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Unexpected distribution patterns of *Carduiceps* feather lice (Phthiraptera: Ischnocera: Philopteridae) on sandpipers (Aves: Charadriiformes: Scolopacidae)

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Abstract. The louse genus *Carduiceps* Clay & Meinertzhagen, 1939 is widely distributed on sandpipers and stints (Calidrinae). The current taxonomy includes three species on the Calidrinae (*Carduiceps meinertzhageni, Carduiceps scalaris, Carduiceps zonarius*) and four species on noncalidrine hosts. We estimated a phylogeny of four of the seven species of *Carduiceps* (the three mentioned above and *Carduiceps fulvofasciatus*) from 13 of the 29 hosts based on three mitochondrial loci, and evaluated the relative importance of flyway differentiation (same host species has different lice along different flyways) and flyway homogenization (different host species have the same lice along the same flyway). We found no evidence for either process. Instead, the present, morphology-based, taxonomy of the genus corresponds exactly to the gene-based phylogeny, with all four included species monophyletic. *Carduiceps zonarius* is found both to inhabit a wider range of hosts than wing lice of the genus *Lunaceps* occurring on the same group of birds, and to occur on *Calidris* sandpipers of all sizes, both of which are unexpected for a body louse. The previously proposed family Esthiopteridae is found to be monophyletic with good support. The concatenated dataset suggests that the pigeon louse genus *Columbicola* may be closely related to the auk and diver louse genus *Craspedonirmus*. These two genera share some morphological characters with *Carduiceps*, but no support was obtained for grouping these three genera together. Based on mitochondrial data alone, the relationships among genera within this proposed family cannot be properly assessed, but some previously suggested relationships within this proposed family are confirmed.

Introduction

Influence of flyways on louse distribution

The most frequent opportunities for transfer of lice between two avian host individuals are during mating (Hillgarth, 1996) or from parents to the young in the nest (Clayton & Tompkins, 1994; Lee & Clayton, 1995). However, lice are likely to exploit any opportunity to transfer among hosts that arises during the host's life cycle. For instance, Brooke & Nakamura (1998) suggested that cuckoos might gain their cuckoo-specific lice when groups of cuckoos gather at caterpillar outbreaks during migration. Communal sand baths, nest holes and theft of nest material have also been proposed as likely opportunities for lateral louse transfer (references in Price *et al.*, 2003).

Gustafsson & Olsson (2012a) suggested that for lice of shorebirds (Charadriiformes), such opportunities may be very frequent outside of mating and nesting, due to the ecology of the host. While host population densities in breeding areas may be low, shorebirds gather into large, dense flocks during migration. These flocks follow specific flyways, which channel different populations of the same species into different wintering areas (e.g. Wilson & Barter, 1998; Tjørve & Tjørve, 2007; Lopes *et al.*, 2008). Migration and wintering flocks often consist of a mixture of shorebirds belonging to different species, genera and even families, and may include shorebird species of very different body sizes. The size difference between two potential

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hosts may impede the success rate of louse dispersal from one host to another (Tompkins *et al.*, 1999; Johnson *et al.*, 2005; Bush & Clayton, 2006). Conversely, the presence of multiple host species of similar size in the same mixed flocks may aid the establishment of lice on novel hosts. Host species like Dunlin (*Calidris alpina*), Sanderling (*Calidris alba*) and Curlew Sandpiper (*Calidris ferruginea*) are of similar size and occur in sympatry along several flyways, with different subpopulations or subspecies restricted to different flyways (Message & Taylor, 2005).

The co-occurrence of potential hosts of similar size in the same wintering area, and the isolation of different populations of the same host species into different flyways may have two different effects on their louse populations, if transfer between hosts happens more frequently during migration than during breeding. Gustafsson & Olsson (2012a) established the term 'flyway differentiation' for the scenario in which different populations of the same host species are parasitized by different louse species depending on the flyway along which hosts migrate. They further suggested that if louse populations on wintering hosts encounter a variety of potential host species of similar body size, and there are no other restrictions to movement between hosts, the lice may spread laterally to parasitize all hosts of similar size along one flyway, a scenario they termed 'flyway homogenization'. Gustafsson & Olsson (2012a) tested these hypotheses for the louse genus *Lunaceps* of sandpipers (*Calidris* sensu lato). They found some evidence for flyway homogenization among some, but not all, hosts of similar size along a flyway. However, flyway differentiation was not seen among any of the *Lunaceps* species sampled from the same host species from multiple flyways.

Most groups of birds are parasitized by multiple genera of chewing lice (Price *et al.*, 2003). In general, co-occurring genera of lice on the same host have differentiated to specialize in different microhabitats of the host. These microhabitat specializations are typically correlated with distinct morphological traits, which are often convergent between distantly related louse genera in the same microhabitat (Johnson *et al.*, 2012). For instance, head lice generally have rounded bodies and large, triangular heads, wing lice (like *Lunaceps*) usually have elongated, slender bodies, and body lice (such as *Carduiceps*) typically have broad, rounded or triangular heads. Two species of lice inhabiting different microhabitats of the same host species may have different rates of straggling to novel hosts, with wing lice being more likely to switch hosts than body lice (Johnson *et al.*, 2002; Page *et al.*, 2004; Whiteman *et al.*, 2004). As flyway homogenization relies on the lice being able to transfer easily between hosts, flyway homogenization may be more common among wing lice than among body lice. By contrast, the potentially more limited capability of dispersal among body lice than among wing lice may suggest that flyway differentiation is more common among body lice than among wing lice.

We present here a phylogeny of the lice in the genus *Carduiceps* that parasitize sandpipers and allies, based on three mitochondrial loci, testing the hypothesis that flyway homogenization may be less common in body lice than in wing lice. Moreover, flyway differentiation may be more common in body lice than in wing lice, as the lesser propensity for dispersal to novel hosts among body lice than among wing lice would tend to isolate the former along different flyways.

Taxonomy and relationships of Carduiceps

Carduiceps was described by Clay & Meinertzhagen (1939) based on head and abdominal characters. The genus mainly parasitizes sandpipers (*Calidris* sensu lato) and godwits (*Limosa* spp.), but also the Terek Sandpiper *Xenus cinereus* and the dowitchers (*Limnodromus* spp.). Most of the hosts of *Carduiceps* are also parasitized by the genus *Lunaceps*, and co-occurrence of lice in these two genera on the same host is common (D. Gustafsson & U. Olsson, Unpublished data). Despite the large overlap in host distribution between these two louse genera (Price *et al.*, 2003; D. Gustafsson & U. Olsson, Unpublished data, 2012b), *Carduiceps* is considered to consist of fewer species than *Lunaceps*. This could imply that lice inhabiting different body parts of sandpipers are subject to different mechanisms or opportunities for lateral spread to novel hosts. However, another explanation may be that *Carduiceps* contains cryptic species and that the current taxonomy of the genus based on Timmermann (1954) is too conservative.

The systematics of ischnoceran chewing lice is poorly known, and all species parasitizing birds are presently placed in one of three families. Of these, the family Heptapsogastridae is limited to Neotropical tinamous (Tinamiformes), Goniodidae is largely limited to wildfowl (Galliformes) and pigeons (Columbiformes), and all other lice are placed in the large and morphologically diverse Philopteridae. The most thorough alternative to this conservative classification was proposed by Eichler (1963), who divided the Ischnocera parasitizing birds into 17 families and 34 subfamilies. Eichler's (1963) proposed subdivision of the Ischnocera has never been widely used, but molecular evidence suggest that at least some of these groups may be meaningful (Cruickshank *et al.*, 2001). In Eichler's (1963) proposed classification, *Carduiceps* is placed in the family Esthiopteridae, which he further subdivided into five subfamilies: Anatoecinae, Aquanirminae, Columbicolinae, Esthiopterinae and Ibidoecinae. *Carduiceps* is placed in the subfamily Anatoecinae in Eichler's (1963) classification scheme. The family Esthiopteridae contains a variety of louse genera occurring on hosts across most of the major divisions of birds (Table 1); however, most of the host groups were placed in the clade Aequorlitornithes by Prum *et al*. (2015). Cruickshank *et al.* (2001) did not find any support for Esthiopteridae, but their analysis included only six of the 15 genera included in the family by Eichler (1963). No species of *Carduiceps* have hitherto been included in any phylogenetic analysis, and the phylogenetic position of this genus in relation to other shorebird lice is unknown. Eichler (1963) placed most of the other ischnoceran shorebird lice in the family Rallicolidae, which was placed together with Esthiopteridae in his 'interfamily' Esthiopteriformia.

We have included representatives of all five of the proposed subfamilies of Esthiopteridae suggested by Eichler (1963), to test whether this family and subfamilies are monophyletic, and

Table 1. Host distribution of the lice in Eichler's (1963) proposed Esthiopteridae.

Louse genus	Host order (Clements *et al.*, 2015)	Host clade (Prum *et al.*, 2015)
*Anaticola**	Anseriformes	Galloanserae
*Anatoecus**	Anseriformes	Galloanserae
*Aquanirmus**	Podicipediformes	Aequorlitornithes
*Ardeicola**	Pelecaniformes	Aequorlitornithes
Ardeiphagus	Pelecaniformes	Aequorlitornithes
*Carduiceps**	Charadriiformes	Aequorlitornithes
*Columbicola**	Columbiformes	Columbaves
*Craspedonirmus**	Gaviiformes, Charadriiformes	Aequorlitornithes
Esthiopterum	Gruiformes	Gruiformes
*Fulicoffula**	Gruiformes	Gruiformes
*Ibidoecus**	Pelecaniformes	Aequorlitornithes
Neophilopterus	Ciconiiformes	Aequorlitornithes
Pessaoiella	Cuculiformes	Columbaves
Turnicola	Charadriiformes	Aequorlitornithes
Turturicola	Columbiformes	Columbaves

In addition to the genera listed, Eichler (1963) included *Stresemanniella* (now *Fulicoffula*), *Abumarkub* (junior synonym of *Neophilopterus*), *Cereopsoecus* and *Flamingobius* (both now *Anatoecus*), and *Parasoricella* and *Soricella* (both now *Columbicola*). *Wilsonia* Eichler, 1940, is preoccupied by *Wilsonia* Khalfin, 1939, and is here replaced with *Pessaoiella* Guimarães, 1940, following Nemésio (2006). Host systematics follows Clements *et al.* (2015). The placement of the Hoatzin (*Opisthocomus hoazin*) in Cuculiformes by Clements *et al*. (2015) does not correspond to its phylogenetic placement in Prum *et al.* (2015). The louse genus *Craspedonirmus* is known mainly from divers (Gaviiformes), but a single species is known from two species of auks (Nelson, 1972). The genera represented in our analyses are marked with an asterisk (*).

where *Carduiceps* is placed in relation to the other genera included in this family by Eichler (1963).

Material and methods

To avoid confusion, the shorebird genus *Calidris* is here abbreviated to *Cal.*, whereas the louse genus *Carduiceps* is abbreviated *Car*. Host taxonomy follows Clements *et al*. (2015).

Sampling

Fresh material of *Carduiceps* was collected from birds following three major flyways (Table 2; East Atlantic, East Asian/Australasian, Pacific Americas) in Sweden during 2007–2008, in Japan and Australia during 2008, and in Canada during 2009. Material from *Cal. ferruginea*, *Cal. canutus* and different subspecies of *Cal. alpina* was collected from two flyways (East Atlantic and East Asian/Australasian). The *Cal. alpina* and *Cal. canutus* samples were collected from host populations considered divergent enough to belong to different host subspecies (Message & Taylor, 2005; Clements *et al.*, 2015; see Table 2). Details about collection of material are the same as in Gustafsson & Olsson (2012a).

All *Carduiceps* species used in this study are listed in Table 2. In addition, representatives of several louse genera belonging to Eichler's (1963) Esthiopteridae and Rallicolidae were included to test the monophyly of Esthiopteridae. Sequences for these lice were obtained from either GenBank or from our own collections (see Table 2). *Carduiceps* lice were assigned to species initially based on the host they were collected from, but later compared with Timmermann (1954).

Extraction and sequencing

Prior to DNA extraction, the head and prothorax were cut off from the posterior part of the body, and extractions were performed on both parts using DNeasy Blood and Tissue Kit (Qiagen, Sollentuna, Sweden), following the manufacturer's instructions, with the following exceptions: extraction was allowed to continue in a water bath for 36 h, and only one elution (with 100 mL elution fluid) was carried out. The exoskeletons were mounted on slides in Canada balsam as vouchers after extraction. All vouchers were deposited at the Natural History Museum, Stockholm (NRM; Swedish material), the Price Institute for Parasitological Research (University of Utah, Salt Lake City, U.S.A.; Canadian and Australian material), or the Yamashina Institute for Ornithology (Chiba, Japan; Japanese Material).

Amplification and sequencing of cytochrome *c* oxidase subunit I (COI) used the primers L6625 and H7005 (Hafner *et al.*, 1994), 12S was sequenced using the primers 12SAI and 12SBI (Simon *et al.*, 1994), and 16S was sequenced using the primers 16SAR and 16SBR (Simon *et al.*, 1994). Polymerase chain reactions (PCRs) were performed using GE Healthcare's Ready-To-Go beads. PCR protocols followed Yoshizawa & Johnson (2003) for 12S and 16S, and Hafner *et al.* (1994) for COI. A small sample from each PCR product was visualized on an ethidium bromide or GelRed (Biotium, Gothenburg, Sweden) gel, and samples showing satisfactory bands were purified using the EZNA Cycle Pure Kit (Omega) or Exonuclease I + FastAP (Fermentas Life Sciences, Helsingborg, Sweden) following the manufacturer's instructions. Sequencing of purified DNA, using the same primers as during PCR, was performed in both the forward and reverse directions at Macrogen Inc., South Korea.

In addition to these mitochondrial markers, three nuclear and one mitochondrial primer sets were examined: elongation factor 1-α (EF1-For3 and EF1-Cho10; Danforth & Ji, 1998), long-wavelength opsin (LWRhF and LWRhR; Mardulyn & Cameron, 1999), NADH dehydroxygenase subunit 5 (F6999 or F7081, and R7495; Yoshizawa, 2004), and LepWG1 and LepWG2a (Brower & DeSalle, 1998). None of these primer sets produced any products visible on ethidium bromide gels. The PCRs using nuclear primer sets were performed in standard, touch-down (Don *et al.*, 1991) and touch-up (Meusnier *et al.*, 2008) mode for all primer sets, with no results. All further analyses were therefore limited to mitochondrial data.

Data treatment

DNA sequences were assembled in SEQMAN II (DNAStar, Inc., Madison, WI, USA) individually for each locus. The 12S and

Table 2. Taxa used in this study.

Taxon information				GenBank accession numbers		
Louse species	Host species	Flyway (location)	Voucher no.	COI	12S	16S
Ingroup						
Carduiceps (*Car.*) *fulvofasciatus*	*Xenus cinereus*	EAs (A)	858	KX865194	–	–
			860	KX865195	–	–
Car. meinertzhageni	*Calidris* (*Cal.*) *alpina alpina*	EAtl (S)	10-1	KX865170	KX865238	–
			19-1	KX865171	KX865239	KX865209
			19-2	KX865172	KX865240	KX865210
	Cal. alpina schinzii	EAtls (S)	224-1	KX865174	KX865245	KX865214
			224-2	KX865175	KX865246	KX865215
	Cal. alpina sakhalina	EAs (J)	775-1	KX865184	–	KX865265
			775-2	KX865185	–	–
Car. scalaris	*Cal. pugnax*	EAtl (S)	321-1	KX865176	–	–
			515-1	JN900135	–	KX865221
			515-2	KX865183	–	KX865222
Car. zonarius	*Cal. acuminata*	EAs (A)	954-1	KX865197	–	KX865228
			956c1	KX865198	–	–
	Cal. alba	EAs (A)	807-1	KX865187	–	–
			808	KX865188	–	–
	Cal. canutus canutus	EAtl (S)	287-1	JN900121	–	KX865217
	Cal. canutus rogersi	EAs (J)	796-1	KX865186	–	KX865223
		EAs (A)	824-1	KX865191	–	KX865226
			853-1	–	–	KX865227
	Cal. ferruginea	EAtl (S)	170	JN900108	KX865242	–
		EAs (A)	845-1	KX865193	–	–
	Cal. mauri	PA (C)	1480-1	KX865199	KX865255	KX865229
			1486	KX865201	KX865257	KX865231
			1502	KX865203	KX865260	KX865234
			1508	KX865204	KX865261	KX865235
	Cal. minuta	EAtl (S)	345-1	–	KX865248	–
	Cal. minutilla	PA (C)	1482	KX865200	KX865256	KX865230
			1493	–	KX865258	KX865232
			1495	KX865202	KX865259	KX865233
			1539	KX865205	KX865262	KX865236
	Cal. pusilla	PA (C)	1546	KX865206	KX865263	–
			1561	KX865207	KX865264	–
			1607	KX865208	–	KX865237
	Cal. ruficollis	EAs (A)	816-1	KX865189	–	KX865224
			817-1	KX865190	–	KX865225
			843-1	KX865192	–	–
Carduiceps sp.[a]	*Lymnocryptes minimus*	EAtl (S)	395a1	KX865180	–	–
Other Esthiopteridae *sensu* Eichler (1963)						
Anaticola crassicornis	*Anas strepera*	–	493	KX865182	KX865254	KX865220
Anaticola rheinwaldi	*Branta bernicla*	–	464	JN900116	KX865252	KX865219
Anatoecus sp.	*Branta bernicla*	–	462	JN900117	KX865251	KX865218
Aquanirmus rollandii	*Rollandia rollandi*	–	–	DQ314505	–	–
Aquanirmus sp.	*Poliocephalus poliocephalus*	–	–	AY314808	AY139889	–
Aquanirmus sp.	*Tachybaptus novaehollandiae*	–	950a	KX865196	–	–
Ardeicola ardeae	*Ardea cinerea*	–	–	AF545677	–	–
Ardeicola geronticorum	*Geronticus calvus*	–	–	AF396545	AF396486	–
Columbicola columbae	*Columba livia*	–	141	KX865173	–	–
Columbicola bacillus	*Streptopelia decocto*	–	375a1	KX865179	KX865250	–
Craspedonirmus immer	*Gavia immer*	–	–	AY314810	AY314852	–
Fulicoffula heliornis	*Heliornis fulica*	–	–	AF545701	–	–
Fulicoffula longipila	*Fulica americana*	–	–	AF380005	–	–
Ibidoecus bisignatus	*Plegadis chihi*	–	–	AY314817	–	–
Outgroups						
Degeeriella fulva	*Buteo lagopus*	–	471	KX865181	KX865253	–
Degeeriella nisus	*Accipiter nisus*	–	350	KX865178	KX865249	–

Table 2. Continued

Taxon information				GenBank accession numbers		
Louse species	Host species	Flyway (location)	Voucher no.	COI	12S	16S
Quadraceps auratus	*Haematopus ostralegus*	–	276	JN900109	KX865247	KX865216
Quadraceps obtusus	*Tringa totanus*	EAtl (S)	69	JN900087	KX865241	KX865211
Rhynonirmus scolopacis	*Gallinago gallinago*	EAtl (S)	334	KX865177	–	–
Saemundsosnia lockleyi	*Sterna paradisaea*	EAtl (S)	215	JN900114	KX865243	KX865212
Saemundssonia sternae	*Sterna hirundo*	EAtl (S)	216	JN900113	KX865244	KX865213

[a]This specimen could not be reliably identified to any species morphologically.
Flyway abbreviations: EAs, East Asian/Australasian; EAtl, East Atlantic; PA, Pacific Americas. Species not following these flyways have been denoted with a '–'. Location abbreviations: A, Australia; C, Canada; J, Japan; S, Sweden. COI, cytochrome *c* oxidase subunit I. 12S sequences for *Degeeriella* spp. were considerably longer than all others and were truncated in both ends to the same lengths as the other aligned sequences. However, full *Degeeriella* 12S sequences were submitted to GenBank. All voucher specimens were deposited at the Price Institute for Parasitological Research (PIPeR), University of Utah, except for the Japanese vouchers, which are deposited at the Yamashina Institute for Ornithology (Chiba, Japan). Voucher numbers for slides are the same as sample numbers. Missing data are denoted with a '–'. Sample identifiers correspond to the same numbers in the figures. The single sample from *Lymnocryptes minimus* is not morphologically identifiable to species level.

16S sequences were aligned by CLUSTALW as implemented in GENEIOUS (Biomatters Ltd, Auckland, New Zealand), followed by manual adjustment to ensure that similar sequences in difficult sections were aligned with each other. The COI sequences were aligned in MEGALIGN (DNA Star, Inc.) and manually inspected and adjusted in SE-AL (http://tree.bio.ed.ac.uk/software/seal/). As useful sequences were obtained for fewer specimens using the 12S and 16S primer sets, these datasets are smaller than the COI dataset. For the combined dataset, a single louse individual from each host species was selected and its individual sequences for the three loci were concatenated in PAUP* (Swofford, 2002). For all host species occurring along more than one flyway, we included one louse individual from each flyway, if possible. Uncorrected p-distances were calculated in PAUP* (Swofford, 2002) for the COI dataset separately in order to compare with previous studies.

Data were phylogenetically analysed using Bayesian inference (BI). The choice of model for the partitions in BI was determined based on the Akaike information criterion (Akaike, 1973) calculated in MRMODELTEST 2 (Nylander, 2004). In COI, first, second and third positions were modelled separately.

Gene trees were estimated by BI using MRBAYES 3.1.2 (Huelsenbeck & Ronquist, 2001, 2005) according to the following: (i) all loci were analysed separately (single-locus analyses, SLAs); (ii) sequences were concatenated all loci together (multilocus analysis). In the multilocus analysis, the data were partitioned by locus and by codon position, using rate multipliers to allow different rates for the different partitions and codon positions (Ronquist & Huelsenbeck, 2003; Nylander *et al.*, 2004). Four Metropolis-coupled Markov chain Monte Carlo chains were run with incremental heating temperature 0.1 for 100×10^6 generations and sampled every 1000 generations, except the 12S dataset, which was run for 50×10^6 generations before convergence occurred. The first 10% of the generations were discarded as 'burn-in', well after the chain likelihood values had become stationary, and the posterior probability (PP) was estimated for the remaining generations. The model fit between an analysis with monophyly constrained to conform with the flyways within each species was compared with the unconstrained model by differences in log Bayes factors as implemented in TRACER v.1.6 (http://tree.bio.ed.ac.uk/software/tracer/).

Results

The alignment of the 12s and 16s sequences revealed some highly incompatible sections, which had to be readjusted manually. For all loci (COI, 12S, and 16S), PPs were calculated under the general time-reversible (GTR) model (Lanave *et al.*, 1984; Tavaré, 1986; Rodríguez *et al.*, 1990), assuming rate variation across sites according to an inverse gamma distribution with six rate categories for all models except COI third positions, in which a discrete gamma (G) distribution with six rate categories was assumed (Yang, 1994). Results of the BI analysis of the combined and COI datasets are shown in Figs 1 and 2, respectively. Results from the analyses of the smaller 12S and 16S datasets are shown in Figures S1 and S2, respectively. Uncorrected p-distances within the Esthiopteridae are shown in Table 3, and distances within *Carduiceps* are shown in Table 4. Uncorrected p-distances within each genus are similar to those reported from other groups (summarized in Gustafsson & Olsson, 2012a). Uncorrected p-distances within each *Carduiceps* species are between 0.0% and 1.2%, which is also similar to that observed in other louse genera (Gustafsson & Olsson, 2012a). The matrices used for this study can be found at http://purl.org/phylo/treebase/phylows/study/TB2:S20287.

Influence of flyways

All four included species of *Carduiceps* are monophyletic in all analyses, typically with high support (Figs 1, 2; Figures S1, S2). Moreover, none of the *Carduiceps* species samples from more than one host flyway unambiguously separated into distinct clades comprising the material from each flyway. Comparisons between unconstrained trees and trees constrained to conform to the flyways resulted in much lower log Bayes

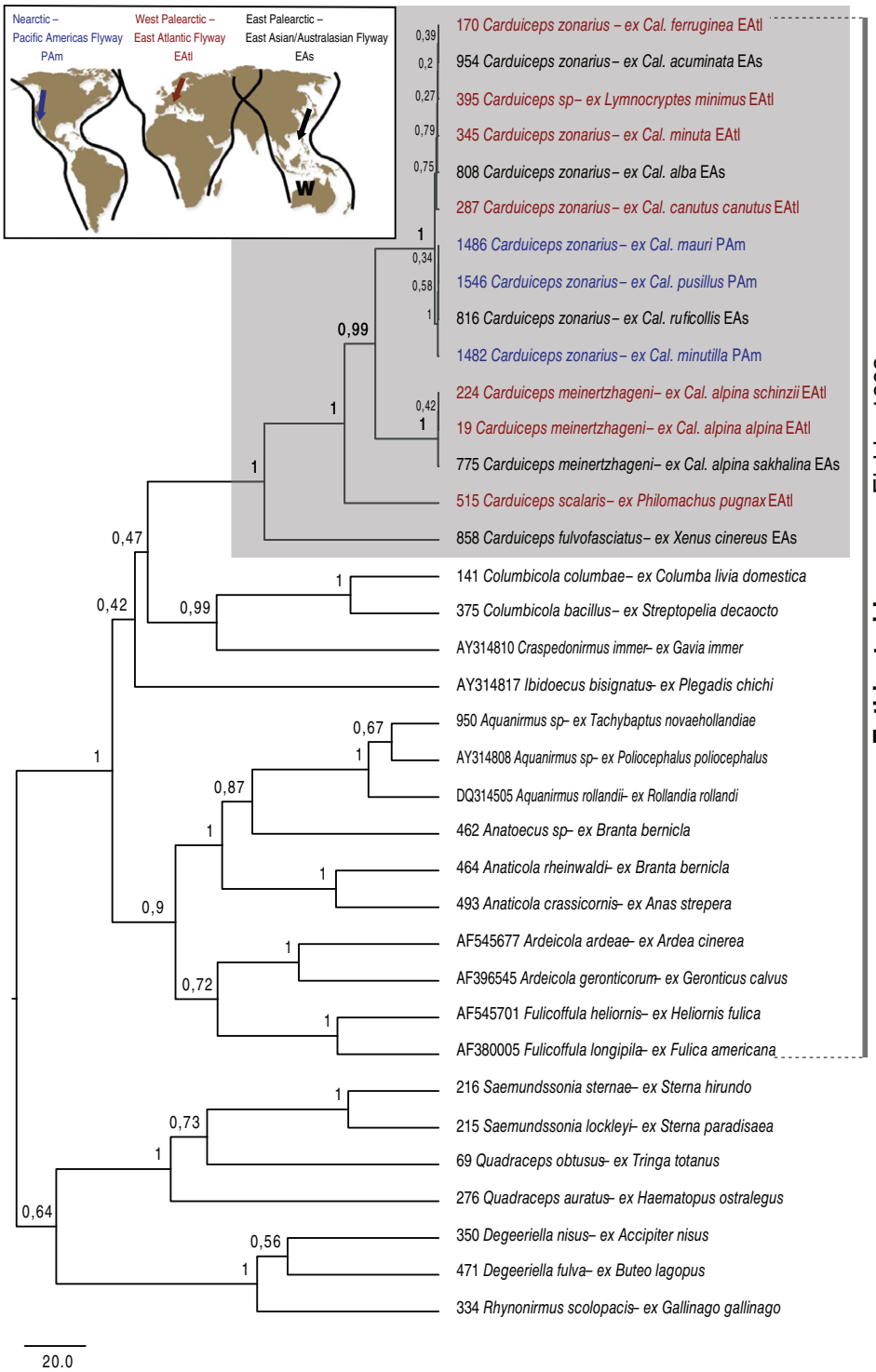

Fig. 1. Majority rule (50%) consensus tree of Esthiopteridae *sensu* Eichler (1963) based on the combined cytochrome *c* oxidase subunit I (COI), 12S and 16S dataset, inferred by Bayesian inference under the GTR + I + G model, except for third codon positions of COI, which used the GTR + G model. Posterior probabilities (≥ 50%) are indicated at the nodes. The specific identity of the host is given directly after the name of each individual louse sample. Numbers before names are sample identifiers (see Table 2). Abbreviations after taxon names correspond to flyway affiliation (PAm, Pacific Americas Flyway; EAtl, East Atlantic Flyway; EAs, East Asian/Australasian Flyway), as outlined in the inset, where arrows denote approximate collection localities for migrating birds, and 'W' approximate collection localities for wintering birds. [Colour figure can be viewed at wileyonlinelibrary.com].

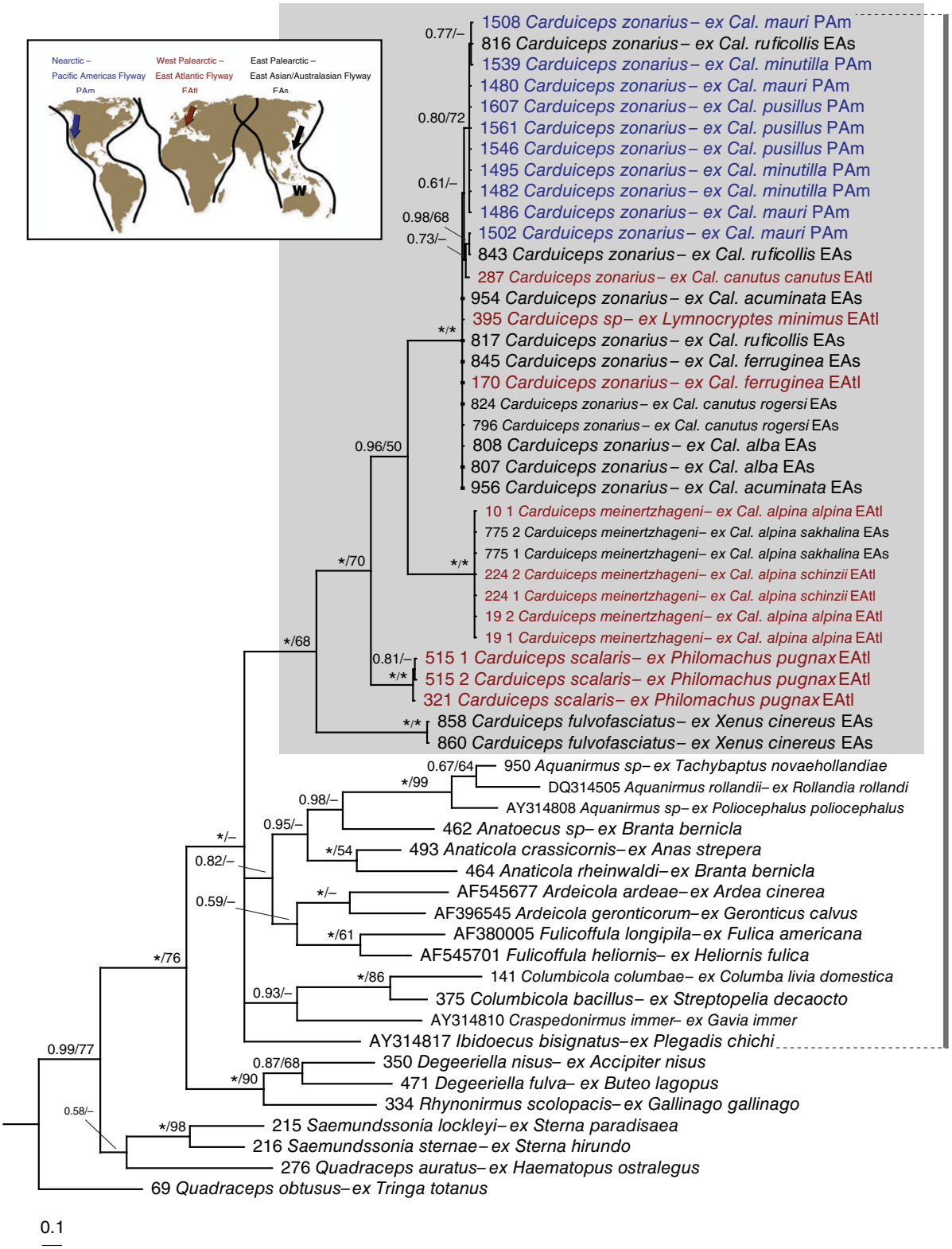

Fig. 2. Majority rule (50%) consensus tree of Esthiopteridae *sensu* Eichler (1963) based on mitochondrial cytochrome *c* oxidase subunit I (COI) sequences, inferred by Bayesian inference under the GTR + G + I model, except for third codon positions of COI, which used the GTR + G model. Posterior probabilities (≥ 50%) are indicated at the nodes. Numbers before names are sample identifiers (see Table 2). Flyway abbreviations at the end of terminals are: PAm, Pacific Americas; EAtl, East Atlantic; EAs, East Asian/Australasian. [Colour figure can be viewed at wileyonlinelibrary.com].

Table 3. Uncorrected p-distances for cytochrome *c* oxidase subunit I (COI) within Esthiopteridae.

	Ac	*Ae*	*Aq*	*Ar*	*Ca*	*Co*	*Cr*	*Fu*	*Ib*
Ac	19.0								
Ae	23.5	–							
Aq	23.9	23.4	14.4						
Ar	24.0	24.0	24.2	18.5					
Ca	25.3	27.0	28.6	25.4	10.7				
Co	26.3	27.6	29.1	26.9	28.4	19.5			
Cr	27.5	28.6	29.4	**30.3**	29.9	26.6	–		
Fu	23.7	22.4	25.6	22.9	25.6	29.0	25.8	17.8	
Ib	25.2	**22.2**	26.1	23.9	26.5	28.9	27.8	23.9	–

Ac, *Anaticola*; *Ae*, *Anatoecus*; *Aq*, *Aquanirmus*; *Ar*, *Ardeicola*; *Ca*, *Carduiceps*; *Co*, *Columbicola*; *Cr*, *Craspedonirmus*; *Fu*, *Fulicoffula*; *Ib*, *Ibidoecus*. All numbers are expressed as percentages, with dashes representing one-taxon clades within which no distances can be measured. Highest and lowest between-genus distances have been bolded.

Table 4. Uncorrected p-distances for the COI dataset within *Carduiceps.*

	C. fulvofaciatus	*C. meinertzhageni*	*C. scalaris*	*C. zonarius*
C. fulvofasciatus	0.5			
C. meinertzhageni	21.8	0.0		
C. scalaris	24.2	18.3	0.4	
C. zonarius	24.3	16.0	18.0	1.2

All numbers expressed as percentages.

factors for the unconstrained tree (AICM difference 1503.333). There is thus no clear support for either flyway homogenization or flyway differentiation in *Carduiceps*.

Significantly, *Car. zonarius* is monophyletic despite being sampled from a large number of hosts from different flyways, and the samples show low genetic variation (Table 4). *Carduiceps zonarius* contains some structure in most datasets; however, this structure is partially contradictory, often with short branch lengths and low support (e.g. Fig. 1). In the COI, 16S and combined datasets, there are tendencies for subdivisions of *Car. zonarius* between material from the Nearctic and the Palaearctic. However, the separation is not complete, as one Palaearctic individual (from *Cal. ruficollis*) is grouped with the Nearctic material, and one Nearctic individual (from *Cal. mauri*) is grouped with the Palaearctic material. The relationships amongst the four species of *Carduiceps* also vary between datasets, and may be heavily affected by missing data.

Eichler's (1963) Esthiopteridae

Our analyses generally result in a basal polytomy for Esthiopteridae (*sensu* Eichler, 1963) (e.g. Fig. 2), with little resolution apart from species in the same genera being grouped together. However, in all analyses, both *Carduiceps* and Esthiopteridae *sensu* Eichler (1963) are monophyletic with high PPs (PP = 1.00). *Carduiceps* is monophyletic with high support (PP = 1.00) in all analyses. The combined analysis (Fig. 1) retrieves monophyletic *Anaticola* (PP = 1.00), *Aquanirmus* (PP = 1.00), *Ardeicola* (PP = 1.00) and *Columbicola* (PP = 1.00). The two duck louse genera, *Anatoecus* and *Anaticola*, are grouped together with the grebe louse genus *Aquanirmus* in all datasets where all three genera were represented (PP = 1.00 in the combined and 12S datasets, but PP = 0.95 in the COI dataset).

The 12S dataset suggests that *Columbicola* and *Craspedonirmus* may be the closest relatives of *Carduiceps* (PP = 0.97); however, this relationship is not recovered with any support in any of the other datasets. One species of *Craspedonirmus* is known from shorebirds, whereas *Columbicola* is specific to pigeons and doves (Price *et al.*, 2003). While there is morphological support for a relationship between these three genera (see Discussion), the lack of support for this group in the concatenated dataset (PP = 0.47) and the COI dataset (in unresolved polytomy) indicates that the relationship may be spurious. Notably, *Craspedonirmus* and *Columbicola* were also placed together in the COI dataset (PP = 0.93).

Discussion

Taxonomic and systematic issues within Carduiceps

The phylogeny reconstructed for *Carduiceps* based on three mitochondrial genes corresponds perfectly with the current taxonomy of the genus (Timmermann, 1954; Table 5), and no changes in the taxonomy of *Carduiceps* are implied by this study. As several of the *Carduiceps* species treated by Timmermann (1954) were not included in these analyses, his division of the genus into three species groups cannot be tested presently. The four included species of *Carduiceps* are all reciprocally monophyletic (Figs 1, 2; Figures S1, S2), but apart from the placement of *Car. fulvofasciatus* as sister to the three other species, there is no supported structure among *Carduiceps* in the combined dataset (Fig. 1). Many of the samples included here were only successfully sequenced for one or two of the three genes. This has probably affected the resolution of the trees, especially the 12S and 16S datasets, which contain the least amount of specimens.

Influence of flyways on host distribution of Carduiceps

We recovered no support for either flyway homogenization or flyway differentiation in *Carduiceps*. *Carduiceps scalaris* and *Car. fulvofasciatus* are both restricted to a single host species, and do not occur on other hosts species samples in the same localities at the same time (data not shown). *Xenus cinereus*, the host of *Car. fulvofasciatus*, also occur salong the West Palearctic flyway, but no samples were obtained from this host population, and its potential division into populations following different flyways could therefore not be tested.

Carduiceps meinertzhageni was sampled from three morphologically distinct host subspecies that migrate along two different flyways (Wenink *et al.*, 1996; Message & Taylor, 2005; but see Marthinsen *et al.*, 2007). Despite this broad sampling range,

Table 5. Taxonomy and host relationships of *Carduiceps.*

Louse name	Host name	Common name
Carduiceps cingulatus (Denny, 1842)	*Limnodromus griseus* (Gmelin, 1789)	Short-billed Dowitcher
	Limnodromus scolopaceus (Say, 1822)	Long-billed Dowitcher
	Limosa limosa (Linnaeus, 1758)	Black-tailed Godwit
Carduiceps clayae Timmermann, 1954	*Limosa fedoa* (Linnaeus, 1758)	Marbled Godwit
Carduiceps fulvofasciatus (Grube, 1851)	*Xenus cinereus* (Güldenstädt, 1775)	Terek Sandpiper
Carduiceps lapponicus Emerson, 1953	*Limosa lapponica* (Linnaeus, 1758)	Bar-tailed Godwit
Carduiceps meinertzhageni Timmermann, 1954	*Calidris alpina alpina* (Linnaeus, 1758)	Dunlin
	Calidris alpina sakhalina (Vieillot, 1816)*	Dunlin
	Calidris alpina schinzii (Brehm & Schilling, 1822)*	Dunlin
	Calidris maritima (Brünnich, 1764)	Purple Sandpiper
	Calidris ptilocnemis (Coues, 1873)	Rock Sandpiper
Carduiceps scalaris (Piaget, 1880)	*Calidris pugnax* (Linnaeus, 1758)	Ruff
Carduiceps subscalaris (Piaget, 1880)	*Phalaropus lobatus* (Linnaeus, 1758)	Red-necked Phalarope
Carduiceps zonarius (Nitzsch [in Giebel], 1866)	*Calidris acuminata* (Horsfield, 1821)	Sharp-tailed Sandpiper
	Calidris alba (Pallas, 1764)	Sanderling
	Calidris bairdii (Coues, 1861)	Baird's Sandpiper
	Calidris canutus canutus (Linnaeus, 1758)	Red Knot
	Calidris canutus rogersi (Mathews, 1913)*	Red Knot
	Calidris ferruginea (Pontoppidan, 1763)	Curlew Sandpiper
	Calidris fuscicollis (Vieillot, 1819)	White-rumped Sandpiper
	Calidris mauri (Cabanis, 1857)	Western Sandpiper
	Calidris himantopus (Bonaparte, 1826)	Stilt Sandpiper
	Calidris melanotos (Vieillot, 1819)	Pectoral Sandpiper
	Calidris minuta (Leisler, 1812)	Little Stint
	Calidris minutilla (Vieillot, 1819)	Least Sandpiper
	Calidris pusilla (Linnaeus, 1766)	Semipalmated Sandpiper
	Calidris pygmaeus (Linnaeus, 1758)	Spoon-billed Sandpiper
	Calidris ruficollis (Pallas, 1776)	Red-necked Stint
	Calidris subminuta (Middendorff, 1853)	Long-toed Stint
	Calidris subruficollis (Vieillot, 1819)	Buff-breasted Sandpiper
	Calidris temminckii (Leisler, 1812)	Temminck's Sandpiper
	Lymnocryptes minimus (Brünnich, 1764)*	Jack Snipe

Taxa marked with an asterisk (*) are a new host record in this paper. All other host relationships follow Price *et al.* (2003).

the sequences from these lice are genetically identical (Table 4), and there is no division between louse populations sampled from the different flyways. Moreover, we have found no specimens of *Car. meinertzhageni* on other host species sampled at the same localities at the same time (data not shown).

The homogeneity of the *Car. meinertzhageni* material across host subspecies may be an effect of recent divergence in these host subspecies (Wenink *et al.*, 1996), with differentiation in *Carduiceps* being slower than in their hosts. This is surprising, as base substitution rates are generally much faster in lice than in their host animals (Johnson *et al.*, 2003a). Alternatively, as different host subspecies may be found in the same flocks during migration and wintering (e.g. Wenink & Baker, 1996), the occurrence of the same *Carduiceps* haplotype on birds sampled from different subspecies may indicate that the lice are capable of dispersal to other subspecies of *Cal. alpina*, but not to other *Calidris* species. No American populations of *Cal. alpina* were sampled, so it is impossible to tell whether there is a split between Old and New World populations of *Car. meinertzhageni*. In addition, two recorded hosts of *Car. meinertzhageni* (Price *et al.*, 2003) with more limited distributions (Message & Taylor, 2005), *Cal. maritima* and *Cal. ptilocnemis*, were not sampled. Johnson *et al.* (2003b) suggested that a very small amount of gene flow, even through an intermediary host, may be enough for speciation to fail even in allopatric species. Small numbers of sandpipers from one flyway regularly visit other flyways, which could potentially be sufficient to stifle speciation. In either case, among the host species studied, dispersing individuals of *Car. meinertzhageni* only seem to have become successfully established on *Cal. alpina*.

In the *Car. zonarius* material there seems to be a slight difference between haplotypes collected from the Pacific Americas flyway and those collected from the two Palaearctic flyways. However, there is no support for a geographic divergence in the phylogenetic analyses, and the genetic distances within this species are comparable to those of the other three *Carduiceps* species, and similar to those reported for other chewing lice (Gustafsson & Olsson 2012a). In two cases, *Carduiceps zonarius* was sampled from the same host species along different flyways (*Cal. canutus* and *Cal. ferruginea*). These samples show no evidence of flyway differentiation between the different flyways. In *Car. zonarius*, the capacity for establishment on different host species seems to be higher than in *Car. meinertzhageni*, but intense sampling efforts have not recovered *Car. zonarius* on

any of the hosts of *Car. fulvofasciatus*, *Car. meinertzhageni* or *Car. scalaris* (data not shown).

Both *Car. meinertzhageni* and *Car. zonarius* thus exhibit host distribution patterns that are structured more by host species than by host biogeography. Palaeoflyways (Kraaijeveld & Nieboer, 2000; Buehler *et al.*, 2006) could perhaps explain some of the patterns, as the present distribution of *Carduiceps* on the calidrines may have been established before or during the last ice age when the hosts may have followed different flyways than they presently do.

Possible limitations for host range in Carduiceps

As the hosts of all four species of *Carduiceps* often occur in mixed flocks in wintering sites, it is difficult to explain why each host species is only parasitized by a single species of *Carduiceps*, and why *Car. zonarius* has not been found on the hosts of the other species of *Carduiceps*. The known hosts of *Car. meinertzhageni* form a monophyletic clade within the sandpipers, but the hosts of *Car. zonarius* do not (Gibson & Baker, 2012).

There is some evidence that wing lice generally cannot successfully colonize new hosts that are much larger or smaller (Tompkins *et al.*, 1999; Johnson *et al.*, 2005; Bush & Clayton, 2006). Whether this is generally true for generalist lice, such as *Carduiceps*, is unknown. The size range of the hosts of *Carduiceps* is large, but *Car. zonarius* occurs on both the smallest sampled hosts (*Cal. ruficollis* and *Cal. minutilla*) and the largest sampled hosts (*Cal. canutus*). *Calidris alpina*, the host of *Car. meinertzhageni*, falls in between these extremes and is similar in size to several of the hosts of *Car. zonarius* (Message & Taylor, 2005). Host size alone may therefore not be a factor in the host distribution of *Carduiceps* lice.

An alternative explanation may be host pigmentation differences (Bush *et al.*, 2010). All the hosts of *Car. meinertzhageni* (including unsampled hosts; Price *et al.*, 2003) are either black-bellied or have mainly dark-grey feathers in at least one plumage (Message & Taylor, 2005), whereas the hosts of *Car. zonarius* are generally white-bellied in all plumages. Lice of the genus *Machaerilaemus* have been found to prefer white parts of feathers over black parts (Kose & Møller, 1999; Kose *et al.*, 1999), suggesting that melanin in bird feathers may deter lice. If *Car. meinertzhageni* has a greater ability to digest melanin, this could give it an advantage over host-switching *Car. zonarius*, and could explain why *Car. meinertzhageni* occurs only on black-bellied or dark-grey hosts. However, *Cal. tenuirostris* is densely black-spotted, but is nevertheless parasitized by *Car. zonarius*. Moreover, all three hosts of *Car. meinertzhageni* also have areas of white body feathers. Bush *et al*. (2006) found no correlation between the amount of melanin in feathers and the abundance of pigeon lice (*Columbicola* and *Campanulotes*), suggesting that the distribution of *Car. meinertzhageni* on black-bellied or dark-grey hosts may be unrelated to host pigmentation patterns.

The most curious aspect of *Carduiceps* distribution lies in comparison with the *Lunaceps* wing lice of the same hosts. In pigeons and doves, wing lice are less species-specific and less geographically structured than body lice (Johnson *et al.*, 2002a; Clayton & Johnson, 2003), which could be related to the greater ability of wing lice to disperse by phoresy on hippoboscid flies (Keirans, 1975; Harbison *et al.*, 2008, 2009; Bartlow *et al.*, 2016). Similar patterns were found in seabird lice (Page *et al.*, 2004). Even in the absence of a host biogeographic structuring according to host flyways, *Carduiceps* would therefore still be expected to be more species-specific than *Lunaceps*. No cases of phoresy involving shorebird lice are known (Keirans, 1975; Bartlow *et al.*, 2016), but *Lunaceps* wing lice would be better placed on its host, topologically, to take advantage of opportunities for spread to new hosts than *Carduiceps* body lice, even in the absence of phoresy. Despite this, *Carduiceps* is both much less geographically structured and less host-specific than *Lunaceps* (Gustafsson & Olsson, 2012a). This implies that some other set of dispersal mechanisms may be available to shorebird lice than to pigeon lice. Continued studies on shorebird louse genera such as *Saemundssonia* and *Quadraceps* may be most instructive in this regard.

Esthiopteridae sensu *Eichler, 1963*

While neither Cruickshank *et al*. (2001) nor Johnson *et al*. (2006) recovered monophyly of the Esthiopteridae, it is suggested to be monophyletic in all of our datasets (PP = 1.00; Figs 1, 2; Figures S1, S2). However, relationships within Esthiopteridae remain obscure, and relationships above the genus level generally have no support in either of our analyses. As only a few species each of the proposed esthiopterids genera were included, few conclusions can be drawn.

Aquanirmus has been grouped quite consistently with the duck lice *Anaticola* and *Anatoecus* in previous molecular studies (Cruickshank *et al.*, 2001; Johnson *et al.*, 2006), but with *Ibidoecus* in morphological studies (Smith, 2001). In this study, *Aquanirmus* groups with the duck lice *Anaticola* and *Anatoecus* in all datasets where all three genera are included.

Ardeicola has a chequered history of having been grouped with the duck lice (Johnson *et al.*, 2003a), the *Philoceanus* complex (Smith, 2001), *Mulcticola* (placed in Rallicolidae by Eichler, 1963; Cruickshank *et al.*, 2001) or even the Amblycera (Cruickshank *et al.*, 2001). In the most inclusive dataset (morphology + genetic data) of Smith *et al.* (2004), *Ardeicola* appears to have no close relatives, but when molecular data are considered alone, they either group with *Falcolipeurus* (parsimony), with the mammal lice (likelihood), or are placed as sister to most of the other genera (Bayesian). This study does not resolve the relationships of *Ardeicola*, except that all datasets where this genus is represented place it inside Esthiopteridae. This placement may be supported by morphology, as aspects of the preantennal area and the male genitalia are similar to those seen in other genera Eichler (1963) placed in Esthiopteridae, but this family has never been satisfactorily circumscribed morphologically.

Columbicola has been separated from other esthiopterids in many previous studies (Cruickshank *et al.*, 2001; Smith, 2001; Johnson *et al.*, 2003a; Smith *et al.*, 2004), but has been placed as sister to *Craspedonirmus* (Smith *et al.*, 2004,

fig. 6a, b) and close to *Fulicoffula* (Johnson & Whiting, 2002) or *Anatoecus* + *Neophilopterus* + *Fulicoffula* + *Cirrophthirius* [the latter placed in Rallicolidae by Eichler (1963)] (Barker *et al.*, 2003). None of these studies have included any *Carduiceps*, and the sister-group relationship between *Columbicola* and *Craspedonirmus* suggested in the combined dataset, and the close relationship between these two and *Carduiceps* suggested by the 12S dataset are novel. *Columbicola* is restricted to pigeons and doves, *Craspedonirmus* to loons and auks, and *Carduiceps* to sandpipers and allies. These host groups do not form a monophyletic group together (e.g. Hackett *et al.*, 2008), suggesting that these relationships are either spurious or not explainable through a simple application of Fahrenholz's rule (i.e. that louse relationships should mirror host relationships; Klassen, 1982).

Carduiceps, *Craspedonirmus* and *Columbicola* are not very similar in gross morphology. However, all three genera share at least two morphological characters: the presence of an arched, transversally continuous preantennal carina arising at the preantennal nodi and the presence of a transversally continuous dorsal postantennal suture immediately posterior to this carina. In all three genera, the suture is extended posteriorly across at least part of each temple, and the *post-nodal seta* (sensu Clay, 1951) and *sensilla 2–3* (sensu Valim & Silveira, 2014) are generally associated with this suture. This head structure is, to our knowledge, not known from any other genus of ischnoceran lice. However, a similar, medianly interrupted carina is found in some members of the *Quadraceps* complex (e.g. *Quadraceps semifissa*; see Timmermann, 1953).

Leaving aside *Columbicola* and *Craspedonirmus*, *Carduiceps* appears to have no close relatives and is not related to any other louse genus on the shorebirds (D. Gustafsson, unpublished data), but seems to represent a separate, very localized, colonization of the Scolopacidae. However, the louse genera included in this study were selected based on their placement in Esthiopteridae by Eichler (1963), and close relatives of *Carduiceps* outside this group may well have been overlooked in the process of outgroup selection.

In short, the relationships within Eichler's (1963) Esthiopteridae are in need of further clarification, requiring greater sampling of genera other than *Columbicola* and *Carduiceps*, and the use of additional unlinked molecular markers, particularly nuclear markers, as well as a morphological revision. In addition, several of the genera included here were represented only in the COI analysis, as data were not available for the other two markers used. Suitable sister groups should also be identified and sampled, to test the phylogenetic position and possible sister-group relationship of *Carduiceps* and *Columbicola* + *Craspedonirmus*. If this sister-group relationship is found to be an artifact of sampling or analysis, on present knowledge this leaves *Carduiceps* with no known close relatives.

Summary

There is no evidence of either flyway homogenization or flyway differentiation in *Carduiceps*. Two host species were sampled from more than one flyway, and in both cases there were no significant differences between louse material from different flyways. The large host range of *Car. zonarius* may be the result of flyway homogenization in the past, but if so, this homogenization is incomplete, as the hosts of the other three *Carduiceps* species sampled migrate along the same flyways and winter in the same areas. Possibly, other features of the hosts' ecology, such as plumage patterns, may explain the structuring of *Carduiceps*.

Eichler's (1963) proposed Esthiopteridae may be monophyletic, as indicated by high Bayesian support across all datasets. However, resolution within this group is poor. One reason may be that appropriate outgroups or sister groups may be lacking, as the phylogeny of lice is incompletely known. Another reason may be that the absence of nuclear markers in this analysis, as well as the few available sequences for most of the genera in this group limit our present understanding of the evolution of this group. In the analysis of the 12S dataset, the dove louse genus *Columbicola* and the loon and auk louse genus *Craspedonirmus* are suggested as the closest relatives to *Carduiceps*. This relationship does not receive any support in the combined analysis, and may be spurious. Nevertheless, the genus *Columbicola* is a widely used model group for many aspects of louse and parasite evolution, and this novel relationship with *Craspedonirmus* and *Carduiceps* requires further study.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: 10.1111/syen.12227

Figure S1. Majority rule (50%) consensus tree of Esthiopteridae *sensu* Eichler (1963) based on mitochondrial 12S sequences, inferred by Bayesian inference under the GTR+G+I model. Posterior probabilities are indicated at the nodes. Numbers before names are sample identifiers (see Table 2).

Figure S2. Majority rule (50%) consensus tree of Esthiopteridae *sensu* Eichler (1963) based on mitochondrial 16S sequences, inferred by Bayesian inference under the GTR + G + I model. Posterior probabilities are indicated at the nodes. Numbers before names are sample identifiers (see Table 2).

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