned sparrow were previously recorded as carrying *B. vulgata* (Kellogg, 1896). However, *Brueelia* from the house finch, which is only weakly supported as sister to *B. vulgata* from the junco and the 2 *Zonotrichia* sparrows, is genetically distinct (average uncorrected COI p-distance = 11.51%). In contrast, the dark-eyed junco (the type host for *B. vulgata*), white-crowned, and white-throated sparrows, which are 3 closely related host species (Spicer and Dunipace, 2004), are parasitized by a strongly supported (MP, ML, and BI = 100%) and genetically indistinct (COI sequence divergence of 0.36%) clade of *B. vulgata*. These 3 host species have similar habitats and geographical ranges.

Myrsidea species:: The phylogenetic analyses for *Myrsidea* show higher levels of genetic differentiation than that found among taxa in the *Brueelia* tree (Fig. 2). Three *Myrsidea incerta* individuals collected from 2 host species, the gray-cheeked thrush (*C. minimus*) and Swainson's thrush (*C. ustulatus*), form a strongly supported clade (MP = 100%, ML = 96%, and BI = 100%), although gray-cheeked and Swainson's thrushes are not each other's closest relatives (Fig. 2; Winker and Pruett, 2006). Uncorrected COI sequence divergence between *M. incerta* individuals from these 2 *Catharus* host species average 0.88%, which is low and nearly matches the uncorrected COI divergence (0%) between 2 *Myrsidea pricei* collected from hermit thrush (*C. guttatus*). Both of these intraspecific louse clades (Fig. 2) are strongly supported. The placement of *Myrsidea* sp. from the ovenbird as sister to *M. incerta* is not strongly supported, and average uncorrected COI sequence divergence between *M. incerta*, *M. pricei*, and *Myrsidea* sp. from the ovenbird is 9.18%. *Myrsidea* from the one-colored becard (*Pachyramphus homochrous*) is strongly supported as sister to this clade (MP = 73%, ML = 76%, and BI = 100%), although the becard is a suboscine passerine and is, therefore, distantly related to the other oscine passerine hosts for lice in this clade.

As we found for *Brueelia*, *Myrsidea* from the Neotropical resident, *C. fuscater*, falls out in a different clade from the *Myrsidea* of migrant *Catharus* (Fig. 2), and this clade contains *Myrsidea* from a wide variety of other Neotropical resident hosts. However, few of the relationships in this clade are strongly supported. Unlike the relationships in the *Brueelia* tree, *Myrsidea* from the slaty-backed nightingale-thrush (*C. fuscater*) is not sister to the *Myrsidea* from wood thrush. Instead, wood thrush *Myrsidea* are weakly supported as sister to the *Myrsidea* from the crimson-backed tanager (*Ramphocelus dimidiatus*), a Central American resident (Fig. 2).

Comparison of phylogenies of *Brueelia* and *Myrsidea* from *Catharus* thrushes

Phylogenetic relationships and divergences within *Brueelia* and *Myrsidea* are incongruent with the phylogenetic history of the *Catharus* thrush hosts (Fig. 3). If cospeciation were common between this monophyletic group of genetically divergent hosts and their chewing lice, one would expect to observe a monophyletic clade of genetically divergent lice from *Catharus* thrushes. Instead, *Brueelia* from migratory *Catharus* thrushes form a genetically indistinct clade. Also, *Brueelia* from the Neotropical resident slaty-backed nightingale-thrush is indistinct from the sister group of *Catharus*, the wood thrush, which is a Neotropical migrant (Fig. 3). Furthermore, these 2 *Catharus* thrush *Brueelia* clades are not closely related (Fig. 1). Two distinct *Myrsidea*, *M. incerta* and *M. pricei*, are found on migratory *Catharus* thrushes and have an average uncorrected COI sequence divergence of 7.39%. However, *M. incerta* is found on both *C. minimus* and *C. ustulatus*, which are distantly related (Fig. 3; Winker and Pruett, 2006), but partially sympatric, host species. The wood thrush, which is sister to all *Catharus* thrushes, hosts a *Myrsidea* sp. that is not closely related to any of the lice from *Catharus* thrushes (Fig. 2).

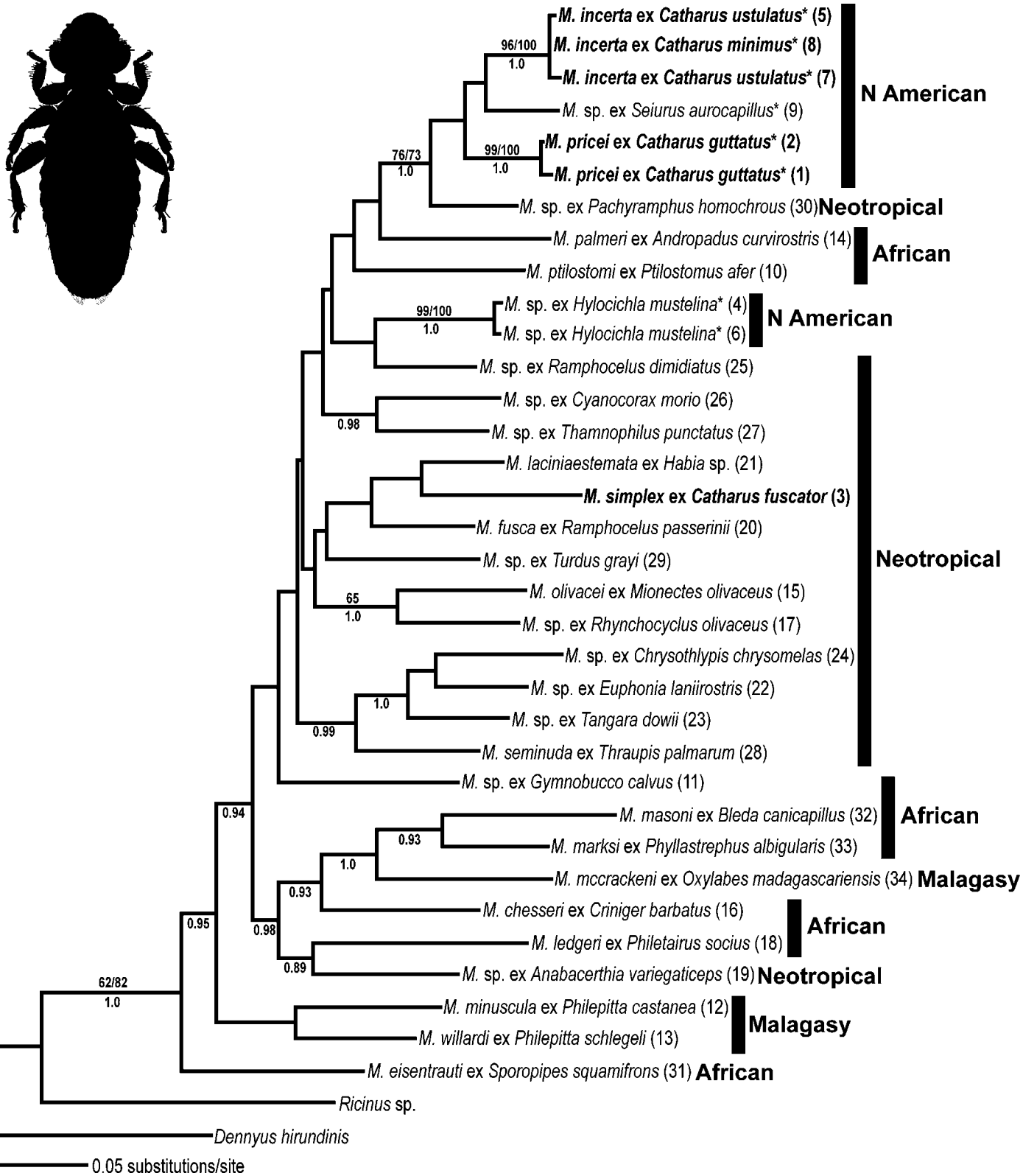

FIGURE 2. BI consensus tree topology including MP and ML bootrap values for 1,000 replicates and BI posterior probabilities (consensus of 5,000,000 sample trees) for species of *Myrsidea* based on 379 bp of COI and 347 bp of EF-1α sequence data. ML/MP bootstrap values are above the node and BI posterior probabilities are below the node. Only bootstrap values >50% and posterior probabilities >90% are shown. Bold taxa are *Myrsidea* chewing lice collected from *Catharus* thrush hosts. Numbers in parentheses next to host name refer to numbers and voucher information listed in Table II. Host labels with an asterisk indicate that the host is a partial or long distance Nearctic migrant. Those without an asterisk are tropical residents.

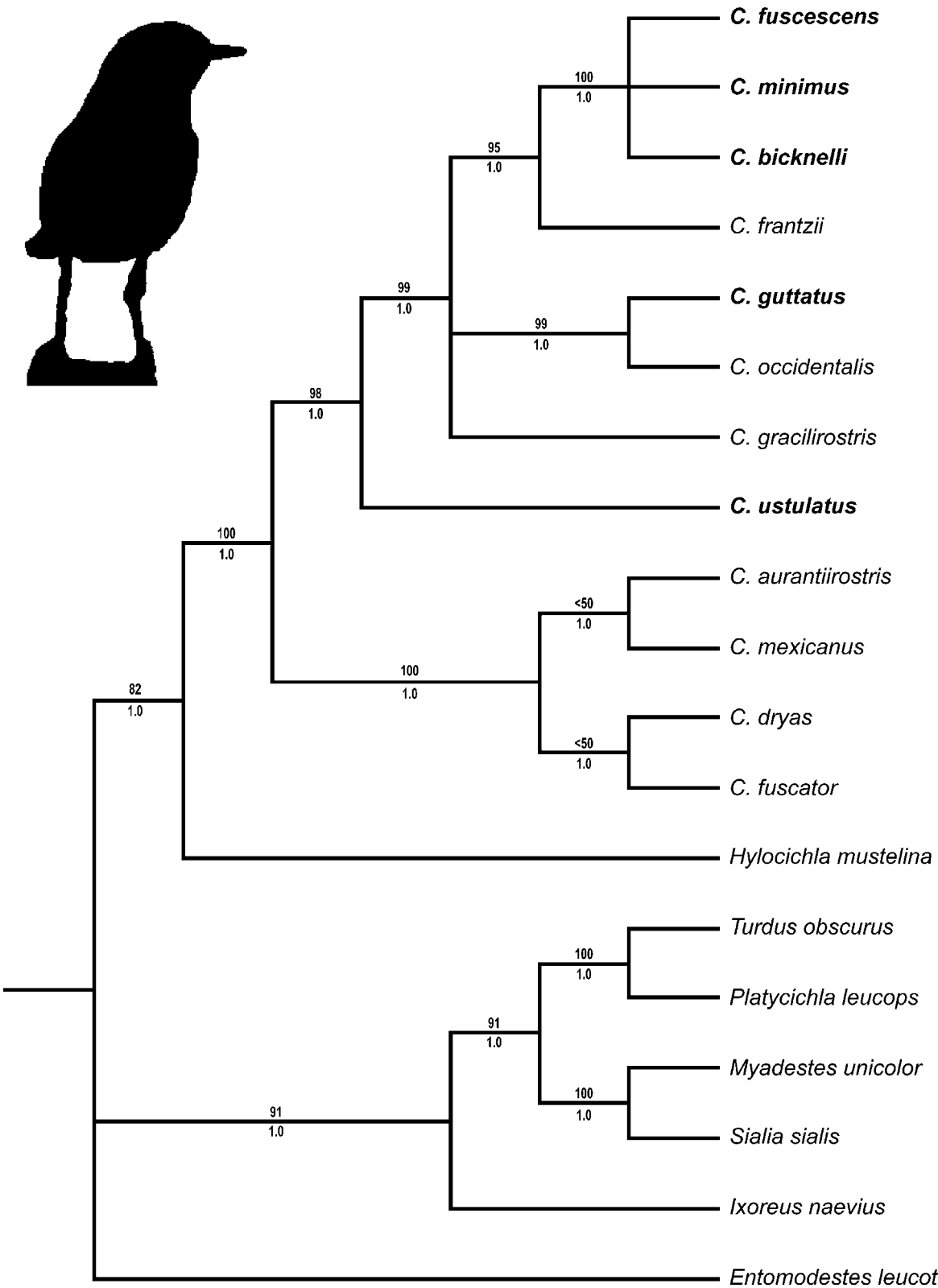

FIGURE 3. Molecular phylogeny of the avian *Catharus* thrush hosts redrawn from Winker and Pruett (2006). Names in bold are Neotropical migrant *Catharus* thrushes.

Geographic analyses

The phylogenetic relationships of *Myrsidea* exhibit biogeographic structure. For example, 1 clade (Fig. 2) includes *Myrsidea* collected from Neotropical resident hosts, another includes *Myrsidea* collected from 2 Malagasy hosts, and a third clade consists mostly of *Myrsidea* from African hosts, except for the scaly-throated foliage-gleaner (*Anabacerthia variegaticeps*), which is Neotropical. Using the Maddison and Slatkin (1992) test, we found that for *Myrsidea*, when biogeographic region where the louse was collected was mapped onto the louse topology, its distribution is significantly different than expected by chance ($P = 0.003$). For *Brueelia*, however, the distribution of biogeographic region on the phylogeny was not significantly different than expected by random chance ($P = 0.593$).

DISCUSSION

Comparison of phylogenies of *Brueelia* and *Myrsidea* species

A comparison of the general phylogenetic patterns for *Brueelia* and *Myrsidea*, concentrating on those codistributed on *Catharus* thrushes, indicates that these chewing louse genera have different levels of host specificity, consistent with hypothesized differences in dispersal. If these genera had cospeciated with their *Catharus* thrush hosts, we would expect to see monophyletic groups of *Brueelia* and *Myrsidea* from *Catharus*, with the parasite tree's branching events mirroring those of the host. However, there is no genetic differentiation among *Brueelia* samples that we collected from *Catharus* hosts. This is consistent with failure to speciate, a phenomenon caused by ongoing gene flow between parasite populations found on different host species (Johnson, Adams et al., 2003; Banks et al., 2006). Many ischnoceran lice, in particular *Brueelia*, are able to attach to hippoboscid flies and hitch a ride to new hosts (Kierans, 1975). This mode of dispersal might explain how a single *Brueelia* sp. can move freely among individuals of all of the migratory *Catharus* thrush species. Phoresis may also be the mechanism by which the tropical resident *C. fuscater* and migrant *H. mustelina* share identical *Brueelia*. We have clarified this molecular result by comparing the voucher *Brueelia* specimens from these hosts to the holotype specimen of *Brueelia concavus*, which is housed in the Museum für Naturkunde der Humboldt-Universität in Berlin, and all 3 voucher specimens morphologically match this type specimen. This is a new host record for *B. concavus* and suggests that a North American Neotropical migrant wood thrush might have picked up *Brueelia* from a tropical resident host. However, the converse could also be true. Regardless, this is one of few definitive demonstrations of a Neotropical migrant and resident host species sharing the same louse species.

Myrsidea differs from *Brueelia* in that, for the most part, distinct *Myrsidea* species inhabit each of the *Catharus* thrush species. This is not true of *M. incerta*, which parasitizes both Swainson's (*C. ustulatus*) and gray-cheeked (*C. minimus*) thrushes, 2 hosts that are not each other's closest relatives (Winker and Pruett, 2006). These results suggest either that *M. incerta* has failed to speciate on Swainson's and gray-cheeked thrushes due to ongoing dispersal/gene flow opportunities between hosts or that a recent successful host-switching event has occurred. Swainson's and gray-cheeked thrushes have overlapping migration routes and wintering and breeding ranges (Mack and Yong, 2000; Lowther et al., 2001), so dispersal between these hosts is possible. Unlike *Brueelia*, *Myrsidea* species are unable to hitchhike on hippoboscid flies (Kierans, 1975); therefore, the mechanism by which these lice disperse between host species is unclear.

Sympatry and similar habitat preferences of hosts might also explain the phylogenetic relationships between *M. incerta* and *M. pricei* from *Catharus* thrushes with *Myrsidea* from ovenbird (Parulidae). The data presented here suggest that *Myrsidea* from *Catharus* thrushes are not monophyletic. Instead, *M. incerta*, from *C. ustulatus* and *C. minimus*, is sister to *Myrsidea* from ovenbird, and these are sister to *M. pricei* (from *C. guttatus*). The hosts of these lice share similar forest understory habitat preferences and geographic distributions, which is consistent with the hypothesis that sympatry of hosts may have provided an opportunity for host switching of *Myrsidea* between *Catharus* thrushes (Turdidae) and ovenbird. However, the relationships within this clade are only weakly supported by bootstrapping; additional data and broader sampling of lice from parulid hosts are needed to assess the support of the phylogenetic history of this clade.

Although a quantitative comparison of branch lengths in the *Brueelia* and *Myrsidea* trees is difficult on account of differences in host taxonomic sampling, one can make a rough comparison of genetic divergence and phylogenetic history of these 2 taxa by comparing their scaled ultrametric trees (Fig. 4). The *Myrsidea* ultrametric tree is relatively deep, and terminal branch lengths are relatively long, with most hosts harboring genetically distinct *Myrsidea*, which suggests that *Myrsidea* have been evolving with their hosts for a considerable time. In contrast, the *Brueelia* ultrametric tree has shallower depth, shorter terminal branches, and many more clades of genetically undifferentiated *Brueelia* from multiple host species. The shallow depth and lower levels of genetic divergence at the terminals might suggest that in comparison with *Myrsidea*, *Brueelia* has colonized its hosts more recently, whereas, the genetically identical *Brueelia* found on multiple host groups indicate relatively low levels of host specificity and relatively more frequent dispersal or host-switching. This matches our prediction that *Brueelia*, which is known to ''hitchhike'' frequently on hippoboscid flies (Kierans, 1975), would show patterns indicative of a relatively higher frequency of dispersal than would *Myrsidea*.

The importance of biogeography

Global biogeographic region has different patterns of signal when mapped onto the *Brueelia* and *Myrsidea* louse phylogenies, suggesting that dispersal between hosts may have occurred at different time scales in the *Brueelia* and *Myrsidea* evolutionary histories. The phylogenetic histories of these genera also show different levels and patterns of genetic divergence and hence, different levels of host specificity. *Myrsidea* has relatively deep branch lengths and high host specificity, whereas *Brueelia* has relatively shallow terminal branches and low host specificity. *Myrsidea* and *Brueelia* phylogenies differ in biogeographic structure, with *Myrsidea* showing significant phylogenetic signal for biogeographic region that is lacking in *Brueelia*. Other studies have pointed out that biogeographic sig-

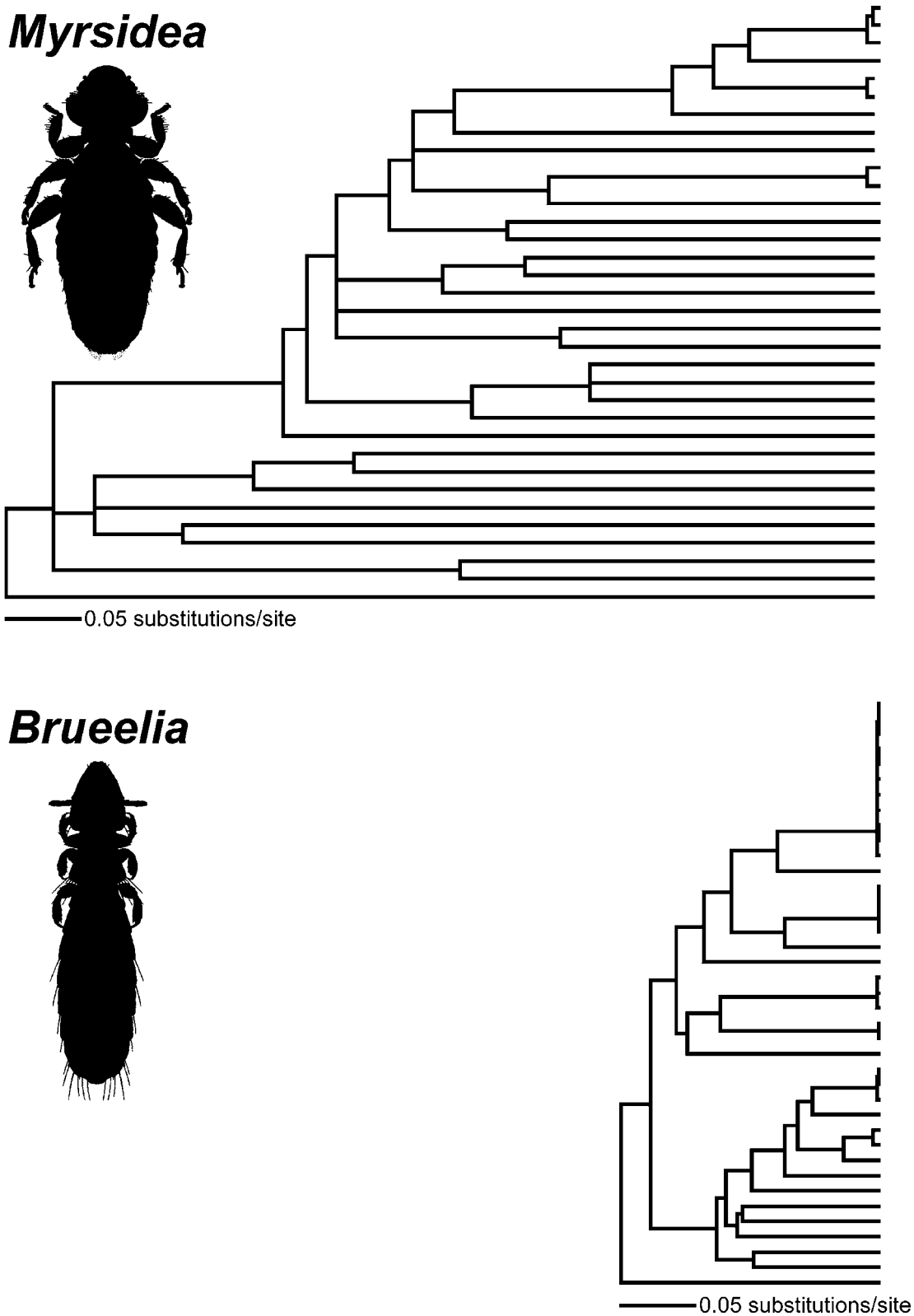

FIGURE 4. Equally scaled (ultrametric) phylogenetic trees for species of *Myrsidea* and *Brueelia* based on COI and EF-1α data for comparison of relative divergence times within each of these genera. Branch lengths were calculated using the GTR+I+G and parameters as estimated in the Modeltest analysis. Outgroups have been pruned from these trees.

nal in parasite phylogenies suggests that sympatry or syntopy of hosts has provided an opportunity for dispersal, or host-switching, or both (Weckstein, 2004; Johnson et al., 2007). However, we would argue that dispersal has played a significant role in both the *Myrsidea* and *Brueelia* evolutionary histories.

For *Brueelia*, recent or ongoing dispersal between hosts has led to failure to speciate (Johnson, Adams et al., 2003; Banks et al., 2006) and the sharing of *Brueelia* species by multiple host taxa. For example, there is geographic overlap in the breeding range, wintering range, and migration routes of the Neotropical migrant *Catharus* thrush hosts. This overlap may create enough opportunities for dispersal and parasite gene flow to result in a single *Brueelia* species infesting all of these host species. The same is true for *Brueelia vulgata* that parasitizes 3 host species from the avian family Emberizidae and an Asian *Brueelia* species that parasitizes 4 host species, each from a different avian family (Fig. 2). As a result of frequent ongoing gene flow among *Brueelia* found on multiple sympatric host taxa, we do not see deep biogeographic structure in the *Brueelia* species level phylogeny. Instead, sympatric hosts often share the same *Brueelia*.

For *Myrsidea*, biogeography appears to be important, suggesting that host switching, rather than ongoing dispersal, is important in their evolutionary history. For example, all of the *Myrsidea* from Neotropical migrants sampled, except for lice from the wood thrush, form a monophyletic clade. *Myrsidea* differs from *Brueelia* in that we found little sharing of genetically identical or similar lice among sympatric hosts. Only 1 *Myrsidea* sampled by us, *M. incerta*, is found on more than 1 host species. This suggests that the frequency of successful dispersal is comparatively lower for *Myrsidea* than for *Brueelia*, which is what one would predict given the inability of *Myrsidea*, and the propensity for *Brueelia*, to hitchhike on hippoboscid flies. Furthermore, ongoing dispersal between host species appears to be limited in *Myrsidea*, so dispersal may more likely be followed by speciation and thus successful host-switching in this genus. In contrast, for *Brueelia*, dispersal events are likely frequent and ongoing, causing failure to speciate among *Brueelia* found on closely related hosts, e.g., *Catharus*, or partial host switching, i.e., no speciation, on morphologically similar sympatric hosts, e.g., *Seiurus* and *Melospiza*. Alternatively, the multihost distributions of *Brueelia*, such as *B. antiqua* and *B. vulgata*, and also *Myrsidea* spp., such as *M. incerta*, from this study, could be due to incomplete host-switching (Clayton, Al-Tamimi, and Johnson, 2003), in which the parasites have recently colonized a new host and either have not had sufficient time to diverge or have maintained genetic contact with the original source population. One can test whether the multihost distributions of parasites are due to ongoing dispersal or recent/incomplete host-switching using population genetic and coalescent analyses (Banks and Paterson, 2005). Future work on multihost parasites identified in this study will focus on comprehensive population level sampling of these lice to test these alternative hypotheses.

New host associations and taxonomic implications

Our analysis of DNA sequence data has implications for chewing louse alpha taxonomy and has allowed us to confirm new host associations and several previously published, but currently unaccepted host associations (Price et al., 2003). First, Price et al. (2003) list 2 *Brueelia* species, *B. antiqua* and *B. zeropunctata*, as being found on the 2 thrushes *C. guttatus* and *C. ustulatus*, respectively. Our genetic data, which show little genetic divergence in *Brueelia* from migrant *Catharus* thrushes and a morphological assessment of the *Brueelia* voucher specimens (vulval setal counts) are consistent with these hosts sharing a single species of *Brueelia*. Furthermore, all of the *Brueelia* that we sampled from migrant *Catharus* are genetically and morphologically undifferentiated, indicating that all of these migrant *Catharus* (*C. guttatus*, *C. ustulatus*, *C. minimus*, and *C. fuscescens*) thrushes share the same louse species. Thus, *B. zeropunctata* may be a junior synonym of *B. antiqua*. Additional work with more comprehensive sampling, including lice from *Catharus* thrush hosts from western North America, should clarify this pattern.

Another thrush louse, *B. concavus*, was previously known only from the Neotropical resident, *C. fuscater*. However, our data show that *H. mustelina*, a migrant thrush that breeds in North America and winters in Central America, carries *Brueelia* that are genetically identical to those found on *C. fuscater*. We compared our voucher specimens from both of these hosts with digital images of the *B. concavus* type specimen and verified that *B. concavus* is found on both *C. fuscater* and *H. mustelina*. *Hylocichla mustelina* winters in sympatry with the resident *C. fuscater*, which might explain how these 2 hosts can share the same louse species. Finally, Price et al. (2003) lists *Brueelia vulgata* as parasitizing only 1 host, *Junco hyemalis*. Although *J. hyemalis* is the type host for *B. vulgata*, Kellogg (1896) also listed the white-crowned sparrow (*Zonotrichia leucophrys gambelli*), golden-crowned sparrow (*Z. atricapilla*), spotted towhee (*P. maculatus*), California towhee (*Pipilo crissalis*), house finch (*Carpodacus mexicanus*), purple finch (*Carpodacus purpureus*), and American robin (*Turdus migratorius*) as hosts for this louse species. However, Price et al. (2003) did not include many of Kellogg's multihost records, because a number of authors (Hopkins, 1951; Ward, 1953; Palma, 1994) have documented erroneous host associations, particularly where Kellogg described parasites with widespread host distributions (R. Palma and R. Price, pers. comm.). We analyzed DNA sequences of *Brueelia* from *Junco hyemalis*, white-throated sparrow (*Zonotrichia albicollis*), *Zonotrichia leucophrys leucophrys*, and *Carpodacus mexicanus*. We found that *B. vulgata* from *J. hyemalis* is nearly genetically identical to *Brueelia* from the sparrows *Z. albicollis* and *Z. leucophrys*. One of these hosts, *Z. albicollis*, is a new host record for *B. vulgata*. Therefore, we believe that the 2 *B. vulgata* records from *Zonotrichia* sparrows reported by Kellogg (1896) are correct. We also analyzed sequence data from 1 house finch *Brueelia* and found that although they are phylogenetically close to the *B. vulgata* from sparrows, they are genetically distinct. This finding is consistent with findings from Carriker (1957), who noted that contrary to Kellogg (1896), the *Brueelia* from *C. mexicanus* was not morphologically the same as the type for *B. vulgata*.

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