



Flyway homogenisation or differentiation? Insights from the phylogeny of the sandpiper (Charadriiformes: Scolopacidae: Calidrinae) wing louse genus *Lunaceps* (Phthiraptera: Ischnocera) ☆

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ABSTRACT

The wing louse genus *Lunaceps*, is the most speciose chewing louse (Phthiraptera) genus inhabiting sandpipers (Charadriiformes: Calidrinae) and is known from almost all sandpiper species. The hosts follow specific flyways from the Arctic breeding grounds to wintering locations in the southern hemisphere, and often form large mixed-species flocks during migration and wintering. We estimated a phylogeny of *Lunaceps* based on three mitochondrial loci, supporting monophyly of the genus but revealing extensive paraphyly at the species level. We also evaluated the relative importance of flyway differentiation (same host species having different lice along different flyways) and flyway homogenisation (different host species having the same lice along the same flyway). We found that while the lice of smaller sandpipers and stints show some evidence of flyway homogenisation, those of larger sandpipers do not. No investigated host species migrating along more than one flyway showed any evidence of flyway differentiation. The host–parasite associations within *Lunaceps* are in no case monophyletic, rejecting strict cospeciation.

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1. Introduction

The Scolopacidae (sandpipers, snipes, curlews and allies; Charadriiformes) are hosts to a diverse louse fauna with several small, but morphologically distinct, genera that are typically found parasitising several host genera (Price et al., 2003). However, there is little correspondence between louse distribution and host phylogeny, and none of these louse genera are limited to a monophyletic group of hosts (e.g., Thomas et al., 2004a; Gibson, 2010). Phylogenetic relationships among the Scolopaci (Aves: Charadriiformes): implications for the study of behavioural evolution (M.Sc. Thesis, Department of Ecology and Evolutionary Biology, University of Toronto; (hereafter: Gibson, 2010)). A good example of this is *Lunaceps*, the most speciose and most widely spread (31 hosts in 12 genera; Price et al., 2003) of the Scolopacidae-specific louse genera. This genus preferentially occurs on the flight feathers and is characterised by certain head and genital characters (Clay and Meinertzhagen, 1939) as well as the long and slender body typical of wing lice (Clay, 1949). The 15 species (Price et al., 2003) have variously been lumped together in a few taxa with wide host distributions (e.g., Waterston, 1915; Emerson, 1972) or

divided into several more host-specific species (e.g., Timmermann, 1954; Price et al., 2003). They mainly parasitise the sandpipers and stints (Calidrinae), but can also be found on all species of curlews (*Numenius*) and godwits (*Limosa*). Here we focus on those species living on the Calidrinae.

The Calidrinae hosts of *Lunaceps* form a monophyletic group within the Scolopacidae. However, until recently no comprehensive and stable phylogeny for this group has been available and many genera have been erected based on single aberrant taxa (e.g., *Philomachus*, *Eurynorhynchus*). Gibson (2010) constructed the first complete phylogeny of the subfamily and clarified most of the relations within it but no formal revision has been made. The other two host groups of *Lunaceps* (*Limosa* and *Numenius*) are not closely related to the Calidrinae (Thomas et al., 2004a; Gibson, 2010). Close relatives of the Calidrinae that are not hosts to *Lunaceps* include the turnstones (*Arenaria*), the shanks (*Tringa* and allies) and the phalaropes (*Phalaropus*) (Gibson, 2010), all of which are instead hosts to the genus *Quadraceps*, a widely spread louse genus on shorebirds (Price et al., 2003). Both of these genera, as well as several of the other Scolopacidae-specific lice and the shorebird head louse genus *Saemundssonina*, were placed in the subfamily Quadraceptinae by Eichler (1963).

Ischnoceran lice have no free-living stage and normally require that two host individuals come into direct contact to disperse. The traditional view of chewing louse evolution has been that dispersal to new hosts typically occurs either during mating (horizontal

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transmission; Hillgarth, 1996) or in the nest (vertical transmission; Clayton and Tompkins, 1994), leading to cospeciation with their hosts (“Fahrenholz’ rule”; Eichler, 1942; Klassen, 1992). However, over recent years it has become increasingly evident that while such mechanisms could explain the distribution and phylogeny of some groups of lice (Paterson et al., 2000; Page et al., 2004; Hughes et al., 2007), other distribution patterns can only be explained by more complex sets of mechanisms (Johnson et al., 2002a,b; Weckstein, 2004). In many cases, host ecology and behaviour have been invoked, such as shared nest holes (Johnson et al., 2002a; Weckstein, 2004), mass feeding aggregations (Brooke and Nakamura, 1998), dust baths (Hoyle, 1938; Clay, 1949) and shared nesting islands (Banks et al., 2006). Scenarios such as these may provide the most important circumstances facilitating lateral dispersal in cases where a group of lice parasitises more than one host order (Johnson et al., 2011).

Most sandpipers follow population-specific flyways (Fig. 1) from the breeding grounds in the Arctic or Subarctic to wintering grounds in the tropics (e.g., Wilson and Barter, 1998; Message and Taylor, 2005; Tjørve and Tjørve, 2007; Lopes et al., 2008), and often form large mixed-species flocks on stop-over and wintering sites, in contrast to the often low densities on breeding

grounds. The structuring of the host populations by different flyways, and their multiple-species flock during migration and wintering could have two important consequences for the louse populations. First, a low migration rate from one flyway to another could lead to the louse populations along each flyway being effectively isolated from each other, resulting in local speciation on the same host species, a situation we here term “flyway differentiation”. Secondly, if communal roosts and the tendency to form large flocks during migration provide sufficient opportunity for lateral transmission to new host species, this could lead to the louse populations being structured geographically, rather than mirroring the host phylogeny. Different host species following the same flyway and using the same stop-over and wintering grounds could come to have the same species of lice, regardless of the phylogenetic relationships of the host species involved. This pattern is here termed “flyway homogenisation” and is essentially the opposite of “Fahrenholz’ rule” in that the phylogenetic patterns of the hosts have little or no influence on the phylogenetic patterns of their lice, with the latter dictated instead by the biogeography of the hosts.

Over time, both processes may influence the louse populations, leading to a situation where a host species along one flyway have the same lice as all other potential host species along that flyway,

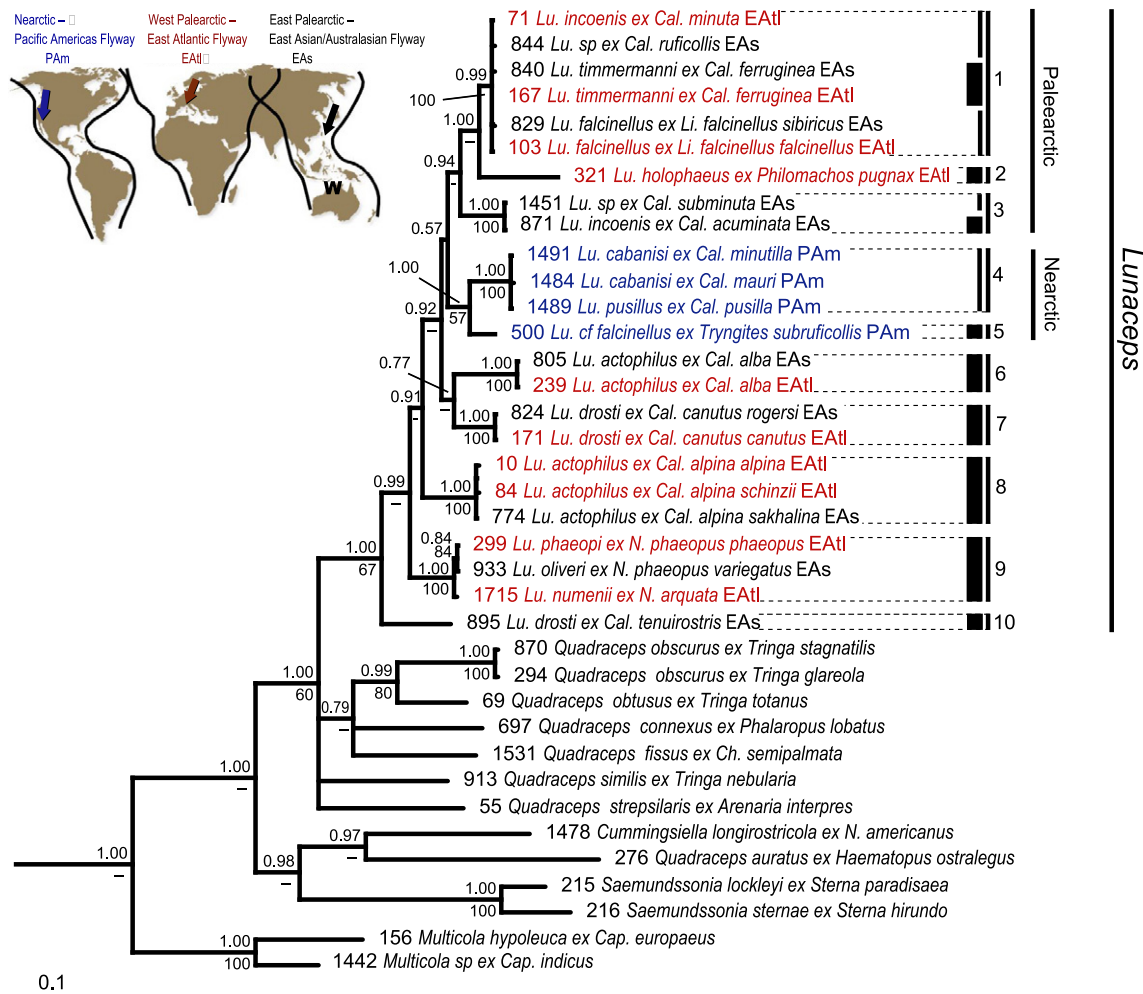


Fig. 1. Majority rule (50%) consensus tree of Quadrateptinae sensu Eichler, 1963. This clade was pruned from a larger phylogeny based on mitochondrial CO1, 12S and 16S sequences, inferred by Bayesian inference under the GTR+G+I model. Posterior probabilities ($\geq 50\%$) are indicated above the nodes and parsimony bootstrap values ($\geq 50\%$) below the nodes. Numbered bars delimit clades discussed in Sections 3 and 4. 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 1). The approximate size of the host is denoted by the narrow (“small sandpipers” and stints, generally smaller than 180 mm) and broad (“large sandpipers”, generally larger than 180 mm) bars (measurements from Message and Taylor, 2005). Abbreviations after taxon names correspond to flyway affiliation (PAm = Pacific American 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.

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