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Cophylogenetic analysis of lice in the *Colpocephalum* complex (Phthiraptera: Amblycera)

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The chewing louse genus *Colpocephalum* parasitizes nearly a dozen distantly related orders of birds. Such a broad host distribution is relatively unusual in lice. However, the monophyly of the genus *Colpocephalum* has never been tested using molecular characters. Using one nuclear and one mitochondrial gene, we inferred a phylogeny for 54 lice from the genus *Colpocephalum* and other morphologically similar genera. The resulting phylogeny demonstrates that *Colpocephalum* itself is not monophyletic. However, these data support the existence of a *Colpocephalum* complex within which several lineages are restricted to particular host orders. These lineages corresponded to previously described genera, some of which are morphologically distinct and currently considered subgenera. Maddison–Slatkin tests were performed on the resulting phylogeny and showed that host order, host family and biogeographic region had significant phylogenetic signal when mapped onto the *Colpocephalum* complex phylogeny. A PARAFIT analysis comparing the overall *Colpocephalum* complex phylogeny to a host phylogeny revealed significant congruence between host and parasite trees. We also compared the cophylogenetic history of *Colpocephalum* and their hosts to that of a second distantly related feather louse genus, *Degeeriella*, which also infests diurnal birds of prey. Using PARAFIT to identify individual host–parasite links that contributed to overall congruence, there was no evidence of correlated cophylogenetic patterns between these two louse groups, suggesting that their host distribution patterns have been shaped by different evolutionary processes.

KEYWORDS

avian chewing lice, phylogenetics, systematics

1 | INTRODUCTION

Chewing louse genera are typically restricted to a single avian host family or order. However, the louse genus *Colpocephalum* Nitzsch, 1818 (Phthiraptera: Amblycera: Menoponidae), as currently defined (Price, Hellenthal, Palma, Johnson, & Clayton, 2003), is found on 11 distantly related avian host orders. The type species of this genus is a parasite of White Stork (*Ciconia ciconia* (Linnaeus)), and other *Colpocephalum* species have been described from a variety of different avian host orders including falcons (Falconiformes), pelicans and relatives (Pelecaniformes), gamebirds (Galliformes), flamingos and relatives (Ciconiiformes), and pigeons (Columbiformes) (Price et al., 2003). Species placed within *Colpocephalum* are united by a comb of ctenidia on the sternites and femora and the presence of black occipital and pre-ocular nodi (connected by a diffuse band-like thickening of the dorsal head roof). A diversity of other menoponid genera also fall within the *Colpocephalum* complex based on shared morphological features, and these other genera are each restricted to specific avian host orders (e.g., *Psittacobrosus* Carriker, 1954 on Psittaciformes and *Ciconiphilus* Bedford, 1939 on Ciconiiformes). Some of these genera were

morphologically well described or were adequately redescribed as part of a taxonomic revision, whereas others were not. Many of these poorly described genera were erected based on host associations or because of the presence of a single highly derived character. Thus, taxonomic revisions and checklists (Hopkins & Clay, 1952; Price & Emerson, 1966; Price et al., 2003) synonymized these 24 poorly described genera in the complex, placing them within the genus *Colpocephalum* and only those genera with detailed descriptions identifying significant morphological differences were retained. As a result, in both past and present taxonomic classifications, the genus *Colpocephalum* is a dumping ground and the *Colpocephalum* complex as a whole has poorly defined generic limits.

The monophyly of *Colpocephalum* has never been tested in a modern phylogenetic framework. If *Colpocephalum* is monophyletic, then interordinal and interfamilial host switching is likely rampant because the host orders and families of this louse genus are not closely related and instead are scattered across the avian tree of life (Hackett et al., 2008; Jarvis et al., 2014; Prum et al., 2015). Furthermore, many of the host orders do not come into direct or indirect contact, and thus, it is unlikely that they share closely related parasites. Recently, molecular phylogenetic data have called into question the validity of many louse genera that parasitize distantly related hosts. For example, the ischnoceran louse genus *Degeeriella* Neumann, 1906, which parasitizes hawks (Accipitriformes) and falcons (Falconiformes), consists of two distinct, distantly related non-sister lineages, one specific to each host order (Catanach & Johnson, 2015).

Clay (1969) placed a number of additional genera into the *Colpocephalum* complex based on morphological characters of the head and legs. Interestingly, these genera have not been synonymized with *Colpocephalum* and many are codistributed on the same bird groups as *Colpocephalum* sensu stricto (sensu Hopkins & Clay, 1952; Price & Beer, 1963a,b). The majority of these other genera in the *Colpocephalum* complex have not been included in a molecular phylogeny, and therefore, the relationships and monophyly of these genera with respect to *Colpocephalum* are unclear.

One of these morphologically similar genera is *Kurodaia* Uchida, 1926, which is differentiated from *Colpocephalum* sensu stricto by the lack of strongly defined occipital nodi on the head and differences in the female genitalia (Price & Beer, 1963c,d). Furthermore, within *Kurodaia*, Price and Beer (1963b) recognized two subgenera, one parasitizing diurnal birds of prey (*Kurodaia*) and the other parasitizing owls (*Conciella* Eichler, 1949). No species of *Kurodaia* was included in Marshall's (2003) morphological phylogenetic analysis of Amblycera, but a molecular phylogeny with limited taxonomic sampling and sequences from two genes (Johnson et al., 2003) recovered *Colpocephalum* and *Kurodaia* as sister taxa. However, Johnson et al. (2003) only included single representatives of these genera in their phylogeny, and therefore, monophyly of the genera and subgenera within the *Colpocephalum* complex could not be assessed.

Here we reconstruct a phylogeny for *Colpocephalum* and *Kurodaia* to: (i) test the monophyly of *Colpocephalum* (including previously recognized subgenera and synonymized genera, (ii) test the validity of *Kurodaia* and included subgenera and (iii) directly compare the phylogeny of these lice to that for *Degeeriella* (Catanach & Johnson, 2015), which is distributed on some of the same groups of birds. The goal of this comparison is to evaluate whether codistributed parasites exhibit correlated divergence events as a result of concordant evolutionary events such as shared vicariance.

2 | MATERIAL AND METHODS

2.1 | Specimen acquisition

Lice were collected from avian hosts in various ways, including ethyl acetate fumigation of freshly collected host specimens or dust ruffling and manual searches of hosts that were banded and released (Clayton, Gregory, & Price, 1992; Walther & Clayton, 1997). In total, 39 *Colpocephalum* and 11 *Kurodaia* were included (Table 1). To test the monophyly of *Colpocephalum* and *Kurodaia,* we also included representatives of eight additional genera considered members of the *Colpocephalum* complex by Clay (1969). When possible, we included DNA sequences from multiple host individuals (up to four specimens per host species), particularly from geographically widespread host species.

2.2 | DNA sequencing

For each specimen, we made two small incisions, one between the head and thorax as described by Valim and Weckstein (2011) and a second between two abdominal sclerites. We then placed the specimen in digestion buffer. We used the QIAamp DNA Micro Kit (Qiagen, Valencia, CA) for DNA extraction following a modified version of the protocol for total genomic DNA from tissues. Modifications include lengthening the incubation period in step 4 to 36 hr, incubating the sample for 10 min at 70°C in step 6, and decreasing the amount of Buffer AE in elution step (step 12) to 50 μl (which was repeated twice in different 1.5-ml collection tubes). During step 12, once pipetted to the filter, the Buffer AE was incubated for 5 min at 70°C prior to centrifugation rather than performing step 13. Specimen exoskeletons were retained, cleared and mounted on a microslide in balsam as vouchers, following the general protocols of Palma (1978). All slides were permanently deposited in the insect collections at either the Illinois Natural History Survey or the Field Museum of Natural History.

TABLE 1 Included samples

Louse species	Voucher code	Locality	Host species	Host order	Host family	COI	COIL	EF-1α
Ciconiphilus decimfasciatus	Cisp.Bustr.7.18.2014.13	Brazil	*Butorides striata*	Pelecaniformes	Ardeidae	x	x	
Anseriphilus sp.	Ciconiphilus sp RF 49		*Cygnus olor*	Anseriformes	Anatidae	x		x
Colpocephalum alecturae	Cwsp.Allat.8.19.2013.7	Australia	*Alectura lathami*	Galliformes	Megapodiidae		x	x
Colpocephalum cf. *turbinatum*	Kusp.Bulac.1.31.2014.6	Malawi	*Bubo lacteus*	Strigiformes	Strigidae	x	x	
Colpocephalum cristatae	Cwsp.Cabur.2.21.2013.4	Bolivia	*Chunga burmeisteri*	Cariamiformes	Cariamidae		x	
Colpocephalum cucullare	Cwsp.Saser.5.21.2014.2	Kenya	*Sagittarius serpentarius*	Accipitriformes	Sagittariidae		x	
Colpocephalum fregili	Cwsp.Coalb.1.31.2014.8	Malawi	*Corvus albus*	Passeriformes	Corvidae	x	x	
Colpocephalum fregili	Cwsp.Coalc.1.31.2014.9	Malawi	*Corvus albicollis*	Passeriformes	Corvidae	x	x	
Colpocephalum heterosoma	Cwsp.Phand.5.24.2013.4	Argentina	*Phoenicoparrus andinus*	Phoenicopteriformes	Phoenicopteridae	x	x	x
Colpocephalum heterosoma	Cwsp.Phchi.5.24.2013.3	Argentina	*Phoenicopterus chilensis*	Phoenicopteriformes	Phoenicopteridae		x	x
Colpocephalum ibicter	Cwsp.Ibame.7.18.2014.6	Peru	*Ibycter americanus*	Falconiformes	Falconidae			x
Colpocephalum indi	Cwsp.Icmis.2.21.2013.9	USA	*Ictinia mississippiensis*	Accipitriformes	Accipitridae	x		x
Colpocephalum kelloggi	Cwsp.Caaur.2.21.2013.2	USA	*Cathartes aura*	Accipitriformes	Cathartidae	x	x	x
Colpocephalum kelloggi	Cwsp.Caaur.8.2.2013.14	Canada	*Cathartes aura*	Accipitriformes	Cathartidae	x		x
Colpocephalum nanum	Cwsp.Accoo.10.31.2014.6	Canada	*Accipiter cooperii*	Accipitriformes	Accipitridae	x	x	x
Colpocephalum nanum	Cwsp.Bujam.8.2.2013.13	Canada	*Buteo jamaicensis*	Accipitriformes	Accipitridae		x	x
Colpocephalum nanum	Cwsp.Bujam.8.2.2013.7	Canada	*Buteo jamaicensis*	Accipitriformes	Accipitridae		x	x
Colpocephalum nanum	Cwsp.Bulag.1.31.2014.5	USA	*Buteo lagopus*	Accipitriformes	Accipitridae		x	
Colpocephalum napiforme	Cwsp.Bulag.10.31.2014.9	Canada	*Buteo lagopus*	Accipitriformes	Accipitridae	x	x	x
Colpocephalum polybori	Cwsp.Cache.5.24.2013.7	USA	*Caracara cheriway*	Falconiformes	Falconidae	x	x	x
Colpocephalum sp.	Cwsp.Lecay.7.18.2014.5	Peru	*Leptodon cayanensis*	Accipitriformes	Accipitridae		x	
Colpocephalum sp.	Cwsp.Faamu.5.21.2014.4	Kenya	*Falco amurensis*	Falconiformes	Falconidae		x	
Colpocephalum spinicollis	Cwsp.Thsp.2.21.2013.10	Australia	*Threskiornis spinicollis*	Pelecaniformes	Threskiornithidae	x	x	
Colpocephalum subzerafae	Cwsp.Faber.2.21.2013.7	Australia	*Falco berigora*	Falconiformes	Falconidae	x	x	
Colpocephalum subzerafae	Cwsp.Facol.8.19.2013.6	Canada	*Falco columbarius*	Falconiformes	Falconidae			x
Colpocephalum subzerafae	Kufas.Facol.8.19.2013.4	Canada	*Falco columbarius*	Falconiformes	Falconidae		x	x
Colpocephalum turbinatum	Cwsp.Bugal.5.24.2013.1	Ecuador	*Buteo galapagoensis*	Accipitriformes	Accipitridae	x	x	x
Colpocephalum turbinatum	Cwsp.Ciapp.2.1.2013.6	New Zealand	*Circus approximans*	Accipitriformes	Accipitridae	x	x	x
Colpocephalum turbinatum	Cwsp.Haleu.2.1.2013.9	USA	*Haliaeetus leucocephalus*	Accipitriformes	Accipitridae			x
Colpocephalum turbinatum	Cwsp.Haleu.8.2.2013.4	Canada	*Haliaeetus leucocephalus*	Accipitriformes	Accipitridae	x	x	x
Colpocephalum turbinatum	Cwsp.Hasph.5.24.2013.2	Australia	*Haliastur sphenurus*	Accipitriformes	Accipitridae	x		

(Continues)

TABLE 1 (Continued)

Louse species	Extraction code	Locality	Host species	Host order	Host family	COI	COIL	EF-1α
Colpocephalum turbinatum	Cwsp.Helon.2.1.2013.4	Papua New Guinea	*Henicopernis longicauda*	Accipitriformes	Accipitridae		x	x
Colpocephalum turbinatum	Cwsp.Bulac.1.31.2014.7	Malawi	*Bubo lacteus*	Strigiformes	Strigidae		x	
Colpocephalum unciferum	Cwsp.Peery.2.21.2013.1	USA	*Pelecanus erythrorhynchus*	Pelecaniformes	Pelecanidae	x	x	x
Colpocephalum unciferum	Cwsp.Peery.8.2.2013.9	Canada	*Pelecanus erythrorhynchus*	Pelecaniformes	Pelecanidae		x	x
Cuculiphilus (*Cuculiphilus*) *fasciativentris*	Cqsp.Pimel.7.18.2014.12	Brazil	*Piaya melanogaster*	Cuculiformes	Cuculidae	x		
Cuculiphilus (*Falcophilus*) *alternatus*	Cwsp.Coatr.2.1.2013.10	USA	*Coragyps atratus*	Accipitriformes	Cathartidae	x	x	x
Cuculiphilus (*Cuculiphilus*) sp.	Cqsp.Chkla.4.3.2000.2	Ghana	*Chrysococcyx klaas*	Cuculiformes	Cuculidae	x		x
Kurodaia (*Conciella*) *longipes*	Kusp.Buafr.1.31.2014.15	Malawi	*Bubo africanus*	Strigiformes	Strigidae	x	x	x
Kurodaia (*Conciella*) sp.	Kumag.Stneb.10.31.2014.7	Canada	*Strix nebulosa*	Strigiformes	Strigidae	x		x
Kurodaia (*Kurodaia*) *fulvofasciata*	Kusp.Acpol.2.1.2013.3	Papua New Guinea	*Accipiter poliocephalus*	Accipitriformes	Accipitridae	x	x	
Kurodaia (*Kurodaia*) *fulvofasciata*	Cwsp.Acruf.2.1.2013.2	Fiji	*Accipiter rufitorques*	Accipitriformes	Accipitridae	x	x	x
Kurodaia (*Kurodaia*) *fulvofasciata*	Kuful.Bujam.8.19.2013.2	Canada	*Buteo jamaicensis*	Accipitriformes	Accipitridae		x	x
Kurodaia (*Kurodaia*) *fulvofasciata*	Kusp.Bujam.1.31.2014.4	USA	*Buteo jamaicensis*	Accipitriformes	Accipitridae	x	x	x
Kurodaia (*Kurodaia*) *fulvofasciata*	Kusp.Bumag.1.31.2014.12	Peru	*Buteo magnirostris*	Accipitriformes	Accipitridae	x		
Kurodaia (*Kurodaia*) *fulvofasciata*	Kusp.Icplu.1.31.2014.10	Peru	*Ictinia plumbea*	Accipitriformes	Accipitridae	x	x	
Kurodaia (*Kurodaia*) *haliaeeti*	Cwsp.Pahal.1.31.2014.14	USA	*Pandion haliaetus*	Accipitriformes	Pandionidae	x	x	x
Kurodaia (*Kurodaia*) *haliaeeti*	Cwsp.Pahal.2.21.2013.8	Australia	*Pandion haliaetus*	Accipitriformes	Pandionidae	x	x	x
Kurodaia (*Kurodaia*) *haliaeeti*	Cwsp.Pahal.5.24.2013.8	USA	*Pandion haliaetus*	Accipitriformes	Pandionidae	x		x

(Continues)

TABLE 1 (Continued)

Louse species	Extraction code	Locality	Host species	Host order	Host family	COI	COIL	EF-1α
Kurodaia (*Kurodaia*) *haliaeeti*	Kuhal.Pahal.8.2.2013.2	Canada	*Pandion haliaetus*	Accipitriformes	Pandionidae	x	x	
Microctenia major	Mtsp.Timaj.7.18.2014.15	Brazil	*Tinamus major*	Tinamiformes	Tinamidae	x	x	
Piagetiella bursaepelecani	Qibur.5.1.2000.3	USA	*Pelecanus occidentalis*	Pelecaniformes	Pelecanidae	x		x
Psittacobrosus sp.	Pssp.Amalb.5.4.1999.10	Mexico	*Amazona albifrons*	Psittaciformes	Psittacidae	x		x
Psittacobrosus anduzei	Psand.3.29.1999.3	Mexico	*Eupsittula nana astec*	Psittaciformes	Psittacidae	x		x
Psittacobrosus molinae	Hmsp.Pymel.7.18.2014.14	Brazil	*Pyrrhura melanura*	Psittaciformes	Psittacidae	x	x	
Psittacomenopon impar	Qmsp.Pocry.7.18.2014.16	Malawi	*Poicephalus cryptoxanthus*	Psittaciformes	Psittacidae	x	x	
Psittacomenopon impar	Qmsp.Pomey.7.18.2014.8	Malawi	*Poicephalus meyeri*	Psittaciformes	Psittacidae	x	x	
Trinoton querquedulae	Amsp.Anpla.4.19.1999.3	USA	*Anas platyrhynchos*	Anseriformes	Anatidae	x		x

After extraction, PCR (25 μl reactions) was performed to amplify three fragments of two genes, including two fragments of the mitochondrial protein coding gene: cytochrome oxidase I (COI) and the nuclear protein coding gene: elongation factor-1α (EF-1α). For COI amplification, we used primers L6625 and H7005 (Hafner et al., 1994) and LCO1490 and HCO2198 (Folmer, Black, Hoeh, Lutz, & Vrijenhoek, 1994), and for EF-1α, we used EF1-For3 and EF1-Cho10 (Danforth & Ji, 1998). PCR conditions follow those for Smith, Page, and Johnson (2004) except that an annealing temperature of 50°C was used for EF-1α. Cycle sequencing reactions were performed using 1 μl of BigDye, 2 μl of sequencing buffer, 5.2 μl of 12.5% glycerol and 2 μl of 1 μM primer. The resulting product was submitted for automated sequencing on an ABI 3730xl automated capillary sequencing machine at the University of Illinois Keck Center for Comparative and Functional Genomics. Raw forward and reverse strands for each fragment were assembled in GENEIOUS 8.0.4 (Biomatters Ltd.) and manually reconciled. Resulting consensus sequences were aligned in Geneious using the MUSCLE plugin and exported to SEAVIEW 4.3.0 where they were checked and adjusted by eye (Edgar, 2004; Gouy, Guindon, & Gascuel, 2010). All novel sequences were deposited in GenBank (accession numbers MF443916–MF444025). In addition to our sampling, the following sequences were downloaded from genbank: AF494292.1, AF494293.1, AF545751.1, AF545756.1, AF545757.1, AF545771.1, AF545781.1, AF545797.1, AF545800.1, AF545801.1, and AF545807.1.

2.3 | Phylogenetic analysis

The three gene regions were first analysed separately to ensure that gene trees were not in conflict (posterior probability [PP] greater than .95). Gene trees were inferred using a 40 million generation BEAST 2.3.1 (Drummond & Rambaut, 2007) run under the model selected by PARTITIONFINDER 1.1.1 (Lanfear, Calcott, Ho, & Guindon, 2012) with branchlengths = linked; model_selection = AIC; search = greedy). No major conflicts were found between ingroup taxa, and therefore, we concatenated the gene sequences.

In the combined analysis of the concatenated data set, different models were applied to each partition. Phylogenies based on the combined analysis were inferred using Bayesian Inference (BI) as implemented in BEAST 2.3.1 (Drummond & Rambaut, 2007; 40 million generations, sampled every 1,000 generations, burnin = 10,000), Maximum Likelihood (ML) as implemented in Garli version 2.01. (Zwickl, 2006): 10 independent runs, default settings, automated stop criterion = 50,000) and Maximum Parsimony (MP) as implemented in PAUP* (Swofford, 2003; 1,000 random addition sequences with TBR branch swapping). Bayesian PP and both MP (1,000 replicates of 100 random addition sequences with maxtrees set at 1,000 due to computational constraints)

and ML bootstrap values (500 bootstrap replicates on default settings with automated stop criterion = 50,000) were used to evaluate branch support. In BI analyses, PartitionFinder favoured an eight partition model (each gene/codon position separate with the exception of the 2nd codon position for both regions of COI) with GTR + I + G selected for all COI partitions except the 3rd positions in the fragment amplified by L6625 and H7005 for which HKY + I + G was favoured. PartitionFinder favoured a different model for each EF-1α codon position, selecting TrN + I, HKY + I and GTR + G for codon positions 1, 2 and 3, respectively. During phylogenetic analyses, each partition was treated as unlinked.

2.4 | Cophylogenetic analysis

Phylogenetic signal for host taxonomy (order and family) and host geography was tested using a Maddison and Slatkin (1991) test as implemented with R code (available at www.github.com/juliema/publications, see Bush et al., 2016). Host taxonomy was based on the eBird-Clements checklist (eBird-Clements-v2015-integrated-checklist-August-2015 available through Cornell University: http://www.birds.cornell.edu/clementschecklist/download/). Geography was coded based upon where the host was acquired—Nearctic, Neotropics, Ethiopian, Australasian, Palearctic and Oriental regions. In cases where we sampled multiple host individuals from the same species and geographic region, we pruned tips to limit the tree to a single representative to prevent duplicate samples of the same louse from influencing the results (and biasing results towards finding evidence of significant phylogenetic signal).

Twelve host species of *Colpocephalum* included in this phylogenetic study also harbour *Degeeriella*, a second louse genus parasitizing diurnal birds of prey. These *Degeeriella* species were previously included in a phylogenetic study of the genus (Catanach & Johnson, 2015). Following the methods outlined in Sweet, Boyd, and Johnson (2016), we used the R implementation of PARAFIT (in package "ape"; Legendre, Desdevises, & Bazin, 2002; Paradis, Claude, & Strimmer, 2004) to evaluate whether cophylogenetic patterns were correlated between the two codistributed louse genera. PARAFIT tests for evidence of congruence between host and parasite trees by randomizing the association matrix. In addition to calculating a global measure of congruence, individual links are also evaluated to determine how much each contributes to the global test statistic. This process results in an F1 (more conservative) and F2 (in some instances has greater power) statistic, both of which were retained in our analysis (Legendre et al., 2002). The host trees were created by selecting the relevant species using the Phylogeny Subsets tool from BirdTree.org (Jetz, Thomas, Joy, Hartmann, & Mooers, 2012). A random sampling of 1,000 Ericson All Species trees was downloaded and then summarize into a single tree using TREEANNOTATOR (Drummond & Rambaut, 2007). Parasite trees were pruned in R to remove outgroups and duplicates (where a single louse species was sampled multiple times, based on sequence divergence and tree topology). We used an R script (available at https://github.com/adsweet/cophylogenetic_analyses) to run PARAFIT for 999 permutations to compare the host tree to the *Colpocephalum* tree and the host tree to *Degeeriella* tree.

To determine whether cophylogenetic patterns are correlated between *Colpocephalum* and *Degeeriella*, we analysed a 2 × 2 contingency table of significant and non-significant links for each genus. In instances where two links existed for a single host species from one of these genera (i.e., a host species infested with two *Colpocephalum*, suborder Amblycera), the louse from the other suborder (e.g., Ischnocera) was counted twice. For example, two different species of lice from the *Colpocephalum* complex occur on Red-tailed Hawk (*Buteo jamaicensis* (Gmelin)), whereas only a single *Degeeriella* taxon occurs. The *Degeeriella* link is therefore counted twice to fill the contingency table. We performed a Fisher's exact test (in R) to determine whether patterns between *Colpocephalum* and *Degeeriella* were correlated. A significant test would indicate that these two genera had similar cophylogenetic patterns.

2.5 | Louse identification

After extraction, all louse specimens were mounted permanently on slides and identified using available parasite literature. Many of taxa within *Colpocephalum* and related genera are poorly described and have never been redescribed using modern standards. In our study, we morphologically compared our specimens to those described from the same host (sensu Price et al., 2003). We then compared our specimens with those described or redescribed in taxonomic revisions for lice parasitizing each host group as listed here: Accipitriformes (Price & Beer, 1963b,c), Anseriformes (Clay & Hopkins, 1960; Price & Beer, 1965b), Cariamiformes (Price, 1968), Cathartiformes (Price & Beer, 1963b; Scharf & Price, 1965), Cuculiformes (Scharf & Price, 1965), Falconiformes (Price & Beer, 1963b,c), Galliformes (Mey, 1999; Price & Beer, 1964), Passeriformes (Price & Beer, 1965b), Pelecaniformes (Price, 1970; Price & Beer, 1965a,c), Psittaciformes (Price & Beer, 1966, 1968), Strigiformes (Price & Beer, 1963a,d) and Tinamiformes (Guimarães, 1947). Specimens used in our data set that could not be positively identified to species based on available literature and reference specimens are labelled as "sp.," regardless of their host association. No identification was made based exclusively on host–parasite relationship.

3 | RESULTS

The tree resulting from Bayesian analysis of COI and EF-1α sequences for the *Colpocephalum* complex (Figure 1)

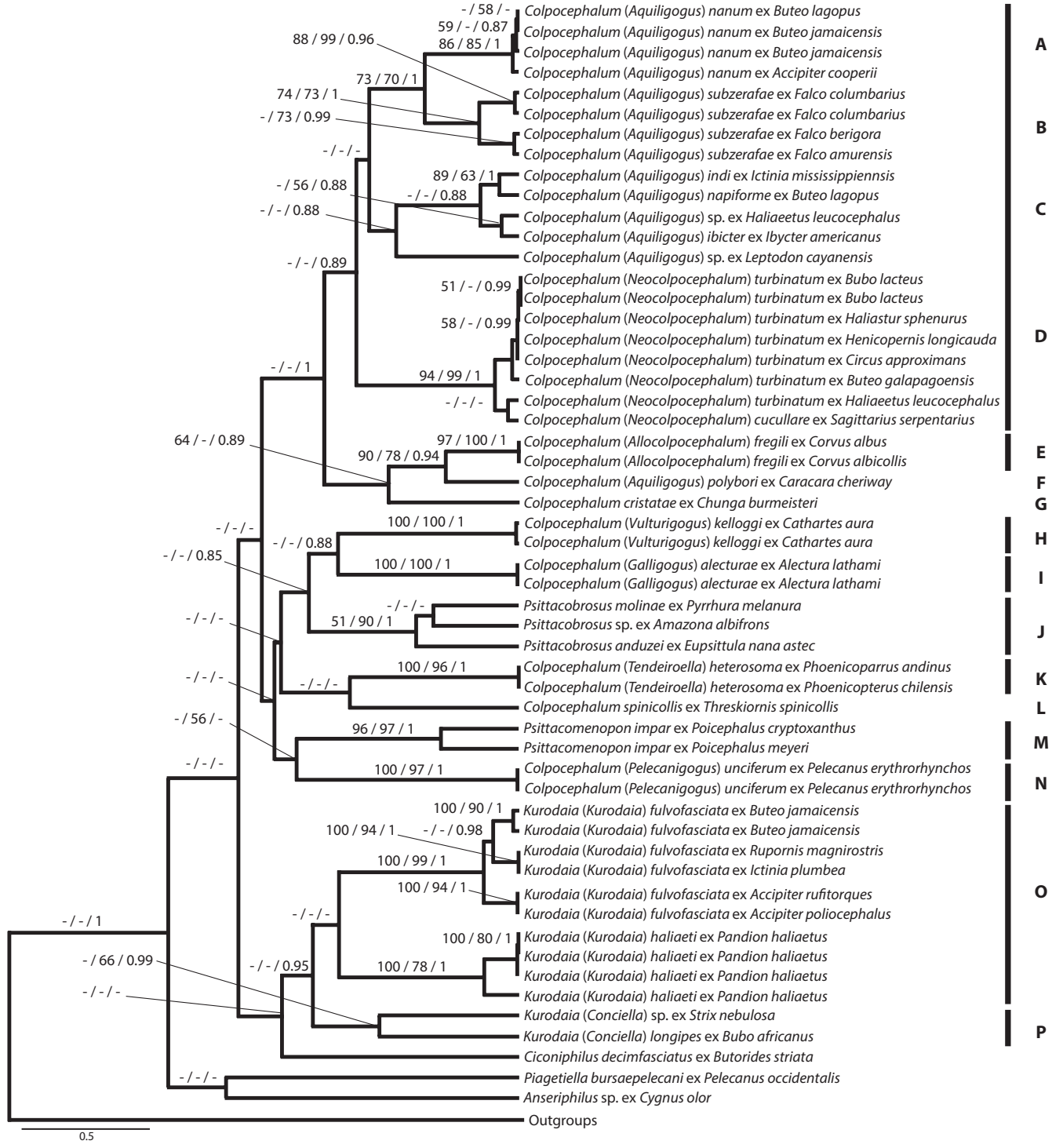

FIGURE 1 Phylogeny of the *Colpocephalum* complex (with outgroups removed). Numbers on branches are Maximum Parsimony bootstrap values (≥50), Maximum Likelihood bootstrap values (≥50) and Bayesian Inference posterior probability values (≥.85). Letters next to clades identify monophyletic groups discussed in the text

indicated that members of *Colpocephalum* were placed in several distinct lineages, most of which parasitize a single host order or clade. Although many of these lineages were strongly supported as monophyletic PP ≥ .95), some lacked statistical support. *Kurodaia* from diurnal and nocturnal birds of prey form a strongly supported (PP = .95; Figure 1, clades O and P) monophyletic group. Whereas support for some *Colpocephalum* and *Kurodaia* lineages was high, support for the relationships among lineages along the backbone of the tree was very low. Furthermore, the tree suggests that *Colpocephalum* is not monophyletic. However, there was not significant support for this result.

Within *Kurodaia,* there are three well-supported (PP > .99) lineages. One includes lice from owls (Strigiformes), from the subgenus *Conciella* (Figure 1, clade P), and this clade is sister to lice from hawks (Accipitriformes) in the subgenus *Kurodaia* (Figure 1, clade O). Although the owl louse clade was well supported in BI, it was not strongly supported in MP or ML (PP = .99, ML = 66). A well-supported clade (PP = 1.0, MP = 100, ML = 78) contained all *Kurodaia* (*Kurodaia*) *haliaeti* (Denny, 1842) sampled from the Osprey (*Pandion haliaetus* Linnaeus) from North America and Australia. The remaining lineage of *Kurodaia*, also from the nominotypical subgenus, was comprised of lice from hawks (Accipitriformes) including Red-tailed Hawk (*Buteo jamaicensis*), Roadside Hawk (*Rupornis magnirostris* Gmelin), Plumbeous Kite (*Ictinia plumbea* (Gmelin)), Fiji Goshawk (*Accipiter rufitorques* (Peale)) and Grey-headed Goshawk (*Accipiter poliocephalus* (Grey)) (PP = 1.0, MP = 100, ML = 98). Within this clade, there are three well-supported lineages: the Red-tailed Hawk lice, Pacific Island *Accipiter* lice (Fiji Goshawk and Grey-headed Goshawk) and a South American lineage (Roadside Hawk and Plumbeous Kite). Each of these lineages has a posterior probability of 1.0 and bootstrap values over 90 in both MP and ML. Although the currently recognized subgenera *Kurodaia* (*Kurodaia*) from diurnal birds of prey and *Kurodaia* (*Conciella*) from owls form reciprocally monophyletic groups in the tree, this node lacked strong statistical support.

Within *Colpocephalum*, one major clade consists of lice primarily found on diurnal and nocturnal birds of prey (Figure 1, clade A–F), whereas a second includes *Colpocephalum* from a variety of other birds, along with two genera of parrot lice, *Psittacomenopon* Bedford, 1930 and *Psittacobrosus* (Figure 1, clade H–N). There are six main lineages within this second major clade (Figure 1, clade H–N), all of them restricted to distinct host groups; however, the relationships among them were not well resolved. The remaining lineages of *Colpocephalum* correspond to groups that some authors have considered as genera or subgenera of *Colpocephalum* (Eichler & Złotorzycka, 1971; Zlotorzycka, 1976; Zlotorzycka, Eichler, & Ludwig, 1974): *Vulturigogus* Eichler & Złotorzycka, 1963 (on New World Vultures; Figure 1, clade H), *Pelecanigogus* Eichler, 1949 (on pelicans and frigatebirds; Figure 1, clade N), *Tendeiroella* Eichler, 1982 (on flamingos; Figure 1, clade K) and *Galligogus* Eichler, 1947 on Australian Brushturkey (Galliformes: *Alectura lathami*; Figure 1, clade I).

Clade A–G contains exclusively *Colpocephalum* from diurnal birds of prey, nocturnal birds of prey, corvids and seriemas. Although this clade was well supported in BI (PP = 1.0), it was not supported in MP or ML. This clade is divided into two lineages. One is comprised of lice from two African corvids (Figure 1, clade E), Crested Caracara (Falconidae: *Caracara cheriway* (Jacquin); Figure 1, lineage F) and Black-legged Seriema (Cariamiformes: *Chunga burmeisteri* (Hartlaub); Figure 1, lineage G), but has weak statistical support (PP = .89, MP = 64).

This clade includes two taxa in the subgenus *Allocolpocephalum* Qadri, 1939 from corvids and a louse from seriema. The other clade (Figure 1, clade A–D) (PP = .89) contains lice from only birds of prey, including owls, hawks and falcons. Within this clade, lice placed in the subgenera *Neocolpocephalum* Ewing, 1933 from Hawks (Accipitriformes) and Owls (Strigiformes) (Figure 1, clade D) and *Aquiligogus* Eichler & Złotorzycka, 1971 from hawks (Accipitriformes) and falcons (Falconiformes) (Figure 1 clades A, B and C) fall into two distinct groups, although monophyly of *Aquiligogus* is not well supported and the monophyly of *Neocolpocephalum* is only strongly supported in BI.

All three Maddison and Slatkin (1991) tests (for host order, host family and host geography) revealed significant evidence of phylogenetic signal ($p < .05$ in all cases) in these characters on the tree. PARAFIT indicated congruence between host and parasite trees for both *Degeeriella* and *Colpocephalum* (global test p-value = .001 for both genera). Although five links within *Degeeriella* were significant (F1 and F2 statistics were identical for each pair), and three links in *Colpocephalum* were significant, no links were shared between the two genera. Furthermore, a Fisher's exact test among the congruent host–parasite links of *Degeeriella* and the host–parasite links of *Colpocephalum* indicates that they were not significantly associated with each other ($p = .27$).

4 | DISCUSSION

Phylogenetic analyses of one mitochondrial and one nuclear gene from a diversity of *Colpocephalum* complex members produced the first molecular phylogeny for this complex of avian lice. Although *Colpocephalum* is not monophyletic in our analysis, its monophyly cannot be ruled out completely because of a number of weakly supported nodes along the backbone of the tree. However, we did find a number of strongly supported clades within the complex, most which correspond to existing genera or subgenera (Figure 2). Our work suggests that either *Psittacomenopon* and *Psittacobrosus* should be treated as subgenera of *Colpocephalum* or many subgenera within *Colpocephalum* should be returned to full generic status. However, without a detailed morphological study of the group, taxonomic recommendations would be premature. Further analyses, including more nuclear gene sequences, are required to determine whether the genus *Colpocephalum* is monophyletic and additional morphological analysis is needed to define generic limits within the complex. Broader taxon sampling, including several genera missing from our study that Clay (1969) placed in the *Colpocephalum* complex, will

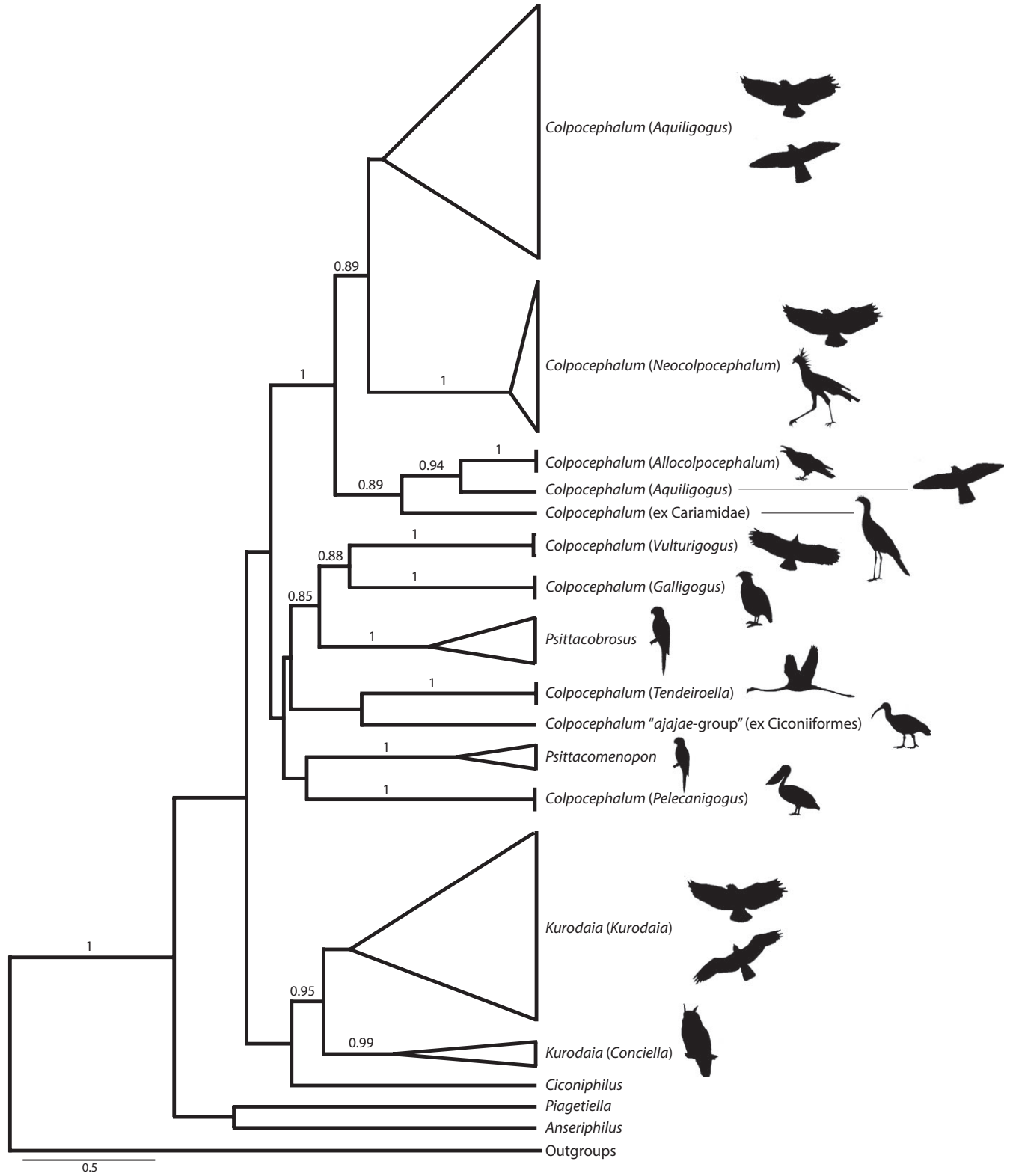

FIGURE 2 Phylogeny of the *Colpocephalum* complex (with outgroups removed) showing subgenera of *Colpocephalum* and *Kurodaia*. Silhouettes represent host orders for louse terminal taxa. Numbers on branches are Bayesian Inference posterior probability values (≥.85)

help clarify taxonomic limits of this group. Furthermore, the addition of data from *Colpocephalum zebra* Burmeister, 1838, the type species of the genus, would be critical for determining which lineages belong in *Colpocephalum* sensu stricto.

Several genera have been synonymized with *Colpocephalum* (Hopkins & Clay, 1952; Price & Emerson, 1966; Price et al., 2003) and are herein treated as subgenera. These include *Vulturigogus* (from New World Vultures),

Pelecanigogus (from pelicans), *Tendeiroella* (from flamingos), *Allocolpocephalum* (from crows) and *Galligogus* (from Australian Brushturkey). Given that we have not conducted a detailed morphological revision of the complex, we believe that treating these taxa as subgenera is the most conservative approach to indicate that these clades are good candidates for elevation to full genera once they have been studied in the context of a more detailed molecular and morphological study.

We sampled both *Tendeiroella* and *Allocopocephalum* from multiple host species. For both of these subgenera, we found that multiple host species share the same morphologically and genetically identical louse species. Other louse taxa are also known to infect multiple host species. For example, based on morphological and genetic data Bueter et al., Weckstein, Johnson, Bates, and Gordon (2009) found that Neotropical migrant thrushes (genus *Catharus*) are parasitized by a single species of *Brueelia*. Escalante et al. (2016) also found clades of closely related (and morphologically similar) lice occurring on distantly related duck hosts. We also sampled other *Colpocephalum* complex subgenera from geographically widespread localities (e.g., lice from *Buteo jamaicensis*), and these were morphologically and genetically identical. Similarly, in a recent study of duck lice by Escalante et al. (2016) clades of lice with virtually no COI genetic divergence were found on host taxa across a wide geographic distribution.

There are two lineages widely distributed on diurnal and nocturnal birds of prey and these are currently treated as subgenera of *Colpocephalum*: *Aquiligogus* and *Neocolpocephalum*. With the exception of the specimen *Colpocephalum* (*Aquiligogus*) *polybori*, each of these subgenera forms a monophyletic clade. Furthermore, the branch lengths on these lineages are similar to those seen in the lineages currently treated as genera within the *Colpocephalum* complex. Although monophyly of *Neocolpocephalum* is well supported (PP = 1.0, MP = 94), support is weak for monophyly of the *Aquiligogus* clade, excluding *Colpocephalum* (*Aquiligogus*) *polybori*. Morphological data were not directly incorporated into this phylogeny, yet the presence of several well-supported clades (Figure 1, clade A–D) suggests that these lineages are distinct evolutionary units and further research may warrant their return to generic status. Some of these lineages do not currently have a name and thus may require the description of new genera/subgenera. For example, the subgenus *Aquiligogus* (Eichler & Złotorzycka, 1971) includes both the *polybori* group (sensu Price & Beer, 1963b) found on caracaras and the *flavescens*-group, and in our phylogenetic reconstructions, these groups are not closely related and therefore may warrant creation of a new subgenus for the *polybori* group.

Our data suggests that there are at least three distinct lineages of *Colpocephalum* complex lice on raptors: *Kurodaia* (comprised of two subgenera: *Kurodaia* and *Conciella* which parasitize diurnal birds of prey and nocturnal owls, respectively), *Colpocephalum* from Accipitridae and Strigidae (comprising two subgenera, *Aquiligogus* and *Neocolpocephalum*) and *Colpocephalum* (*Vulturigogus*) from New World Vultures (Cathartidae).

In this study, all the *Colpocephalum* complex lice sampled from the Falconidae (falcons and caracaras) were embedded within the *Colpocephalum* louse clade, confirming this louse group broadly parasitizes Falconiformes and Accipitriformes, rather than a single host order. Lice collected from falcons (genus *Falco*) were all placed in a single clade (Figure 1, clade B) suggesting a single colonization and subsequent radiation of lice occurred on this host genus. Conversely, lice from Crested Caracara (*Caracara cheriway*) and Red-throated Caracara (*Ibycter americanus* (Boddaert) were not closely related to each other or to lice collected from falcons. Further sampling of lice from other species within the Falconidae, particularly outside of *Falco*, are needed to further understand the non-monophyly of lice parasitizing caracaras (Polyborinae) and falcons (Falconinae). A molecular phylogeny of Falconidae (Fuchs, Johnson, & Mindell, 2015) showed that *Falco* is a recent (7.5 mya) radiation, whereas many of the caracara genera, including *Caracara* and *Ibycter*, diverged significantly earlier (10 mya). This could provide a potential calibration point for future divergence time estimation of *Colpocephalum* complex members.

Lice from owls fell into two different clades in the tree. *Colpocephalum turbinatum* Denny, 1842, from Verreaux's Eagle-Owl (*Bubo lacteus* (Temminck)) was deeply embedded within the *Colpocephalum* (*Neocolpocephalum*) clade, which included a number of *C. turbinatum* specimens from diurnal birds of prey. Within *Kurodaia*, a pair of lice in the subgenus *Conciella* from two owls (Great Grey Owl, *Strix nebulosa* Forster, and Spotted Eagle-Owl, *Bubo africanus* (Temminck)) are each other's closest relatives and are sister to the nominotypical subgenus *Kurodaia*.

A louse from Secretary Bird (*Sagittarius serpentarius* (Miller)), morphologically identified as *Colpocephalum cucullare*, was embedded within the clade of lice identified as *C. turbinatum*. These species are morphologically similar (Price & Beer, 1963b), and the status of the members of this group will require further investigation.

Overall, host taxonomy at both the host order and host family level is highly correlated with louse phylogeny. Host geography also explains louse phylogeny, although with less statistical support. A cophylogenetic analysis using PARAFIT indicated significant congruence between the *Colpocephalum* complex phylogeny and host phylogeny ($p = .001$). Comparing significant links between the two louse genera (*Colpocephalum* and *Degeeriella*) on the same group of hosts did not reveal any correlation between the two. *Degeeriella* complex members are thought to disperse via phoresy, hitchhiking on hippoboscid flies (Bartlow, Villa,

Thompson, & Bush, 2016; Keirans, 1975; J. Weckstein and M. Valim personal observation), whereas *Colpocephalum* is not known to engage in this behaviour. Phoresis by *Degeeriella* has the potential to result in populations of lice that freely move between different host species within a geographic region (Weckstein, 2004). This difference in phoretic behaviour could explain the lack of correlation in cophylogenetic patterns between these two genera of lice.

The *Colpocephalum* complex includes lice parasitizing a wide array of host species. Here we identified monophyletic lineages within this complex that parasitize individual host orders. These lineages could potentially be treated as either subgenera within the large *Colpocephalum* genus, or as full, but closely related genera. Although our analysis found support for these clades, backbone support to determine how lineages are related to each other was lacking. We also lacked molecular grade specimens for many of the type species described from the various *Colpocephalum* complex member lineages. Future studies should include these species so that formal recommendations regarding the taxonomic status of these genera/subgenera can be made. Lastly, a thorough taxonomic review with detailed morphological analysis is needed for this complex.

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