UNIVERSITAT DE BARCELONA

Diversity, ecology and evolution of feather mites in seabirds

Diversidad, ecología y evolución de los ácaros de las plumas en aves marinas

Laura Mihaela Stefan

DOCTORAL THESIS
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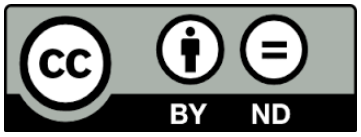

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Evolutiva, Ecología i Ciències Ambientals
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DIVERSIDAD, ECOLOGÍA Y EVOLUCIÓN DE LOS ÁCAROS DE LAS PLUMAS EN AVES MARINAS

Memoria presentada por:
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para optar al grado de Doctora por la Universidad de Barcelona

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“So many mites, so little time”
Barry OConnor

A mi familia,

A Pap,

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CONTENTS

RESUMEN

Los ácaros de las plumas (Astigmata: Analgoidea y Pterolichoidea) son unos de los ectosimbiontes más abundantes y comunes encontrados en aves. Viven de forma permanente en el cuerpo del huésped, están adaptados para ocupar microhabitats bien definidos del huésped y se encuentran en casi todos los grupos de aves. Aunque los ácaros de las plumas han sido ampliamente estudiados a nivel taxonómico, mucha diversidad permanece sin ser descrita y todavía hay muchas preguntas abiertas sobre la biología, ecología y evolución de estos ectosimbiontes. También hay un debate en curso sobre el tipo de simbiosis, es decir, si las interacciones entre las aves y los ácaros son de parasitismo, comensalismo o incluso mutualismo. Por lo tanto, un mejor conocimiento de las comunidades de los ácaros de las plumas en diferentes niveles de su organización biológica (es decir, entre individuos huésped, poblaciones huésped y especies huésped) puede contribuir a nuestra comprensión de la ecología evolutiva de las interacciones entre aves y ácaros, y de la evolución de la biodiversidad de los parásitos en general.

En este contexto, el objetivo principal de esta tesis ha sido investigar los factores evolutivos y ecológicos que influyen la diversidad y la estructura de la comunidad de los ácaros de las plumas en aves marinas (Procellariiformes y Phaethontiformes) del Océano Atlántico y el Mar Mediterráneo. Más específicamente, usando una aproximación de la comunidad de múltiples huéspedes y múltiples especies de ácaros, (1) cuantifiqué la diversidad morfológica y genética de los ácaros de las plumas dentro de diferentes especies y poblaciones de aves marinas; (2) evalué la importancia relativa de la estructura por huésped y estructura geográfica en la evolución y estructura de la población de los ácaros de las plumas en aves marinas; (3) investigué la distribución espacial y la estructura trófica dentro del huésped para identificar los mecanismos y factores inmediatos que modelan la estructura de la infra-comunidad de los simbiontes.

Sobre la diversidad de los ácaros de las plumas en aves marinas, en base a los criterios morfológicos, los resultados muestran que las especies de aves que crían en el Océano Atlántico Nordeste y el Mediterráneo albergan una fauna de ácaros diversa y única compuesta por 38 especies (33 especies en Procellariiformes; cinco especies en Phaenthontiformes) perteneciendo a 10 géneros y tres familias. Todas las especies de aves marinas tenían al menos tres especies de ácaros, mientras que la comunidad más rica estaba compuesta por nueve especies. Cada género de ave albergaba una comunidad distinta de ácaros y solo tres especies de ácaros fueron compartidos por dos géneros cercanos de pardelas. Diecisiete de las 33 especies de ácaros encontradas en Procellariiformes eran especies nuevas, no descritas; descripciones formales de seis especies están incluidas en esta tesis. En conjunto, los datos moleculares correlacionaron bien con las descripciones morfológicas, pero también revelaron la presencia de seis especies cripticas pertenecientes a cuatro géneros de ácaros.

En relación con los factores y procesos de diversificación, los patrones de la estructura genética de los ácaros fueron variables tanto entre los diferentes huéspedes simpátricos y entre la misma especie de huésped en diferentes regiones geográficas. Por lo tanto, la gran mayoría de las especies de ácaros de aves marinas simpátricas exhibió fuertes patrones de estructura genética asociados al huésped. Al comparar las comunidades de ácaros entre especies hermanas del mismo género de huésped, algunas especies de ácaros no estaban genéticamente estructuradas tanto entre huéspedes como entre localidades, mientras que otras especies presentaron un mayor grado de diversidad genética y diferenciación entre poblaciones. Estas diferencias observadas corresponden con el uso de microhabitats en el cuerpo del huésped. Aunque la especialización por huésped parece ser el principal factor de la diversificación de los ácaros, un cierto grado de mezcla entre especies cercanas de huéspedes se produce en caso de los ácaros más generalistas. Adicionalmente, no se encontró ninguna diferenciación genética entre las localidades para los ácaros, sugiriendo que la dispersión de los ácaros se produce regularmente entre las poblaciones de huéspedes.

En cuanto a la ecología y la estructura de la comunidad de los ácaros de las aves marinas, la distribución de dos especies abundantes de ácaros que coocurren en las plumas del vuelo de una sola especies de ave marina, *Calonectris borealis*, mostró una clara segregación espacial entre plumas; una especie prefirió las primarias

centrales, mientras que la otra fue restringida a las primarias más externas. Este patrón fue resultado de una combinación de adaptaciones específicas de hábitat y la competición en curso. Adicionalmente, los análisis isotópicos de la dieta de los ácaros indicaron que las dos especies de ácaros comparten los mismos recursos alimenticios provenientes del huésped, probablemente aceite de la glándula uropígeal complementado con material exógeno.

En conjunto, esta tesis destaca la gran y poco conocida diversidad de los ácaros de las plumas albergada por las aves marinas, proporciona una caracterización exhaustiva de los patrones de las asociaciones entre las aves marinas y los ácaros y contribuye a una mejor comprensión de los procesos ecológicos y evolutivos que conlleva dicha alta diversidad. Esta tesis muestra la importancia del papel esencial de la adaptación al microhábitat para la evolución de la biodiversidad de los ectosimbiontes, tanto por su impacto en la reducción de la competencia para recursos locales como por la probabilidad de dispersión a diferentes escalas espaciales.

ABSTRACT

Feather mites (Astigmata: Analgoidea and Pterolichoidea) are among the most abundant and commonly occurring bird ectosymbionts. They live permanently on the host body, are adapted to inhabit well-defined host microhabitats and are found in almost all avian groups. Although feather mites have been extensively studied at the taxonomic level, much diversity remains undescribed and there are many open questions on the biology, ecology and evolution of feather mites. There is also an ongoing debate on the type of symbiosis, that is, whether bird-feather mite interactions are parasitic, commensalistic or even mutualistic. Therefore, better knowledge of feather mite communities at different levels of their biological organization (i.e., among host individuals, host populations and host species) can contribute to our understanding of the evolutionary ecology of feather mite-bird interactions, and of the evolution of parasite biodiversity in general.

In this context, the main goal of this thesis was to investigate the evolutionary and ecological factors driving the diversity and community structure of feather mites inhabiting seabirds (Procellariiformes and Phaethontiformes) of the north-eastern Atlantic Ocean and Mediterranean Sea. More specifically, using a multi-host and multi-mite species community approach, I (1) quantify feather mite morphological and genetic diversity within different seabird species and populations; (2) evaluate the relative importance of host versus geographic structure in influencing the evolution and population structure of seabird feather mites; (3) investigate the spatial distribution and trophic structure within a host individual to identify the driving mechanisms and proximate factors shaping symbiont infra-community structure.

About the diversity of seabird feather mites, based on morphological criteria, the results show that seabird species breeding in the NE Atlantic Ocean and Mediterranean basin harbour a diverse and unique mite fauna composed of 38 species (33 species in Procellariiformes; five species in Phaenthontiformes) belonging to 10 genera and three families. All seabird species hosted at least three feather mite species, while the richest community was composed of nine mite species. Each seabird genus harboured a distinct feather mite community and only three mite species were shared by two related shearwater genera. Seventeen of the 33 mite species found to inhabit the Procellariiformes were new, undescribed species; official descriptions of six are included in this thesis. Overall, molecular data correlated well with morphological species descriptions, but also revealed the presence of six putative cryptic species belonging to four mite genera.

In relation to factors and processes of diversification, the patterns of mite genetic structure were variable both among different sympatric hosts and among the same host species in different geographic regions. Thus, the great majority of mite species from sympatric seabirds exhibited strong host-associated patterns of genetic structure. When comparing mite communities among sibling host species from the same genus, some mite species were genetically unstructured among hosts and localities, whereas other mite species showed higher degree of genetic diversity and among population differentiation. These observed differences correspond to microhabitat use on the host body. Although host-specialization appeared to be the main driving factor of feather mite diversification, some degree of mixing between closely related host species occur for more generalist mites. In addition, no genetic differentiation among localities was found for feather mites, suggesting that mite dispersal regularly occurs between host populations.

Related to the question on the ecology and community structure of seabird feather mites, the distribution of two widely abundant mite species that co-occur on the flight feathers of a single seabird species, *Calonectris borealis*, showed clear spatial segregation among feathers; one species preferred the central primaries, whereas the other was restricted to the outermost primaries. This pattern resulted from a combination of habitat-specific adaptations and ongoing competition. In addition, isotopic analyses of mite diet indicated that the two mite species share the same host food resources, probably preen gland oil complemented with exogenous material.

Altogether, this thesis highlights the vast and largely unrecognized diversity of feather mites harboured by seabirds, provides a comprehensive characterization of the patterns of seabird-feather mite species/lineages associations and contributes to a better understanding of the ecological and evolutionary processes that have lead to their high diversity. It demonstrates, in particular, the essential role of microhabitat adaptation for the evolution of ectosymbiont biodiversity, both due to its impact on reducing local resource competition and conditioning dispersal probability at different spatial scales.

GENERAL INTRODUCTION

GENERAL INTRODUCTION

1. SYMBIOTIC INTERACTIONS

Host-symbiont interactions are defined as long and intimate associations between two or more organisms, which are phylogenetically and biologically distant. **The symbiont** is an organism intimately associated with and metabolically dependent upon a larger organism (the host) for the completion of a major part of its life cycle. In turn, **the host** is an organism that harbours a symbiotic species, typically providing it with food resources and shelter (Combes 2001, Leung and Poulin 2008). These associations can take three principal forms namely parasitism, mutualism and commensalism. In **parasitism** one species (the parasite) benefits through the use of resources gathered by the other species (the host) and, thus, the parasite has a negative impact on the host. **Mutualism** is a relationship in which both species benefit from their interaction, whereas in **commensalism**, one member benefits from the relationship, whereas the other, normally the host, neither gains nor loses. The line among these different types of associations is relative. Depending on local environmental conditions, the interaction between two organisms can change from mutualistic or commensalistic to parasitic, or the reverse. For example, if local resources are high, the presence of a parasite may have no detectable effect on host fitness, representing therefore a commensalistic interaction; this is often the case for macroparasites when found in low intensities in a host population (e.g., McCoy et al. 2002). In other cases, a mutualistic relationship may become parasitic when the local environment changes, such is the case of cleaner fishes (Grutter and Bshary 2003, Cheney and Côté 2005), fig-pollinating wasps (Machado et al. 2001), *Wolbachia* bacteria (Weeks et al. 2007), endosymbiotic dinoflagellates (Sachs and Wilcox 2006) or branchiobdellid worms (Brown et al. 2012).

Among the different types of host-symbiont interactions, those involving parasites are the most common and the most widely studied. Indeed, parasitism is an extremely successful lifestyle considering the number of extant parasite species and the number of times it has evolved independently (De Meeûs and Renaud 2002, Poulin and Morand 2004). Parasites also show a remarkable diversity of life-history strategies and have evolved a wide range of adaptations that allow them to exploit hosts as resources (Huyse et al. 2005, Barrett et al. 2008). Almost all metazoan species host one or more parasitic species, indicating that parasite diversity probably surpasses that of free-living organisms (Price 1980). Furthermore, owing to their diversity and effects on hosts, parasites play key roles in ecosystems and it is well documented that complex assemblages of macroparasites (helminths and arthropods) and microparasites (viruses, bacteria and protozoans) impact food webs and influence ecosystem energetics (Hudson et al. 2006, Dobson et al. 2008, Lafferty et al. 2008). Despite this, small-bodied species and/or species with weak negative effects often escape researchers' attention and are more difficult to study. Consequently, certain parasite taxa have received little attention, and we are still far from having a complete inventory of extant parasite diversity (Poulin and Morand 2000).

One reason for the underestimation of parasite biodiversity is the presence of **cryptic species**. Cryptic species are genetically distinct, but morphologically indistinguishable (or seem so, without detailed studies) and therefore erroneously classified as a single species (Bickford et al. 2007; Nadler and Pérez-Ponce de León 2011). The presence of cryptic species can have important implications for the estimation of true parasite biodiversity (Poulin and Morand 2000, Poulin 2011) as well as for testing the factors involved in the diversification process (Johnson et al. 2007; Light and Hafner 2007). Molecular techniques are the gold-standard to identify cryptic species. Many parasite groups, such as nematodes, trematodes, cestodes, acanthocephalans, blood parasites, intestinal flagellates or avian lice, have been found to harbour cryptic diversity (Cepicka et al. 2005, Sehgal et al. 2006, Grillo et al. 2007, Leung et al. 2009, Malenke et al. 2009, Martínez-Aquino et al. 2009, Lavikainen et al. 2010, Razo-Mendivil et al. 2010). In addition, available data point out to an uneven distribution of cryptic species among different groups of parasites, for instance, with more among trematodes than other helminths (Poulin 2011). Despite of the potential of molecular techniques

to uncover this diversity, recent studies have called for caution and claim that in order to correctly delimit species, DNA sequence data should be combined with additional sources of information such as morphology, ecology, biogeography and/or behavioral traits (Bickford et al. 2007; Nadler and Pérez-Ponce de León 2011; Jörger and Schrödl 2013).

In sum, we lack knowledge about the real diversity of most ectosymbiont groups, with only a fraction of the estimated number of species described. By studying and characterizing the symbiont diversity, in my thesis I have attempted to help fill this gap.

2. DIVERSIFICATION PATTERNS AND PROCESSES

One key question that remains unanswered in the field of symbiotic interactions is about the mechanisms driving the high diversification and adaptation of parasites. Studying the proximate factors influencing the evolution and organisation of parasite communities and understanding relationships with the host can provide important insight in this regard. The mode and the outcome of interspecific interactions depend on a wide range of **host and parasite life history traits**. Transmission mode, dispersal ability, mode of reproduction, life cycle complexity and host specificity are considered among the most important parasite features shaping the host-parasite interactions (Criscione et al. 2005, Barrett et al. 2008). Parasite **reproductive mode** is a complex trait that strongly influences the genetic structure and evolutionary potential of populations (Mazé-Guilmo et al. 2016). Although sexual reproduction is common, many parasites exhibit hermaphroditic, parthenogenetic, and strict clonal reproduction, or a mix of these reproductive modes. For most parasites, the main **mode of transmission** is horizontal, between related or unrelated host individuals via a variety of mechanisms (e.g. direct contact, vector-borne transmission or environmental dispersal). But, in some cases, transmission can be vertical, parasite passing directly from parent to offspring without a dispersal stage per se (Barrett et al. 2008). Parasitic organisms also display different **life cycles**, ranging from species that complete their entire life cycle on a single host to species that exhibit multiple stages on different host species, through to species that alternate between parasitic and free-living phases. **Host specificity** is another defining feature of a parasitic organism, reflecting the breadth of a parasite's ecological niche and determining the likelihood that a parasite will successfully colonize new habitats or new hosts (Poulin and Mouillot 2003, Poulin and Keeney 2008). Many parasite taxa are highly host-specific, infecting only one or a few phylogenetically-related host species, whereas others are generalists, exploiting many alternative host species. The level of host specificity of a parasite may simply be due to limited opportunities for dispersal and colonization (Clayton et al. 1992, Johnson et al. 2002, Whiteman et al. 2004), but may also be determined by specific parasite adaptations to particular host structures (e.g. feather or hair structure), such that a parasite is incapable of surviving and reproducing on foreign hosts (Tompkins and Clayton 1999, Reed et al. 2000). The evolution of host specificity is directly linked to diversification in that it can be an intermediate step in the process of host-associated speciation.

In turn, different **host life-history traits**, such as spatial structure (population size and distribution), longevity, resistance or behaviour, may also influence the outcome of host-parasite associations, and ultimately parasite population dynamics (Huyse et al. 2005, Bruyndonckx et al. 2009, Mazé-Guilmo et al. 2016). Hosts represent a patchy and dynamic resource that varies spatially and temporally and to which parasites must continuously adapt. The lack of a free-living stage increases the dependence of the parasite on its hosts, and consequently parasite dispersal is limited to host movements (Criscione 2008, but see Mazé-Guilmo et al. 2016). Furthermore, if hosts are long-lived, then parasites populations are likely to be more stable, while, if host are short-lived, parasites populations are more likely to experience extinction and colonization processes (Barrett et al. 2008). Host availability and geographic range, physiological body condition and the phylogenetic relatedness to alternative hosts can also select for different degree of parasite specificity (Fallon et al. 2005, Krasnov et al. 2005, 2006, Edwards and Vidrine 2006).

Because of this, the evolution and diversification of symbionts is tightly linked to that of the host. Studying host-symbiont associations and their evolutionary patterns can give insights into the driving processes and factors that have generated these interactions. The evolution of symbionts and host-symbiont associations has been studied at both macroevolutionary and microevolutionary levels. **Macroevolution** refers to evolutionary changes at or above the species level and over extended periods of time (geological scale), whereas **microevolution** refers to any evolutionary change below the level of species that occurs on a small scale (within and among populations) and over short time intervals (ecological time).

Studies on the macroevolutionary scale are useful to understand the origins of specific lineages and the patterns of diversification. Several possible processes may explain patterns of symbiont-host associations. One of the most common processes is **cospeciation** (or association by descent), where one symbiont species speciates in response to the speciation of the host species and which is highlighted by congruent host and symbiont phylogenies (Brooks 1988). However, a number of processes can lead to different evolutionary trajectories in host and symbionts and non-specific host-symbiont associations (Paterson and Banks 2001, Johnson et al. 2003). For instance, **host switching** (or association by colonization) occurs when a symbiont species successfully colonise a new host species, whereas **duplication** (or intrahost speciation) take place when a symbiont speciates in the absence of host speciation and results in several closely related symbiont species on the same host species. Another evolutionary event is **inertia** where a symbiont species does not speciate despite speciation of its host, resulting in the same symbiont species being present on several descendant host species. **Sorting events** occur when symbiont species are entirely, or apparently, removed from host species, and can involve **extinction** or "**missing the boat**" (the absence of symbionts on the founder population of hosts potentially caused by the aggregated distribution of macrosymbiont populations).

Evolutionary patterns and host-symbiont associations will be directly influenced by the life-history features of both host and symbiont, as outlined in section 1 (Clayton and Johnson 2003, Clayton et al. 2004). Strict cospeciation may occur when host-switching is prevented by the low mobility of the symbiont and the asocial lifestyle of the host, with many examples coming from avian lice (Johnson and Clayton 2003, Johnson et al. 2002), tetrapod monogeneans (Verneau et al. 2002, Bentz et al. 2003) and bacterial endosymbionts (Hosokawa et al. 2006). The frequency of macroevolutionary events (cospeciation, host switching, duplication, sorting events) may be also influenced by different ecological factors that reflect the distribution and abundance of the host and parasites. For instance, any factor that causes a parasite to be patchily distributed over the range of its host may increase the probability of parasite duplication, whereas a parasite may undergo extinction if is typically found only in small numbers on host individuals (Clayton et al. 2004). Recently, Hoberg and Brooks (2008) developed the concept of macroevolutionary mosaic, according to which the diversification and persistence of complex host-parasite systems results from episodic events of geographical colonization (host-switching) alternating with periods of regional stability and co-speciation.

At the microevolutionary scale, the diversity and structuring of symbiont communities depend on the genetic variation and ecology of the interacting species. There has been a recent increase in the number of studies documenting the population genetic structure of host-parasite associations and the factors and processes acting at this scale (Bruyndonckx et al. 2010, Brouat et al. 2011, Mazé-Guilmo et al. 2016). The population dynamics of a parasite species has important implications for evolutionary processes, such as host-race formation, adaptation to host defences and the evolution of drug resistance (Blouin et al. 1995). The degree of parasite genetic structure can be influenced by different parameters, including parasite host specificity, parasite infrapopulation size, host geographic distribution, parasite dispersal rates and host behaviour (Johnson et al. 2002, McCoy et al. 2003, Weckstein 2004, Huyse et al. 2005). Thus, immobile or asocial hosts, unstable heterogeneous external environments, complex parasite life cycles, small effective parasite population sizes, high host specificity or parasite vertical transmission are among the factors that may increase the genetic structure of parasite populations (Nadler 1995, Huyse et al. 2005), although the relative importance of these determinants can vary strongly with parasite species (Mazé-Guilmo et al. 2016). Parasite dispersal among host

populations is considered one of the most important factors influencing the dynamics and coevolution of species interactions. Differences in dispersal abilities of parasites may lead to differing degrees of host-specificity and, ultimately, may drive differences in population genetic structures and the degree of congruence between host and parasite lineages (Johnson et al. 2002, Whiteman et al. 2004, Mazé-Guilmo et al. 2016).

In this thesis, I use feather mites as biological model to investigate patterns and processes of diversification in symbiotic organisms by applying a community and comparative approach. For this purpose, I have first examined the morphological and genetic diversity of multiple ectosymbionts occurring on multiple hosts. Then, to investigate the processes and factors involved in their diversification; I compared the population genetic structure of multiple feather mites co-occurring on the same or closely related hosts that differ in various life-history traits and spatial distributions.

3. FEATHER MITES AS ECTOSYMBIONTS OF BIRDS

Among bird ectosymbionts, feather mites (class Arachnida: subclass Acari) are the most abundant, obligatory ectosymbionts of birds, developing their entire life cycle on the host body. Because of their extraordinary ecological and evolutionary diversity, these ectosymbionts offer a unique system for studying the ecology and evolution of interspecific interactions. Feather mites have been extensively studied at the taxonomic level (Gaud and Atyeo 1996), although much diversity remains undescribed. In contrast, basic questions on the biology, ecology and genetic structure of feather mites remain largely unsolved (Proctor and Owens 2000, Proctor 2003). Better knowledge of feather mite community structure within and among bird host species can accelerate our understanding of the evolutionary ecology of this interaction (Doña et al. 2015), and of the evolution of ectosymbiont diversity in general.

3.1. DIVERSITY OF FEATHER MITES

Birds typically host a rich feather mite fauna, with some host species carrying as many as 25 different species (ex: green conure, *Aratinga holochlora*, Pérez 1997). Despite their great diversity and wide distribution among hosts, only about 2 500 species of feather mites have been described so far, representing only a small part of the estimated number of species (Gaud and Atyeo 1996) (Figure 1). Feather mites have been grouped into two superfamilies in the suborder Astigmata (Analgoidea and Pterolichoidea) and are reported from all avian orders, except Rheiformes (Mironov and Proctor 2008). Analgoidea represent almost 50% of the acarofauna on non-passeriform birds, while on passeriform birds, their supremacy is practically absolute (Dabert and Mironov 1999). The host orders with the greatest recorded number of mite families are the Passeriformes, Charadriiformes, Coraciiformes, Piciformes and Apodiformes, but this likely reflects the interest showed for these avian orders rather than the true mite richness per se (Proctor 2003). Feather mites have developed complex associations with their avian hosts. Almost all extant avian orders have their own specific feather mite fauna and usually, a particular feather mite species inhabits a single avian genus or species (Gaud and Atyeo 1996, Dabert and Mironov 1999). However, some variation in this pattern exists: mite species found on a few or several closely-related hosts and mite species present on a wide range of unrelated birds (e.g. *Analges passerinus* found on 27 species of passerine birds from different genera and families; some species of *Brephosceles* found on Gaviiformes, Procellariiformes, Anseriformes, Gruiformes and Charadriiformes). The most widely distributed, i.e. generalist, feather mite family is Xolalgidae, known from 16 avian orders (Atyeo and Gaud 1996, Proctor and Owens 2000).

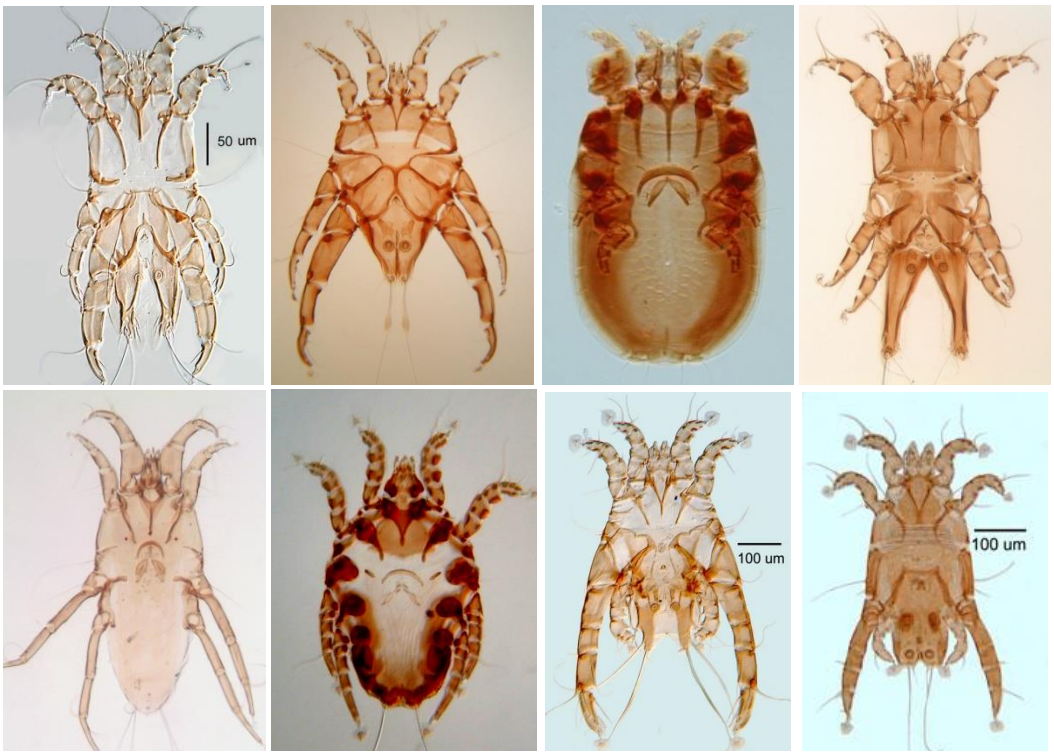

Figure 1. Diversity of feather mite species, from left to right and from top to bottom: *Gymnalloptes sp.* (Xolalgidae); *Laminalloptes minor* (Alloptidae); *Microspalax brevipes* (Alloptidae); *Brephosceles sp.* (Alloptidae); *Opetiopoda bulweriae* (Xolalgidae); *Zachvatkinia sp.* (Avenzoariidae); *Scutomegninia microfalcifera* (Avenzoariidae); *Scutulanyssus sp.* (Pteronyssidae) (Photos by Heather Proctor and Laura M. Stefan).

3.2. EVOLUTION OF FEATHER MITES

The origins and evolutionary relationships of feather mites are difficult to interpret due to the lack of direct fossil records. It is believed that the first feather mites originated from ancestors who inhabited bird nests (pyroglyphid-like nidicoles mites) in Cretaceous, 65-130 million years ago. Despite this shortcoming, there is a general agreement that feather mites represent a diphyletic group, with the Pterolichoidea derived from one ancestral astigmatan lineage and the Analgoidea from another (Dabert and Mironov 1999, Klimov and OConnor 2008). According to the hypothesis formulated by Atyeo and Gaud (1979), the Pterolichoidea originated first in the late Cretaceous during the radiation of non-passeriform birds, whereas analgoid mites invaded the Passeriformes in the Eocene, 55-40 mya. However, Dabert and Mironov (1999) proposed another hypothesis. In their opinion, the Analgoidea were the first feather mites occupying the least harsh microhabitats on the bird's body (skin surface and soft downy feathers), and later, pterolichoid mites colonized the vane surfaces of the feathers. A recent molecular study based on three nuclear genes renders the superfamily Analgoidea as paraphyletic assemblage that includes the ancestors of the mammalian and free-living lineages (pyroglyphid mites), while superfamily Pterolichoidea form a sister clade to the mite assemblage mention above (Klimov and OConnor 2008). This finding questions the traditional classification of these mites, which largely relies on host preferences, and indicates that alternative characters should be taken into account.

To date, most phylogenetic studies have been conducted at family and genus levels and were based on morphological characters: e.g. superfamily Analgoidea (Figure 2) (Dabert and Mironov 1999), Avenzoariidae (Mironov 1991), subfamily Avenzoariinae (Mironov and Dabert 1999), Epidermoptidae and Dermationidae (Mironov et al. 2005), Alloptidae (Mironov 2007), Xolalgidae (Mironov 2005), subfamily Pterodectinae

(Mironov 2009) or genus Metapteronyssus (Mironov and Wauthy 2006). However, a few studies based on molecular data also exist: subfamily Avenzoariinae (Dabert et al. 2001), Proctophyllodidae (Knowles and Klimov 2011), psoroptidian mites (feather and fur mites) (Klimov and OConnor 2008).

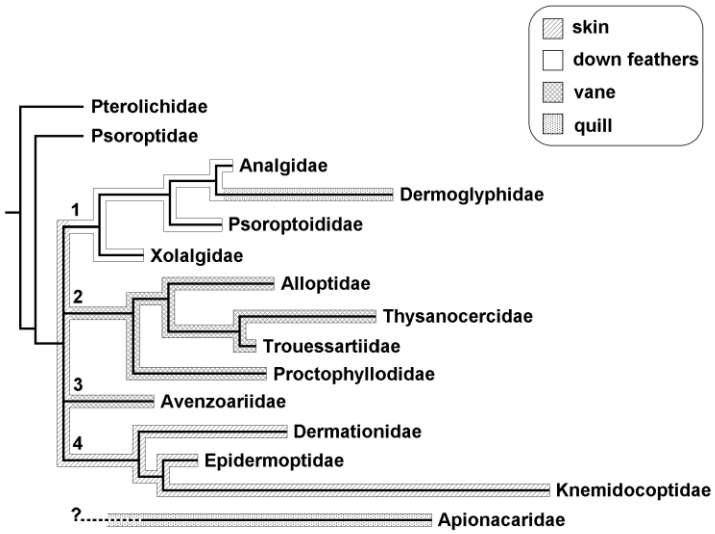

Figure 2. Phylogeny of the superfamily Analgoidea compared with the microhabitats occupied by mites from particular families (from Dabert and Mironov 1999). The Pterolichidae (superfamily Pterolichoidea) and Psoroptidae (superfamily Psoroptoidea) are outgroups. The position of the Apionacaridae is unresolved. The numbers indicate the clusters obtained based on the cladistic analysis of 32 morphological characters: cluster 1 corresponds to mites living in the down feathers and quills, clusters 2 and 3 contain mites inhabiting vane surfaces and cluster 4 includes skin mites.

Due to their high diversity and high degree of specialization, it is assumed that feather mites have cospeciated with their avian hosts (Dabert and Mironov 1999, Mironov and Dabert 1999, Dabert et al. 2001, Ehrnsberger et al. 2001, Dabert 2004, Mironov 1991, 2005, 2007, 2009). At the macroevolutionary level, several morphological and molecular studies have tested coevolutionary hypotheses. All demonstrated a considerable degree of cospeciation, but other evolutionary events, such as duplications, extinctions and host switching, have also been reported. Although many studies have investigated the co-evolutionary relationships between feather mites and their avian hosts at the family and genus level, very few studies have explored feather mite-host associations at the species level and below (Dabert et al. 2015). This level of study is however critical in order to identify the processes and factors involved in the diversification and specialization of these group of symbionts.

3.3. ECOLOGY OF FEATHER MITES

The **life-cycle** of feather mites is highly dependent of their bird hosts. That is, feather mites develop their entire life cycle on the host's body, which includes four motile feeding stages: six-legged larva, two nymphal instars (proto- and tritonymph) and adult (Proctor 2003). Females and tritonymphs are thought to be the main dispersal stage due to their relative size and mobility, along with their ability to reproduce rapidly after colonizing a new host individual (Mironov 2000). After moulting, females become fertilized and start laying eggs quite quickly after moving to new hosts. As for tritonymphs, they moult rapidly after arriving on new hosts and then copulate with the males. Sexual dimorphism is strong in some feather mite lineages and is normally expressed in the final, adult stage. The most common male modifications include bifurcation of the posterior idiosoma, enlargement of the third pair of legs (e.g. Xolalgidae, Avenzoariidae), presence of ventral suckers (adanal discs) used to hold the female during copulation, enlarged and flattened terminal setae (e.g. Pterolichidae), enlarged chelicerae (e.g. Falculiferidae) or skewed body symmetry (e.g. Alloptidae,

Freyanidae, Kramerellidae) (Dubinin 1951, Gaud and Atyeo 1996, Proctor 2003). Feather mites are primarily oviparous with females producing one large, sausage-shaped egg at a time, although some evidence of seasonal ovoviviparity has been observed in some species (Proctor 2003). In spring and summer females produce eggs with thin shells, whereas in autumn females produce thick-shelled eggs that hatch the following spring. For most mite species, colonization of new hosts occurs almost exclusively through direct physical contact between conspecifics: vertically from parents to fledglings or horizontally between adults during courtship, mating and communal roosting. However, some rare examples of indirect transmission are also known by phoresy on hippoboscid flies (OConnor 1982, Gaud and Atyeo 1996, Jovani et al. 2001, Proctor 2003, Proctor and Jones 2004).

Feather mites are highly specialized ectosymbionts, being adapted to inhabit well-defined host microhabitats including the vane surface of contour feathers, soft down feathers, the surface of the skin or subcutaneous layers, and even the interior of feather quills (Gaud and Atyeo 1996, Dabert and Mironov 1999, Proctor 2003) (Figure 3). Most feather mites are adapted to live on the ventral surface of flight feathers, in narrow corridors between barbs, which represent a very stressful environment with strong aerodynamic forces and low humidity (Proctor 2003). Due to these extreme conditions, feather mites display complex and specific morphological adaptations like dorso-ventrally flattened and heavy sclerotized body, reduced dorsal setae, short and laterally-inserted legs, and well developed membranous foot discs (ambulacra) that act as hold-fast organs (Dabert and Mironov 1999, Proctor 2003). In contrast, feather mites that live in soft downy feathers don't need a strong sclerotization as air disturbance is minimal here. The body setae of these mites tend to be long and fine, as in ancestral free-living mites and help mites orient themselves in their habitat and detect substrate vibrations, which may denote the presence of conspecifics (Dabert and Mironov 1999, Proctor 2003). Syringicolous mites (those living in the feather quills) have ovoid or cylindrical bodies with poorly sclerotized opisthosomas and legs with ventral insertions. Finally, dermicolous mites (those living on or under the epidermis of birds) have round, dorso-ventrally flattened and poorly sclerotized bodies and short hooked legs for grasping skin (Dabert and Mironov 1999, Proctor 2003).

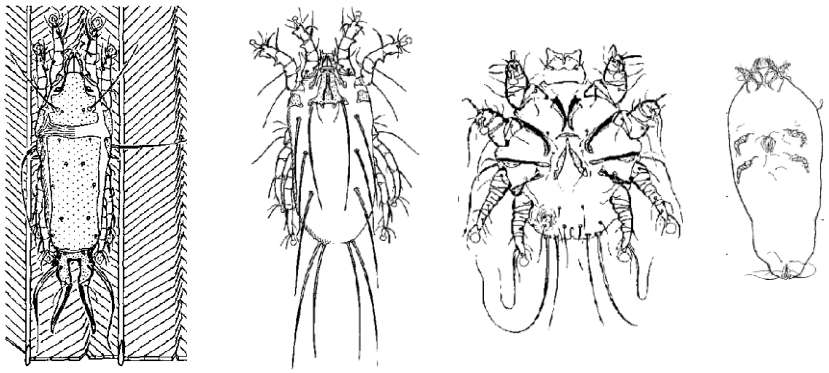

Figure 3. Feather mite morphotypes associated with main microhabitats on the host body. From left to right: vane-dwelling mites, down mites, skin mites and quill mites. Figure modified from Dabert and Mironov 1999.

In order to understand the evolution and diversity of feather mites it is fundamental to increase our knowledge about their ecology. The **ecological niche** of a species can be define as the global environmental requirements of a species to complete its life cycle, and includes its impact on resource availability and on other organisms in the community (Leibold 1995). According to classic niche theory, species can coexist in heterogeneous environments by reducing interspecific competition via niche partitioning (Schoener 1983). Therefore, coexistence requires some niche difference between species that increases the strength of intra-specific competition relative to that of inter-specific competition. There are different types of niche partitioning, such as **trophic partitioning**, when different species specialize on distinct food resources in sympatric habitats, and **spatial niche partitioning**, when species share the same resource but use distinct subsets of the habitat. Segregation patterns among co-occurring species are difficult to study mainly due to the lack of sufficient

replicates that limits the detection and analysis of general patterns of community structure. In this regard, obligate symbionts are good models for understanding the dynamics of niche partitioning over small spatial scales, because in these systems spatial and trophic resources are limited to the body of the host and each host represents a replica of a discrete habitat patch (Mouillot et al. 2003). The distribution of permanent symbionts on or within a host can be influenced by intrinsic host factors and environmental factors, although structuring can also arise due to the interspecific competition.

The distribution of feather mites has been examined both among and within different feather types (Choe and Kim 1989, Bridge 2003, Jovani and Serrano 2004, Pap et al. 2005, Jovani et al. 2006, Mestre et al. 2011). The majority of these studies show a general pattern with high concentrations of mites on the central wing feathers, low densities or complete absence on the external wing feathers and an avoidance of the first secondary feather, although a few exceptions to these patterns have been reported (Bridge 2003). The distribution of feather mites among and within feathers can be affected by environmental factors (air turbulence, friction between feathers, temperature, sunlight and humidity) (Choe and Kim 1989, Wiles et al. 2000, Jovani and Serrano 2004, Mestre et al. 2011), as well as feather structure, particularly barb height, grooming behaviour (preening and scratching) of birds or host moulting status (Jovani and Serrano 2001, Bridge 2003, Jovani et al. 2006, Pap et al. 2006). Other studies have investigated the abundance, prevalence and spatial distribution of feather mites within host individuals. Mite abundance may be shaped by particular host traits, such as body size (Galván et al. 2012), size of the uropygial gland (Galván and Sanz 2006), but also by the species composition of feather mites living on a bird (Fernández-Ganzález et al. 2013) or by external environmental factors (Meléndez et al. 2014). In this thesis, I examined the spatial and trophic segregation of feather mites co-occuring in a seabird host in order to test if these mites follow the distribution patterns mentioned above and to determine the role of interspecific competition for resources in shaping within-host distributional patterns.

Apart from how mite species interact each other and establish their niche, an important question about the ecology of feather mites that still remains unclear is about the nature of the ecological interaction between feather mites and birds. Although some studies consider feather mites as parasites, having a negative impact on their hosts (Thompson et al. 1997, Harper 1999, Figuerola et al. 2003), other authors consider them to be commensals or even mutualists (Blanco et al. 1997, 1999, Dowling et al. 2001, Pap et al. 2005, Galván and Sanz 2006, Brown et al. 2006, Galván et al. 2012). More likely there is a continuum and which depends on the species and the ecological/evolutionary context of the interaction. A gap in our knowledge on the biology of feather mites that helps define the nature of their interaction with the host relates to their diet; what do feather mites feed on? It is often assumed that feather mites feed principally on uropygial gland oil (predominantly waxes and fatty acids), along with algae, bacteria, fungal spores and pollen grains trapped between the feather barbs (Proctor and Owens 2000, Blanco et al. 2001, Galván et al. 2008). Direct studies on the trophic habits of these organisms are difficult due to their small size and particular host use. However, indirect tools, such as the use of stable isotopes can provide powerful tools for studying the trophic relationships within cryptic communities (Inger and Bearhop 2008) (BOX 1). Stable isotopes have been successfully applied to study trophic interactions in different host-parasite systems, including both endoparasites, such as intestinal nematodes and cestodes (Deudero et al. 2002, Persson et al. 2007), and ectoparasites, such as lice, fleas and bat flies (Voigt and Kelm 2006, Gómez-Díaz and González-Solís 2010), and could be a good approach to disentangling the feeding preferences of feather mites.

4. STUDY MODEL: SEABIRDS AND THEIR FEATHER MITES

4.1. SEABIRD HOSTS

Seabirds refer to various orders and families of birds that have adapted to life within the marine environment, and for which the sea represents the main source of food. Currently, “true” seabirds include six orders: Sphenisciformes (penguins), Procellariiformes (albatrosses, petrels and shearwaters), Pelecaniformes

(pelicans), Suliformes (gannets, boobies, cormorants, frigatebirds), Phaethontiformes (tropicbirds) and Charadriiformes (skuas, gulls, terns, skimmers, waders and auks), 15 families, and about 300 species. Seabirds are widespread and exploit a broad spectrum of marine habitats, from littoral to pelagic and from tropical to polar environments. One of the most important key features of seabird ecology is colonial breeding, which, in many species, can lead to the aggregation of hundreds of thousands, and sometimes millions, of individuals during the breeding season (Coulson 2001).

BOX 1: Stable isotopes in ecological research

Most chemical elements naturally occur in a number of forms, which differ in the number of neutrons they contain in the nucleus. These various forms are known as the stable isotopes of an element, and are distinct from radiogenic isotopes in that they do not decay over time. Although stable isotopes have identical chemical properties, they vary in their masses, causing small differences in their kinetic features. Although many known elements have at least two stable isotopes, only those elements related to the biosphere (plants, animals), the hydrosphere (water) and the atmosphere (gaseous) – i.e. carbon (C), nitrogen (N), hydrogen (H), oxygen (O) and sulphur (S) – are relevant to ecological research. Differences in relative abundance of these isotopes can be measured using a mass spectrometer and expressed as the ratio of heavy to light forms, which can then be standardized against an international reference sample.

Stable isotopes are so useful in ecological research because even very small differences in mass cause subtle differences in their behaviour during chemical reactions and diffusion which alter the ratio of heavy to light isotopes. This process, known as isotopic fractionation, leads to variation in isotope signatures among different organisms and across different habitats. Thus, the isotope ratios observed in animal tissues can be used to make inferences about their diet and the type of habitats in which they live (Inger and Bearhop 2008).

Stable isotopes are intrinsic markers reflecting the signatures of different dietary sources in the tissues of consumers in a predictable manner (Hobson and Clark 1992). Nitrogen ($^{15}N/^{14}N$) is typically used to infer the trophic position of consumers, and increases by approximately 2.5‰-5‰ with each trophic level (DeNiro and Epstein 1981), whereas carbon ($^{13}C/^{12}C$) is typically used to describe the diet sources, and shows only a limited enrichment between trophic levels (0-1‰) (DeNiro and Epstein 1978).

Procellariiformes (albatrosses, petrels, shearwaters, storm petrels and diving petrels) are an order of approximately 117 species which are almost exclusively pelagic, coming only to land to breed in large and dense colonies on remote oceanic islands (Brooke 2004). Most species show strong natal philopatry and fidelity to their breeding sites, characteristics which should promote genetic isolation and differentiation among populations. This order includes four families: Diomedeidae (albatrosses), Procellariidae (petrels and shearwaters), Hydrobatidae (storm petrels) and Pelecanoididae (diving petrels) (Gaston 2004). Procellariiformes have a few unifying morphological characteristics, such as external tubular nostrils used for olfaction, grooved, hooked bills and webbed feet set well back on the body. They exhibit a "slow-pace' life-history strategy: long-lived species, delayed sexual maturation and breeding age, low annual reproductive rate and relatively long chick-rearing periods (Brooke 2004). Both sexes are similar in size and plumage, and all species tend to have darker plumage on the back, in different combinations of black, gray and brown tones that only change with age in albatrosses and giant petrels (Gaston 2004). Procellariiformes have a cosmopolitan distribution, occurring in all the major oceans and seas of the world, with nearly two-thirds of all species breeding in the southern hemisphere. In the northern hemisphere, many species breed in the Mediterranean Sea and in different archipelagos of the Atlantic Ocean. Despite their broad distribution and high diversity, Procellariiformes are among the most endangered seabird taxon, the main threats being loss of island breeding

habitats due to human activities, introduced predators in their breeding colonies and mortality associated with commercial fisheries (Baker et al. 2002, Butchart et al. 2004, Donlan and Wilcox 2008).

In this thesis, I focused mainly on procellariiform species as hosts to feather mites. The focal species all breed in temperate and sub-tropical regions of the North-East Atlantic Ocean and Mediterranean Sea and include several species of Procellariidae (*Calonectris* and *Puffinus* shearwaters, Bulwer's petrel and gadfly petrels) and Hydrobatidae (storm petrels). I have also included data from one phaethontiform species (*Phaethon aethereus*) that breeds sympatrically with the Procellariiformes in the study region (Table 1, Figures 4 and 5). This seabird species is predominantly white, 90-105 cm long (including 46-56 cm tail streamers), with elongated central tail feathers, and large, powerful and slightly decurved red bill. The main species nesting in the Mediterranean Basin are the Scopoli´s shearwater (*Calonectris diomedea*), the Mediterranean shearwater (*Puffinus yelkouan*) and the European storm-petrel subspecies *Hydrobates pelagicus melitensis*, whereas all the other species included in this study breed in the NE Atlantic Ocean: Cory´s shearwater (*Calonectris borealis*), Cape Verde shearwater (*Calonectris edwardsii*), Manx shearwater (*Puffinus puffinus*), Macaronesian shearwater (*Puffinus baroli*), Boyd's shearwater (*Puffinus boydi*), Bulwer's petrel (*Bulweria bulwerii*), Cape Verde petrel (*Pterodroma feae*), the band-rumped storm-petrel (*Hydrobates castro*), European storm-petrel subspecies *Hydrobates pelagicus pelagicus* and red-billed tropicbird (*Phaethon aethereus*) (see BOX 2 for details on each seabird species). These seabird species exhibit different degrees of migratory behaviour, which may influence the dispersal of feather mites among different host populations and ultimately among different host taxa (see Table 1).

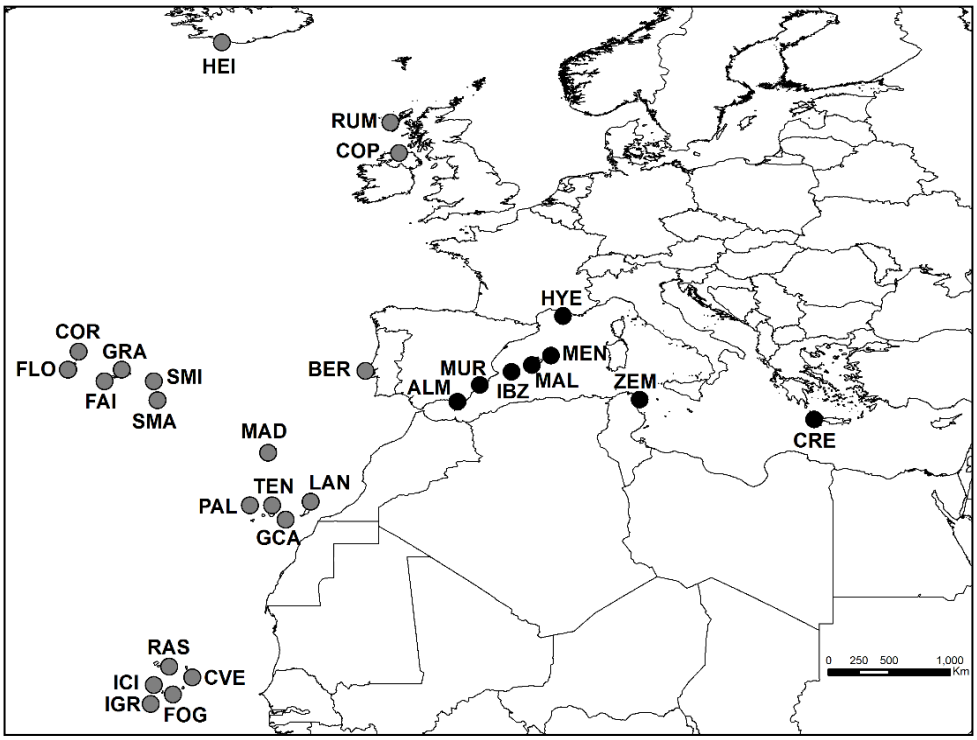

Figure 4. The distribution map of the 28 seabird breeding colonies included in this study. Black circles represent the Mediterranean colonies (CRE – Crete, ZEM – Zembra, HYE – Hyeres, MEN – Menorca, MAL – Mallorca, IBZ – Ibiza, MUR – Murcia, ALM - Almeria) and the grey circles the Atlantic colonies (HEI – Heimaey, RUM – Halival-Rum, COP – Copeland, BER – Berlengas, MAD – Madeira, COR – Corvo, FLO – Flores, FAI – Faial, GRA – Graciosa, SMI – São Miguel, SMA – Santa Maria, LAN – Lanzarote, TEN – Tenerife, GCA – Gran Canaria, PAL – La Palma, RAS – Raso, CVE – Curral Velho, FOG – Fogo, IGR – Ilheu Grande, ICI – Ilheu Cima). See Table 1 for details on the different species present in each colony.

BOX 2: Seabird species breeding in NE Atlantic and Mediterranean Sea

Order Procellariiformes, Fam. Procellariidae

***Calonectris* shearwaters** are highly pelagic seabirds found mostly in the northern hemisphere and which breed on isolated oceanic areas. They have a strongly contrasting plumage between the back and the underside, with grey-brown upper parts and white lower areas. Currently, this group includes the streaked shearwater (*C. leucomelas*), which breeds predominantly in Japan and on several islands around Taiwan, South Korea and eastern China, and three species of the Cory's shearwater complex: Scopoli's shearwater, *C. diomedea*, Cory´s shearwater, *C. borealis* and Cape Verde shearwater, *C. edwardsii*. The Scopoli's shearwater (623g) breeds mainly from the Iberian coast to the Adriatic and Aegean Seas; the Cory's shearwater (852g) breeds mainly in the northeastern Atlantic Ocean from Canary to Azores Archipelagos and the Cape Verde shearwater (440g) nests exclusively on the Cape Verde Archipelago (Warham 1990, Thibault et al. 1997; Gómez-Díaz et al. 2006; Sangster et al. 2012). Recently, one population of the Cory's shearwater was discovered on Terreros Island (Almeria, Spain) within the Mediterranean basin (Gómez-Díaz et al. 2006).

***Puffinus* shearwaters** are a diverse group of pelagic, small- to medium-sized petrels (150-508g) with a worldwide distribution. However, they are most abundant and diverse in the cool temperate seas around Australasia (Warham 1990, Austin 1996). The main *Puffinus* taxa breeding in the northeast Atlantic Ocean are the Manx shearwater *P. puffinus*, the Macaronesian shearwater *P. baroli* and the Boyd's shearwater *P. boydi*, whereas the Mediterranean shearwater *P. yelkouan* and the Balearic shearwater *P. mauretanicus* nest in Mediterranean Sea. The Manx shearwater is a small seabird (447 g) breeding on different islands from Britain and Ireland, with just two small Welsh islands, Skokholm and Skomer, holding a substantial proportion of the global breeding population (around 150 000 breeding pairs). The Macaronesian shearwater is a small non-migratory seabird species (157g), breeding in the Azores, Madeira, Desertas, Salvagens and Canary Islands, whereas the Boyd's shearwater (150g) is restricted to the Cape Verde archipelago. The Mediterranean shearwater (420g), considered as threatened by the IUCN, is endemic to the Mediterranean Sea, including the Black Sea, and breeds on French, Italian, Maltese, Greek and Croatian islands (Sangster et al. 2002, Bourgeois and Vidal 2008, Militão et al. 2013). The Balearic shearwater (508g) is endemic to the Balearic archipelago and is classified by the IUCN as critically endangered.

Bulwer's petrel (*Bulweria bulwerii*) is a small procellariiform seabird (80-120g) with dark plumage and a lighter band at the top of the wings, which shows a pan-tropical and subtropical distribution, including the Atlantic, Pacific and Indian oceans (Brooke 2004, Ramos et al. 2015). Within the Atlantic, this species breeds on some islets and islands from the Macaronesian archipelago, including the Azores, Madeira, Salvagens, Canary Islands and the Cape Verde Islands. Bulwer's petrel is abundant in Madeira (>90% of the Atlantic population) where the population is estimated at 10,000 breeding pairs, whereas in the Cape Verde islands the population holds more than 1,000 pairs (Jacob Gonzalez-Solís, personal communication). In the Azores archipelago, it is quite rare with only one known colony of approximately 50 breeding pairs (Hazevoet 1995, Nunes and Vicente 1998, Bried and Bourgeois 2005).

Gadfly petrels (genus *Pterodroma*) are some of the most threatened and least known of all seabirds, which breed in small numbers in mountainous areas of difficult access of remote islands, returning to colonies only at night (Ramos et al. 2016). Three species of gadfly petrels are breeding in the north-east Atlantic Ocean: Zino's petrel *P. Madeira* (227g), found on Madeira Island, Desertas petrel *P. deserta* (325g), nesting on Bugio Island (in the Desertas Islands, only 50 km south-east of Madeira Island), and the Cape Verde petrel *P. feae* (284g), breeding on four distinct islands in the Cape Verde archipelago: Santo Antão, Fogo, São Nicolau and Santiago (Ratcliffe et al. 2000, Zino et al. 2008, Gangloff et al. 2013). The three taxa display a clear allochrony in timing of breeding. However, the taxonomic status of these three species is still controversial. The three taxa are of conservation concern showing low population sizes (around 80 breeding pairs on Madeira Island, 150-180 pairs in Bugio Island and 500-1000 pairs in Cape Verde archipelago) (Shirihai et al. 2010, Gangloff et al. 2013).

BOX 2 (Continued)

Order Procellariiformes, Fam. Hydrobatidae

Storm petrels are almost as widespread as the procellariids, being found mostly in the Northern Hemisphere. The band-rumped storm-petrel *Hydrobates castro* (also known as the Madeiran storm petrel) is a small and extremely mobile pelagic procellariiform seabird (45g) with a widespread tropical and subtropical distribution in both the Atlantic and Pacific Oceans. Birds breed on isolated islands in Japan, Hawaii, Galapagos and north-east and central Atlantic in the Macaronesian archipelago (including Madeira, Salvagens, Canary Islands, Cape Verde Islands, Ascension and St Helena Islands) (Monteiro and Furness 1998, Brooke 2004). This species exhibits an unusual breeding phenology, with some populations having one single, synchronous breeding season (e.g. Japan and Cape Verde) and others having two main reproductive periods separated by a non breeding interval (e.g. Azores, Madeira and Galapagos Islands) (Monteiro and Furness 1998, Friesen et al. 2007). The European storm-petrel *H. pelagicus* is the smallest seabird in the world (average mass 20g), which breeds along the European Atlantic coast and in Mediterranean Sea. This species is split into two subspecies*: H. p. melitensis*, which breeds around the Mediterranean Sea from east Spain to Greece and possibly Turkey, and *H. p. pelagicus*, found in the north-east Atlantic Ocean, breeding from Iceland and Norway to northwest France, northern Spain and the Canary Islands (Hémery and d'Elbée 1985, Cagnon et al. 2004).

Order Phaethontiformes, Fam. Phaethontidae

Red-billed tropicbirds (*Phaethon aethereus*) are found in the tropical zones of the Pacific and Atlantic Oceans, and in the north of the Indian Ocean. Despite their wide distribution, the world population of red-billed tropicbirds is small, estimated to be less than 8000 pairs (Castillo-Guerrero et al. 2011). This species is mainly pelagic, breeding on small remote oceanic islands and it seems that is a non-migratory bird, some adults remaining in vicinity of their colonies all year-round. In NE Atlantic Ocean, this species occurs in several islets of the Cape Verde archipelago including Raso Island.

4.2. SEABIRD FEATHER MITES

Seabirds harbour a wide range of ectosymbonts, including lice, mites (Janovy Jr. 1997, Clayton and Price 1999, Proctor and Owens 2000), fleas and ticks (Janovy Jr. 1997, Dietrich et al. 2011). Among them, feather mites are particularly interesting because they show the greatest species richness. Most published studies on seabird feather mites have been limited to descriptive systematics and taxonomy, with very few investigations of their ecological and evolutionary relationships with the avian hosts. The large majority of these studies were focused on feather mites from Charadriiformes (Choe and Kim 1989, Dabert 1992, Mironov 1992, 2005, 2007, Mironov and Dabert 1999, Dabert et al. 2001, 2015, Bridge 2002, 2003, Badek and Dabert 2006, Mironov and Palma 2006, Negm et al. 2013). To date, studies documenting the feather mite fauna of procellariiform seabirds are relatively scarce (Dubinin 1949, Černý 1967, Peterson 1971, Fitzpatrick and Threlfall 1977, Bourgeois and Threlfall 1979, Horne and Rounsevell 1982, Atyeo and Gaud 1991, Gaud and Atyeo 1996, Mironov 1989a, b, 1991, 2014). All feather mite species identified to date belong to six families: Alloptidae, Avenzoariidae, Dermationidae, Epidermoptidae, Xolalgidae and Freyanidae (Gaud and Atyeo 1996, Proctor 2003), with *Microspalax*, *Zachvatkinia* and *Brephosceles* being the most common genera found on Procellariiformes (Peterson 1971, Mironov 1989a, Atyeo and Gaud 1991). Moreover, only few studies have examined the evolutionary relationships between feather mites and their seabird hosts (Dabert and Mironov 1999, Mironov 2005, 2007). For instance, feather mites of the genus Zachvatkinia showed a clear pattern of co-speciation with their primary hosts (Procellariiformes) and with their secondarily inhabited host group (Charadriiformes) (Dabert and Mironov 1999). Other studies investigated the coevolutionary trends of the feather mite families Xolalgidae and Alloptidae with non-passerine birds and aquatic birds. Although alloptid

and xolalgid mites generally coevolved with their hosts, these mites also have experienced duplications, numerous extinctions and host switching from one bird order to another (Mironov 2005, 2007). In general, these studies have focused on higher-order mite taxa, while work examining their trophic and spatial ecology and patterns of diversification at the microevolutionary level are currently lacking.

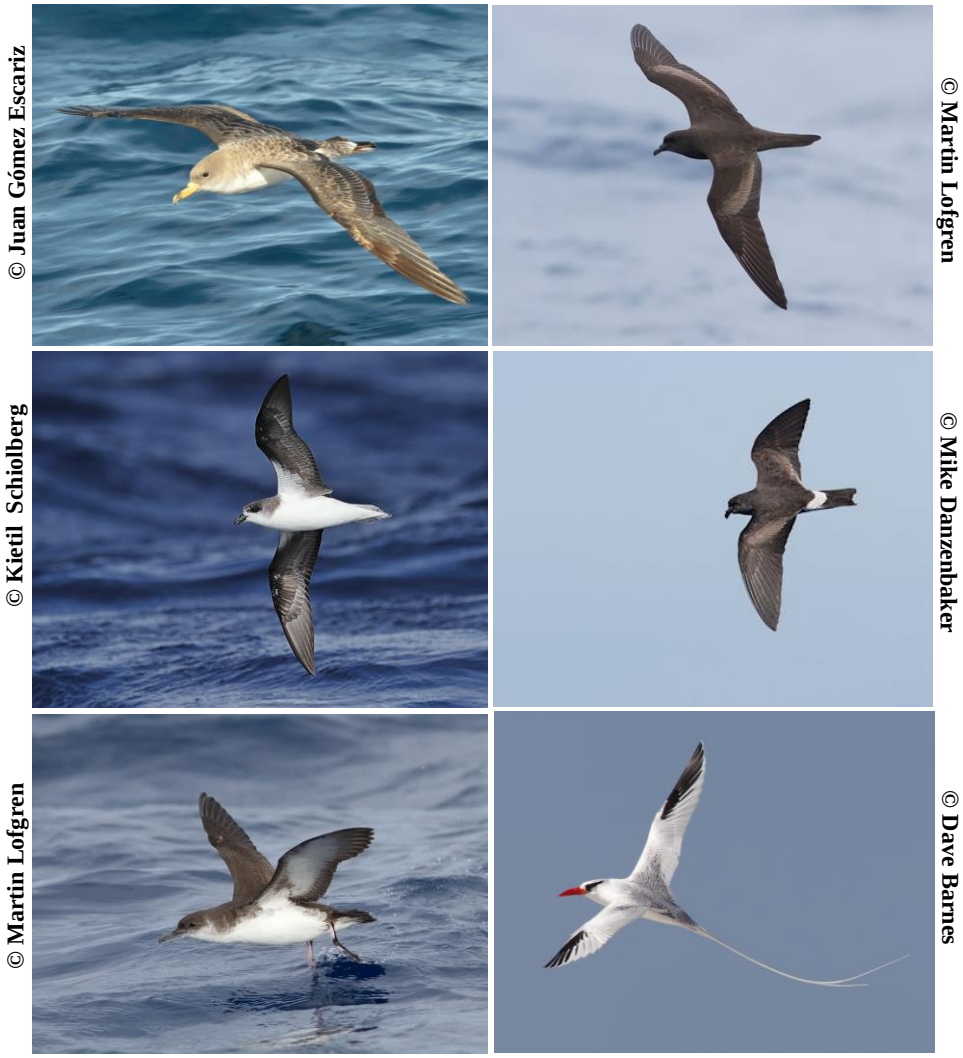

Figure 5. Examples of Procellariiformes, from left to right and from top to bottom:
Scopoli's shearwater *Calonectris diomedea* (Family Procellariidae)
Bulwer's petrel *Bulweria bulwerii* (Family Procellariidae)
Fea's petrel *Pterodroma feae* (Family Procellariidae)
Band-rumped storm petrel *Hydrobates castro* (Family Hydrobatidae)
Manx shearwater *Puffinus puffinus* (Family Procellaridae)
Red-billed tropicbird *Phaethon aethereus* (Family Phaethontidae)

Table 1. Details of the migratory routes and wintering areas of the seabird species examined in this thesis. The abbreviations used for the breeding colonies are shown in Figure 1.

Species name	Scientific name	Breeding colonies	Migratory behavior (wintering areas)	References
Scopoli´s shearwater	*Calonectris diomedea*	MUR, MEN, MAL, IBZ, HYE, ZEM, CRE	Eastern South Atlantic associated with the Benguela Current Western Indian Ocean associated with the Agulhas Currents Western South Atlantic associated with the Brazilian Current Northeast tropical Atlantic associated with the Canary Current	González-Solís et al. 2007
Cory´s shearwater	*Calonectris borealis*	ALM, MAD, BER, GCA, LAN, TEN, COR, FLO, FAI, GRA, SMI, SMA	Eastern South Atlantic associated with the Benguela Current Western Indian Ocean associated with the Agulhas Currents Western South Atlantic associated with the Brazilian Current Northeast tropical Atlantic associated with the Canary Current	González-Solís et al. 2007
Cape Verde shearwater	*Calonectris edwardsii*	RAS, CVE	Brazil and Falklands/Malvinas confluence off the Uruguayan coast	González-Solís et al. 2009
Manx shearwater	*Puffinus puffinus*	HEI, COP, RUM	Restricted area of the Patagonian shelf, close to the Argentinean coast south of the Río de la Plata	Guilford et al. 2009
Macaronesian shearwater	*Puffinus baroli*	LAN, SMA	North Atlantic region, around the colony during breeding and non-breeding periods	Neves et al. 2012
Boyd's shearwater	*Puffinus boydi*	RAS, ICI	Performs short migrations to the Central Atlantic Some individuals occasionally remain around the Cape Verde Islands	Zajková et al. in preparation
Mediterranean shearwater	*Puffinus yelkouan*	HYE	Aegean and Black Seas, or the coasts of north Africa (Tunisia and Algeria) and Egypt Some birds remain in the western Mediterranean near their breeding colonies	Militão et al. 2013
Bulwer's petrel	*Bulweria bulwerii*	LAN, PAL, SMA, RAS, ICI, IGR	Mid-equatorial Atlantic Ocean (north of the Saint Peter and Saint Paul archipelago)A small proportion of birds from the northernmost populations (Azores, Salvages and Canary Islands) undertake a leapfrog migration, spending the winter south of the Tropic of Capricorn	Ramos et al. 2015
Cape Verde petrel	*Pterodroma feae*	FOG	Remains around the breeding area (Cape Verde archipelago)	Ramos et al. 2016
European storm-petrel	*Hydrobates pelagicus*	IBZ, MEN, ALM, COP	The subspecies that breeds in the Atlantic migrates to South Africa and up to 200 miles south of Cape Agulhas and some birds overwinter close to the coasts of Mauritania and Rio de Oro The migration of the birds breeding in the Mediterranean is unknown, although most evidences suggest they move to the central Mediterranean	Onley and Scofield 2013 Martínez et al. 2016 submmited
Band-rumped storm-petrel	*Hydrobates castro*	MAD, BER, LAN, GRA, SMA, RAS, CVE, ICI, IGR	it is unclear whether these birds undertake systematic migrations after breedingmay migrate to the western Atlantic, being found from Canada southward to the nutrient-rich upwellings off northeast Brazil	Brooke 2004

OBJECTIVES

OBJECTIVES, ASSUMPTIONS AND PREDICTIONS

The main goal of this thesis was to investigate the diversity as well as the evolutionary and ecological factors and processes involved in the diversification and community structure of feather mites within procellariiform (11 species of petrels and shearwaters) and phaethontiform (one species) seabirds breeding in the north-eastern Atlantic Ocean and Mediterranean Sea. In order to achieve this main goal, we established three main objectives: 1) To quantify feather mite diversity within different populations of procellariiform birds. Five papers are presented that include the description of these communities and some of the new species that were discovered. 2) To characterise the relative role of host versus geographic factors in shaping the genetic structure of mite communities. This was carried out by comparing mite community structure both among different sympatric hosts, and among the same host species in different geographic regions. 3) To investigate the spatial and trophic structure of feather mites within a host individual to identify the proximate factors shaping symbiont community structure.

Chapter 1: DIVERSITY OF SEABIRD FEATHER MITES

In this chapter, I quantify the feather mite diversity in different populations and species of seabirds across a wide geographic scale. The number of taxonomic studies on feather mites has experienced a notable increase in recent years, with many new species being described from different avian orders and species (Mironov and OConnor 2014, Dabert and Mironov 2015, Hernandes and Mironov 2015, Mironov et al. 2015, Wang and Proctor 2015). However, the true feather mite diversity of seabirds, particularly Procellariiformes (petrels and shearwaters), is poorly known and we expected to find a rich feather mite community on these hosts, including cryptic species. As expected, these communities were very rich with thirty-eight mite morphological species recorded, 17 of which are new species. Six of these new species are described integrating morphological and molecular data. I also made some corrections to the systematics of the feather mite genus *Laminalloptes*.

1.1 **L.M. Stefan**, W. Isbert, E. Gómez-Díaz, S.V. Mironov, K.D. McCoy, J. González-Solís (2016) Feather mite diversity and community structure in NE Atlantic and Mediterranean seabirds. In preparation

1.2 **L.M. Stefan**, E. Gómez-Díaz, S. Mironov (2013) Three new species of the feather mite subfamily Ingrassiinae (Acariformes: Xolalgidae) from shearwaters and petrels (Procellariiformes: Procellariidae). *Zootaxa* 3682: 105-120

1.3 **L.M. Stefan**, K. D. McCoy, S. Mironov (2014) A new species of the feather mite genus *Rhinozachvatkinia* (Acari: Avenzoariidae) from *Calonectris* shearwaters (Procellariiformes: Procellariidae): integrating morphological descriptions with DNA barcode data. *Folia Parasitologica* 61: 90-96

1.4 S.V. Mironov, **L.M**. **Stefan,** J.González-Solís (2015) New species of the feather mite genus *Promegninia* Gaud & Atyeo (Acari: Avenzoariidae) from petrels and shearwaters (Procellariiformes: Procellariidae). *Systematic Parasitology* 90: 91-103

1.5 S.V. Mironov, **L.M**. **Stefan** (2016) On identification of species in the feather mite genus *Laminalloptes* Dubinin, 1955 (Acari: Alloptidae). *Acarina* 24: 77-85

Chapter 2: DIVERSIFICATION PROCESSES. HOST VERSUS SPATIAL GENETIC STRUCTURE OF SEABIRD FEATHER MITE COMMUNITIES

The host species of feather mites have relatively wide distributions, but with clear delimitations at a population level. As feather mites develop their entire life cycle on the host body and should evolve in close association with their avian hosts, we expected to find highly divergent communities on different host species and/or strong population genetic structure among distinct geographic locations. The relative force of community structure related to host species versus geography can inform us about the role of each factor in generating and maintaining mite diversity. Here, I characterize the genetic structure of feather mite communities in relation to both host species (controlling for geography) and geography (controlling for host species).

2.1 **L.M. Stefan**, E. Gómez-Díaz, S.V. Mironov, J. González-Solís, K.D. McCoy (2016) Host-specificity and cryptic diversity of seabird feather mites: integrating morphological and genetic data. In preparation

2.2 **L.M. Stefan**, E. Gómez-Díaz, J. González-Solís, K.D. McCoy (2016) Contrasting patterns of diversity and genetic structure in ectofaunal communities of long-lived seabirds. In preparation

Chapter 3: SPATIAL DISTRIBUTION AND TROPHIC ECOLOGY OF SEABIRD FEATHER MITES

Feather mite species occupy very well defined habitats on the feathers. Thus, if more than one mite species inhabits the feathers of a seabird species, we would expect mite species to spatially segregate among bird feathers, and this niche partitioning to be induced by either space or resource use. This chapter focuses on the spatial distribution and trophic structure of two dominant and morphologically specialized feather mite species inhabiting the flight feathers of Cory´s shearwater *Calonectris borealis* to determine whether interspecific competition for resources drives within host distributional patterns.

3.1 **L.M. Stefan**, E. Gómez-Díaz, E. Elguero, H.C. Proctor, K.D. McCoy, J. González-Solís (2015) Niche partitioning of feather mites within a seabird host, *Calonectris borealis*. *PLoS ONE* 10: e0144728.

SUPERVISERS' REPORT

SUPERVISORS' REPORT

Dr. Karen D. McCoy and **Dr. Elena Gómez-Díaz,** co-supervisors of the doctoral thesis entitled: *"***Diversity, ecology and evolution of feather mites in seabirds***"* certify that the dissertation presented here has been carried out by **Laura Mihaela Stefan** in its totality and grants her the right to defend her thesis in front of a scientific committee.

As supervisors, we have participated in the design, guidance and correction of earlier drafts of the manuscripts written by the doctoral candidate. The contribution of the doctoral candidate and the impact factor (Thomson Institute for the Scientific Information) of each article is detailed below:

FEATHER MITE DIVERSITY AND COMMUNITY STRUCTURE IN NE ATLANTIC AND MEDITERRANEAN SEABIRDS
L.M. Stefan, W. Isbert, E. Gómez-Díaz, S.V. Mironov, K.D. McCoy, J. González-Solís (2016)
In preparation
L. M. Stefan has contributed to the study design, data analysis and scientific writing.

THREE NEW SPECIES OF THE FEATHER MITE SUBFAMILY INGRASSIINAE (ACARIFORMES: XOLALGIDAE) FROM SHEARWATERS AND PETRELS (PROCELLARIIFORMES: PROCELLARIIDAE)
L.M. Stefan, E. Gómez-Díaz, S.V. Mironov (2013)
Zootaxa 3682, 105-120
Impact Factor (2015/2016): 0.994
L. M. Stefan has contributed to the study design, data analysis and scientific writing.

A NEW SPECIES OF THE FEATHER MITE GENUS *RHINOZACHVATKINIA* (ACARI: AVENZOARIIDAE) FROM C*ALONECTRIS* SHEARWATERS (PROCELLARIIFORMES: PROCELLARIIDAE): INTEGRATING MORPHOLOGICAL DESCRIPTIONS WITH DNA BARCODE DATA
L.M. Stefan, K.D. McCoy, S.V. Mironov (2014)
Folia Parasitologica 61, 90-96
Impact Factor (2015/2016): 1.271
L. M. Stefan has contributed to the study design, data analysis and scientific writing.

NEW SPECIES OF THE FEATHER MITE GENUS *PROMEGNINIA* GAUD & ATYEO (ACARI: AVENZOARIIDAE) FROM PETRELS AND SHEARWATERS (PROCELLARIIFORMES: PROCELLARIIDAE)
S.V. Mironov, **L.M. Stefan**, J. González-Solís (2015)
Systematic Parasitology 90, 91-103
Impact Factor (2015/2016): 1.316
L. M. Stefan has contributed to the study design, data analysis and scientific writing.

ON IDENTIFICATION OF SPECIES IN THE FEATHER MITE GENUS *LAMINALLOPTES* DUBININ, 1955 (ACARI: ALLOPTIDAE)
S.V. Mironov, **L.M. Stefan** (2016)
Acarina 24, 77-85
Impact Factor (2015/2016): No Impact Factor
L. M. Stefan has contributed to the study design, data analysis and scientific writing.

HOST-SPECIFICITY AND CRYPTIC DIVERSITY OF SEABIRD FEATHER MITES: INTEGRATING MORPHOLOGICAL AND GENETIC DATA
L.M. Stefan, E. Gómez-Díaz, S.V. Mironov, J. González-Solís, K.D. McCoy (2016)
In preparation
L. M. Stefan has contributed to the study design, data analysis and scientific writing.

CONTRASTING PATTERNS OF DIVERSITY AND GENETIC STRUCTURE IN ECTOFAUNAL COMMUNITIES OF LONG-LIVED SEABIRDS
L.M. Stefan, E. Gómez-Díaz, J. González-Solís, K.D. McCoy (2016)
In preparation
L. M. Stefan has contributed to the study design, data analysis and scientific writing.

NICHE PARTITIONING OF FEATHER MITES WITHIN A SEABIRD HOST, *CALONECTRIS BOREALIS*
L.M. Stefan, E. Gómez-Díaz, E. Elguero, H.C. Proctor, K.D. McCoy, J. González-Solís (2015)
PLOS ONE 10: e0144728
Impact Factor (2015/2016): 3.057
L. M. Stefan has contributed to the study design, sampling collection, data analysis and scientific writing.

We also certify that none of the manuscripts included in this doctoral thesis has been used as a part of another doctoral thesis.

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CHAPTER 1

DIVERSITY OF SEABIRD FEATHER MITES

1.1 FEATHER MITE DIVERSITY AND COMMUNITY STRUCTURE IN NE ATLANTIC AND MEDITERRANEAN SEABIRDS

Laura M. Stefan, Wolf Isbert, Elena Gómez-Díaz, Sergey V. Mironov, Karen D. McCoy, Jacob González-Solís

In preparation

LA DIVERSIDAD Y ESTRUCTURA DE LA COMUNIDAD DE LOS ÁCAROS DE LAS PLUMAS EN AVES MARINAS DEL NE ATLÁNTICO Y MEDITERRÁNEO

RESUMEN

Los ácaros de las plumas (Astigmata: Pterolichoidea y Analgoidea) son los ectosimbiontes más comunes y diversos asociados con las aves, pero sólo una pequeña parte de su verdadera diversidad se ha descrito y examinado hasta ahora. Las aves marinas son huéspedes particularmente interesantes porque albergan una comunidad rica de ácaros de las plumas y crían en grandes colonias, a veces con contacto directo entre diferentes especies. En el presente estudio hemos explorado la diversidad y la estructura de la comunidad de los ácaros de las plumas en Procelariformes que crían en el Océano Atlántico del Nord-Este y Mar Mediterráneo. Hemos investigado las infracomunidades de ácaros en 11 especies de aves marinas en 28 colonias de cría. En base a criterios morfológicos, hemos identificado un total de 33 especies de ácaros, de los cuales 11 eran nuevas especies y seis recientemente descritas en base al material recogido en este muestreo. Las especies pertenecen a ocho géneros y tres familias: *Zachvatkinia, Rhinozachvatkinia, Promegninia* (Avenzoariidae), *Microspalax*, *Brephosceles*, *Plicatalloptes* (Alloptidae), *Ingrassia* and *Opetiopoda* (Xolalgidae). Entre los huéspedes, la mayor riqueza de los ácaros se encontró en las pardelas del genero *Calonectris* (nueve especies) y el petrel de Bulwer (*Bulweria bulwerii*; ocho especies), mientras que el petrel de Cabo Verde (*Pterodroma feae*) albergó la riqueza más baja (tres). Entre las 11 especies nuevas, cuatro se encontraron en el petrel de Bulwer y tres en las pardelas del género *Puffinus*. A nivel de la comunidad, nuestros resultados mostraron que la comunidad de los ácaros fue claramente estructurada por el género de huésped, mientras que la estructuración geográfica de los ácaros dentro del mismo género de huésped (entre las especies dentro de un género de huésped) o dentro de una misma especie de huésped (a través de varias localidades de muestreo) fue relativamente débil y, a veces insignificante. En cambio, tres especies de ácaros fueron compartidas por dos géneros cercanos de pardelas, *Calonectris* y *Puffinus*. Entre todas las colonias de cría, el archipiélago de Cabo Verde mostro la diversidad más alta de ácaros de las plumas, actuando como un punto caliente de la biodiversidad para estos ectosimbiontes. Este estudio destaca la inmensa y en gran parte no conocida diversidad de los ácaros de las plumas albergados por las aves marinas. Nuestros resultados también muestran la necesidad de investigar cuidadosamente datos genéticos, morfológicos y ecológicos de estos ectosimbiontes para entender mejor los procesos que han llevado a su alta diversidad.

FEATHER MITE DIVERSITY AND COMMUNITY STRUCTURE IN NE ATLANTIC AND MEDITERRANEAN SEABIRDS

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ABSTRACT

Feather mites (Astigmata: Pterolochoidea and Analgoidea) are the most common and diverse ectosymbionts associated with birds, but only a small part of their true diversity have been described and examined so far. Seabirds are particularly interesting hosts because they harbour a rich feather mite community and breed in large colonies, sometimes in close contact among species. In the present study we explored the diversity and community structure of feather mites in Procellariiformes breeding in the north-east Atlantic Ocean and Mediterranean Sea. We examined feather mite infracommunities in 11 seabird species at 28 breeding colonies. Based on morphological criteria, we identified a total of 33 feather mite species, of which 11 were undescribed and six recently described based on the material collected in this survey. These species belonged to eight genera and three families: *Zachvatkinia*, *Rhinozachvatkinia*, *Promegninia* (Avenzoariidae), *Microspalax*, *Brephosceles*, *Plicatalloptes* (Alloptidae), *Ingrassia* and *Opetiopoda* (Xolalgidae). Among hosts, the highest feather mite richness was found on *Calonectris* shearwaters (nine species) and Bulwer's petrel (*Bulweria bulwerii*; eight species), whereas Cape Verde Petrel (*Pterodroma feae*) harboured the lowest (three). Amongst the 11 new species, four were found in Bulwer's petrel and three in *Puffinus* shearwaters. At community level, our results showed that the mite community was clearly structured by host genera, whereas the geographic structuring of feather mites within host genera (i.e. among host species within a host genus) or within a single host species (across several sampling localities) was relatively weak and sometimes negligible. Instead, three mite species were shared by two closely related host genera, *Calonectris* and *Puffinus* shearwaters. Among all breeding colonies, Cape Verde Archipelago showed the highest feather mite diversity, which suggest it may act as biodiversity hotspot for these avian ectosymbionts. This study highlights the vast, and largely unrecognized, diversity of feather mites harboured by seabirds. Our findings also illustrate the need to carefully investigate genetic, morphologic and ecological data on these ectosymbionts for better understanding the processes that have lead to their high diversity.

Key-words: Procellariiformes, Astigmata, ectosymbionts, community assemblage, seabird-mite associations, host specificity

INTRODUCTION

Host specificity is a fundamental feature of symbionts (commensals, mutualists or parasites) which reflects the breadth of a symbiont's ecological niche and determines the likelihood that a symbiont will successfully colonize new habitats or adapt to new hosts (Poulin and Mouillot 2003, Poulin and Keeney 2008). Although parasites are considered to be highly host specific, important variation in specificity occurs among and within parasite taxa. Thus, some parasite taxa are highly host-specific, infecting only one or sometimes a few phylogenetically-related host species, whereas others are generalists, showing low host specificity and exploiting many (alternative) host species (Poulin 1997). For example, among fish parasites, monogeneans seem to be the most host-specific of all fish parasites, whereas acanthocephalans and cestodes show little host specificity (Poulin 1992). In birds, chewing lice and mites are seen as highly host-specific, while others, like fleas and ticks, are considered more generalists (Clayton and Price 1999, Proctor 2003, Dietrich et al. 2011). Specialist parasites seemed to prefer larger hosts than generalists do, which is probably related to their longer host life expectancy, since long-lived host may provide a more stable environment not subjected to unexpected changes (Sasal et al. 1999). Typically, the parasite population is unevenly distributed among its different host species, with a parasite species usually achieving high levels of infection in one host species (the principal host) and being less abundant in the other host species. In this sense, infection parameters like prevalence and intensity of infection can be used as a measure of host-specificity (Poulin 2005). Differences in the distribution and species richness of parasites among their different host species could be explained by host phylogeny but also by a wide array of ecological factors (e.g. host diet, body size, habitat, population size, metabolism, longevity, immune response, behaviour, geographic range, latitude) among different host species (Poulin 1995, Morand and Harvey 2000, Møller and Rózsa 2005, Nunn et al. 2005, Poulin 2005, Felsõ and Rózsa 2006, Hughes and Page 2007). It is expected that parasite richness increases with host body size, as larger-bodied hosts offer a larger surface area and more niches for colonization (Poulin 1995). Regarding the parasite species richness in seabirds, Hughes and Page (2007) found that patterns of louse diversity were explained only by a few host characteristics, especially host population size and geographic range.

Feather mites (Astigmata: Pterolichoidea and Analgoidea) are the most common and diverse group of ectosymbionts associated with birds that live exclusively on the body of their hosts (Dabert and Mironov 1999, Proctor 2003). They are adapted to inhabit different parts of the plumage such as flight feathers, large coverts of the wings or soft downy feathers and even the skin or the interior of feather quills (Gaud and Atyeo 1996, Proctor 2003, OConnor 2009). The large majority of known feather mite species is supposed to feed on uropygial gland secretions (predominantly waxes and fatty acids) and scurf, bacteria, fungi and pollen grains trapped between the feather barbs, usually without causing structural damage on the feathers (Proctor and Owens 2000, Blanco et al. 2001, Galván et al. 2008). Feather mites are considered to be highly specialized symbionts that depend and have evolved adaptations to the feather morphology and probably to the nature of the uropygial secretions (Proctor and Owens 2000, Proctor 2003). In general, almost all avian orders have their own specific feather mite faunas (Gaud and Atyeo 1996, Dabert and Mironov 1999). They usually are highly host-specific, so a particular feather mite species inhabits a single avian species or several closely related host species from the same genus (Gaud and Atyeo 1996, Dabert and Mironov 1999), although there are cases of mite species living on different host genera (e.g. *Analges passerinus* found on 27 species of small passerines from different genera and families; some species of *Brephosceles*, found on Gaviiformes, Procellariiformes, Anseriformes, Gruiformes and Charadriiformes). The most widely distributed feather mite family is Xolalgidae, known from 16 avian orders (Gaud and Atyeo 1996, Proctor 2003). However, these patterns must be taken with caution, since, despite their great diversity and wide distribution among hosts, only about 2 500 species of feather mites have been described so far, that likely represent a small part of their true diversity. However, it is assumed that the total number of feather mite species could be around 10 000 or even greater (Peterson 1975, Gaud and Atyeo 1996).

Seabirds, particularly Procellariiformes, are interesting hosts because they harbour a rich and diverse community of ectosymbionts composed of fleas, ticks, lice and mites (Clayton and Price 1999, Proctor 2003,

Adams et al. 2005, Dietrich et al. 2011). In addition, most seabirds breed in large and dense colonies on remote oceanic islands, sometimes in close contact with other seabird species, thus providing good opportunities for ectosymbiont transmission within and among host species. Interestingly, procellariiformes show two fundamental traits that constitute opposite forces in term of ectosymbiont dispersal and community structuring: they are highly mobile pelagic species, with a cosmopolitan distribution over all the major oceans of the world, but also show strong interannual fidelity and natal philopatry to their breeding sites (Brooke 2004, McCoy et al. 2013, 2016). To date, several studies have documented the feather mite fauna of procellariiform seabirds from various oceanic areas (Dubinin 1949, Černý 1967, Fitzpatrick and Threlfall 1977, Bourgeois and Threlfall 1979, Mironov 1989a, b, 2014). All feather mite species recorded from procellariiforms belong to six families: Alloptidae, Avenzoariidae, Dermationidae, Epidermoptidae, Xolalgidae and Freyanidae (Gaud and Atyeo 1996, Proctor 2003), with *Microspalax*, *Zachvatkinia* and *Brephosceles* being the most common genera found on these seabirds (Peterson 1971, Mironov 1989a, Atyeo and Gaud 1991). However, little information is available on feather mite community of petrels breeding on remote islands in the NE Atlantic and Mediterranean. Indeed, six new mite species, *Rhinozachvatkinia calonectris*, *Promegninia calonectris*, *Promegninia buweriae*, *Opetiopoda bulweriae*, *Ingrassia calonectris* and *Ingrassia micronota*, have been recently described based on the feather mite survey examined in the present study (Stefan et al. 2013, 2014, Mironov et al. 2015).

Therefore, the aims of the present study are: 1) to investigate the feather mite diversity within different populations of procellariiform seabirds, particularly Procellariidae and Hydrobatidae, breeding on islands distributed across the Mediterranean Sea and the north-eastern Atlantic archipelagos and 2) to examine patterns of community structure among these seabird feather mites.

MATERIAL AND METHODS

STUDY SPECIES AND SAMPLING

Our study focused on 11 procellariiform species, nine belonging to Procellariidae (Scopoli´s shearwater, *Calonectris diomedea*; Cory´s shearwater, *Calonectris borealis*; Cape Verde shearwater, *Calonectris edwardsii*; Manx shearwater, *Puffinus puffinus;* Mediterranean shearwater, *Puffinus yelkouan*; Macaronesian shearwater, *Puffinus baroli*; Boyd's shearwater, *Puffinus boydi*; Bulwer´s petrel, *Bulweria bulwerii* and Cape Verde petrel, *Pterodroma feae*) and two belonging to Hydrobatidae (band-rumped storm-petrel, *Hydrobates castro* and European storm-petrel, *Hydrobates pelagicus*). Overall, we collected samples from 28 breeding colonies, eight across the Mediterranean Sea (including Balearic Islands, Creta, Zembra, Hyeres, Murcia, Almeria) and 20 across the North-East Atlantic Ocean (including Iceland, Ireland, Scotland, Madeira, Berlengas, Azores archipelago, Canary Islands and Cape Verde archipelago) (Table 1, Figure 1). Bird captures and mite sampling were performed in accordance with good animal practices as defined by the current European legislation and under permission from corresponding governmental authorities of Spain, Portugal, France, Tunisia, Greece, North Ireland, Scotland, Iceland and Cape Verde. From 2003 to 2012, we collected feather mites from adult birds using the dust-ruffling method (Walther and Clayton 1997), except in Cory´s and Scopoli´s shearwaters. Due to their large body size, in these two species dust-ruffling was impractical and therefore we collected mites by visual inspection in barbs of primary and body feathers. In these two species, nearly all specimens harboured at least on mite species, but in any case visual detection would be lower than mite detection by dust-ruffling, and therefore prevalence of each mite species between these two methods should be treated with caution. All samples were stored in absolute ethanol at -20^{o}C for subsequent morphological identifications. In total, we collected and examined 931 feather mite samples covering all hosts and all geographic locations.

MORPHOLOGICAL IDENTIFICATIONS

Mites were cleared in lactic acid for 24h and mounted on microscope slides in PVA medium (BioQuip Products, Rancho Dominguez, California). The slides were cured on slide warmers at 40^{o}C for 4 days and then examined using a Leica DM 5000B light microscope with differential interference contrast (DIC) illumination.

Mites were identified in collaboration with Sergey Mironov using corresponding publications and keys for bonnetelline mites (Mironov 1989a, b), xolalgid mites (Dabert and Ehrnsberger 1991, Mironov and Palma 2006) and alloptid mites (Peterson and Atyeo 1968, Peterson 1971, Atyeo and Gaud 1991, Mironov 1996). Feather mite specimens were deposited in the Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia (ZISP).

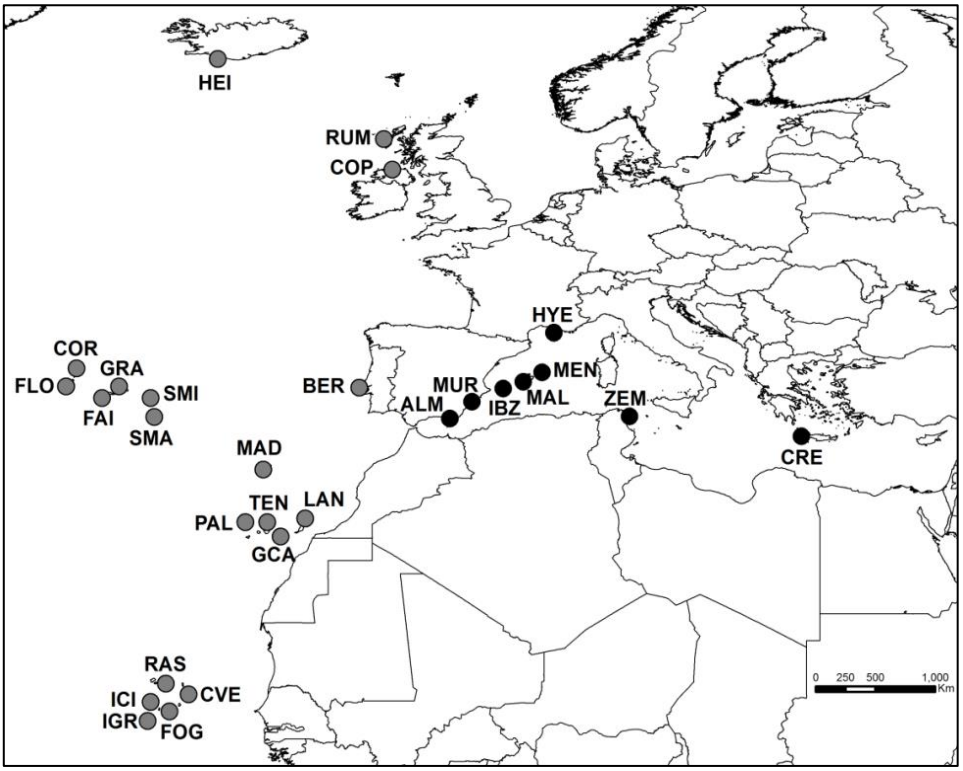

Figure 1. Map of the study area showing the 28 sampling localities for feather mites in procellariiform seabird species across the North-East Atlantic Ocean (grey circles) and Mediterranean Sea (black circles). Colony abbreviations are shown in Table 1.

FEATHER MITE COMMUNITY ANALYSES

For the analysis on the geographic structure of mite communities, due to the relatively low number of samples obtained in some localities and the large number of localities sampled, nearby breeding colonies were grouped by archipelagos. Therefore, Mallorca, Menorca and Ibiza were grouped into Balearic Islands; Tenerife, Gran Canaria, Lanzarote and La Palma were grouped into Canary Islands; Corvo, Flores, Faial, Graciosa, Sao Miguel and Santa Maria were grouped into Azores Islands; Raso, Curral Velho, Fogo, Ilhéu Cima and Ilhéu Grande were grouped into Cape Verde archipelago. The European storm-petrel was uneven and sparse and therefore not included in the analyses of mite community structure.

All analyses conducted in this study were based on presence-absence of each feather mite species for each examined host. Ecological terms for symbiont/parasite populations and communities follow Bush et al. (1997). Prevalence was calculated as the number of birds harbouring a particular symbiont species divided by the number of examined birds. Overall mite prevalence was calculated for each host species and each geographic location and compared among them by means Fisher's exact test using Quantitative Parasitology 3.0 software (QP3.0) (Rozsa et al. 2000). The Whittaker beta diversity and two different parameters for ectosymbiont species richness (Chao 2 and Jackknife1) were calculated for each host species and each breeding colony using PAST software (version 2.17c) (Hammer et al. 2001). Chao 2 is a non-parametric incidence-based estimator of species richness, whereas Jackknife 1 is a first-order jackknife estimator of species richness. The observed species richness (Sobs) were calculated and species accumulation curves were generated for each procellariiform species pooling data from the different sampling areas. Species accumulation curves represent

Table 1. Sample size of host examined and harbouring feather mites by seabird species and locality. The following abbreviations were used for the host species: CALDIO – *Calonectris diomedea*, CALBOR – *Calonectris borealis*, CALEDW – *Calonectris edwardsii*, PUFPUF – *Puffinus puffinus*, PUFYEL – *Puffinus yelkouan*, PUFBOY – *Puffinus boydi*, PUFBAR – *Puffinus baroli*, BULBUL – *Bulweria bulwerii*, PTEFEA – *Pterodroma feae*, HYDCAS – *Hydrobates castro* and HYDPEL – *Hydrobates pelagicus*.

Country	Locality	Code	Area	Code	Region	Code	Lat/Long	Host scientific name	Host abbreviation	Number of examined birds
Spain	Murcia	MUR			Western Mediterranean	WM	37°34'59"N/00°58'59"W	*Calonectris diomedea*	CALDIO	9
Spain	Ibiza	IBZ	Balearic Is.	BI	Western Mediterranean	WM	38°57'42"N/01°11'53"E	*Calonectris diomedea*	CALDIO	21
								Hydrobates pelagicus	HYDPEL	30
Spain	Mallorca	MAL	Balearic Is.	BI	Western Mediterranean	WM	39°39'58"N/02°34'53"E	*Calonectris diomedea*	CALDIO	9
Spain	Menorca	MEN	Balearic Is.	BI	Western Mediterranean	WM	39°48'07"N/04°17'16"E	*Calonectris diomedea*	CALDIO	7
								Hydrobates pelagicus	HYDPEL	3
France	Hyeres	HYE			Western Mediterranean	WM	43°00'32"N/06°12'38"E	*Calonectris diomedea*	CALDIO	4
								Puffinus yelkouan	PUFYEL	11
Tunisia	Zembra	ZEM			Western Mediterranean	WM	37°07'33"N/10°48'10"E	*Calonectris diomedea*	CALDIO	15
Spain	Almeria	ALM			Western Mediterranean	WM	37°20'56"N/01°39'02"W	*Calonectris borealis*	CALBOR	12
								Hydrobates pelagicus	HYDPEL	1
Greece	Crete	CRE			Eastern Mediterranean	EM	35°36'38"N/23°34'49"E	*Calonectris diomedea*	CALDIO	5
Iceland	Heimaey	HEI			Northern NE Atlantic	NNEA	63°27'00"N/20°15'00"W	*Puffinus puffinus*	PUFPUF	11
Ireland	Copeland	COP			Northern NE Atlantic	NNEA	54°40'29"N/05°31'44"W	*Puffinus puffinus*	PUFPUF	16
								Hydrobates pelagicus	HYDPEL	2
Scotland	Halival-Rum	RUM			Northern NE Atlantic	NNEA	57°00'05"N/06°19'21"W	*Puffinus puffinus*	PUFPUF	5
Portugal	Madeira	MAD			Central NE Atlantic	CNEA	32°20'40"N/16°29'08"W	*Calonectris borealis*	CALBOR	34
								Hydrobates castro	HYDCAS	6
Portugal	Berlengas	BER			Central NE Atlantic	CNEA	39°24'32"N/09°29'38"W	*Calonectris borealis*	CALBOR	16
								Hydrobates castro	HYDCAS	2
Spain	Gran Canaria	GCA	Canary Is.	CI	Central NE Atlantic	CNEA	27°50'40"N/15°47'19"W	*Calonectris borealis*	CALBOR	30
Spain	Lanzarote	LAN	Canary Is.	CI	Central NE Atlantic	CNEA	29°17'29"N/13°31'57"W	*Calonectris borealis*	CALBOR	12
								Puffinus baroli	PUFBAR	6
								Bulweria bulwerii	BULBUL	3
								Hydrobates castro	HYDCAS	1
Spain	Tenerife	TEN	Canary Is.	CI	Central NE Atlantic	CNEA	28°26'59"N/16°13'59"W	*Calonectris borealis*	CALBOR	8
Spain	La Palma	PAL	Canary Is.	CI	Central NE Atlantic	CNEA	28°48'54"N/17°45'54"W	*Bulweria bulwerii*	BULBUL	3
Portugal	Corvo	COR	Azores Is.	AI	Central NE Atlantic	CNEA	39°40'28"N/31°06'21"W	*Calonectris borealis*	CALBOR	15
Portugal	Flores	FLO	Azores Is.	AI	Central NE Atlantic	CNEA	39°22'29"N/31°11'50"W	*Calonectris borealis*	CALBOR	14
Portugal	Faial	FAI	Azores Is.	AI	Central NE Atlantic	CNEA	38°31'27"N/28°44'48"W	*Calonectris borealis*	CALBOR	12
Portugal	Graciosa	GRA	Azores Is.	AI	Central NE Atlantic	CNEA	39°03'20"N/27°57'17"W	*Calonectris borealis*	CALBOR	23
								Hydrobates castro	HYDCAS	4
Portugal	Sao Miguel	SMI	Azores Is.	AI	Central NE Atlantic	CNEA	37°43'02"N/25°25'59"W	*Calonectris borealis*	CALBOR	5

Country	Locality	Code	Area	Code	Region	Code	Lat/Long	Host scientific name	Host abbreviation	Number of examined birds
Portugal	Santa Maria	SMA	Azores Is.	AI	Central NE Atlantic	CNEA	36°56'31"N/25°10'17"W	*Calonectris borealis*	CALBOR	29
								Puffinus baroli	PUFBAR	4
								Bulweria bulwerii	BULBUL	17
								Hydrobates castro	HYDCAS	5
Cape Verde	Raso	RAS	Cape Verde	CV	Southern NE Atlantic	SNEA	16°36'36"N/24°36'00"W	*Calonectris edwardsii*	CALEDW	44
								Puffinus boydi	PUFBOY	29
								Bulweria bulwerii	BULBUL	31
								Hydrobates castro	HYDCAS	139
Cape Verde	Curral Velho	CVE	Cape Verde	CV	Southern NEAtlantic	SNEA	15°58'10"N/22°47'22"W	*Calonectris edwardsii*	CALEDW	20
								Hydrobates castro	HYDCAS	36
Cape Verde	Fogo	FOG	Cape Verde	CV	Southern NE Atlantic	SNEA	14°59'28"N/24°22'12"W	*Pterodroma feae*	PTEFEA	77
Cape Verde	Ilhéu Cima	ICI	Cape Verde	CV	Southern NE Atlantic	SNEA	14°58'11"N/24°38'21"W	*Puffinus boydi*	PUFBOY	29
								Bulweria bulwerii	BULBUL	30
								Hydrobates castro	HYDCAS	54
Cape Verde	Ilhéu Grande	IGR	Cape Verde	CV	Southern NE Atlantic	SNEA	14°58'09"N/24°41'20"W	*Bulweria bulwerii*	BULBUL	20
								Hydrobates castro	HYDCAS	12

the Sobs as well as two non-parametric methods (Chao2, Jackknife 1) and estimate the mite species number which would be collected as the number of samples approaches infinity. The analyses were conducted with PERMANOVA+ for PRIMER v6 software (Anderson et al. 2008). The calculations included all mite species detected. For the following analyses we used mite species exhibiting prevalence above 5% in single sampled areas unless otherwise indicated.

Mite infracommunities (all infrapopulations within an individual bird) were used as replicate samples in community similarity analyses using the PRIMER software package. We performed non-metric multi-dimensional scaling (NMDS) based on Jaccard similarities to obtain an ordination of mite infracommunities in individual birds from different host species or geographic locations. To assess the effects of host species or locality on the composition and structure of mite communities we used permutational multivariate analysis of variance (PERMANOVA) with host species or locality as a fixed factor. Permutation *P*-values were obtained under a reduced model of permutation of raw data (9999 permutations) and the Sum of Squares Type I (sequential). For these analyses we did not transform the data and added a dummy species with value 1 for all host individuals in order to include those seabirds harbouring no feather mites. In order to assess significant correlation between spatial variation in mite assemblages of host species and the absolute geographical distance between sampling areas we used the RELATE routine in the PRIMER v6 package. This Mantel-type test determined Spearman's correlation coefficients between the two similarity matrices (9999 permutations). This analysis was based on procellariiform species which had been sampled in more than one area with at least one infested host.

Patterns and similarities in biometric measures of the different procellariiform species were analysed and identified by means of a principal component analysis (PCA) using PRIMER v6. In the PCA analysis we included six biometric measures typically used for determining the size of the birds: bill length, bill depth at base, bill depth at nostril, maximum head length, tarsus length and wing length. All measurements were taken using a digital caliper (±0.01 mm), except for wing length, which was measured using a ruler (±0.5 mm). The first axis (PC1) explained the main share of the total variability and its values were used as a proxy o the body size of the individuals. We analysed the relationship between body size and mite community richness including all mite species using simple linear regression and Pearson's correlation. Furthermore, we conducted a one-way Analysis of Covariance (ANCOVA) to analyse the relationship between body size and mite community richness within each host species, with mite species number as dependent variable, locality as a fix factor and the PC1 of each individual host as a co-variable. This analysis was performed only on procellariiform species which had been sampled in more than one area.

Data on mite species richness per host species were analyzed for normality and homogeneity of variance (Shapiro-Wilk's test; Kolmogorov-Smirnov test and Levene's test). Since these variables did not approach normality even after logarithmic transformation, we used non-parametric statistics (Kruskal Wallis, Mann Whitney U test). These calculations as well as the simple linear regression and ANCOVA mentioned above were conducted with SPSS Statistics 17.0.

RESULTS

MORPHOLOGICAL DIVERSITY OF FEATHER MITES

On 11 studied procellariiform species we found 33 species of feather mite belonging to eight genera and three families: *Zachvatkinia*, *Rhinozachvatkinia*, *Promegninia* (Avenzoariidae), *Microspalax*, *Brephosceles*, *Plicatalloptes* (Alloptidae), *Ingrassia* and *Opetiopoda* (Xolalgidae) (Supplementary Information – Tables S1 and S2). Overall, we found 11 species of the feather mite genus *Brephosceles*, six of the genus *Zachvatkinia*, five in each of the genera *Microspalax* and *Ingrassia*, two in each of the genera *Zachvatkinia* and *Promegninia* and one

species in each of the genera *Plicatalloptes* and *Opetiopoda*. The highest number of feather mite species was found on two *Calonectris* shearwaters (nine species on Scopoli´s shearwater and eight on Cape Verde shearawater and Bulwer´s petrel), whereas Cape Verde petrel and Mediterranean shearwater harboured the lowest number of species (three). The species accumulation curves on mite richness reached a plateau for most host species (Bulwer´s petrel, Scopoli´s and Cory´s shearwaters, Boyd´s and Manx shearwaters, band-rumped strom-petrel) and Chao2 and Jackknife1 estimates conformed with this trend (see Supplementary Information – Figure S1). Rarefaction curves did not reach the asymptote for four host species (Cape Verde shearwater, Mediterranean shearwater, Macaronesian shearwater and Cape Verde petrel) indicating that mite richness for these host species may be slightly understimated.

The number of mite species varied among host species. For instance, among *Calonectris* species, Scopoli´s, Cape Verde and Cory´s shearwaters were inhabited by five, eight and nine mite species, respectively. Five mite species (*Z. ovata*, *M. brevipes*, *B. puffini*, *B. sp.4* and *Plicatalloptes sp.1*) were shared by all *Calonectris* hosts, three mite species (*I. calonectris*, *R. calonectris* and *P. calonectris*) were found only on Cory´s and Cape Verde shearwaters, while only one mite species, *M. ardennae*, was restricted to Cory´s shearwaters breeding in the northernmost colonies from NE Atlantic Ocean, such as Madeira, Berlengas and Azores archipelago. Regarding *Puffinus* shearwaters, Manx shearwaters and Boyd´s shearwaters were found to host six feather mite species, followed by Macaronesian shearwaters and Mediterranean shearwaters with four and three mite species, respectively. The mite species found on all *Puffinus* hosts were *Z. sp.1*, *B. puffini* and *I. dubinini*. Eight mite species were isolated from Bulwer´s petrels and three species from Cape Verde petrels (*Z. sp.3*, *M. pterodromae* and *B. disjunctus*). Finally, five and six mite species were found to inhabit band-rumped storm-petrels and European storm-petrels, respectively, from which only one species, *B. lanceolatus*, was shared by these two hosts (Tables 1, Supplementary Information – Tables S1 and S2). At the host genus level, in general, each bird genus harboured distinct feather mite species, except three mite species (*M. brevipes*, *B. puffini* and *P. sp.1*) shared by *Calonectris* and *Puffinus* shearwaters. The genus *Hydrobates* hosted the highest number of mite species (10), followed by *Calonectris* with nine species, *Bulweria* with eight species, *Puffinus* with six species and *Pterodroma* with only three mite species. Many feather mite genera, such as *Zachvatkinia*, *Microspalax*, *Brephosceles* and *Ingrassia*, co-occurred in multiple species of procellariiform seabirds, whereas *Rhinozachvatkinia*, *Promegninia* and *Plicatalloptes* were restricted to two host genera and *Opetiopoda* to one host species, the Bulwer´s petrel. Furthermore, each host genus/species carries only one mite species of a given genus, except *Microspalax*, where two different species inhabited Cory´s shearwaters, and *Brephosceles*, where two or more species co-occur on the same host genus/species and even on the same individual host. All examined seabird species harboured at least two *Brephosceles* species, except Cape Verde petrel with only one species (*B. disjunctus*) and European storm-petrel with three species. Finally, at the host family level, we found 23 mite species on the nine seabird species belonging to family Procellariidae and 10 mite species on the two seabird species belonging to the family Hydrobatidae.

Among the 33 feather mite species found on procellariiform seabirds, eleven corresponded to new undescribed species, of which six belonged to the genus *Brephosceles*, three to the genus *Zachvatkinia*, one to *Rhinozachvatkinia* and one to *Plicatalloptes*. The host harbouring the highest number of new species was Bulwer´s petrel with four species, followed by *Puffinus* shearwaters with three, *Calonectris* shearwaters and European storm-petrels with two species each and Cape Verde petrels with only one species. Only one new species (*P. sp.1*) was shared by two shearwater species. Some new host records have also been identified. Thus, *Z. ovata* and *Z. oceanodromae* have been found on Cape Verde shearwaters and band-rumped storm-petrels, respectively; *M. brevipes* was isolated from Cape Verde shearwaters and all *Puffinus* species included in this study; *B. puffini* was found on all host species belonging to *Calonectris* and *Puffinus* genera; *B. disjunctus* on Cape Verde petrels; *B. lanceolatus* on European storm-petrels, *I. oceanodromae* on band-rumped storm-petrels and *I. dubinini* on all *Puffinus* species examined here (see Supplementary Information – Tables S1 and S2).

When looking to the feather mite distribution by locality, we found the highest number of mite species in Cape Verde Archipelago with 27 species, followed by Canary Islands with 13 species, Madeira with 12 species and Azores and Balearic Islands with 11 species each, whereas the remaining Mediterranean colonies (Almeria, Murcia, Crete, Hyeres and Zembra) showed the lowest number of mite species (between three and five).

FEATHER MITE COMMUNITY STRUCTURE

From the 895 seabirds sampled in this study, 631 were infected with at least one mite species (931 and 655, respectively, if European storm-petrel was included). Overall, prevalence was 70.5% (CI: 67.4–73.4) including Scopoli´s and Cory´s shearwaters, while overall prevalence was 57.1% (CI: 53.1–61.0) when excluding these two host species for which a different sampling method was applied. Host species with high overall mite prevalence were Scopoli´s and Cory´s shearwaters (100%), Cape Verde shearwater (92.2%), Manx shearwater (90.6%) and Mediterranean shearwater (81.8%), whereas those with low prevalence were Cape Verde petrel and Macaronesian shearwater (36.4% and 20%, respectively) (Table 2). However, although nearly all Cory´s and Scopoli´s shearwaters certainly harboured at least one mite species, their 100% prevalence is an artefact of the sampling method used (see methods). Both estimators of species richness, Chao 2 and Jackknife 1, gave roughly similar results (Table 2). Chao 2 species richness estimator ranged from 1 for band-rumped storm-petrels breeding in Azores Is. to 9.8 for Bulwer´s petrels nesting in Canary Is. Regarding Jackknife 1 estimator, species richness ranged from 1for band-rumped storm-petrels breeding in Azores Is. to 10 for Cory´s shearwaters in the same breeding area. Overall, the values showed by Jackknife 1 were slightly higher than those of Chao 2 estimator.

We considered common feather mite species as those with a prevalence > 5% and found in host species in at least 50% of the sampled localities (Table 3). Eight mite species (*M. brevipes*, *Z. ovata*, *Z. sp.1*, *B. puffini*, *B. sp.4*, *B. sp.5*, *Plicatalloptes sp.1* and *I. dubinini*) were found to inhabit several species of *Calonectris* and *Puffinus* shearwaters across all their breeding colonies. Furthermore, two mite species (*M. brevipes* and *B. puffini*) were widely distributed among all sampled locations, while *Plicatalloptes sp.1* and *Z. ovata* were found in 12 and 11 breeding colonies, respectively.

The NMDS ordination based on relative similarities of feather mite infracommunities showed a clear separation among **the five seabird genera** (*Calonectris*, *Puffinus*, *Bulweria*, *Pterodroma* and *Hydrobates*; Figure 2A) with some overlapping between *Calonectris* and *Puffinus* samples. In contrast, the NMDS ordination showed little separation among **the five sampled regions** (NNEA, CNEA, SNEA, WM, EM; Figure 2B). The PERMANOVA exhibited significant effect for both factors, host genus (Pseudo-$F_{4,\ 822}$ = 106.3; $P_{(perm)}$ = 0.0001) and region (Pseudo-$F_{4,\ 822}$ = 7.7; $P_{(perm)}$ = 0.0001) on the mite communities, but also revealing a significant interaction between them (Pseudo-$F_{4,\ 822}$ = 8.6; $P_{(perm)}$ = 0.0001). Therefore, we performed separate analyses for each factor including post-hoc pairwise contrasts. When performed separately, the PERMANOVA indicated significant difference in feather mite infracommunity composition among both, the five host genera (Pseudo-$F_{4,\ 890}$ = 99.8; $P_{(perm)}$ = 0.0001) and among the five geographic regions (Pseudo-$F_{4,\ 890}$ = 36.3; $P_{(perm)}$ = 0.0001), but explaining 28.8 % and 21.8 % of the observed variation, while the residual variation was 37.2% and 41.5%, respectively. The greater F value for the factor host genus indicated a stronger effect of this factor. Pairwise contrasts between all genera and regions indicated significant differences in the mite community structure (all P ranging from 0.0001 to 0.02) except for the regions WM – EM (P > 0.05).

Table 2. Feather mite richness (prevalence - P%; mean and total species number; estimates for diversity and richness) by procellariiform seabirds species and locality across the NE Atlantic and Mediterranean (N1 = number of examined birds, N2 = number of infected birds). Birds sampled using a different method (direct sampling of barbs from primary and body feathers) are marked with *.

Host species	Locality/Area	N1	Overall P% (95%CI)	N2	Species number (mean ±SD)	Total species number	Whittaker (beta diversity)	Estimate of parasite species richness Chao 2 (± SD)	Estimate of parasite species richness Jackknife 1 (± SD)
BULBUL	Azores Is.	17	64.7 (40.6–83.4)	11	1.1 ±0.3	2	0.8	2.0 (± 0.1)	2.0 (± 0.0)
	Canary Is.	6	66.7 (27.1–93.7)	4	1.8 ±0.5	6	2.4	9.8 (± 4.6)	9.8 (± 0.8)
	Cape Verde	81	65.4 (54.3–75.4)	53	1.9 ±1.0	8	3.2	8.0 (± 0.0)	8.0 (± 0.0)
	Total	104	65.4 (55.8–74.1)	68	1.8 ±1.0	8	3.6	8.0 (± 0.0)	8.0 (± 0.0)
CALBOR*	Almeria	12	100.0 (75.5–100.0)	12	1.3 ±0.5	3	1.3	3.0 (± 0.4)	3.9 (± 0.9)
	Azores Is.	98	100.0 (96.1–100.0)	98	1.7 ±1.0	9	4.2	9.0 (± 0.2)	10.0 (± 1.0)
	Berlengas	16	100.0 (79.1–100.0)	16	2.3 ±1.2	7	2.0	7.0 (± 0.2)	7.0 (± 0.0)
	Canary Is.	50	100.0 (92.5–100.0)	50	2.0 ±1.0	7	2.5	7.0 (± 0.4)	8.0 (± 1.0)
	Madeira	34	100.0 (90.2–100.0)	34	2.1 ±1.2	8	2.8	8.0 (± 0.1)	9.0 (± 1.0)
	Total	210	100.0 (98.2–100.0)	210	1.9 ±1.1	9	3.8	9.0 (± 0.0)	9.0 (± 0.0)
CALDIO*	Balearic Is.	37	100.0 (90.9–100.0)	37	1.8 ±1.0	5	1.7	5.0 (± 0.1)	5.0 (± 0.0)
	Creta	5	100.0 (50.0–100.0)	5	2.2 ±0.8	4	0.8	4.8 (± 1.8)	5.6 (± 1.0)
	Hyeres	4	100.0 (48.3–100.0)	4	1.8 ±0.5	3	0.7	3.0 (± 0.3)	3.8 (± 0.8)
	Murcia	9	100.0 (67.7–100.0)	9	1.7 ±0.7	4	1.4	4.0 (± 0.4)	4.9 (± 0.9)
	Zembra	15	100.0 (77.8–100.0)	15	1.9 ±0.6	5	1.7	5.0 (± 0.4)	5.9 (± 0.9)
	Total	70	100.0 (94.6–100.0)	70	1.8 ±0.9	5	1.7	5.0 (± 0.0)	5.0 (± 0.0)
CALEDW	Cape Verde	64	92.2 (82.9–96.9)	59	3.0 ±1.6	8	1.7	8.0 (± 0.5)	8.9 (± 1.0)
HYDCAS	Azores Is.	9	100.0 (67.7–100.0)	9	1.0 ±0.0	1	0.0	1.0 (± 0.0)	1.0 (± 0.0)
	Berlengas	2	100.0 (22.4–100.0)	2	1.0 ±0.0	2	1.0	2.5 (± 1.1)	3.0 (± 0.0)
	Canary Is.	1	100.0 (5.1–100.0)	1	1.0 ±0.0	1	0.0	x	x
	Cape Verde	241	39.8 (33.8–46.3)	96	1.6 ±0.8	5	2.1	5.0 (± 0.0)	5.0 (± 0.0)
	Madeira	6	100.0 (58.9–100.0)	6	1.2 ±0.4	4	2.4	4.4 (± 1.1)	5.7 (± 1.1)
	Total	259	44.0 (38.0–50.2)	114	1.5 ±0.8	5	2.3	5.0 (± 0.0)	5.0 (± 0.0)

Host species	Locality/Area	N1	Overall P% (95%CI)	N2	Species number (mean ±SD)	Total species number	Whittaker (beta diversity)	Estimate of parasite species richness Chao 2 (± SD)	Estimate of parasite species richness Jackknife 1 (± SD)
PUFBAR	Azores Is.	4	0	0	0.0 ±0.0	0	x	x	x
	Canary Is.	6	33.3 (6.3–72.9)	2	3.0 ±1.4	4	0.3	4.2 (± 0.6)	5.0 (± 1.0)
	Total		20.0 (3.7–55.3)	2	3.0 ±1.4	4	0.3	4.2 (± 0.6)	5.0 (± 1.0)
PUFBOY	Cape Verde	58	72.4 (59.5–83.0)	42	2.3 ±1.4	6	1.6	6.0 (± 0.0)	6.0 (± 0.0)
PUFPUF	Heimaey	11	90.9 (59.7–99.5)	10	2.9 ±1.8	6	1.1	6.0 (± 0.2)	6.0 (± 0.0)
	Copeland	16	87.5 (62.8–97.7)	14	2.1 ±1.1	5	1.4	5.0 (± 0.4)	5.9 (± 0.9)
	Halival-Rum	5	100.0 (50.0–100.0)	5	3.2 ±1.1	6	0.9	6.0 (± 0.2)	6.8 (± 0.8)
	Total	32	90.6 (75.3–97.4)	29	2.6 ±1.4	6	1.3	6.0 (± 0.0)	6.0 (± 0.0)
PUFYEL	Hyeres	11	81.8 (50.0–96.7)	9	1.4 ±0.7	3	1.1	3.0 (± 0.4)	3.9 (± 0.9)
PTEFEA	Cape Verde	77	36.4 (26.0–48.0)	28	1.1 ±0.3	3	1.7	3.0 (± 0.4)	3.9 (± 1.0)

Table 3. The most common feather mite species found in procellariform seabirds of the NE Atlantic and Mediterranean, showing a prevalence > 5% and found in at least 50 % of the sampled localities for each host species. Abbreviations of seabird hosts and sampling localities are shown in Table 1.

Mite species	**Host species**	**Locality**
Microspalax brevipes	All *Calonectris* species	All localities
	All *Puffinus* species	
Brephosceles puffini	All *Calonectris* species	All localities
	PUFPUF, PUFBAR, PUFBOY	
Plicatalloptes sp.1	All *Calonectris* species	MUR, ZEM, CRE, BI, HEI, COP, RUM, BER, MAD, AI, CI, CV
	PUFPUF, PUFBOY	
Zachvatkinia ovata	All *Calonectris* species	ALM, MUR, HYE, ZEM, CRE, BI, BER, MAD, AI, CI, CV
Brephosceles sp.4	All *Calonectris* species	ZEM, BI, BER, MAD, AI, CI, CV
Zachvatkinia sp.1	All *Puffinus* species	HYE, HEI, COP, RUM, CI, CV
Ingrassia dubinini	All *Puffinus* species	HYE, HEI, COP, RUM, CI, CV
Brephosceles sp.5	PUFPUF, PUFBOY	HEI, COP, RUM, CV
Ingrassia calonectris	CALEDW	CV
	CALBOR	MAD, AI, CI
Rhinozachvatkinia calonectris	CALEDW	CV
	CALBOR	AI
Microspalax ardennae	CALBOR	BER, MAD, AI
Brephosceles sp.1	BULBUL	AI, CI, CV
Zachvatkinia sp.2	BULBUL	AI, CI, CV
Microspalax bulweriae	BULBUL	CI, CV
Ingrassia micronota	BULBUL	CI, CV
Zachvatkinia sp.3	PTEFEA	CV
Brephosceles disjunctus	PTEFEA	CV
Zachvatkinia oceanodromae	HYDCAS	BER, MAD, AI, CI, CV
Brephosceles decapus	HYDCAS	BER, MAD, CV

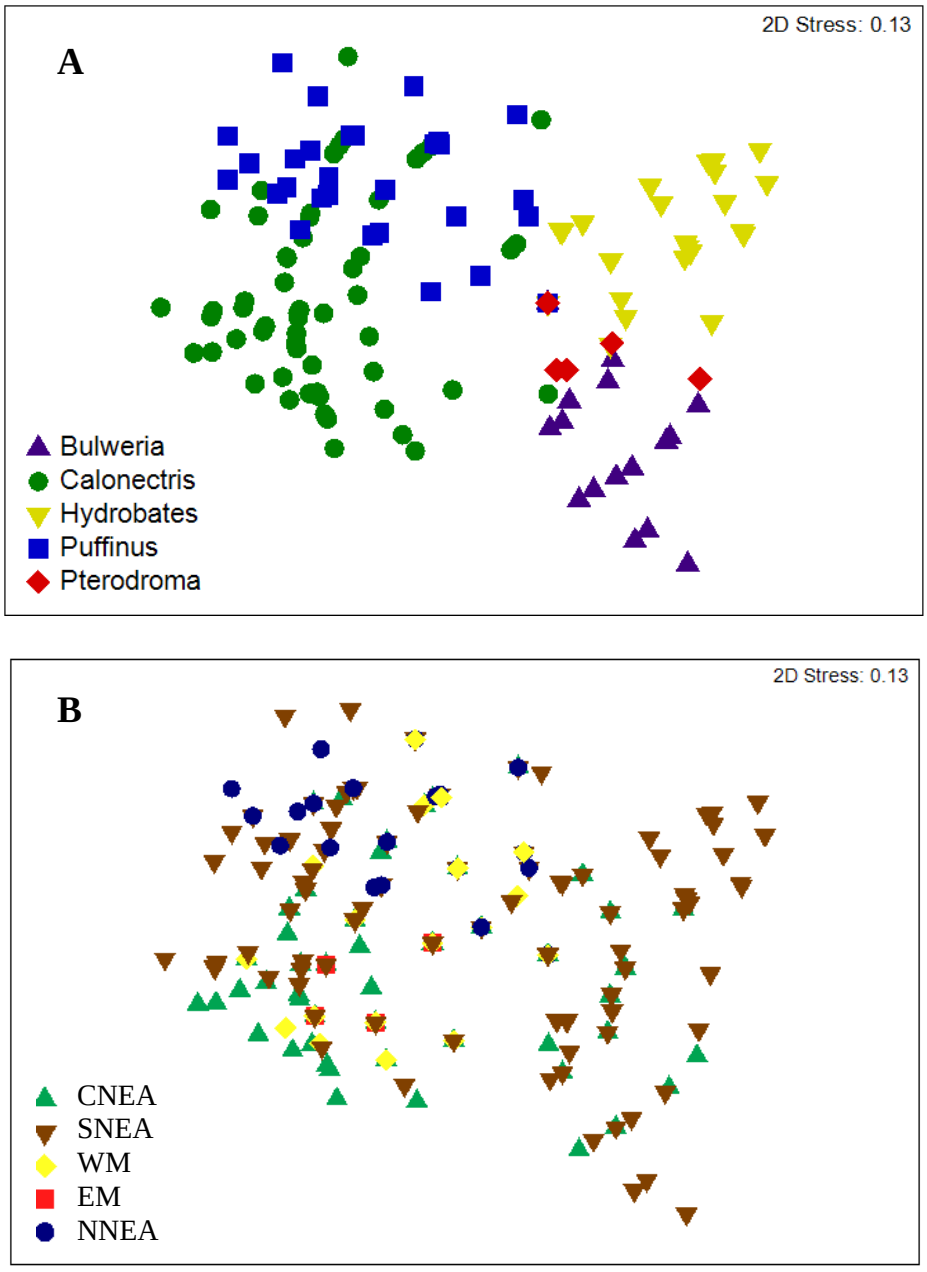

Figure 2. Non-metric multidimensional scaling ordination plot based on Jaccard similarities in mite species occurrence (data non-transformed) for (A) feather mite infracommunities of five procellariiform genera and (B) feather mite infracommunities of these five host genera presented as pooled data from five sampled regions, showing the higher importance of the factor host genus on the mite community structure. Abbreviations of the geographical regions are shown in Table 1.

Further detailed analyses were conducted on two procellariid genera, ***Puffinus* and *Calonectris***, for which a complete sampling from different bird species and geographic locations was conducted. For these seabird genera the visual inspection of NMDS ordination does not suggest a clear structure of mite infracommunities by host species (Figure 3A and B), but the PERMANOVA indicated significant difference in feather mite infracommunity composition in both genera, the *Puffinus* species (Pseudo-$F_{3, 107}$ = 3.1; $P_{(perm)}$ = 0.001) (Figure 3A) and the *Calonectris* species (Pseudo-$F_{2, 341}$ = 15.8; $P_{(perm)}$ = 0.0001) (Figure 3B). Host species factor explained only 12.2 and 15.1 % of the observed variation, respectively, while there was a substantial residual variation of 40.3 and 38.1 %, respectively. In total, three to six mite species were found in *Puffinus* species from different areas with a significantly different overall prevalence ranging from 20.0 to 90.6 % (Fisher's P < 0.001). The pairwise comparisons of prevalence resulted in significant differences only between Macaronesian shearwater and the three other species. Average similarities within individuals of the same *Puffinus* species ranged from 44.3 % for Manx shearwater to 73.0 % for Macaronesian shearwater, whereas similarities between different host species ranged from 41.2 % (Macaronesian shearwater – Manx shearwater) to 52.0 % (Macaronesian shearwater – Mediterranean shearwater). The pairwise contrast exhibited significant differences between most of the *Puffinus* spp. (P < 0.05) except for the pairs Boyd´s – Manx shearwaters and Boyd´s – Mediterranean shearwaters (P > 0.05). Significant differences in the mean number of mite species have been found among the four *Puffinus* species (Kruskal Wallis test: H/Chisquare = 9.348, P < 0.05), with differences only among Macaronesian shearwater (mean ± SD: 0.6 ± 1.3) and Manx shearwater (2.3 ± 1.5) (Mann Whitney test: Z = -2.50, P = 0.03) and Boyd´s shearwater (1.7 ± 1.6) and Manx shearwater (Mann Whitney test: Z = -2.04, P = 0.04) and marginal non-signficant between Manx shearwater and Mediterranean shearwater (1.2 ± 0.9) (Mann Whitney test Z:-2.18; P = 0.06). For the three *Calonectris* species the within group similarities ranged from 45.4 % (Cape Verde shearwater) to 54.9% (Scopoli´s shearwater) and calculated similarities between species were lowest in Cory´s – Cape Verde shearwaters (41.2 %) and highest in Cory´s – Scopoli´s shearwaters (51.0 %). Mean mite species richness in *Calonectris* species showed no significant difference between Cory´s shearwater (1.9 ± 1.0) and Scopoli´s shearwater (1.8 ± 0.9) (Mann Whitney test Z:-0.42; p > 0.05), while the value for the Cape Verde shearwater was higher (2.8 ± 1.7) but we decided not to test these difference because sampling methods for Cory's and Scopoli's shearwaters differed from those for Cape Verde shearwaters (see methods).

Regarding the structuring of feather mite communities by breeding localities within a host species, we focused **on two *Calonectris* species, the Scopoli´s and the Cory´s shearwaters**, due to their broad geographical distribution. The number of mite species ranged from three in Hyeres to five in Balearic Is. and Zembra for Scopoli´s shearwater and from three in Almeria to nine in Azores Is. for Cory´s shearwater (Table 2). Significant differences in the mean mite species richness have been found among the breeding colonies for Cory´s shearwater (Kruskal Wallis test: H/Chisquare = 11.7, P = 0.02), whereas no differences have been detected between the sampling areas for Scopoli´s shearwater (Kruskal Wallis test: H/Chisquare = 2.8, P > 0.05). For Cory´s shearwaters, pairwise comparisons revealed that mite species numbers differed significantly between Azores Is. and Canary Is and Berlengas, respectively, and between Almeria and the areas Canary Is, Madeira and Berlengas (Mann Whitney Z: -1.9 – 2.39; P < 0.05). The NMDS based on the mite species communities showed a lack of clear separation by breeding localities for Scopoli´s shearwaters in the Mediterranean Sea (Figure 4A), which was also confirmed by PERMANOVA (Pseudo-$F_{4, 65}$ = 1.3; $P_{(perm)}$ =0.23). This result indicates no geographic structuring of these mite communities. The pairwise contrast between areas showed overall high within group similarities ranging from 50.0 % (Murcia) to 69.3 % (Crete), and partly comparable similarities between groups with the lowest value between Murcia – Zembra (44.2 %) and the highest between Creta – Hyeres (70.2 %), indicating no separation of Crete from the Western Mediterranean areas. In the case of the Cory´s shearwaters breeding in the North-East Atlantic and Mediterranean (one colony in Almeria), the NMDS ordination showed some separation of mite communities by breeding localities (Figure 4B), and PERMANOVA indicated a significant geographic structuring (Pseudo-$F_{4, 205}$ = 13.2; $P_{(perm)}$ = 0.0001), with the factor locality explaining 19.6 % of the variation.

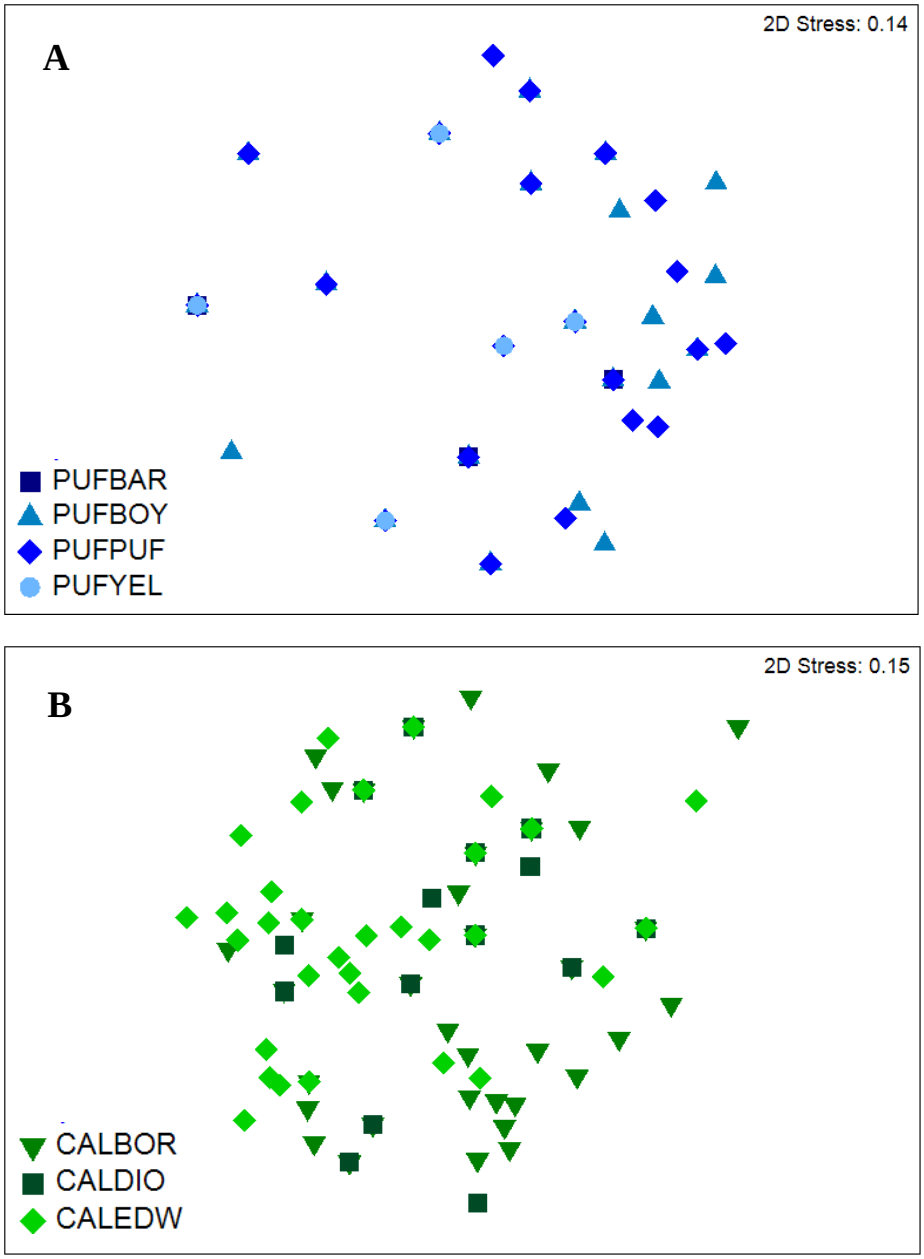

Figure 3. Non-metric multidimensional scaling ordination plot based on Jaccard similarities in mite species occurrence (data non-transformed) for (A) mite infracommunities of four species of *Puffinus* and (B) three species of *Calonectris* revealing no clear separation at species level. Data were pooled when host species were sampled in different areas (see Table 2). Abbreviations of the species are shown in Table 1.

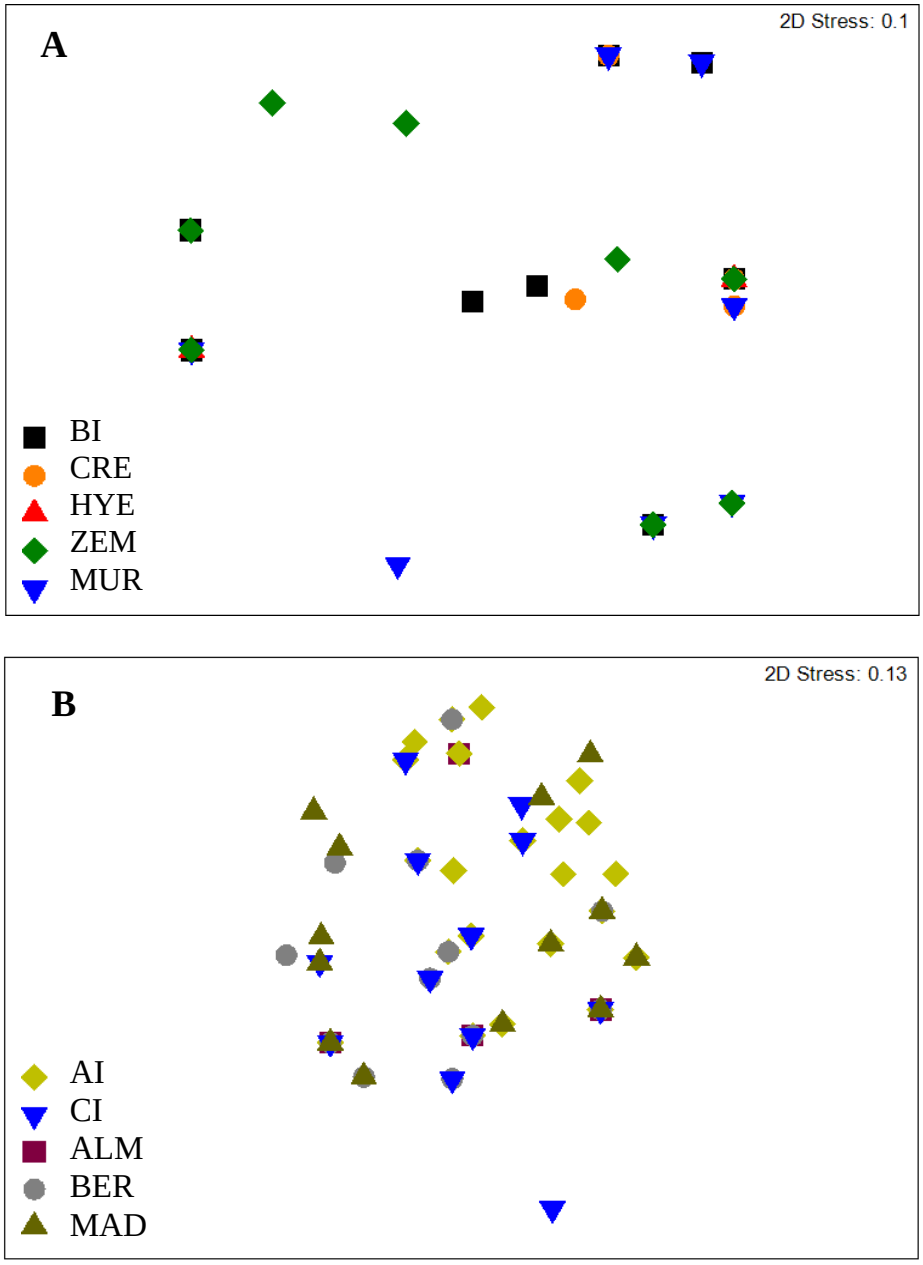

Figure 4. Non-metric multidimensional scaling ordination plot based on Jaccard similarities (data non-transformed) for mite infracommunities of (A) Scopoli´s shearwaters and (B) Cory´s shearwaters across their corresponding sampling localities. For both host species, no clear separation of mite infracommunities between localities was observed. Abbreviations of the geographical areas are shown in Table 1.

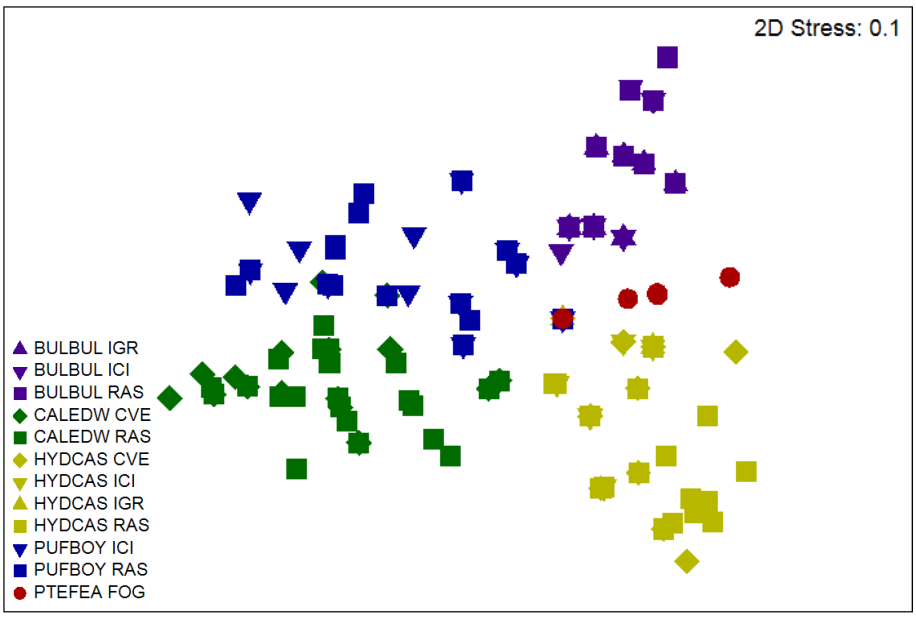

Figure 5. Non-metric multidimensional scaling ordination plot based on Jaccard similarities (data non-transformed) of mite infracommunities for five procellariiform species breeding in different localities of the Cape Verde archipelago. Each host species and sampled locality is represented by its own colours and icons, respectively. Abbreviations of the species and localities are shown in Table 1.

Pairwise contrast revealed significant different structuring in mite communities between the five sampled areas ($P < 0.05$), except between Canary Is. and Almeria, and Canary Is. and Berlengas. Within group similarities ranged between 45.1 % (Berlengas) and 63.1 % (Almeria) while between the areas similarities varied, with the highest values for Almeria – Canary Is (59.4 %) and Almeria – Azores Is (56.6 %) and lowest values for Berlengas – Madeira (40.2 %) and Berlengas – Azores Is (39.7 %). To test for the effect of geographic distance (among breeding localities of each host species) on the similarity of the mite communities, we correlated the matrix with the similarity index among mite communities with the matrix among geographic distances for each host species. Significant effect of the geographic distance on the similarity of the mite communities was found only for Cory´s shearwater, although *rho* was relatively low (RELATE: *rho* = 0.176, P = 0.0001).

Considering potential differences in the mite communities **on a smaller geographical scale**, data on mite infracommunities of five host species (Cape Verde shearwater, Boyd´s shearwater, Bulwer´s petrel, Cape Verde petrel and band-rumped storm-petrel) breeding in the **Cape Verde archipelago** were analysed. In these five host species, overall mite prevalence ranged from 36.4 to 92.2 %, exhibiting a significant difference (Fisher's $P < 0.001$) (Table 2). The NMDS ordination showed a clear separation of the mite communities by host species, some of which were sampled in the same localities (Figure 5). Nevertheless, the PERMANOVA revealed significant effects of both factors, host species (Pseudo-$F_{3, 509} = 59.4$; $P_{(perm)} = 0.0001$) and sampling locality (Pseudo-$F_{4, 509} = 15.5$; $P_{(perm)} = 0.0001$), on the mite communities, although showing a significant interaction between both factors (Pseudo-$F_{4, 509} = 4.4$; $P_{(perm)} = 0.0001$). Owing to this interaction, we performed separate analyses for each factor including post-hoc pairwise contrasts in cases of significance. When performed separately, the PERMANOVA indicated significant differences in mite community composition among the five host species (Pseudo-$F_{4, 516} = 52.1$; $P_{(perm)} = 0.0001$) and among the five localities (Raso, Curral Velho, Fogo, Ilheu Cima and Ilheu Grande) (Pseudo-$F_{4, 516} = 11.4$; $P_{(perm)} = 0.0001$). The factor host species exhibited a greater F value, which indicated a stronger effect on the mite community by this factor and explained 26.0 % of the observed variation compared to

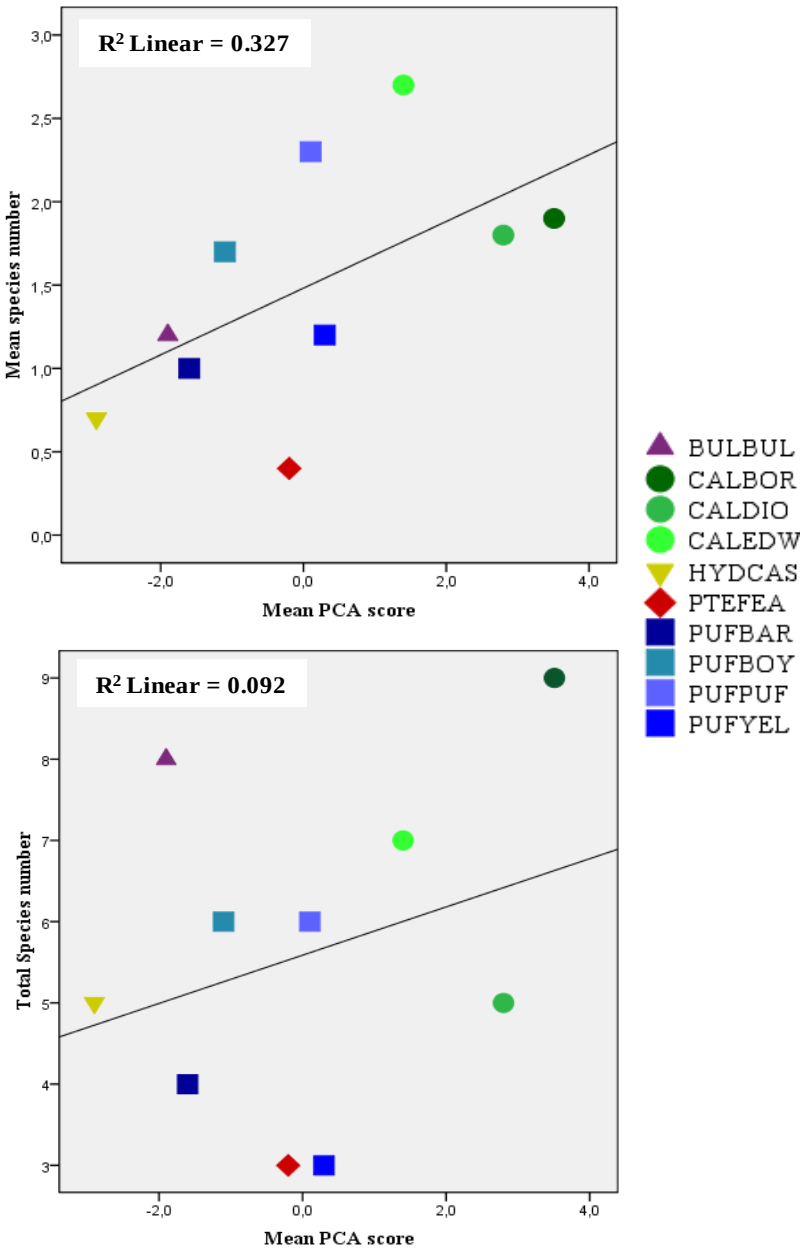

Figure 6. Regression plot indicating the relationship between the mite (A) **mean** species number and (B) **total** species number contrasted with PC1 of the PCA for 10 host species. Data collected from the same host species in different areas were pooled (see Table 2). Data was not transformed. Graph A exhibits a clear trend between both variables, while no trend was observed for the total species number and PC1. Abbreviations of the host species are shown in Table 1.

13.5 % explained by the factor locality. In both tests the residual variation was 35.1% and 39.9%, respectively. The pairwise contrasts between all host species and localities revealed significant differences in the mite community structure ($P < 0.01$ – $P = 0.0001$). Considering the main factor host species, similarities were low between Cape Verde shearwater and the other species ranging from 25.9 % (Bulwer´s petrel) to 31.1 % (Boyd´s shearwater). The average similarities were higher between Bulwer´s petrel and band-rumped storm-petrel (48.9 %), Bulwer´s petrel and Cape Verde petrel (51.8%) and Cape Verde petrel and band-rumped storm-petrel (63.8%).

The PCA analysis of six biometric measures of 10 procellariiform species revealed that PC1 accounted for 97.8 % of the total variation present (Eigenvalue = 6.85). This analysis comprised a sligtly smaller number of samples (792 individuals) as measurements were not available for all birds. The PC1 had very similar negative high loadings of all parameters measured (0.376 – 0.381) and no positive loading was observed. The visualization of the relationship between biometric measures and mite mean and total species number, by means of a regression plot, showed a tendency of larger host species to harbour a greater mean number of mite species ($R^2 = 0.33$), although, this relationship was marginally not significant (ANOVA $F_{1,8} = 3.89$, $P = 0.08$) (Figure 6A). No relationship could be observed between the total mite species number and the PC1, this relationship being marginally not significant ($R^2 = 0.09$; ANOVA: $F_{1,8} = 0.81$, $P > 0.05$) (Figure 6B). We performed one-way Analysis of Covariance (ANCOVA) to assess a potential relationship between body size (the co-variable PC1) and the mite species (dependent variable) at intraspecific host level, but correcting by the sampling locality (fix factor). However, in all analysed host species the co-variable did show a significant influence on mite species richness (all $P > 0.05$).

DISCUSSION

Seabirds are known to harbour rich ectofaunal communities, including ticks, fleas, mites and lice, but their feather mite communities have been poorly investigated. Furthermore, almost no information on feather mites living on seabirds breeding in the Mediterranean Sea and different archipelagos from north-east Atlantic Ocean is available. The present study revealed that the 11 procellariiform species breeding in these areas harboured a diverse and unique mite fauna composed by 33 species belonging to eight genera and three families. The most common feather mite species reported from these bird hosts belong to the genera *Brephosceles* (with 11 species), *Zachvatkinia* (with six species), *Microspalax* and *Ingrassia* (with five species each). Among all mite species found, one third (11 species) corresponded to new undescribed species (six of them recently described in Stefan et al. 2013, 2014, Mironov et al. 2015). These findings just show the poor investigation of the acarofauna of these host species, so far. Birds frequently harboured more than one feather mite species, and all seabird species examined in this study hosted at least three feather mite species (e.g. Mediterranean shearwater and Cape Verde petrel), with *Calonectris* shearwaters and Bulwer´s petrel presenting the highest mite richness, with nine and eight species, respectively. Species accumulation curves on mite richness reached a plateau in most host species, indicating that we detected all common mite species harboured by these seabirds. However, in four procellariiform species (Cape Verde shearwater, Mediterranean shearwater, Macaronesian shearwater and Cape Verde petrel) the asymptote was not reached, indicating a slight underestimation of their mite richness and therefore, further detailed sampling may reveal more mite species in these hosts.

Concerning the different genera of feather mites detected in this study, to date, 10 species of feather mite genus ***Microspalax*** Megnin and Trouessart, 1884 (Alloptidae) have been described, all associated with shearwaters (Procellariidae) and storm-petrels (Hydrobatidae); however it is assumed that many species still need to be described (Atyeo and Gaud 1991). Here, we found five *Microspalax* species, of which two, *M. brevipes* and *M. ardennae*, were associated with *Calonectris* and *Puffinus* shearwaters. The genus ***Zachvatkinia*** Dubinin, 1949 (Avenzoariidae) currently includes 15 species, of which only five are known from Procellariiformes of the families Diomedeidae, Procellariidae and Hydrobatidae (Mironov 1989a, 1992, Mironov and Stefan 2013, Negm et al. 2013). Other members of this genus are associated with gulls, terns and crab plovers (Charadriiformes: Laridae, Dromadidae). We identified six *Zachvatkinia* species on procellariiform seabirds breeding in Mediterranean and NE Atlantic areas, of which three appeared to be undescribed new species from petrels of the genera *Puffinus*, *Bulweria* and *Pterodroma*. Each *Zachvatkinia* species was restricted to a single host genus. Feather mites of the genus *Zachvatkinia* share their habitat on the wing feathers of procellariiform birds with two closely related avenzoariid genera, ***Rhinozachvatkinia*** and ***Promegninia***, which are restricted to these host orders (Dabert and Mironov 1999). Little information is available in the literature on feather mites about these two genera, with only

four species described so far for each genus (Gaud and Atyeo 1967, Mironov 1989b, 2014, Stefan et al. 2014, Mironov et al. 2015). In the present study we found two *Promegninia* species hosted by *Calonectris* shearwaters and Bulwer´s petrel, respectively, and two *Rhinozachvatkinia* species inhabiting the *Calonectris* shearwaters and European storm-petrel (this being a new species). Eighteen of the approximately 50 feather mite species of the genus ***Brephosceles*** Hull, 1934 (Alloptidae) form symbiotic associations with procellariiform seabirds and normally, two or more species of *Brephosceles* co-occur on the same host species and even on the same individual host (Peterson 1971). Here, eleven *Brephosceles* species were identified on the eleven procellariiform hosts and more than a half (six) represented undescribed new species. All examined seabird species harboured at least two species, except Cape Verde petrel with only one species, *B. disjunctus*. Furthermore, *B. puffini* was previously known only from *Puffinus* hosts, like *P. gravis* and *P. griseus* (Peterson 1971), whereas we found this species being shared by *Calonectris* and *Puffinus* shearwaters breeding in Mediterranean and NE Atlantic areas. Although, to date, no mites belonging to the genus *Brephosceles* were reported from Bulwer´s petrel, we identified three new mite species on this seabird host. The feather mite genus ***Plicatalloptes*** Dubinin, 1955 (Alloptidae) included so far seven species described from Ciconiiformes and Pelecaniformes (Mironov 1996), however we found one new species of this genus to be shared by the two related *Calonectris* and *Puffinus* shearwater genera. Feather mite genus ***Ingrassia*** Oudemans, 1905 (Xolalgidae) includes 28 species, with the majority of them (19) being associated with Charadriiformes and only six species being described from Procellariiformes (Stefan et al. 2013). Most extensive studies of diversity of this genus have been carried out in the Palaearctic region (Gaud 1974, Chirov and Mironov 1990, Dabert 2000) and in Africa (Gaud 1972). Five species of *Ingrassia* were found on five procellariiform genera, each host genus harbouring its own *Ingrassia* species. The genus ***Opetiopoda*** Gaud and Atyeo, 1981 was another xolalgid mite genus found in this study; it currently includes two species associated exclusively with Procellariiformes (Stefan et al. 2013). From the 11 studied seabird species, only Bulwer´s petrel hosted one species of *Opetiopoda* (*O. bulweriae*).

At community level, we found a clear specialization of feather mite communities by host genus at both large (among five large geographic regions) and small geographic scale (Cape Verde Archipelago). That is, the main seabird genera (*Calonectris*, *Puffinus*, *Bulweria*, *Pterodroma* and *Hydrobates*) harboured a distinct feather mite community. However, *Calonectris* and *Puffinus* shearwaters shared some mite species, a finding that could be explained by the close phylogenetic relationship between these two procellariid genera (Kennedy and Page 2002). The same pattern has been found at a smaller geographic scale (e.g. within Cape Verde Archipelago), where feather mite communities were clearly structured by host genus (each represented by a single species), even when these species breed in the same islets, some time in relatively close contact or at least sharing the same breeding habitat or even burrows.

Feather mite communities also appeared somewhat different among host species of a given host genus (e.g. *Calonectris* and *Puffinus*), indicating some structure among closely related host species possibly resulting from their parapatric distributions. For example, the three Calonectris species exhibit a parapatric distribution, which suggest a very limited contact between individuals of these host species and, therefore, a limited mite transmission among them, which probably result in a more clear structuring of their mite communities. Interestingly, mite community composition of Cape Verde shearwaters was more similar to that of the Scopoli´s shearwaters, despite a closer geographic proximity between Cape Verde and Cory´s shearwaters. This may mirror a closer relateness between Scopoli´s and Cape Verde shearwaters, whereas Cory´s shearwater would be the ancient clade. Indeed, a molecular study on *Calonectris* shearwaters estimated that Scopoli´s and Cory´s shearwaters have split 1 MYA ago, whereas the separation of Cape Verde shearwater from Scopoli´s shearwater probability occurred about 700,000 years ago (Gómez-Díaz et al. 2006). Some differences have also been observed in the mite species richness between the three *Calonectris* species. From the nine mite species found to inhabit these seabird hosts, five species (*Z. ovata, M. brevipes, B. puffini, B. sp.4* and *P. sp.1*) were shared by all three shearwater species,

three species (*R. calonectris, P. calonectris* and *I. calonectris*) were found only on two hosts (Cory´s shearwater and Cape Verde shearwater), whereas one species, *M. ardennae*, was restricted to Cory´s shearwaters breeding in the northenmost Atlantic colonies. This may suggest either different levels of host specificity exhibited by these mite species or some mite species have been missed during sampling, and particularly for the Scopoli´s shearwater which showed the lowest mite species richness among the three host species. However, this explanation is less likely since the sampling strategy used for this species was identicial to that used for the Cory´s shearwater (see methods) and overall sample sizes were greater for Scopoli´s shearwaters than for Cape Verde shearwaters.

Overall, our findings are in agreement with the hypothesis that differences in the relative infection levels (measured as prevalence, intensity or abundance) by a symbiont are proportional to the taxonomic or phylogenetic distance between different host species (Poulin 2005). However, previous studies have shown that other factors, such as ecological similarities among host species (e.g. similar diet, host habitat), may be as important in shaping parasite communities as host phylogeny (Bush et al. 1990, Poulin 2005). For example, in this study some differences in feather mite communities were also observed among five large geographic regions (Western Mediterranean, Eastern Mediterranean, Northern NE Atlantic, Central NE Atlantic and Southern NE Atlantic), but these appeared less marked than the patterns of mite community structure by host. Nevertheless, the relatively high degree of specialization exhibited by seabird feather mites could be inflated by the incomplete sampling of closely related host species. Indeed, some of the mite species detected in the present study were the first record for the host species, but had been previously found in other closely related host species, indicating one should be careful in concluding on the degree of host specificity of feather mites before all closely related host species have been thoroughly sampled.

After the present extensive survey across the NE Atlantic and Mediterranean seabirds, the Cape Verde archipelago was the richest locality in feather mite species, with 27 out of 33 mite species found in this region. In this way, these islands may represent an important biodiversity hotspot for avian feather mites. Although based on molecular data, similar results have also been reported for *Ornithodoros* seabird ticks (Gómez-Díaz et al. 2012). The high feather mite diversity observed in Cape Verde Islands is accompanied by a lower diversity found in the remaining Atlantic breeding colonies and Mediterranean Sea, which could indicate a colonization process of these seabird genera from tropics to more temperate areas. However, molecular data are needed to confirm hypotheses about the origin and phylogeography of these seabird feather mites.

When looking to the composition of mite community among breeding colonies within a host species, no geographic structuring has been observed for Scopoli´s shearwaters in the Mediterranean Sea, whereas certain degree of segregation of mite communities was found among localities for Cory´s shearwaters. The community structure observed in Cory´s shearwaters corresponds to a similarity by distance, as shown by the correlation between the matrice with the similarity index in mite communities and that with the geographic distances among sampled localities. Similar results have been reported for parasites of fish hosts, where adjacent localities displayed similar parasite communities than distant ones (Poulin and Morand 1999, Vidal-Martínez and Poulin 2003).

Furthermore, although not significant, there was a clear trend in larger seabird species to harbour a greater number of mite species. That is, on average *Calonectris* and *Puffinus* shearwaters, tended to host a greater number of species than the smaller seabirds, such as Bulwer´s petrels and European storm-petrels. On the contrary, overall mite species richness of each host species was not related to their body size. This apparent contradiction may just result from the fundamentally different processes driving them. The number of mite species for a given bird may increase with the body mass of its species possibly because larger seabirds provide more micro-habitats for mite species not to compite among them. Overall host species richness, however, is possibly driven by evolutionary

processes, such as mite co-speciation, when two lineages of the same host species become isolated for a certain period.

In conclusion, our results revealed a highly diverse feather mite community harboured by procellariiform seabirds breeding in the NE Atlantic Ocean and Mediterranean Sea, with 33 mite species identified, one third of which was represented by undescribed new species. In addition, feather mites showed a high degree of specialization at host genus level, whereas the geographic structuring of feather mites within host genera (i.e. among host species within a host genus) or within a single host species (across several sampling localities) was relatively weaker and sometimes negligible. This vast feather mite diversity supported by seabirds shows the need to carefully investigate these mite communities combining genetic, morphologic and ecological data for better understanding the processes that have led to their high diversity and specialization on their seabird hosts.

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SUPPLEMENTARY INFORMATION

Table S1. Morphological diversity of feather mites harboured by 11 procellariiform species breeding in the Mediterranean Sea and northeastern Atlantic Ocean ordered by host species. Species nominated as sp.1, sp.2, etc. are undescribed new species. * represents new host records.

Host species	Feather mite species	Locality	Region
Calonectris diomedea	*Zachvatkinia ovata*	Murcia, Ibiza, Mallorca, Menorca, Hyeres, Crete, Zembra	Mediterranean
	Microspalax brevipes	Murcia, Ibiza, Mallorca, Menorca, Hyeres, Crete, Zembra	Mediterranean
	Brephosceles puffini *	Murcia, Ibiza, Menorca, Hyeres, Crete, Zembra	Mediterranean
	Brephosceles sp.4	Ibiza, Zembra	Mediterranean
	Plicatalloptes sp.1	Murcia, Ibiza, Mallorca, Menorca, Crete, Zembra	Mediterranean
Calonectris borealis	*Zachvatkinia ovata*	Almeria	Mediterranean
		Madeira, Berlengas, Gran Canaria, Lanzarote, Tenerife, Corvo, Flores, Faial, Graciosa, Sao Miguel, Santa Maria	NE Atlantic
	Microspalax brevipes	Almeria	Mediterranean
		Madeira, Berlengas, Gran Canaria, Lanzarote, Tenerife, Corvo, Flores, Faial, Graciosa, Sao Miguel, Santa Maria	NE Atlantic
	Microspalax ardennae	Madeira, Berlengas, Corvo, Flores, Graciosa, Santa Maria	NE Atlantic
	Brephosceles puffini *	Almeria	Mediterranean
		Madeira, Berlengas, Gran Canaria, Lanzarote, Tenerife, Corvo, Flores, Faial, Graciosa, Sao Miguel, Santa Maria	NE Atlantic
	Brephosceles sp.4	Madeira, Berlengas, Gran Canaria, Lanzarote, Corvo, Flores, Faial, Graciosa, Sao Miguel	NE Atlantic
	Plicatalloptes sp.1	Madeira, Berlengas, Gran Canaria, Lanzarote, Tenerife, Corvo, Flores, Faial, Graciosa, Santa Maria	NE Atlantic
	Ingrassia calonectris	Madeira, Lanzarote, Flores, Santa Maria	NE Atlantic
	Rhinozachvatkinia calonectris	Corvo, Flores, Graciosa, Santa Maria	NE Atlantic
	Promegninia calonectris	Madeira, Berlengas, Gran Canaria, Corvo	NE Atlantic
Calonectris edwardsii	*Zachvatkinia ovata* *	Raso, Curral Velho	NE Atlantic
	Microspalax brevipes *	Raso, Curral Velho	NE Atlantic
	Brephosceles puffini *	Raso, Curral Velho	NE Atlantic
	Brephosceles sp.4	Raso, Curral Velho	NE Atlantic
	Plicatalloptes sp.1	Raso, Curral Velho	NE Atlantic
	Ingrassia calonectris	Raso, Curral Velho	NE Atlantic
	Rhinozachvatkinia calonectris	Raso, Curral Velho	NE Atlantic
	Promegninia calonectris	Raso	NE Atlantic
Puffinus puffinus	*Zachvatkinia sp.1*	Heimaey, Copeland, Halival-Rum	NE Atlantic
	Microspalax brevipes *	Heimaey, Copeland, Halival-Rum	NE Atlantic

Host species	Feather mite species	Locality	Region
	Brephosceles puffini *	Heimaey, Copeland, Halival-Rum	NE Atlantic
	Brephosceles sp.5	Heimaey, Halival-Rum	NE Atlantic
	Plicatalloptes sp.1	Heimaey, Copeland, Halival-Rum	NE Atlantic
	Ingrassia dubinini *	Heimaey, Copeland, Halival-Rum	NE Atlantic
Puffinus boydi	*Zachvatkinia sp.1*	Raso, Ilhéu Cima	NE Atlantic
	Microspalax brevipes *	Raso, Ilhéu Cima	NE Atlantic
	Brephosceles puffini *	Raso, Ilhéu Cima	NE Atlantic
	Brephosceles sp.5	Raso	NE Atlantic
	Plicatalloptes sp.1	Raso, Ilhéu Cima	NE Atlantic
	Ingrassia dubinini *	Raso, Ilhéu Cima	NE Atlantic
Puffinus baroli	*Zachvatkinia sp.1*	Lanzarote	NE Atlantic
	Microspalax brevipes *	Lanzarote	NE Atlantic
	Brephosceles puffini *	Lanzarote	NE Atlantic
	Ingrassia dubinini *	Lanzarote	NE Atlantic
Puffinus yelkouan	*Zachvatkinia sp.1*	Hyeres	Mediterranean
	Brephosceles puffini *	Hyeres	Mediterranean
	Ingrassia dubinini *	Hyeres	Mediterranean
Pterodroma feae	*Zachvatkinia sp.3*	Fogo	NE Atlantic
	Microspalax pterodromae	Fogo	NE Atlantic
	Brephosceles disjunctus *	Fogo	NE Atlantic
Bulweria bulwerii	*Zachvatkinia sp.2*	La Palma, Santa Maria, Raso, Ilhéu Cima, Ilhéu Grande	NE Atlantic
	Microspalax bulweriae	La Palma, Raso, Ilhéu Cima, Ilhéu Grande	NE Atlantic
	Brephosceles sp.1	Lanzarote, Santa Maria, Raso, Ilhéu Cima, Ilhéu Grande	NE Atlantic
	Brephosceles sp.2	Raso, Ilhéu Cima	NE Atlantic
	Brephosceles sp.3	Ilhéu Cima	NE Atlantic
	Ingrassia micronota	Lanzarote, Raso, Ilhéu Cima, Ilhéu Grande	NE Atlantic
	Opetiopoda bulweriae	Lanzarote, Raso	NE Atlantic
	Promegninia bulweriae	La Palma, Raso, Ilhéu Cima	NE Atlantic
Hydrobates castro	*Zachvatkinia oceanodromae* *	Madeira, Berlengas, Lanzarote, Graciosa, Santa Maria, Raso, Curral Velho, Ilhéu Cima, Ilhéu Grande	NE Atlantic
	Microspalax cymochoreae	Madeira, Raso, Curral Velho, Ilhéu Cima	NE Atlantic
	Brephosceles decapus	Madeira, Berlengas, Raso, Curral Velho	NE Atlantic
	Brephosceles lanceolatus	Raso, Curral Velho, Ilhéu Cima	NE Atlantic
	Ingrassia oceanodromae *	Madeira, Raso, Curral Velho, Ilhéu Cima	NE Atlantic
Hydrobates pelagicus	*Zachvatkinia hidrobatidii*	Ibiza	Mediterranean
	Rhinozachvatkinia sp.1	Ibiza	Mediterranean
	Brephosceles pelagicus	Ibiza, Menorca	Mediterranean
	Brephosceles lanceolatus *	Ibiza, Menorca	Mediterranean
	Brephosceles sp.6	Ibiza	Mediterranean
	Ingrassia oceanica	Ibiza	Mediterranean

Table S2. Morphological diversity of feather mites harboured by 11 procellariiform species breeding in the Mediterranean Sea and northeastern Atlantic Ocean ordered by feather mite species. Species nominated as sp.1, sp.2, etc. are undescribed new species. * represents new host records.

Feather mite species	Host species	Locality	Region
Fam. Avenzoariidae			
Zachvatkinia ovata	*Calonectris diomedea*	Murcia (Spain)	Mediterranean
		Ibiza, Mallorca, Menorca (Balearic Is. - Spain)	Mediterranean
		Hyeres (France)	Mediterranean
		Crete (Greece)	Mediterranean
		Zembra (Tunisia)	Mediterranean
	Calonectris borealis	Almeria (Spain)	Mediterranean
		Madeira (Portugal)	NE Atlantic
		Berlengas (Portugal)	NE Atlantic
		Gran Canaria, Lanzarote, Tenerife (Canary Is. - Spain)	NE Atlantic
		Corvo, Flores, Faial, Graciosa, Sao Miguel, Santa Maria (Azores Is. - Spain)	NE Atlantic
	Calonectris edwardsii *	Raso, Curral Velho (Cape Verde)	NE Atlantic
Zachvatkinia oceanodromae	*Hydrobates castro* *	Madeira (Portugal)	NE Atlantic
		Berlengas (Portugal)	NE Atlantic
		Lanzarote (Canary Is. - Spain)	NE Atlantic
		Graciosa, Santa Maria (Azores Is. - Spain)	NE Atlantic
		Raso, Curral Velho, Ilhéu Cima, Ilhéu Grande (Cape Verde)	NE Atlantic
Zachvatkinia hidrobatidii	*Hydrobates pelagicus*	Ibiza (Balearic Is. - Spain)	Mediterranean
Zachvatkinia sp.1	*Puffinus puffinus*	Copeland (Northern Ireland)	NE Atlantic
		Heimaey (Iceland)	NE Atlantic
		Halival-Rum (Scotland)	NE Atlantic
	Puffinus boydi	Raso, Ilhéu Cima (Cape Verde)	NE Atlantic
	Puffinus baroli	Lanzarote (Canary Is. - Spain)	NE Atlantic
	Puffinus yelkouan	Hyeres (France)	Mediterranean
Zachvatkinia sp.2	*Bulweria bulwerii*	La Palma (Canary Is. - Spain)	NE Atlantic
		Santa Maria (Azores Is. - Spain)	NE Atlantic
		Raso, Ilhéu Cima, Ilhéu Grande (Cape Verde)	NE Atlantic
Zachvatkinia sp.3	*Pterodroma feae*	Fogo (Cape Verde)	NE Atlantic
Rhinozachvatkinia calonectris	*Calonectris borealis*	Corvo, Flores, Graciosa, Santa Maria (Azores Is. - Spain)	NE Atlantic
	Calonectris edwardsii	Raso, Curral Velho (Cape Verde)	NE Atlantic
Rhinozachvatkinia sp.1	*Hydrobates pelagicus*	Ibiza (Balearic Is. - Spain)	Mediterranean
Promegninia calonectris	*Calonectris borealis*	Madeira (Portugal)	NE Atlantic
		Berlengas (Portugal)	NE Atlantic

Feather mite species	Host species	Locality	Region
		Gran Canaria (Canary Is. - Spain)	NE Atlantic
		Corvo (Azores Is. - Spain)	NE Atlantic
	Calonectris edwardsii	Raso (Cape Verde)	NE Atlantic
Promegninia bulweriae	*Bulweria bulwerii*	La Palma (Canary Is. - Spain)	NE Atlantic
		Raso, Ilhéu Cima (Cape Verde)	NE Atlantic
Fam. Alloptidae			
Microspalax brevipes	*Calonectris diomedea*	Murcia (Spain)	Mediterranean
		Ibiza, Mallorca, Menorca (Balearic Is. - Spain)	Mediterranean
		Hyeres (France)	Mediterranean
		Crete (Greece)	Mediterranean
		Zembra (Tunisia)	Mediterranean
	Calonectris borealis	Almeria (Spain)	Mediterranean
		Madeira (Portugal)	NE Atlantic
		Berlengas (Portugal)	NE Atlantic
		Gran Canaria, Lanzarote, Tenerife (Canary Is. - Spain)	NE Atlantic
		Corvo, Flores, Faial, Graciosa,	NE Atlantic
		Sao Miguel, Santa Maria (Azores Is. - Spain)	
	Calonectris edwardsii *	Raso, Curral Velho (Cape Verde)	NE Atlantic
	Puffinus puffinus *	Copeland (Northern Ireland)	NE Atlantic
		Heimaey (Iceland)	NE Atlantic
		Halival-Rum (Scotland)	NE Atlantic
	Puffinus boydi *	Raso, Ilhéu Cima (Cape Verde)	NE Atlantic
	Puffinus baroli *	Lanzarote (Canary Is. - Spain)	NE Atlantic
Microspalax ardennae	*Calonectris borealis*	Madeira (Portugal)	NE Atlantic
		Berlengas (Portugal)	NE Atlantic
		Corvo, Flores, Graciosa, Santa Maria (Azores Is. - Spain)	NE Atlantic
Microspalax bulweriae	*Bulweria bulwerii*	La Palma (Canary Is. - Spain)	NE Atlantic
		Raso, Ilhéu Cima, Ilhéu Grande (Cape Verde)	NE Atlantic
Microspalax pterodromae	*Pterodroma feae*	Fogo (Cape Verde)	NE Atlantic
Microspalax cymochoreae	*Hydrobates castro*	Madeira (Portugal)	NE Atlantic
		Raso, Curral Velho, Ilhéu Cima (Cape Verde)	NE Atlantic
Brephosceles puffini	*Calonectris diomedea* *	Murcia (Spain)	Mediterranean
		Ibiza, Menorca (Balearic Is. - Spain)	Mediterranean
		Hyeres (France)	Mediterranean
		Crete (Greece)	Mediterranean
		Zembra (Tunisia)	Mediterranean
	Calonectris borealis *	Almeria (Spain)	Mediterranean
		Madeira (Portugal)	NE Atlantic
		Berlengas (Portugal)	NE Atlantic
		Gran Canaria, Lanzarote, Tenerife (Canary Is. - Spain)	NE Atlantic

Feather mite species	Host species	Locality	Region
		Corvo, Flores, Faial, Graciosa, Sao Miguel, Santa Maria (Azores Is. - Spain)	NE Atlantic
	Calonectris edwardsii *	Raso, Curral Velho (Cape Verde)	NE Atlantic
	Puffinus puffinus *	Copeland (Northern Ireland)	NE Atlantic
		Heimaey (Iceland)	NE Atlantic
		Halival-Rum (Scotland)	NE Atlantic
	Puffinus boydi *	Raso, Ilhéu Cima (Cape Verde)	NE Atlantic
	Puffinus baroli *	Lanzarote (Canary Is. - Spain)	NE Atlantic
	Puffinus yelkouan *	Hyeres (France)	Mediterranean
Brephosceles decapus	*Hydrobates castro*	Madeira (Portugal)	NE Atlantic
		Berlengas (Portugal)	NE Atlantic
		Raso, Curral Velho (Cape Verde)	NE Atlantic
Brephosceles pelagicus	*Hydrobates pelagicus*	Ibiza, Menorca (Balearic Is. - Spain)	Mediterranean
Brephosceles lanceolatus	*Hydrobates castro*	Raso, Curral Velho, Ilhéu Cima (Cape Verde)	NE Atlantic
	Hydrobates pelagicus *	Ibiza, Menorca (Balearic Is. - Spain)	Mediterranean
Brephosceles disjunctus	*Pterodroma feae* *	Fogo (Cape Verde)	NE Atlantic
Brephosceles sp.1	*Bulweria bulwerii*	Lanzarote (Canary Is. - Spain)	NE Atlantic
		Santa Maria (Azores Is. - Spain)	NE Atlantic
		Raso, Ilhéu Cima, Ilhéu Grande (Cape Verde)	NE Atlantic
Brephosceles sp.2	*Bulweria bulwerii*	Raso, Ilhéu Cima (Cape Verde)	NE Atlantic
Brephosceles sp.3	*Bulweria bulwerii*	Ilhéu Cima (Cape Verde)	NE Atlantic
Brephosceles sp.4	*Calonectris diomedea*	Ibiza (Balearic Is. - Spain)	Mediterranean
		Zembra (Tunisia)	Mediterranean
	Calonectris borealis	Madeira (Portugal)	NE Atlantic
		Berlengas (Portugal)	NE Atlantic
		Gran Canaria, Lanzarote (Canary Is. - Spain)	NE Atlantic
		Corvo, Flores, Faial, Graciosa, Sao Miguel (Azores Is. - Spain)	NE Atlantic
	Calonectris edwardsii	Raso, Curral Velho (Cape Verde)	NE Atlantic
Brephosceles sp.5	*Puffinus puffinus*	Heimaey (Iceland)	NE Atlantic
		Halival-Rum (Scotland)	NE Atlantic
	Puffinus boydi	Raso (Cape Verde)	NE Atlantic
Brephosceles sp.6	*Hydrobates pelagicus*	Ibiza (Balearic Is. - Spain)	Mediterranean
Plicatalloptes sp.1	*Calonectris diomedea*	Murcia (Spain)	Mediterranean
		Ibiza, Mallorca, Menorca (Balearic Is. - Spain)	Mediterranean
		Crete (Greece)	Mediterranean
		Zembra (Tunisia)	Mediterranean
	Calonectris borealis	Madeira (Portugal)	NE Atlantic
		Berlengas (Portugal)	NE Atlantic
		Gran Canaria, Lanzarote, Tenerife (Canary Is. - Spain)	NE Atlantic

Feather mite species	Host species	Locality	Region
		Corvo, Flores, Faial, Graciosa, Santa Maria (Azores Is. - Spain)	NE Atlantic
	Calonectris edwardsii	Raso, Curral Velho (Cape Verde)	NE Atlantic
	Puffinus puffinus	Copeland (Northern Ireland)	NE Atlantic
		Heimaey (Iceland)	NE Atlantic
		Halival-Rum (Scotland)	NE Atlantic
	Puffinus boydi	Raso, Ilhéu Cima (Cape Verde)	NE Atlantic
Fam. Xolalgidae			
Opetiopoda bulweriae	*Bulweria bulwerii*	Lanzarote (Canary Is. - Spain)	NE Atlantic
		Raso (Cape Verde)	NE Atlantic
Ingrassia calonectris	*Calonectris borealis*	Madeira (Portugal)	NE Atlantic
		Lanzarote (Canary Is. - Spain)	NE Atlantic
		Flores, Santa Maria (Azores Is. - Spain)	NE Atlantic
	Calonectrisedwardsii	Raso, Curral Velho (Cape Verde)	NE Atlantic
Ingrassia dubinini	*Puffinus puffinus* *	Heimaey (Iceland)	NE Atlantic
		Copeland (Northern Ireland)	NE Atlantic
		Halival-Rum (Scotland)	NE Atlantic
	Puffinus boydi *	Raso, Ilhéu Cima (Cape Verde)	NE Atlantic
	Puffinus baroli *	Lanzarote (Canary Is. - Spain)	NE Atlantic
	Puffinus yelkouan *	Hyeres (France)	Mediterranean
Ingrassia micronota	*Bulweria bulwerii*	Lanzarote (Canary Is. - Spain)	NE Atlantic
		Raso, Ilhéu Cima, Ilhéu Grande (Cape Verde)	NE Atlantic
Ingrassia oceanodromae	*Hydrobates castro* *	Madeira (Portugal)	NE Atlantic
		Raso, Curral Velho, Ilhéu Cima (Cape Verde)	NE Atlantic
Ingrassia oceanica	*Hydrobates pelagicus*	Ibiza (Balearic Is. - Spain)	Mediterranean

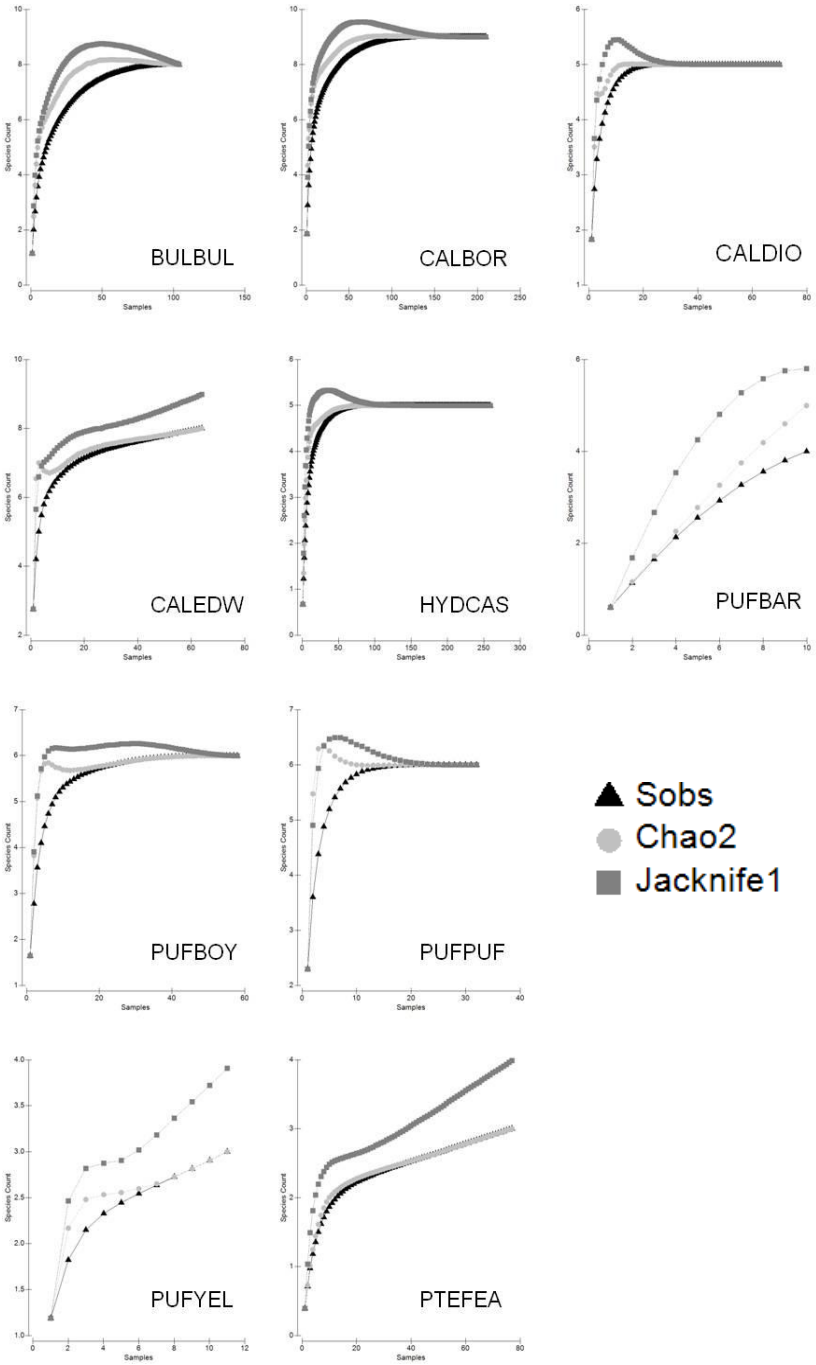

Figure S1. Mite species accumulation curves for 10 procellariiform host species. Data is pooled over all sampled areas. Species observed (Sobs) - black triangles; Chao2 estimator - light grey circles; Jackknife1 - dark grey squares.

1.2 THREE NEW SPECIES OF THE FEATHER MITE SUBFAMILY INGRASSIINAE (ACARI: XOLALGIDAE) FROM SHEARWATERS AND PETRELS (PROCELLARIIFORMES: PROCELLARIIDAE)

Laura M. Stefan, Elena Gómez-Díaz, Sergey V. Mironov

Zootaxa, 3682: 105-120, 2013

TRES NUEVAS ESPECIES DE ÁCAROS DE LAS PLUMAS DE LA SUBFAMILIA INGRASSIINAE (ACARIFORMES: XOLALGIDAE) EN PARDELAS Y PETRELES (PROCELLARIIFORMES: PROCELLARIIDAE)

RESUMEN

Se describen tres nuevas especies de ácaros de las plumas de la subfamilia Ingrassiinae (Acariformes: Astigmata: Xolalgidae) en pardelas y petreles (Procellariiformes: Procellariidae) del noreste del Océano Atlántico: *Ingrassia calonectris* **sp. n.** en *Calonectris borealis* (Cory) (huésped tipo) y *Calonectris edwardsii* (Oustalet), *Ingrassia micronota* **sp. n.** y *Opetiopoda bulweriae* **sp. n.** en *Bulweria bulwerii* (Jardine and Selby).

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Three new species of the feather mite subfamily Ingrassiinae (Acariformes: Xolalgidae) from shearwaters and petrels (Procellariiformes: Procellariidae)

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Abstract

Three new species of the feather mite subfamily Ingrassiinae (Acariformes: Astigmata: Xolalgidae) are described from shearwaters and petrels (Procellariiformes: Procellariidae) in the North-East of Atlantic Ocean: *Ingrassia calonectris* **sp. n.** from *Calonectris borealis* (Cory) (type host) and *Calonectris edwardsii* (Oustalet), *Ingrassia micronota* **sp. n.** and *Opetiopoda bulweriae* **sp. n.** from *Bulweria bulwerii* (Jardine and Selby).

Key words: Acariformes, feather mites, Xolalgidae, Ingrassiinae, systematics, Aves, Procellariiformes

Introduction

Feather mites (Acariformes: Astigmata) are a very diverse and abundant group of astigmatan mites that live permanently on the body of birds. They are highly specialized ectosymbionts adapted to inhabit well-defined host microhabitats including flight feathers, down, skin and even feather quills (Gaud & Atyeo 1996; Proctor 2003; OConnor 2009). Feather mites have been reported from all avian orders, including penguins, which were traditionally believed to be mite-free because of their strongly modified plumage and subaquatic lifestyle (Mironov & Proctor 2008). Despite their great diversity and wide distribution among hosts, only about 2500 species of feather mites have been described until now, which likely represent only a very small part of the true world mita fauna. It is assumed that the potential number of feather mite species could be twice as great as the number of recent avian species (Peterson 1975).

In the present paper we described three new species of the feather mite subfamily Ingrassiinae (Analgoidea: Xolalgidae), two from the genus *Ingrassia* Oudemans, 1905 and one from the genus *Opetiopoda* Gaud and Atyeo, 1981, from three species of Procellariiformes.

The representatives of the subfamily Ingrassiinae, as for all Xolalgidae, are relatively small-sized and generally weakly sclerotized feather mites that mainly inhabit the downy parts of covert feathers and feed on uropygial gland secretions (Gaud & Atyeo 1996; Mironov 2005). Mites of this subfamily have been recorded from hosts belonging to 16 avian orders (Gaud & Atyeo 1981a, 1996; Mironov & Proctor 2008). In a generic revision of the family Xolalgidae, Gaud and Atyeo (1981a, 1981b) gave uniform diagnoses for genera and listed all valid species that were known up to that time. Within the subfamily Ingrassiinae these authors recognized 57 species in 14 genera. Subsequent investigations of the systematics and biodiversity of ingrassiines were mainly dedicated to mites from Charadriiformes (Chirov & Mironov 1990; Dabert & Ehrnsberger 1991; Vasyukova & Mironov 1991; Dabert 2000; Mironov & Palma 2006) and Psittaciformes (Atyeo & Gaud 1987; Mejía-Gonzalez & Pérez 1988; Pérez 1995, 1996; Dabert *et al.* 2007) and to much less extent to those from other avian orders, such as Falconiformes, Pelecaniformes, Strigiformes and Sphenisciformes (Mironov 1997; Mironov & Galloway 2002;

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Dabert *et al*. 2008; Mironov & Proctor 2008). A morphology-based phylogenetic analysis of the family Xolalgidae supported the monophyly of the subfamily Ingrassinae and most of its genera (Mironov 2005).

Material and methods

The material was collected by Drs. Jacob González-Solís and Elena Gómez-Díaz from 2003 to 2012 from live procellariiform birds breeding on different archipelagos in the North-East of Atlantic Ocean: Cape Verde, Azores and Madeira. Bird capturing and handling, and mite sampling were made in accordance with good animal practice as defined by the current European legislation and under permissions from corresponding governmental authorities of Spain, Portugal and Cape Verde. Feather mites, sampled using the dust-ruffling method (for *C. edwardsii* and *B. bulwerii*) (Clayton & Moore 1997; Walther & Clayton 1997) or direct sampling of barbs from primary feathers (for *C. borealis*), were cleared in lactic acid for 24h and mounted on microscope slides in PVA medium (BioQuip Products, Rancho Dominguez, California). The descriptions of the new species follow the standard used for xolalgid mites (Dabert & Ehrnsberger 1991; Mironov & Palma 2006). Drawings were made using a Leica DM 5000B light microscope with DIC illumination and camera Lucida.

Morphological terms and the leg chaetotaxy follow Gaud and Atyeo (1996). Idiosomal chaetotaxy also follows these authors with corrections for coxal setae proposed by Norton (1998). All the measurements are in micrometers (μm). The measuring techniques for particular structures are as follows:

(i) length of idiosoma is measured from the anterior margin of the propodosoma to the lobar apices (in males) and to the posterior margin of opisthosoma (in females); width of idiosoma is measured as the widest portion of the humeral area;
(ii) hysterosoma is measured from the level of the sejugal furrow on lateral margins of the body to the lobar apices or posterior margin of opisthosoma;
(iii) distance between setae of the same pair is the direct distance between their bases, and distance between different pairs of setae is the shortest distance between the transverse levels formed by the setae of respective pairs;
(iv) hysteronotal shield length in males is the greatest length from the anterior margin to the lobar apices bearing setae *h3*; width is measured at the anterior margin;

The taxonomic system and scientific names of birds follow Clements *et al*. (2012) and Sangster *et al.* (2012). All type and additional materials are deposited in ZISP—Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia.

Taxonomy

Family Xolagidae Dubinin, 1953

Subfamily Ingrassiinae Gaud and Atyeo, 1981

Genus *Ingrassia* Oudemans, 1905

Type species: *Megninia veligera* Oudemans, 1904 by original designation.

Ingrassia is the most species-rich genus within the subfamily Ingrassiinae, including 26 species up to now (Černý 1967; Gaud 1972; Gaud & Atyeo 1981a; Chirov & Mironov 1990; Dabert & Ehrnsberger 1991; Vasyukova & Mironov 1991; Dabert 2000; Mironov & Palma 2006; Mironov and Proctor 2008). Its representatives have been recorded on hosts from 6 orders of aquatic birds: Anseriformes, Charadriiformes, Pelecaniformes, Podicipediformes, Procellariiformes and Sphenisciformes.

The majority of currently known *Ingrassia* species (19) are associated with charadriiform avian hosts, with only few species described from other avian orders mentioned above. The most extensive studies of diversity of

Ingrassia have been carried out in the Palaearctic region (Vitzthum 1921; Dubinin 1949; Gaud 1974; Chirov & Mironov 1990; Vasyukova & Mironov 1991; Dabert 2000) and in Africa (Gaud 1972). Identification keys to species of *Ingrassia* are available only for those associated with Charadriiformes from Africa (Gaud 1972) and Northern Eurasia (Chirov & Mironov 1990; Vasyukova & Mironov 1991). To date, only four species of *Ingrassia* are known from procellariiform birds: *Ingrassia dubinini* (Černý 1967) from Procellariidae (*Puffinus* spp.), *I. oceanica* (Vitzthum 1921) and *I. oceanodromae* (Černý 1967) from Hydrobatidae (*Hydrobates pelagicus* Linnaeus and *Oceanodroma leucorhoa* Vieillot, respectively) and *I. antarctica* (Gaud 1952) from Pelecanoididae (*Pelecanoides georgicus* Murphy and Harper). Most species known from avian hosts other than charadriiforms are need in of modern redescriptions.

***Ingrassia calonectris* sp. n.**
(Figs. 1–3)

Type material. Male holotype (ZISP 5032), 1 male paratype from *C. borealis* Cory (Procellariidae), PORTUGAL, Azores Archipelago, 9 June 2003, col. J. González-Solís and E. Gómez-Díaz; 1 female paratype (ZISP 5033), same host and location, 16 August 2003, col. J. González-Solís and E. Gómez-Díaz.

Additional material. 1 male (ZISP 5034) from *C. borealis*, PORTUGAL, Madeira Archipelago, Desertas Island, 19 September 2005, col. E. Gómez-Díaz; 1 male (ZISP 5035) from same host and same locality, 21 September 2005, col. J. González-Solís; 3 males and 1 female (ZISP 5036) from *C. edwardsii*, CAPE VERDE, Cape Verde Archipelago, Boa Vista, Curral Velho Islet, 9 July 2007, col. J. González-Solís; 2 males and 2 females (ZISP 5037) from same host and same locality, 12 July 2006, col. J. González-Solís; 2 males and 1 female (ZISP 5038) from same host, CAPE VERDE, Cape Verde Archipelago, Raso Island, 7 June 2008, col. P. Rodrigues; 5 males and 4 females (ZISP 5039–5041) from same host and same locality, 8 March 2007, col. J. González-Solís.

Description. MALE (holotype, measurements for paratype in parentheses): length of idiosoma from anterior end to bases of setae *h3* 290 (290), greatest width 195 (205), length of hysterosoma 155 (155). Prodorsal shield: narrow longitudinal plate with strongly attenuate anterior and posterior ends, membranous longitudinal crest present in the anterior one third of this shield, length 80 (75), greatest width 20 (20), posterior end strongly extending beyond level of scapular setae *se* (Fig. 1A). Setae *se* separated by 73 (68) situated on finely striated tegument, setae *si* slightly anterior to level of setae *se*. Scapular shields wide, inner margin convex, smooth, without suprategumental extension. Hysteronotal shield: anterior margin roughly sinuous, length of shield from anterior end to bases of setae *h3* 175 (173). Setae *c2* and *d2* filiform, 20–30 long, much shorter than humeral macrosetae *cp*. Supranal concavity ovate, open posteriorly into terminal cleft. Length of terminal cleft from anterior end of concavity to base of setae *h3* 83 (85), greatest width of terminal cleft 45 (50). Terminal membranous extensions on lobar apices tongue-like, with longitudinal striae, length from base of setae *h3* to apices of terminal extensions 33 (33), width at base 23 (20), length of incision between extensions 30 (30). Setae *ps1* situated approximately at level of setae *h2*. Distance between dorsal setae: *c2*:*c2* 123 (123), *c2*:*d2* 33 (35), *d2*:*e2* 50 (50), *e2*:*h3* 70 (75), *h3*:*h3* 38 (40), *ps1*:*ps1* 28 (28).

Sternum about 2/3 of total length of epimerites I. Inner ends of epimerites IIIa free, widely separated from each other (Fig. 1B). Setae *4b* situated on ends of epimerites IIIa and extending to level of lobar apices. Pregenital apodeme (epiandrium) bow-shaped, 8 (9) long, 28 (27) wide. Genital apparatus small, 9 (10) × 20 (21). Adanal shields present, represented by small L-shaped sclerites between levels of setae *g* and *ps3.* Anal shields small, represented by minute transverse sclerites between setae *ps3* and anal suckers. Epimerites IVa present, long, almost completely enclosing coxal fields IV. Central part of coxal fields IV not sclerotized. Diameter of anal suckers 18 (20). Distance between ventral setae: *4b:4b* 40 (38), *4b:3a* 23 (25), *4b:g* 38 (38), *g:ps3* 23 (25), *ps3:h3* 25 (25).

Tarsi I, II each with a well-expressed apico-dorsal extension. Tibia I and II with spine-shaped ventral processes (Figs. 3A, B). Tibia III with flat spine-like extension at base of solenidion φ; tarsus III widened at base, with crest a long lateral margin and with small finger-like apical extension, length of tarsus III 65 (73) (Fig. 3C). Tarsus IV with finger-like apical extension bearing setae *d*, *e* (Fig. 3D). Legs IV excluding pretarsus 123 (123) long, articulation of genu and tibia at level of setae *h2;* tarsus IV extending by distal half beyond level of terminal membranous extensions.

FEMALE (paratype): Length of idiosoma 305, greatest width 175, length of hysterosoma 180. Prodorsal

shield: narrow longitudinal plate with slightly attenuated ends; anterior end bifurcated with short longitudinal crest (about 1/5 of total length of the shield); posterior end with small incision or straight and extending to midlevel between scapular setae and *c2*; length 90, greatest width 20 (Fig. 2A). Scapular setae *si* and *se* situated on finely striated tegument. Setae *se* separated by 75, setae *si* slightly anterior to level of *se*. Scapular shields with smooth inner margin. Humeral shields well-developed without antero-mesal extensions. Setae *c3* short, subequal to total length of femur and genu III. Hysteronotal shield: a longitudinal plate occupying median part of hysterosoma; anterior end with median extension, lateral margins unevenly sinuous, posterior part noticeably narrowed and truncate, extending slightly beyond level of setae *e2*; length 125, greatest width 38. Setae *c2*, *d2*, and *e2* filiform, about 20 long, noticeably shorter than trochanters III. Setae *d1*, *d2*, and *e1* situated on lateral margins of hysteronotal shield, setae *c2*, *e2* situated on striated tegument. Distance between dorsal setae: *c2*:*d2* 58, *d2*:*e2* 65, *e2*:*h3* 55, *h3*:*h3* 28.

Sternum slightly shorter than half the -length of epimerites I. Epigynum thick, bow-shaped, 13 long, 35 wide, tips bearing bases of setae *4b*. Apodemes of oviporus long, posterior ends narrowed and rounded, extending to midlevel of epimerites IVa (Fig. 2B). Setae *4b* long, almost extending to posterior tips of oviporus apodemes, setae *g*, *3a*, *4a* short, not exceeding the length of femoragenu III, IV. Setae *h3* approximately half as long as setae *h2*.

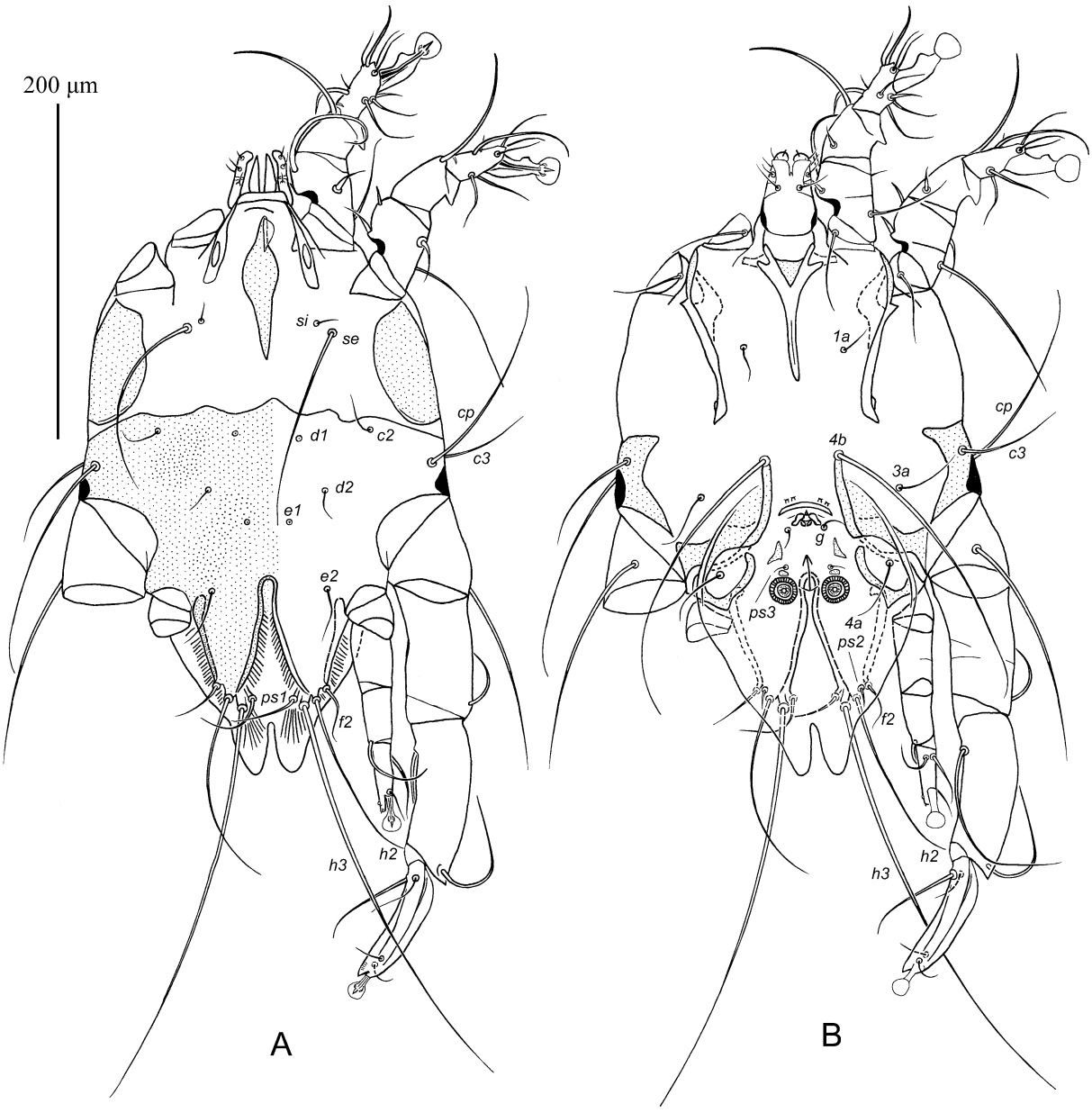

FIGURE 1. *Ingrassia calonectris* **sp. n.**, male. A—dorsal view, B—ventral view.

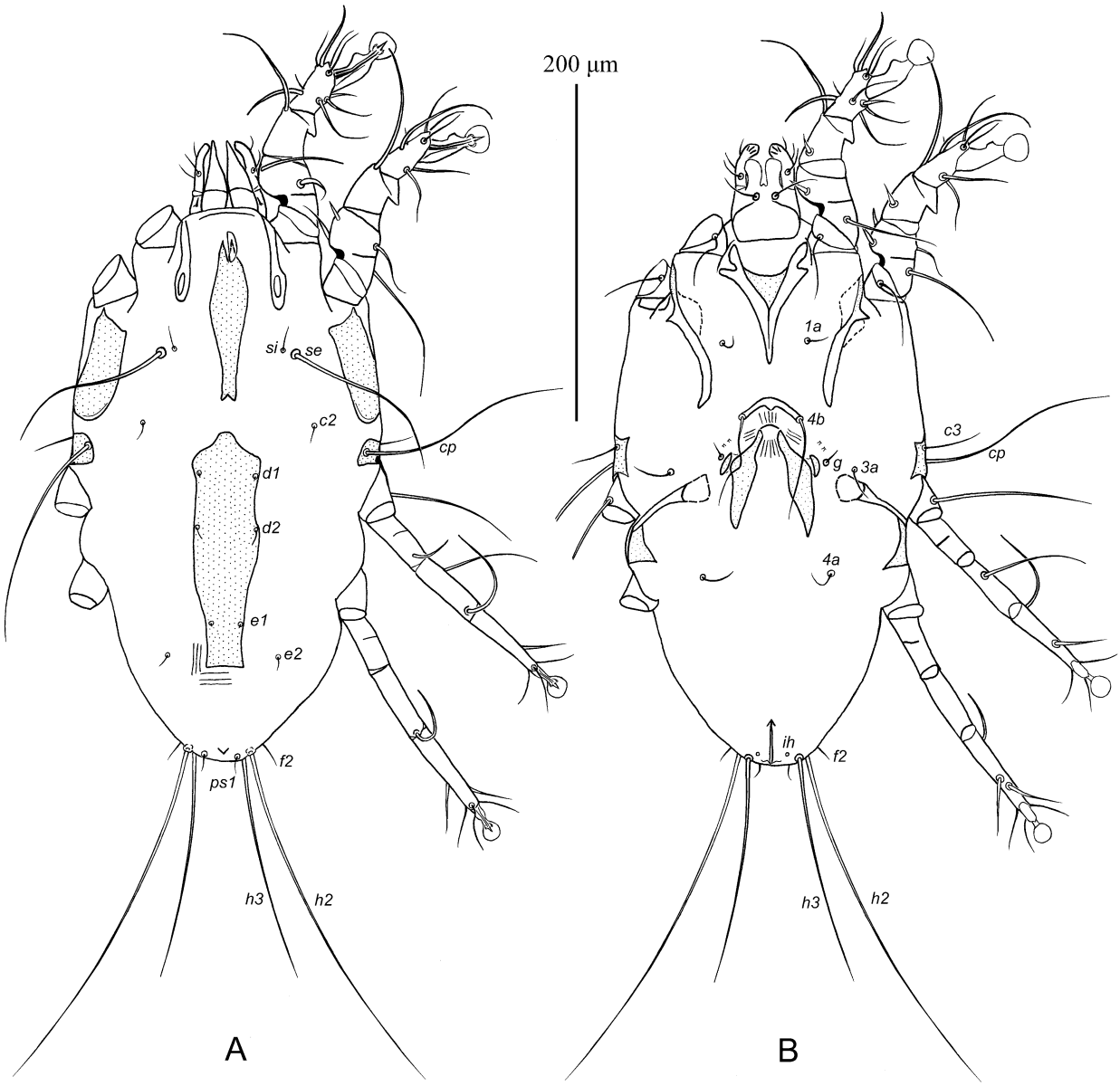

FIGURE 2. *Ingrassia calonectris* **sp. n.**, female. A—dorsal view, B—ventral view.

Legs I, II as in the male. Tarsus IV extending beyond posterior end of opisthosoma. Tarsi III, IV without apical spines, length of tarsi III and IV 50 and 58, respectively (Figs. 3E, F). Setae *sR*III subequal to total length of corresponding femur, genu and tibia. Seta *w* of tarsus III and setae *r, w* of tarsus IV noticeably thickened in basal part.

Differential diagnosis. The new species *Ingrassia calonectris* **sp. n.** is most similar to *I. dubinini* Černý, 1967 by having in both sexes the prodorsal shield relatively narrow (much less than half the distance between scapular setae *se*) with strongly attenuate posterior end, and by the presence of the membranous median crest on the anterior part of this shield. *Ingrassia calonectris* differs from that species by the following features: in males, the middle part of the prodorsal shield has distinctly convex lateral margins, the anterior margin of the hysteronotal shield is roughly sinuous, and tarsi III have an angular apicodorsal extension at the base of solenidion *φ*; in females, the posterior end of the prodorsal shield is truncate or bidentate, the posterior end of the hysteronotal shield is truncate and extends beyond the level of setae *e2*. In males of *I. dubinini*, the prodorsal shield does not have lateral convex extensions, the anterior margin of the hysteronotal shield is slightly convex, and the apices of tarsi III lack an extension at the base of solenidion φ; in females, the prodorsal shield has an acute posterior end, and the posterior end of the hysteronotal shield is angular and does not extend to the level of setae *e2*.

Etymology. The specific epithet is taken from the generic name of the type host.

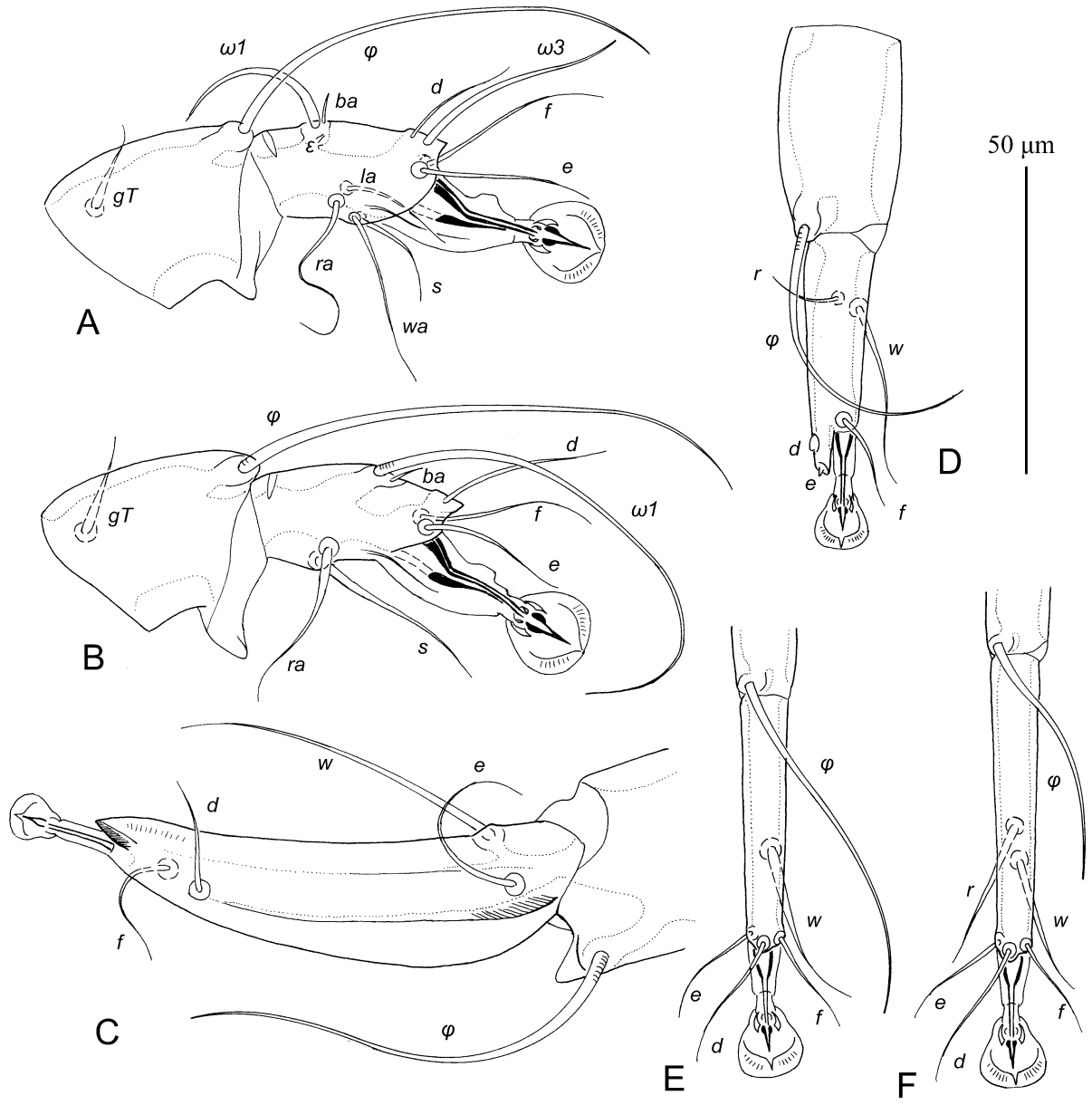

FIGURE 3. *Ingrassia calonectris* **sp. n.**, details of legs. A–D—male, E–F—female. A—tarsus and tibia I, dorsal view, B—tarsus and tibia II, dorsal view, C—tarsus III, dorsal view, D—tarsus and tibia IV, dorsal view, E—tarsus III, dorsal view, F—tarsus IV, dorsal view.

Ingrassia micronota sp. n.

(Figs. 4–6)

Type material. Holotype male (ZISP 5042), 5 male and 5 female paratypes (ZISP 5043, 5044) from *B. bulwerii* (Jardine and Selby) (Procellariidae), CAPE VERDE, Cape Verde Archipelago, Raso Island, 5 July 2006, col. J. González-Solís and E. Gómez-Díaz.

Additional material. 4 males and 2 females (ZISP 5045) from *B. bulwerii*, CAPE VERDE, Cape Verde Archipelago, Ilhéu Grande Island, 30 June 2009; 2 females (ZISP 5046) from same host and same locality, 28 June 2009; 4 males and 2 females (ZISP 5047, 5048) from same host, CAPE VERDE, Cape Verde Archipelago, Ilhéu de Cima Island, 24 February 2012; 2 males and 2 females (ZISP 5049–5051) from *B. bulwerii*, same location, 26 February 2012; collector in all cases J. González-Solís.

Description. MALE (holotype, range for 5 paratypes in parentheses): Length of idiosoma from anterior end to bases of setae *h3* 290 (265–280), greatest width 185 (175–185), length of hysterosoma 160 (140–155). Prodorsal shield: narrow longitudinal plate with slightly attenuate anterior and posterior ends, anterior half with longitudinal membranous crest, length 80 (73–83), greatest width 13 (13–15), posterior end extending slightly beyond level of scapular setae *se*, *si* (Fig. 4A). Setae *se* separated by 58 (50–63), situated on small circular plates. Scapular shields wide, inner margin rough, without suprategumental extension. Hysteronotal shield: anterior margin with three blunt-angular extensions, length of shield from anterior margin to bases of setae *h3* 178 (155–168). Setae *c2* approximately half as long as macrosetae *cp*; setae *d2* about 2/3rd the length of setae *cp*, extending approximately to level of setae *h3*. Supranal concavity ovate almost closed posteriorly. Length of terminal cleft from anterior end of supranal concavity to base of setae *h3* 88 (75–85), greatest width of terminal cleft 33 (25–33). Terminal membranous extensions on lobar apices tongue-like, with longitudinal striae, length from base of setae *h3* to apices 33 (25–35), width at base 23 (20–23), length of incision between terminal extensions 28 (20–30). Setae *ps1* situated approximately at level of setae *h2*. Distance between dorsal setae: *c2*:*c2* 100 (100), *c2*:*d2* 28 (20–25), *d2*:*e2* 55 (48–55), *e2*:*h3* 75 (63–73), *h3*:*h3* 40 (33–35), *ps1*:*ps1* 25 (23).

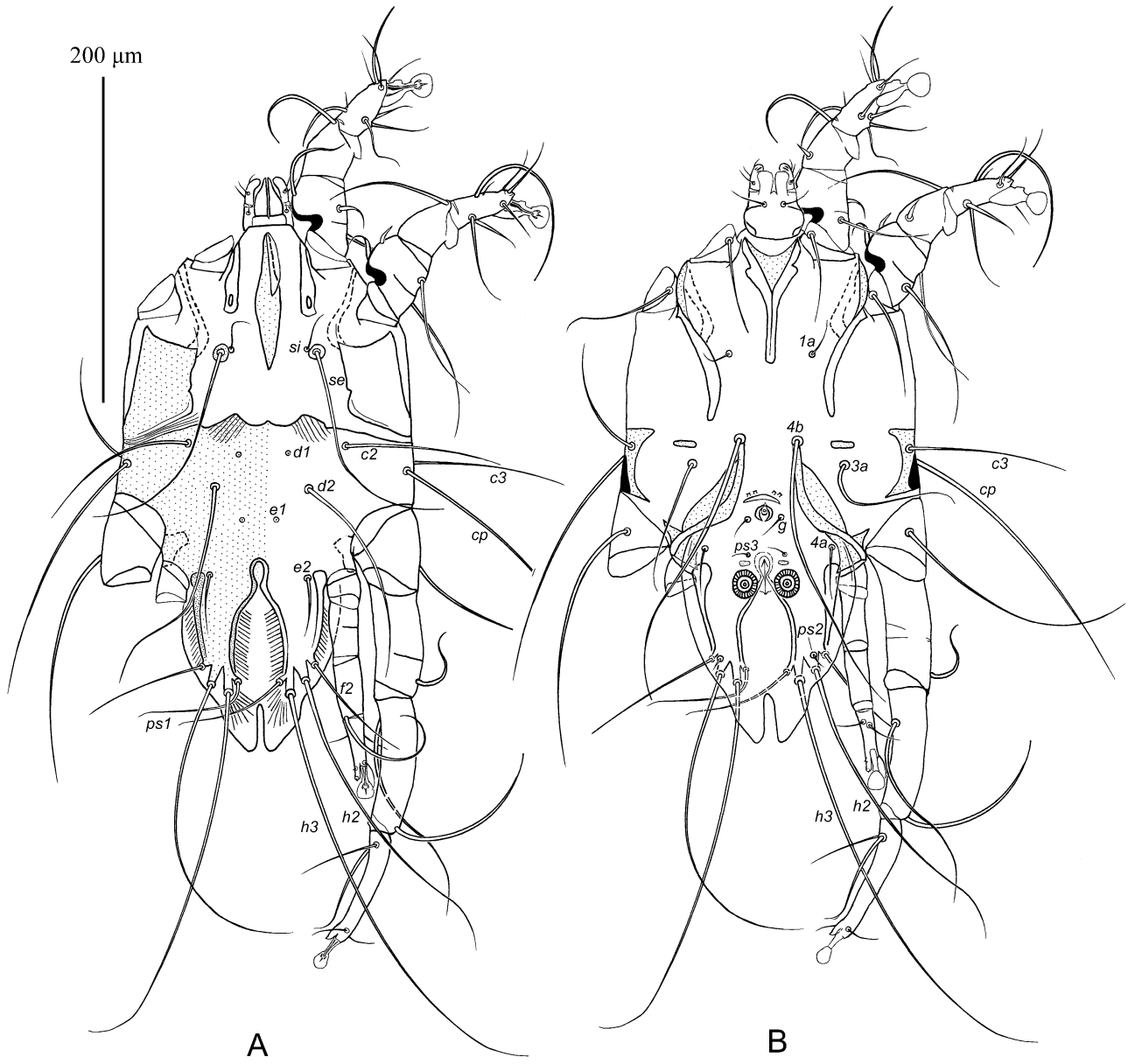

FIGURE 4. *Ingrassia micronota* **sp. n.** male. A—dorsal view, B—ventral view.

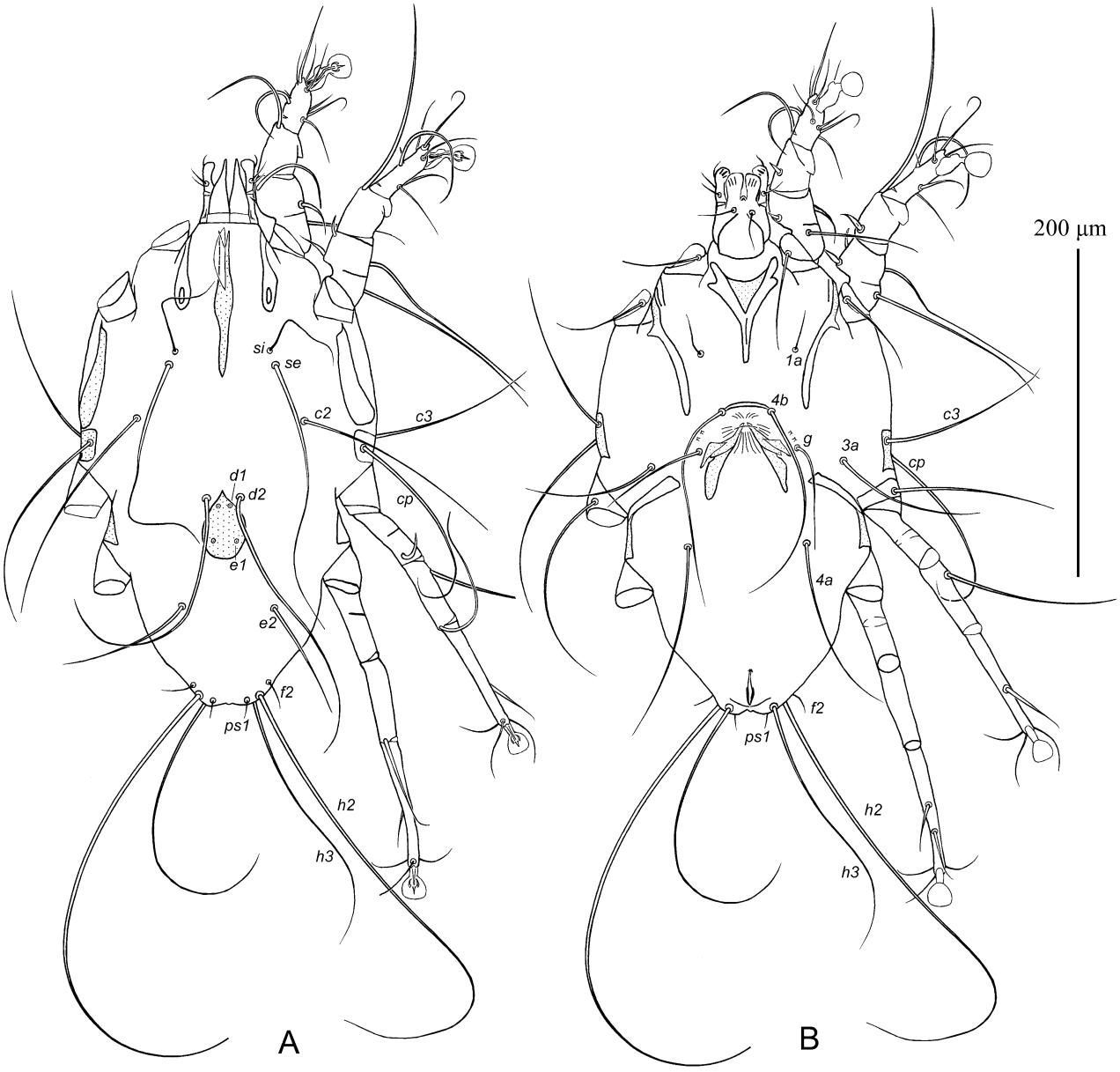

FIGURE 5. *Ingrassia micronota* **sp. n.**, female. A—dorsal view, B—ventral view.

Sternum about ½ of total length of epimerites I. Inner ends of epimerites IIIa free, widely separated from each other (Fig. 4B). Setae *4b* situated on ends of epimerites IIIa and extending slightly beyond lobar apices. A pair of small sclerites (apparently derivatives of epimerites III) situated just above setae *3a* (Fig. 4B). Adanal shields absent. Pregenital apodeme small, slightly curved. Genital apparatus small, genital arch ring-shaped, 12 (10–13) long, 11 (10–12) wide. Anal shields present, situated between setae *ps3* and anal suckers. Epimerites IVa not developed. Coxal fields IV not sclerotized. Diameter of anal suckers 15 (13–15). Distance between ventral setae: *4b:4b* 35 (33–35), *4b:3a* 13 (10–13), *4b:g* 48 (38–43), *g:ps3* 25 (20–23), *ps3:h3* 25 (20–25).

Tarsi I, II each with well-expressed apico-dorsal extension. Tibia I with acute ventral process, tibia II with rounded ventral process (Figs. 6A, B). Tibia III without apical spine, solenidion *φ* situated on rounded distal end of this segment; tarsus III narrow, without crest on lateral margin, with small finger-like apical extension, length of tarsus III 78 (68–75) (Fig. 6C). Tarsus IV with finger-like apical extension bearing setae *d*, *e* (Fig. 6D). Legs IV excluding pretarsus 125 (120–125) long; articulation of genu and tibia approximately at level of setae *f2;* tarsus IV extending by distal half beyond the level of terminal membrane apices.

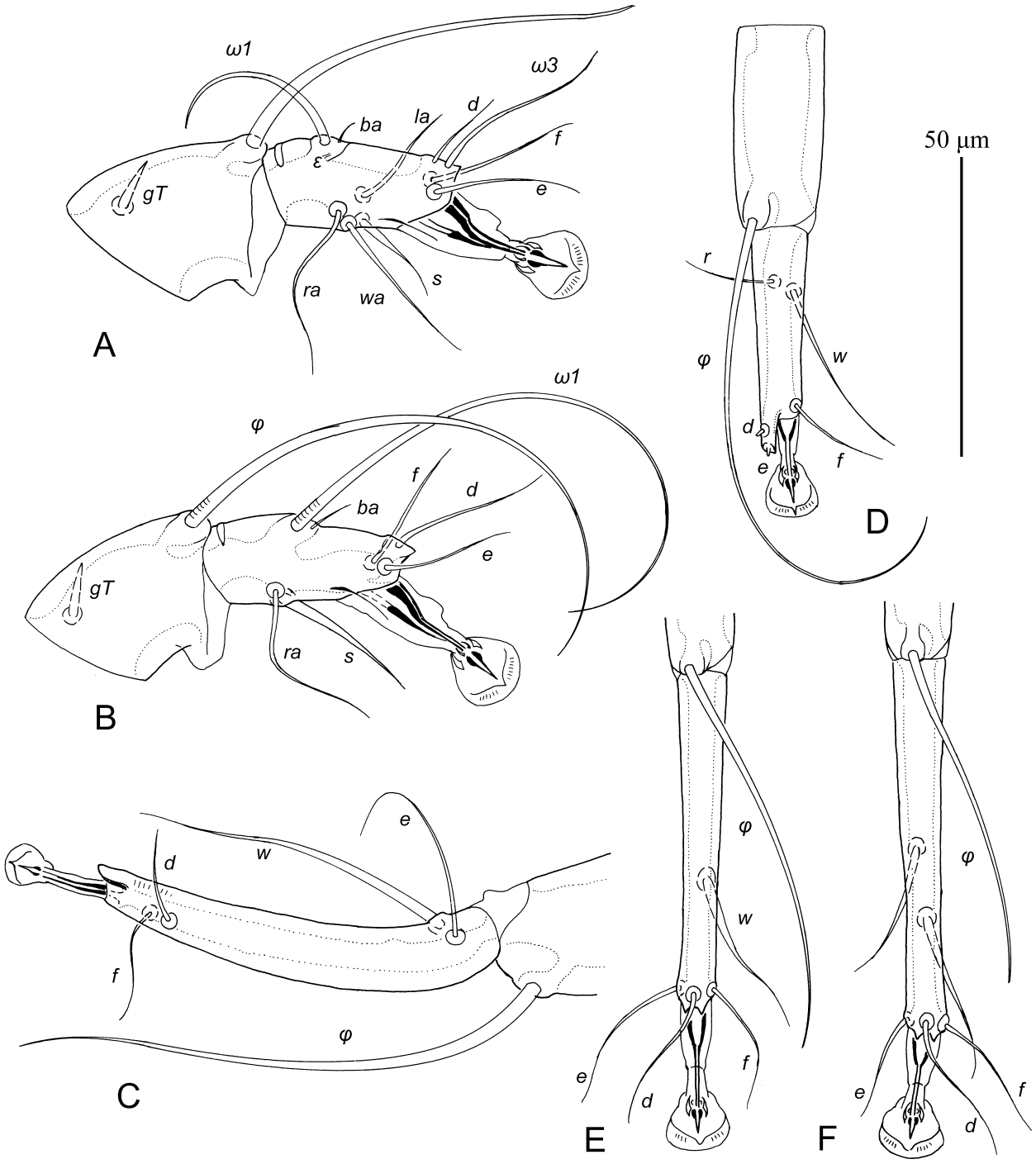

FIGURE 6. *Ingrassia micronota* **sp. n.**, details of legs. A–D—male, E–F—female. A—tarsus and tibia I, dorsal view, B—tarsus and tibia II, dorsal view, C—tarsus III, dorsal view, D—tarsus and tibia IV, dorsal view, E—tarsus III, dorsal view, F—tarsus IV, dorsal view.

FEMALE (range for 5 paratypes): Length of idiosoma 285–305, greatest width 165–210, length of hysterosoma 150–200. Prodorsal shield: narrow longitudinal plate with strongly attenuated posterior end and bifurcated anterior end; longitudinal membranous crest present in the anterior part of this shield; posterior end of shield extending slightly beyond level of setae *se*; length 80–88, greatest width 10–13 (Fig. 5A). Scapular setae *si* and *se* situated on finely striated tegument, setae *si* situated noticeably anterior to level of setae *se*. Setae *se* separated by 58–88. Scapular shields narrow, inner margin of them smooth, slightly convex. Humeral shields small without antero-mesal extension. Setae *c3* longer than total length of trochanter, femur and genu III. Hysteronotal shield: very small longitudinal plate, teardrop-shaped, with acute anterior end and bearing setae *d1* and *e1*; length

along midline 38–43, greatest width 23–30. Setae *c2*, *d2*, and *e2* situated on striated tegument. Setae *c2* and *d2* subequal in length to humeral setae *cp*. Setae *d2* strongly moved to midline, situated at level of anterior end of hysteronotal shield, tips of these setae extending beyond posterior end of opisthosoma. Setae *e2* extending slightly beyond posterior end of opisthosoma. Distance between dorsal setae *c2*:*d2* 48–63, *d2*:*e2* 58–65, *e2*:*h3* 53–63, *h3*:*h3* 20–30.

Sternum shorter than half total length of epimerites I. Epigynum thin, slightly curved transverse sclerite, 5–8 long, 25–30 wide, with tips touching to bases of setae *4b*. Apodemes of oviporus long, posterior ends narrowed and rounded, extending to midlevel of epimerites IIIa. Setae *g*, *3a*, *4a*, *4b* long, exceeding lengths of femoragenu III, IV. Setae *g*, *3a*, and *4b* extending to or beyond level of seta *4a* bases; setae *4a* extending beyond posterior end of opisthosoma. Setae *h3* approximately half as long as setae *h2*.

Legs I, II as in the male. Distal half of tibia IV and tarsus IV extending beyond posterior end of opisthosoma. Tarsi III, IV with pair of short dorso-apical spines; length of tarsi III and IV 68–70 and 70–78, respectively (Figs. 6E, F). Setae *sR*III subequal to total length of corresponding femur, genu and tibia. Seta *w* of tarsus III and setae *r*, *w* of tarsus IV noticeably thickened in basal part.

Differential diagnosis. As for the species described above, *I. micronota* **sp. n.** is also most similar to *I. dubinini* Černý, 1967 by the structures of the prodorsal shield in both sexes. *Ingrassia micronota* differs from *I. dubinini* by the following characters: in both sexes, the dorsal crest of the prodorsal shield is approximately half as long as the shield; in males, the bases of setae *se* are situated on small circular plates, setae *d2* are long and almost extend to the lobar apices; in females, the hysteronotal shield is represented by a small teardrop-shaped sclerite (38–43 long) in the middle of the hysterosoma and encompasses only bases of setae *d1*, *e1*. In both sexes of *I. dubinini*, the dorsal crest of the prodorsal shield is no longer than one third the length of the shield; in males, the bases of setae *se* as well as setae *si* are situated on striated tegument, setae *d2* are short and do not extend to bases of setae *e2*; in females, the hysteronotal shield is represented by a longitudinal plate (70–80 long) with the acute posterior end and encompasses only bases of setae *d1*, *e1* and *d2*.

Etymology. The specific epithet refers to a very small hysteronotal shield in females.

Genus *Opetiopoda* Gaud and Atyeo, 1981

Type species: *Opetiopoda anadermura* Gaud and Atyeo, 1981 by original designation.

Prior to now, the genus *Opetiopoda* has been monobasic, including only the type species *O. anadermura* Gaud and Atyeo, 1981 from *Puffinus pacificus* (Gmelin) (Procellariiformes: Procellariidae). This genus represents the most morphologically basal lineage within the subfamily Ingrassiinae (Mironov 2005). This is the only genus within the subfamily that retains all four pairs of median hysteronotal setae (*c1*, *d1*, *e1* and *h1*). In addition, mites of the genus *Opetiopoda* also retain a full set of ventral setae on tarsi I and II (*la*, *ra*, *wa*, and *s*).

Opetiopoda bulweriae sp. n.
(Figs. 7–10)

Type material. Male holotype (ZISP 5030) from *B. bulwerii* (Jardine and Selby) (Procellariidae), SPAIN, Canary Islands, Lanzarote, Montaña Clara, 19 April 2007, col. J. González-Solís and 4 female paratypes (ZISP 5031) from same host, CAPE VERDE, Cape Verde Archipelago, Raso Island, 5 July 2006, col. J. González-Solís and E. Gómez-Díaz.

Description. MALE (holotype): Length of idiosoma from anterior end to bases of setae *h3* 308, greatest width 162, length of hysterosoma 175. Prodorsal shield fused with scapular shields forming entire dorsal shield covering prodorsum; borders between these shields marked by longitudinal furrows; greatest length of prodorsal shield 133, width at posterior margin 119 (Fig. 7A). Anterior part of prodorsal shield with a pair of longitudinal crests diverging posteriorly. Setae *c1* situated on prodorsal shield near its posterior margins. Scapular setae *se* separated by 77, setae *si* situated slightly posterior to level of setae *se*. Hysteronotal shield: anterior angles fused with humeral shields, length of shield from anterior end to bases of setae *h3* 170, width at anterior margin about 90, lateral parts with longitudinal furrows stretching from anterior margin to bases of setae *f2*. Opisthosomal lobes

narrow, attenuate apically, with seta *h3* on lobar apices. Supranal concavity a narrow median groove. Terminal cleft angular, narrow; length from anterior end to lobar apices 57. Interlobar membrane narrow, occupying entire margin of terminal cleft and forming acute terminal extensions 15 long on lobar apices. Distance between dorsal setae: *c2*:*d2* 15, *d2*:*e2* 84, *e2*:*h3* 35, *h3*:*h3* 33, *h2*:*h2* 49, *ps2*:*ps2* 55.

Sternum about 3/4th of total length of epimerites I. Inner ends of epimerites IIIa free, widely separated, bearing setae *4b* on their inner ends. Genital apparatus small, 7.5 × 10, with pair of ovate paragenital sclerites. Setae *4a* and *g* arranged in transverse row posterior to base of genital arch. Adanal shield present, represented by roughly rectangular plate situated anterior to anal opening and anal suckers and bearing setae *ps3*. Adanal apodemes present, represented by uneven longitudinal sclerites stretching from base of genital apparatus to lateral margins of anal area. Epimerites IVa absent. Anal suckers ovate, corolla with indentations, diameter along long axis 18. Distance between ventral setae: *4b:4b* 28, *4b:4a* 66, *4b:ps3* 55.

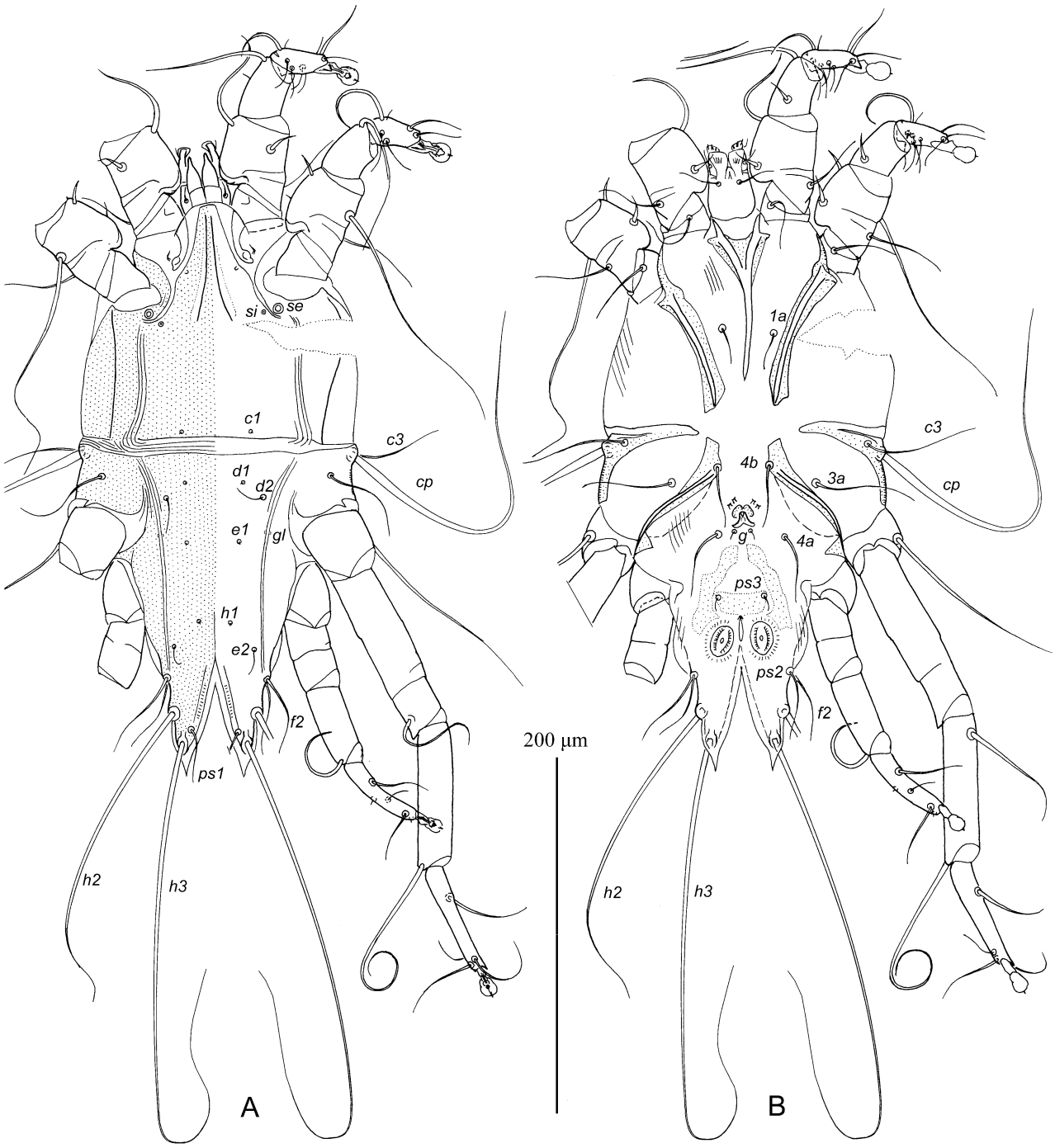

FIGURE 7. *Opetiopoda bulweriae* **sp. n.**, male. A—dorsal view, B—ventral view.

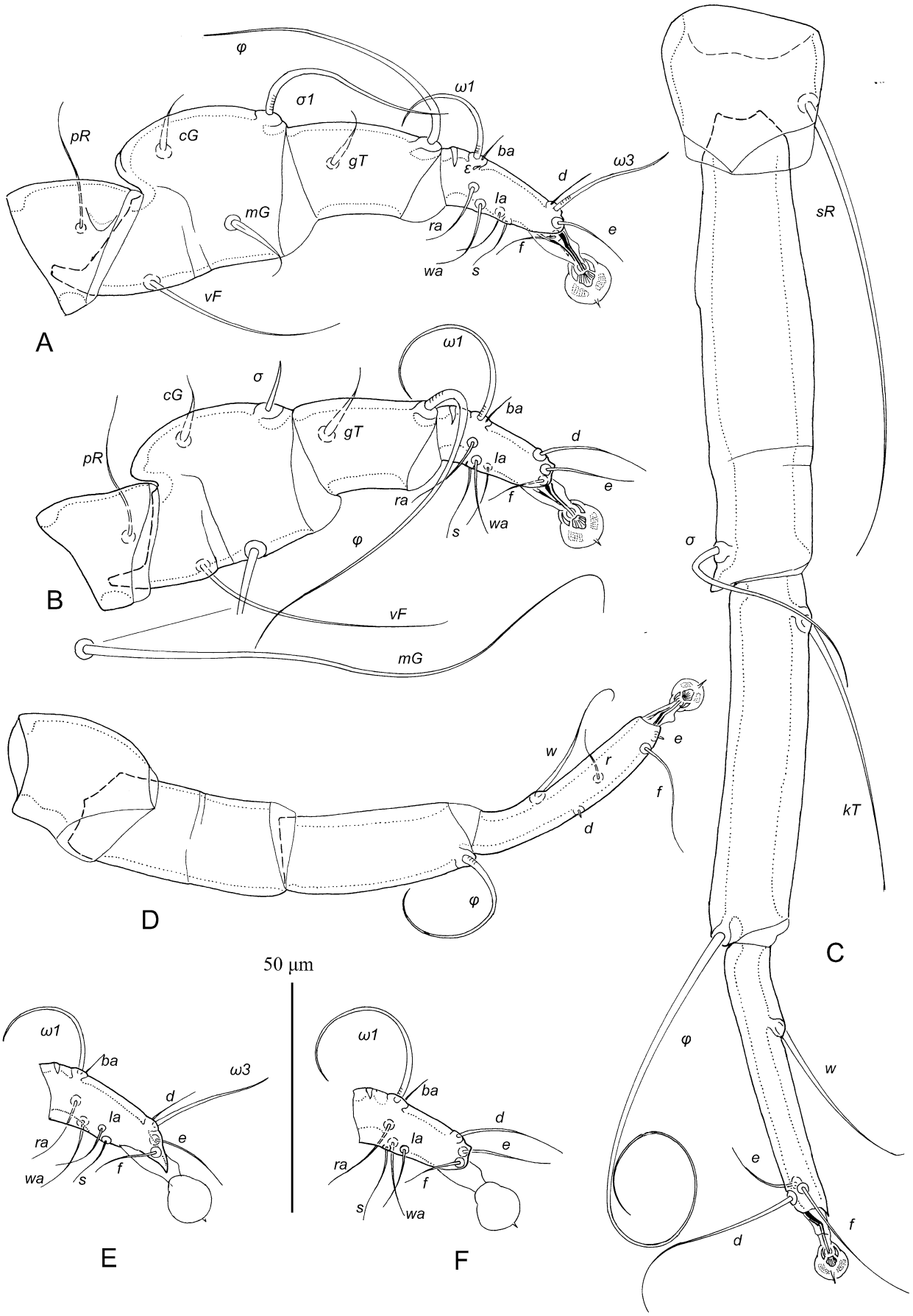

FIGURE 8. *Opetiopoda bulweriae* **sp. n.**, legs of male. A–D—dorsal view of legs I–IV, respectively, E—tarsus I, ventral view, F—tarsus II, ventral view.

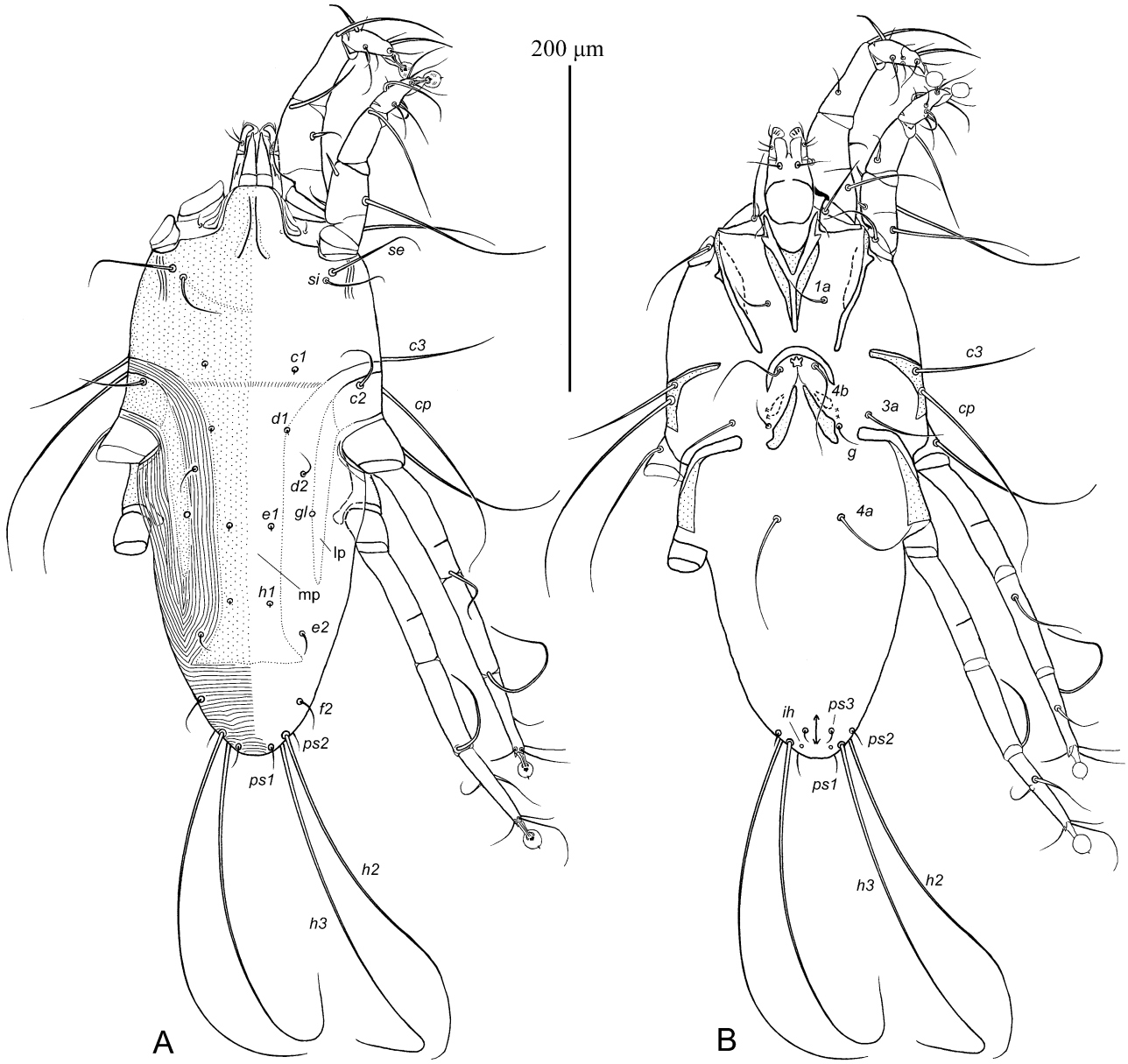

FIGURE 9. *Opetiopoda bulweriae* **sp. n.**, female. A—dorsal view, B—ventral view. lp—lateral piece of hysteronotal shield, mp—median piece of hysteronotal shield.

Tarsus I with paraxial apical hook, tarsus II without apical spine (Figs. 8A, B, E, F). Tibia I, II without ventral processes. Tibia III with small distal spine-like extension at base of solenidion *φ*; tarsus III with small apical spine-like extension, length of tarsus III 62 (Fig. 8C). Tarsus IV 49 long, setae *e* situated apically, seta *d* situated at midlevel of segment (Fig. 8D). Legs IV, excluding pretarsus, 148 long, extending beyond lobar apices by full tarsus IV.

FEMALE (range for 4 paratypes): Length of idiosoma 345–365, greatest width 160–170, length of hysterosoma 230–250. Prodorsal shield fused laterally with scapular shields forming integral shield completely covering prodorsum and encompassing bases of setae *se*, *si*, and *c1*; length of prodorsal shield along midline 123–133 (Fig. 9A). Scapular setae *se* 38–48 long, not exceeding half-wide of idiosoma, their bases separated by 98–105. Hysteronotal shield represented by three separate pieces, median piece and a pair of lateral ones. Anterior end of median piece fused with the prodorsal shield with the border between them marked by narrow longitudinally striated furrow; length of median piece along midline 165–185, width at anterior margin 75–83, width at posterior margin 50–53. Setae *d1, e1, h1* situated on median piece of hysteronotal shield. Setae *d2, e2* situated on striated

tegument. Setae *h1* situated anterior to level of setae *e2*. Lateral pieces of hysteronotal shield represented by narrow longitudinal bands, their anterior ends fused with corresponding humeral shields, posterior ends extend beyond level of trochanters IV. Hysteronotal gland openings *gl* situated on lateral pieces of hysteronotal shield at level of trochanters IV. Distance between dorsal setae: *c2*:*d2* 50–53, *d2*:*e2* 100–103, *e2*:*h3* 60–73, *h3*:*h3* 30–38. Setae *h3* and *h2* approximately subequal in length.

Sternum formed by fused epimerites I approximately half as long as total length of these epimerites. Epimerites I surrounded by narrow sclerotized areas. Epigynum semicircular, thin, 25–28 long, 43–45 wide, tips not reaching level of genital papillae (Fig. 9B). Apodemes of oviporus short, slightly extending beyond inner tips of epimerites IIIa. Setae *4b* long, extending slightly beyond posterior ends of oviporus apodemes.

Tarsi I, II without paraxial apical spine (Figs. 10A, B). Tibiae I, II without ventral processes. Tarsi III, IV with small apico-dorsal and apico-ventral spines (Figs. C, D). Legs IV extend beyond posterior end of opisthosoma by full tarsus and distal part of tibia.

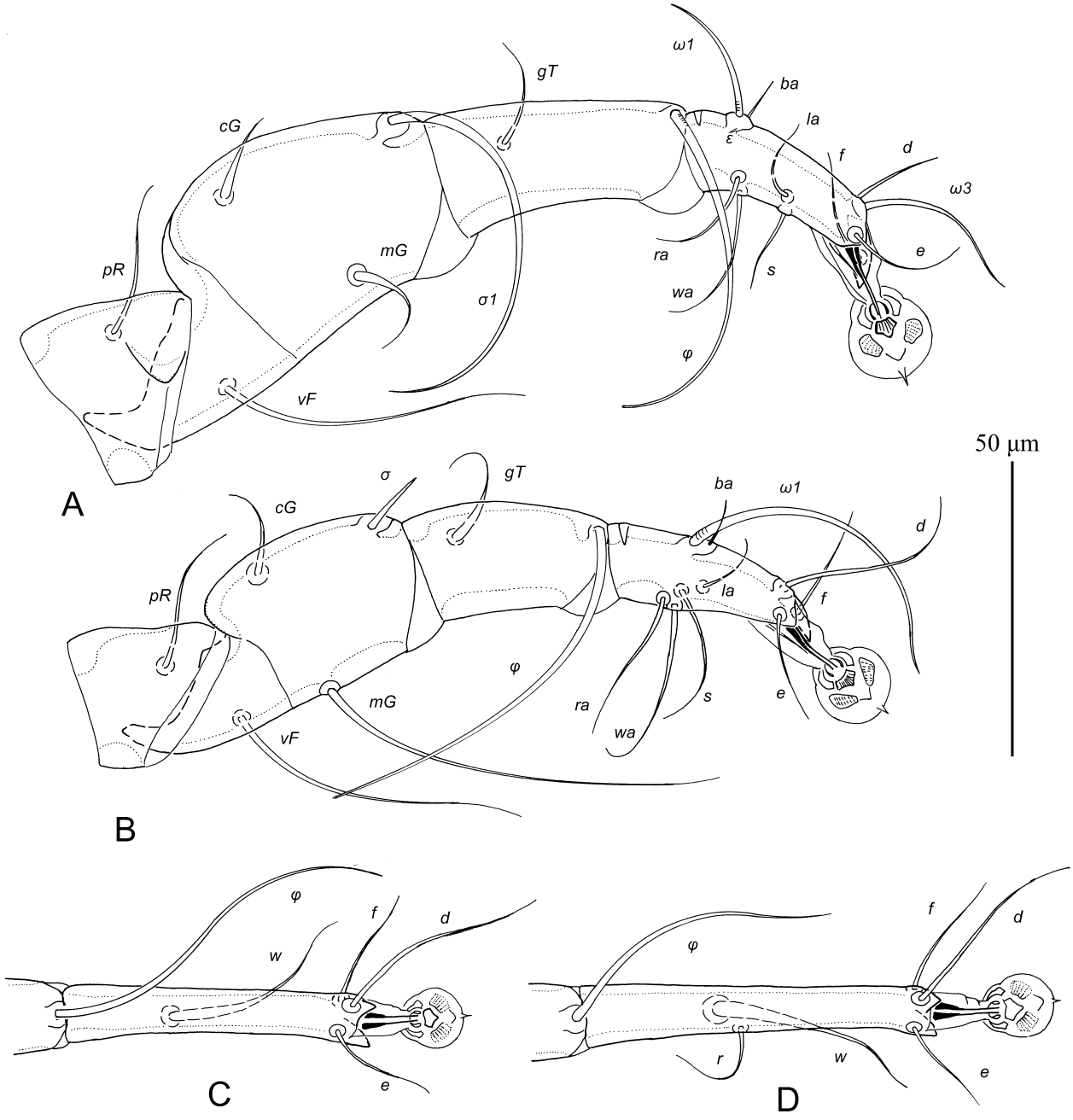

FIGURE 10. *Opetiopoda bulweriae* **sp. n.**, legs of female. A—tibia and tarsus I, B—tibia and tarsus II, C—tarsus III, D—tarsus IV.

Differential diagnosis. The new species *Opetiopoda bulweriae* **sp. n.** clearly differs from *O. anadermura* Gaud and Atyeo, 1981 by the following features. In males, the entire shield covering the prodorsum is separated from the hysteronotal shield by a band of striated tegument, legs IV extend beyond the opisthosomal lobe apices by the full tarsus IV, the adanal shield is present, and setae *4a* are situated posterior to the level of the genital apparatus; in females, the hysteronotal shield is split into the median part fused with hysteronotal shield and a pair of narrow lateral parts, of which the anterior ends are fused with the corresponding humeral shields, setae *d2* and *e2* are situated on striated tegument, setae *h1* are situated anterior to *e2*, macrosetae *h2* and *h3* are subequal in length, the epigynum is semicircular and does not extend to the level of the genital papillae, and setae *4a* are long and extend beyond the posterior ends of folds of oviporus. In males of *O. anadermura*, the shield covering the prodorsum is fused with the hysteronotal shield, legs IV extend beyond the lobar apices by only the pretarsus, the adanal shield is absent, and setae *4a* are situated at the level of the genital apparatus; in females, the hysteronotal shield is entire and encompasses bases of setae *d2* and *e2*, setae *h1* and *e2* are situated at the same transverse level, setae *h3* are approximately half as long as setae *h2*, the epigynum is represented by a high and narrow arch extending by its tips to the genital papillae, and setae *4a* are extremely short and do not extend even to the midlevel of the epigynum.

Etymology. The specific epithet derives from the generic name of the type host and is a noun in the genitive case.

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1.3 A NEW SPECIES OF THE FEATHER MITE GENUS *RHINOZACHVATKINIA* (ACARI: AVENZOARIIDAE) FROM C*ALONECTRIS* SHEARWATERS (PROCELLARIIFORMES: PROCELLARIIDAE): INTEGRATING MORPHOLOGICAL DESCRIPTIONS WITH DNA BARCODE DATA

Laura M. Stefan, Karen D. McCoy, Sergey V. Mironov

Folia Parasitologica, 61: 90-96, 2014

UNA NUEVA ESPECIE DE ÁCAROS DE LAS PLUMAS DEL GÉNERO *RHINOZACHVATKINIA* (ACARI: AVENZOARIIDAE) EN PARDELAS DEL GÉNERO *CALONECTRIS* (PROCELLARIIFORMES: PROCELLARIIDAE): INTEGRANDO DESCRIPCIONES MORFOLÓGICAS CON DATOS DE CÓDIGOS DE BARRAS DE ADN

RESUMEN

Rhinozachvatkinia calonectris sp. n., una nueva especie de ácaros de las plumas del género *Rhinozachvatkinia* Mironov, 1989 (Avenzoariidae: Bonnetellinae), es descrita en dos especies de pardelas del noreste del Océano Atlántico, *Calonectris edwardsii* (Oustalet) (huésped tipo) y *Calonectris borealis* (Cory) (Procellariiformes: Procellariidae). La descripción morfológica de la nueva especie se completó con datos de la secuencia del gen mitocondrial del citocromo c oxidasa subunidad I. Se fija formalmente el estado genérico completo de *Rhinozachvatkinia*, originalmente establecido como subgénero de *Zachvatkinia* Dubinin, 1949, y se discuten brevemente sus relaciones sistemáticas.

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A new species of the feather mite genus *Rhinozachvatkinia* (Acari: Avenzoariidae) from *Calonectris* shearwaters (Procellariiformes: Procellariidae): integrating morphological descriptions with DNA barcode data

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Abstract: *Rhinozachvatkinia calonectris* sp. n., a new species of the feather mite genus *Rhinozachvatkinia* Mironov, 1989 (Avenzoariidae: Bonnetellinae), is described from two species of shearwaters in the North-East of the Atlantic Ocean, *Calonectris edwardsii* (Oustalet) (type host) and *Calonectris borealis* (Cory) (Procellariiformes: Procellariidae). We completed the morphological description of this new feather mite species with sequence data on the mitochondrial cytochrome *c* oxidase subunit I gene fragment (COI). The full generic status of *Rhinozachvatkinia,* originally established as a subgenus of *Zachvatkinia* Dubinin, 1949, is formally fixed and its systematic relationships are briefly discussed.

Keywords: Bonnetellinae, ectoparasites, taxonomy, morphology, molecular study, new species, mites, birds, COI

Feather mites (Astigmata: Pterolichoidea and Analgoidea) are the most common ectosymbionts associated with birds and develop their entire life cycle on their hosts. The approximately 2 500 species described to date have been reported from all recent avian orders (Gaud and Atyeo 1996, Proctor 2003, Mironov and Proctor 2008). The majority of known feather mite species live permanently on the surface of wing feathers, where they feed on uropygial gland secretions and detritus associated with the feather barbs (Blanco and Tella 2001, Galván et al. 2008).

In the present study, we describe a new species of the feather mite genus *Rhinozachvatkinia* Mironov, 1989 (Avenzoariidae: Bonnetellinae) found on two species of shearwaters, *Calonectris borealis* (Cory) and *Calonectris edwardsii* (Oustalet) (Procellariiformes: Procellariidae). To date, only three species of *Rhinozachvatkinia* have been described from three procellariiform hosts belonging to different families: *Rhinozachvatkinia graciosa* Mironov, 1989 from *Pachyptila desolata* (Gmelin) (Procellariidae), *Rhinozachvatkinia pelecanoidi* Mironov, 1989 from *Pelecanoides georgicus* (Murphy et Harper) (Pelecanoididae) and *Rhinozachvatkinia zygoloba* Mironov, 1989 from *Oceanodroma leucorrhoa* (Vieillot) (Hydrobatidae) (Mironov 1989a).

Feather mites of the genus *Rhinozachvatkinia* share their habitat on the wing feather of procellariiform birds with two closely related avenzoariid genera, *Promegninia* Gaud et Atyeo, 1967 and *Zachvatkinia* Dubinin, 1949. The genus *Promegninia* is monotypic and known only from albatrosses (Procellariiformes: Diomedeidae) (Gaud and Atyeo 1967). The genus *Zachvatkinia* currently includes 15 species, of which five are known from procellariiforms of the families Diomedeidae, Procellariidae and Hydrobatidae, whereas remaining species are associated with gulls, terns and crab plovers (Charadriiformes: Laridae and Dromadidae) (Mironov 1989b, 1991a,b, 1992, Mironov and Stefan 2013, Negm et al. 2013). These three mite genera constitute the *Zachvatkinia* generic group within the subfamily Bonnetellinae – see Mironov and Dabert (1999).

It is necessary to note that *Rhinozachvatkinia* was originally established as a subgenus of *Zachvatkinia* by Mironov (1989a). Later, Mironov and Dabert (1999) carried out a phylogenetic analysis of Avenzoariidae and showed that *Rhinozachvatkinia* is much closer to *Promegninia* than to *Zachvatkinia* sensu stricto. Although these authors treated *Rhinozachvatkinia* as a genus in their work, they did not formally declare its full generic status. Therefore, we formally fix its status as a full genus in the present paper.

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MATERIALS AND METHODS

The material used in the present study was collected by Jacob González-Solís, Elena Gómez-Díaz and Teresa Militão from 2003 to 2008 from living birds breeding on the Cape Verde and Azores Archipelagos using the dust-ruffling method (for *C. edwardsii*; see Walther and Clayton 1997) or direct sampling of barbs from primary feathers (for *C. borealis*). Bird captures and mite sampling were carried out under permissions from the corresponding Governments authorities of Portugal and Cape Verde. All animals were handled in accordance with good animal care practices as defined by the current European legislation.

Collected material was preserved in vials with absolute ethanol. For morphological identifications, feather mites were cleared in lactic acid for 24 h and mounted on microscope slides in PVA medium (BioQuip Products, Rancho Dominguez, California). The new species description follows the standards used for avenzoariid mites (Atyeo and Gaud 1981, Mironov 1989b, Mironov and Dabert 1997). General morphological terms and leg chaetotaxy follow Gaud and Atyeo (1996), idiosomal chaetotaxy also follows these authors with corrections proposed by Norton (1998). All measurements are in micrometres (μm). Drawings were made using a Leica DM 5000B light microscope with DIC illumination and camera lucida.

Prior to mounting on slides, six individual mites were subjected to DNA extraction using the nondestructive method described by Dabert et al. (2008). A 609-bp fragment of the COI gene was amplified using the primers bcdF05 (5'-TTTTCTACHAAYCATAAAGATATTGC-3') and bcdR04 (5'-TATAAACYTCDGGATGNCCAAAAAA-3') (Dabert et al. 2008). Polymerase chain reactions (PCRs) were carried out in a total volume of 25 μl containing 2 μl 10× reaction buffer with $MgCl_2$ (15 mM) (Roche Diagnostics, Meylan, France), 1.5 mM $MgCl_2$, 0.15 mM of each dNTP, 0.4 μM of each primer, 1.25 U *Taq* DNA polymerase (Roche Diagnostics) and 3 μl of DNA template. Amplification conditions consisted of an initial step of 5 min at 95 °C, followed by 35 cycles of 30 sec at 95 °C, 1 min 30 sec at 50 °C, 1 min at 72 °C, with a final step of 5 min at 72 °C. PCR products were separated by electrophoresis in 2% agarose gel and visualized under UV light. Samples containing visible bands were sent for sequencing to Beckman Coulter Genomics (France; GenBank Accession nos. KF111269–KF111274). Bioedit version 7.0.5.3 (Hall 1999) was used to assemble, edit and align sequences and all variable sites were confirmed by visual inspections of the chromatograms. Pairwise distances between sequences were computed with MEGA 4 (Tamura et al. 2007) using K2P distance model (Kimura 1980).

The taxonomic system and scientific names of birds follow Clements et al. (2012) and Sangster et al. (2012). Type and additional materials are deposited in the Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia (ZISP).

RESULTS

Family **Avenzoariidae** Oudemans, 1905

Subfamily **Bonnetellinae** Atyeo et Gaud, 1981

Genus ***Rhinozachvatkinia*** Mironov, 1989 stat. n.

As it was noticed above, the genus *Rhinozachvatkinia* was originally established as a subgenus of the genus *Zachvatkinia* by Mironov (1989a). Later on, Mironov and Dabert (1999) proved that this taxon is phylogenetically closer to the genus *Promegninia* than to *Zachvatkinia* in a strict sense, but did not formally fix its full generic status.

Rhinozachvatkinia is clearly distinguished from the genus *Zachvatkinia* by the following set of characters: in both sexes, the subcapitulum is elongated and its distal part is noticeably narrowed (more expressed in females than in males), genual setae *mG*I are narrow lanceolate or spiculiform; in males, the lateral membranes of opisthosomal lobes are absent, the anterior ends of coxal fields IV are widely separated from each other, distance between them is equal to or wider than the genital arch; in females, the anterior margin of hysteronotal shield is distinct (Mironov 1989a,b). The two former characters also differentiate this genus from *Promegninia*. Within the *Zachvatkinia* generic group, the genera *Promegninia* and *Rhinozachvatkinia* could be referred to as small-sized representatives of this grouping; the idiosoma lengths of these mites do not exceed 450 μm in males and 400 μm in females, whereas in *Zachvatkinia* these lengths are over 600 μm and 450 μm, respectively.

Type species: *Zachvatkinia* (*Rhinozachvatkinia*) *graciosa* Mironov, 1989 by original designation.

Other species: *Rhinozachvatkinia pelecanoidi* Mironov, 1989, *R. zygoloba* Mironov, 1989 and one species described below.

Rhinozachvatkinia calonectris sp. n. Figs. 1–4

Male (Figs. 1, 3, 4A,B) (holotype, measurements for one paratype in parentheses). Length of idiosoma from anterior end to end of opisthosomal lobes 440 (420), greatest width at level of humeral shields 210 (185). Subcapitulum moderately narrowed in anterior part, lateral margins with small tooth-like extensions, length including palps 62 (63), greatest width 46 (48), width at bases of palps 29 (32) (Fig. 4A). Chelicerae slightly narrowed in anterior part, 65 (63) long.

Prodorsal shield: pear-shaped, strongly narrowed in anterior part, without median ridges, with pair of ovate desclerotized patches, posterior margin convex, posterolateral margins rounded or with short angular extension, not encompassing bases of setae *se*, length along midline 95 (93), greatest width 63 (63) (Fig. 1A). Setae *vi* paired. Setae *si* situated on lateral margins of prodorsal shield, setae *se* situated on small circular plates near prodorsal shield, distance between setae *se* 80 (80). Length of hysterosoma from level of sejugal furrow to lobar apices 315 (300). Setae *c3* narrowly lanceolate, 15 (15) long.

Hysteronotal shield: anterior margin sinuous with noticeable concavities lateral to setae *c1*, anterior angles acute and almost touching humeral shields, greatest length from anterior margin to level of setae *h3* 275 (270), width at anterior margin 125 (125). Opisthosomal

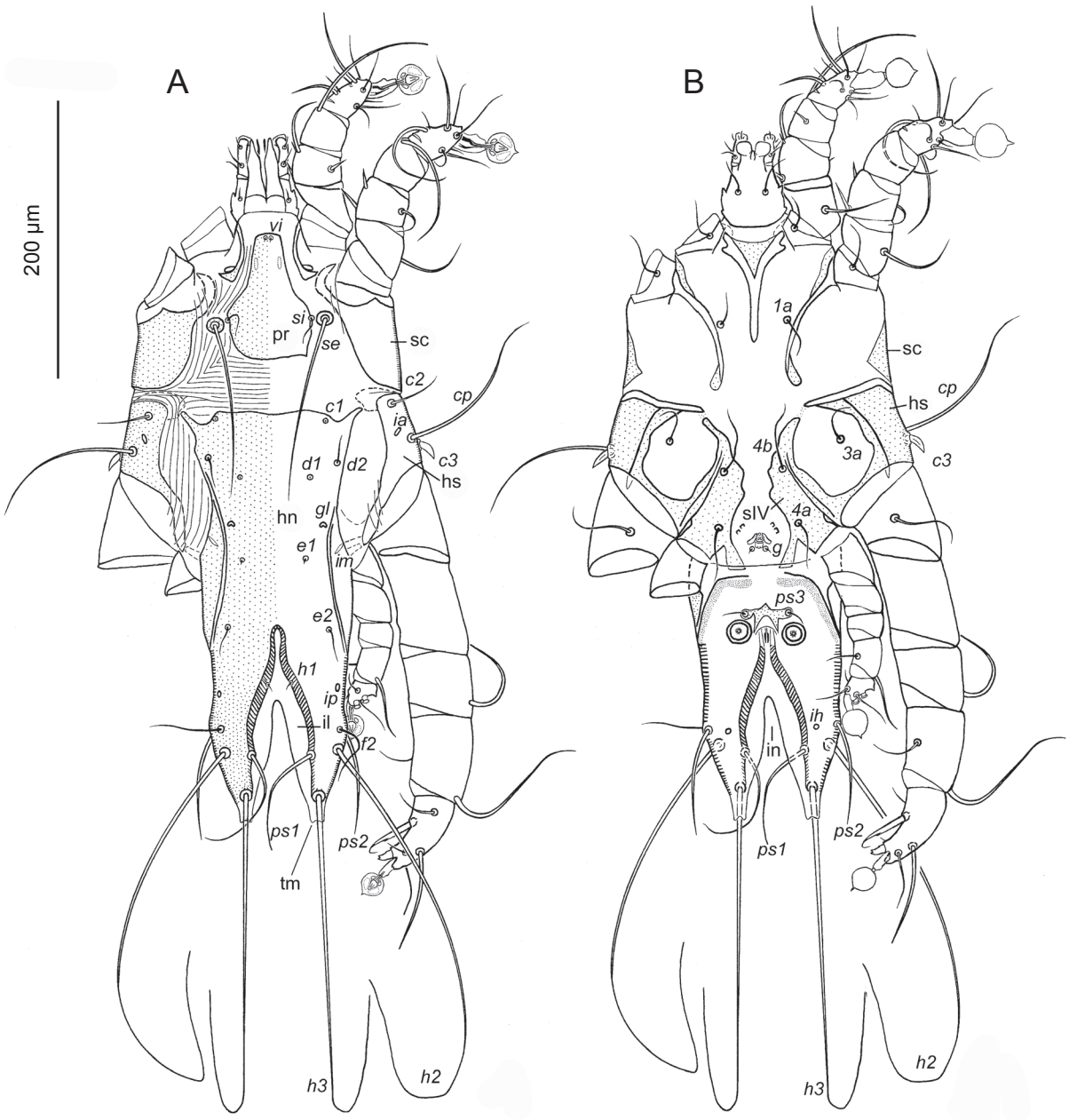

Fig. 1. *Rhinozachvatkinia calonectris* sp. n. from *Calonectris edwardsii*; male. **A** – dorsal view; **B** – ventral view. *Abbreviations*: *ia*, *im*, *ip* and *ih* – cupules; hn – hysteronotal shield; hs – humeral shield; il – interlobar membrane; in – incision in interlobar membrane; pr – prodorsal shield; sc – scapular shield; sIV – sclerotized area of coxal fields IV; tm – terminal membrane.

lobes long, strongly narrowed apically, well separated from each other. Terminal cleft between lobes deep and relatively narrow, extending to level of setae *e2*, length including supranal concavity 138 (140), greatest width 40 (35). Inner margins of opisthosomal lobes without ledge, outer margins of lobes slightly convex, apical part posterior to bases of setae *h3* represented by narrow bidentate membranes (Fig. 1A). Lateral membranes not developed.

Interlobar membrane around two times narrower than lobe width at level of setae *ps2*, gradually narrowing to bases of setae *h3*. Incision in interlobar membrane not extending to level of setae *h1*, length of incision from anterior end to level of lobar apices 88 (90). Distance between dorsal setae *c2* : *d2* 45 (33), *d2* : *e2* 118 (120), *e2* : *h2* 88 (85), *h2* : *h3* 30 (33), *ps1* : *h3* 28 (30), *d1* : *d1* 43 (35), *e1* : *e1* 40 (45), *h2* : *h2* 83 (80), *h3* : *h3* 53 (50). Setae *ps1* 85 (75) long, around two times longer than *f2*, extending beyond lobar apices.

Sternum about half as long as total length of epimerites I. Coxal fields III almost closed. Sclerotized areas of coxal fields IV widely separated from each other and anterior to genital apparatus (Fig. 1B). Setae *3a* situated anterior to level of setae *4b*. Genital apparatus small, length 8 (7), width 15 (14), branches of genital arch short. Genital

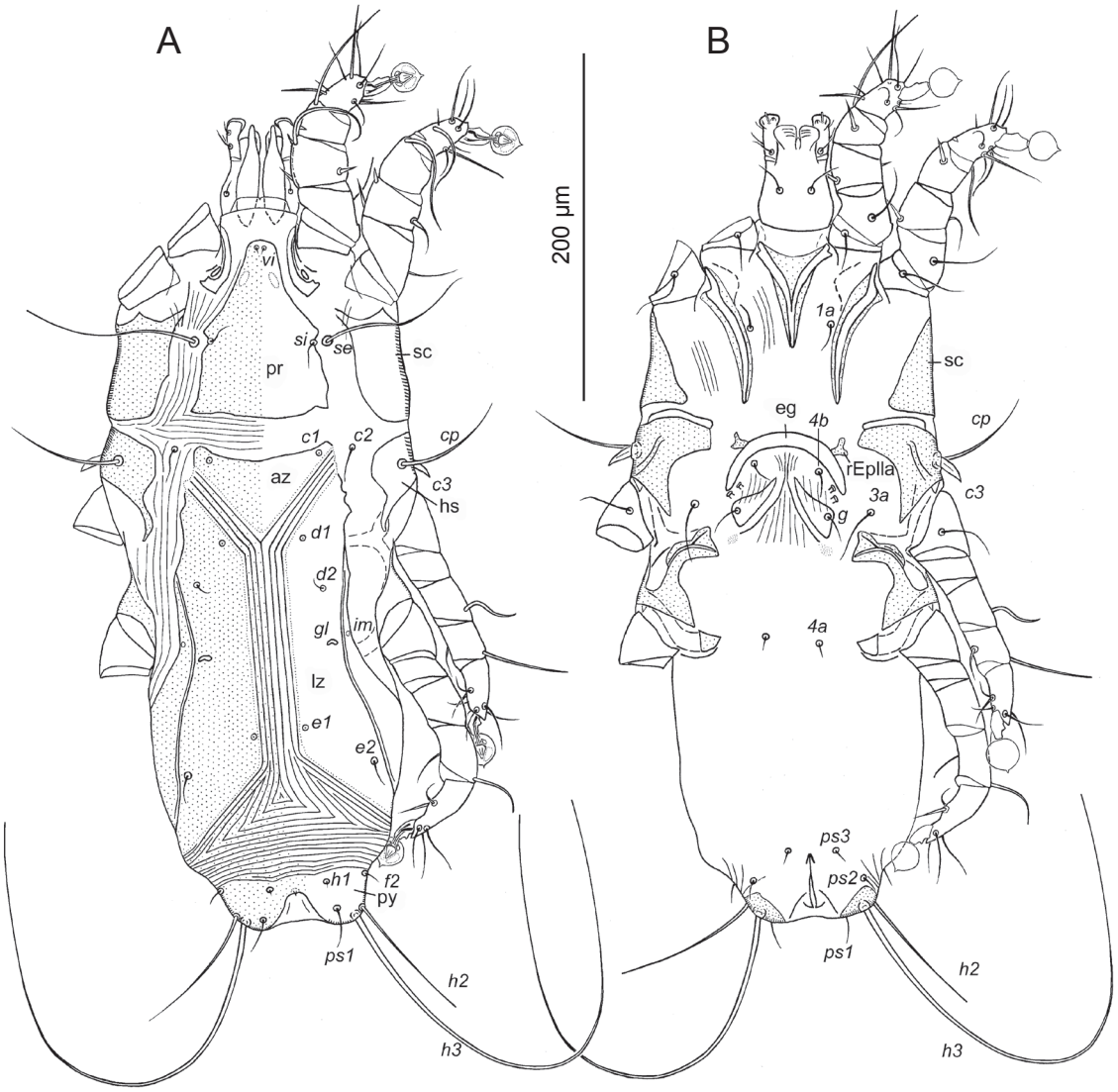

Fig. 2. *Rhinozachvatkinia calonectris* sp. n. from *Calonectris edwardsii*; female. **A** – dorsal view; **B** – ventral view. *Abbreviation*: az – anterior sclerotized zone of hysteronotal shield; eg – epigynum; hs – humeral shield; *im* – cupules; lz – lateral sclerotized zone of hysteronotal shield; pr – prodorsal shield; py – pygidial shield; rEpIIa – rudimentary sclerite of epimerites IIa; sc – scapular shield.

shields absent, setae *g* situated on striated tegument immediately posterior to genital arch. Adanal shields fused each other forming star-like structure, its lateral branches bear setae *ps3* (Fig. 4B). Diameter of adanal suckers 16 (17). Adanal apodemes narrow, poorly sclerotized. Distance between setae: *4b* : *4b* 48 (30), *g* : *g* 10 (10), *4a* : *g* 18 (13), *g* : *ps3* 45 (48), *ps3* : *ps3* 30 (28).

Tarsi I, II with scarcely distinct apical spine-like processes (Fig. 3A,B). Setae *mG* on genu I narrow spine-shaped, on genu II filiform. Setae *cG* of genua I, II narrow spine-like. Tarsus III 60 (62) long (Fig. 3C). Tarsus IV with one dorso-basal spine (Fig. 3D).

Female (Figs. 2, 4C–E) (range for two paratypes). Length of idiosoma 410–445, width 175–190. Gnathosoma shaped as in male, lateral margins without tooth-like extensions, length of subcapitulum including palps 69–72, greatest width 49–51, width at bases of palps 37–39 (Fig. 4D). Palps not enlarged basally. Chelicerae slightly narrowed in anterior part, 72–75 long.

Prodorsal shield: strongly narrowed in anterior part, posterior part roughly rectangular; length along median line 100–113, greatest width 75–85 (Fig. 2A). Setae *vi* paired. Setae *si* situated on lateral margins of prodorsal shield, setae *se* situated on striated tegument near lateral margins of shield, distance between setae *se* 80–85. Length of hysterosoma from sejugal furrow to posterior margin of opisthosoma 295–305. Setae *c3* narrowly lanceolate, 13–15 long.

Hysteronotal shield: with three dotted parts separated from each other by striated areas, anterior zone and a pair of lateral zones; posterior margin of hysteronotal shield medially indistinct (Fig. 2A). Anterior zone triangular in

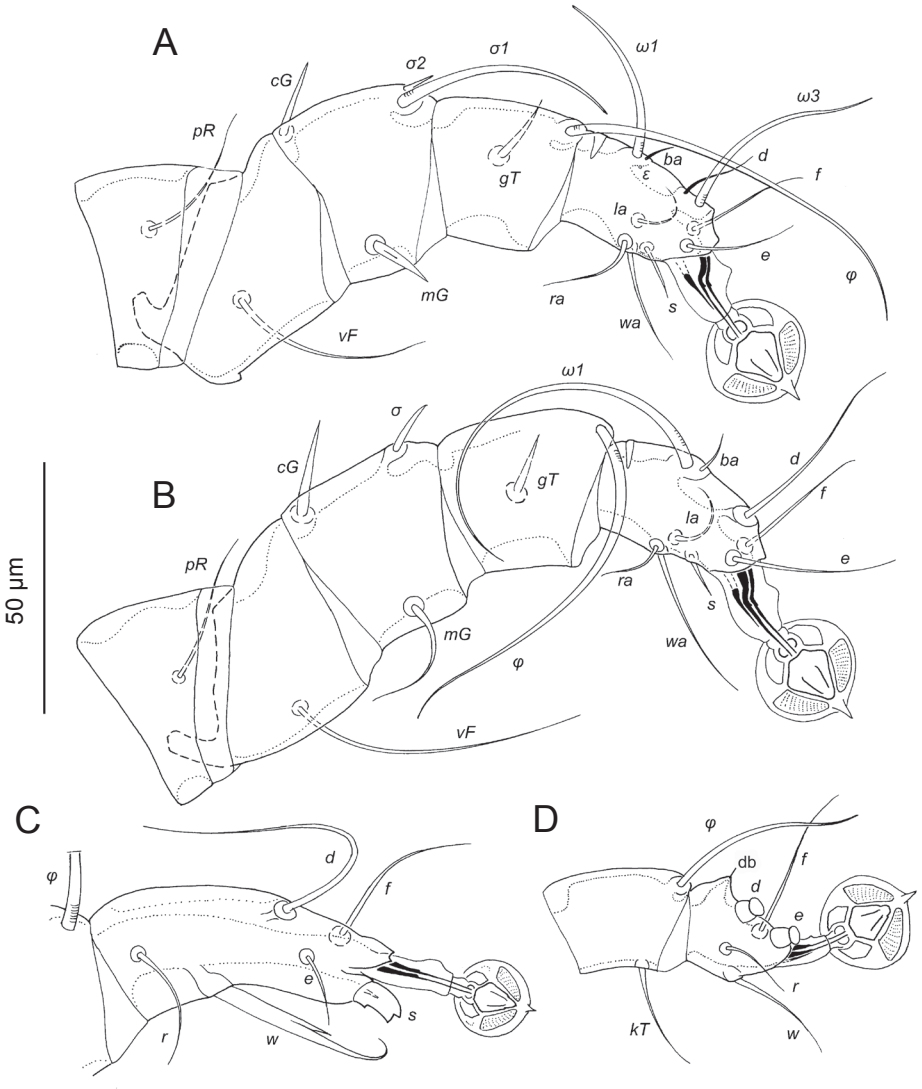

Fig. 3. *Rhinozachvatkinia calonectris* sp. n. from *Calonectris edwardsii*; legs of male. **A** – leg I; **B** – leg II; **C** – tarsus III; **D** – tibia and tarsus IV. *Abbreviation*: db – dorso-basal spine of tarsus IV.

shape, small, and bear setae *c1*. Lateral zones bear setae *d1*, *d2*, *e1*, *e2* and hysteronotal gland opening *gl*. Greatest length of hysteronotal shield (from anterior margin to posterior ends of lateral dotted zones) 238–250, width at anterior margin 85–90, width at posterior margin 120–125. Distance between dorsal setae *c2* : *d2* 75–85, *d2* : *e2* 110, *e2* : *h3* 85–88, *h3* : *h3* 60–68, *d1* : *d1* 45–50, *e1* : *e1* 28–30.

Pygidial shield 28–33 long, 85–90 wide. Epimerites I fused into Y, sternum about one third of total length of epimerites, bases of epimerites not thickened. Epigynum semicircular, thick, extending to level of anterior genital papillae (Fig. 2B), length 38–43, width 60–75. Rudimentary sclerites rEpIIa small and fused with epigynum. Setae *g* situated at level of setae *3a* or slightly posterior.

Legs I, II as in male. Tarsi III, IV with small apical spine-like extension (Fig. 4C,E). Leg IV not extending to posterior end of the body.

Type host: Cape Verde shearwater *Calonectris edwardsii* (Oustalet) (Procellariiformes, Procellariidae).

Type locality: Cape Verde, Boa Vista Island, Curral Velho Islet.

Date of collection: 12 July 2006, collected by Jacob González-Solís.

Type material: Male holotype; one male and two female paratypes.

Deposition of material: Male holotype (ZISP 5021-1), one male (ZISP 5022) and two female paratypes (ZISP 5021-2, 5023).

Additional material: one male (ZISP 5024) from *C. edwardsii*, Cape Verde, Raso Island, 21 March 2008, collected by Teresa Militão; one female (ZISP 5025) from *C. edwardsii*, Cape Verde, Boa Vista Island, Curral Velho Islet, 8 July 2007, collected by Jacob González-Solís; one male and one female (ZISP 5026-1, 5026-2) from Cory's shearwater *Calonectris borealis* (Cory), Portugal, Azores Archipelago, Graciosa Island, Praia, 9 August 2003, collected by Jacob González-Solís; one male (ZISP 5027) from

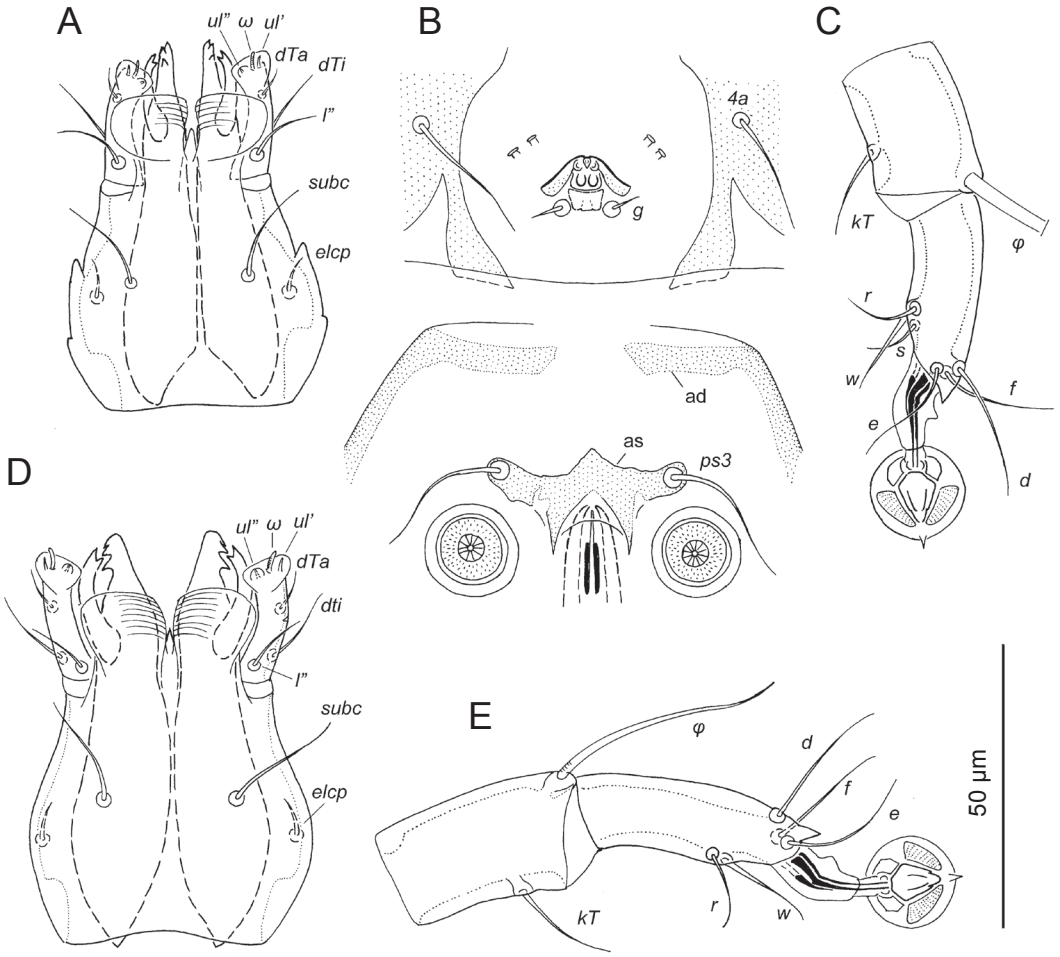

Fig. 4. *Rhinozachvatkinia calonectris* sp. n. from *Calonectris edwardsii;* details. **A** – gnathosoma of male, ventral view; **B** – genital and anal areas of male; **C** – tibia and tarsus III of female; **D** – gnathosoma of female, ventral view; **E** – tibia and tarsus IV of female. *Abbreviations*: ad – adanal apodeme; as – adanal shield.

C. borealis, Portugal, Azores Archipelago, Santa Maria Island, Vila, 9 June 2003, collected by Elena Gómez-Díaz; one male and one female (ZISP 5028-1, 5028-2) from *C. borealis*, Portugal, Azores Archipelago, Flores Island, Faja Lopo Vaz, 16 August 2003, collected by Jacob González-Solís; one male (ZISP 5029) from *C. borealis*, Portugal, Azores Archipelago, Corvo Island, Pesqueiros, 20 August 2003, collected by Elena Gómez-Díaz.

Etymology: The specific epithet is taken from the generic name of the type host and is a noun in apposition.

Differential diagnosis: Among three previously described species, *Rhinozachvatkinia calonectris* sp. n. is most similar to *R. graciosa* Mironov, 1989 described from *Pachyptila desolata* from Georgia Island (Mironov 1989) by having long and well separated opisthosomal lobes and star-shaped adanal shield in males.

The new species differs from *R. graciosa* by the following features: in both sexes, scapular setae *se* are situated off the prodorsal shield and subhumeral setae *c3* are lanceolate; in males, the terminal membranes are bidentate, setae *4b* are situated posterior to the level of setae *3a*, and the adanal apodemes are narrow L-shaped; in females, the hysteronotal shield is separated by striated areas into three dotted zones (the anterior zone and a pair of lateral ones), and the rudimentary sclerites rEpIIa are small and fused to the epigynum.

In both sexes of *R. graciosa*, scapular setae *se* are situated on the prodorsal shield, and subhumeral setae *c3* are spiculiform; in males, the terminal membranes are acute apically, setae *4b* are situated anterior to the level of setae *3a*, and the adanal apodemes are teardrop-shaped; in females, the hysteronotal shield has two lateral dotted parts, and the rudimentary sclerites rEpIIa are represented by a pair of transverse sclerites distinctly separated from the epigynum.

DNA barcode. We sequenced a 609-pb fragment of the mitochondrial cytochrome *c* oxidase subunit I (COI) gene for one male paratype (Acc. No. KF111273, ZISP 5022), four males (Acc. No. KF111274, ZISP 5024; Acc. No. KF111270, ZISP 5026-1; Acc. No. KF111269, ZISP 5027; Acc. No. KF111272, ZISP 5029) and one female

(Acc. No. KF111271, ZISP 5028-2) from additional material collected as described above. The average genetic distance (K2P) among the *R. calonectris* COI sequences was 1.2% (SE 0.3). The majority of nucleotide substitutions were synonymous and only two amino acid changes were detected (substitution of valine with isoleucine at positions 124 and 157).

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1.4 NEW SPECIES OF THE FEATHER MITE GENUS *PROMEGNINIA* GAUD & ATYEO (ACARI: AVENZOARIIDAE) FROM PETRELS AND SHEARWATERS (PROCELLARIIFORMES: PROCELLARIIDAE)

Sergey V. Mironov, Laura M. Stefan, Jacob González-Solís

Systematic Parasitology, 90: 91-103, 2015

NUEVAS ESPECIES DE ÁCAROS DE LAS PLUMAS DEL GÉNERO *PROMEGNINIA* GAUD & ATYEO (ACARI: AVENZOARIIDAE) EN PARDELAS Y PETRELES (PROCELLARIIFORMES: PROCELLARIIDAE)

RESUMEN

Dos nuevas especies de ácaros de las plumas del género *Promegninia* Gaud & Atyeo, 1967 (Avenzoariidae: Bonnetellinae) son descritas en procelariformes del noreste del Océano Atlántico: *Promegninia bulweriae* n. sp. en el petrel de Bulwer *Bulweria bulwerii* (Jardine & Selby) y *P. calonectris* n. sp. en la pardela cenicienta *Calonectris borealis* (Cory) Procellariiformes: Procellariidae). Los machos de *P. bulweriae* n. sp. se distinguen más claramente de las otras especies conocidas del género por tener el tercer par de patas cortas que se extienden solamente al nivel de los ápices lobares y tarsos III cónicos cortos con seta ventral *w* lanceolada; las hembras de esta especies se caracterizan por la ausencia de escleritos adicionales en ángulos postero-laterales del escudo prodorsal. Los machos de *P. calonectris* difieren de las otras especies conocidas en tener lamelas terminales bidentadas en los ápices lobares y escudo adanal completo; las hembras de esta especie se distinguen por tener escudos pigidiales bien desarrollados y un escudo histeronotal que incluye las bases de las setas *c2*. También se obtuvieron datos de las secuencias del fragmento de ADN mitocondrial de la subunidad I del citocromo oxidasa I (COI) para las nuevas especies. Se proporcionan un diagnóstico actualizado para *Promegninia* y una clave de identificación para las especies conocidas.

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New species of the feather mite genus *Promegninia* Gaud & Atyeo (Acari: Avenzoariidae) from petrels and shearwaters (Procellariiformes: Procellariidae)

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Abstract Two new species of the feather mite genus *Promegninia* Gaud & Atyeo, 1967 (Avenzoariidae: Bonnetellinae) are described from procellariids in the northeasterm Atlantic Ocean: *Promegninia bulweriae* n. sp. from the Bulwer's petrel *Bulweria bulwerii* (Jardine & Selby) and *P. calonectris* n. sp. from the Cory's shearwater *Calonectris borealis* (Cory) (Procellariiformes: Procellariidae). Males of *P bulweriae* n. sp. are most clearly distinguished from the other known species in the genus by having short legs III extending only to the level of lobar apices and short conical tarsi III with lanceolate ventral seta *w*; females of this species are characterised by the absence of additional sclerites at postero-lateral angles of the prodorsal shield. Males of *P. calonectris* differ from the other known species in having bidentate terminal lamellae on the lobar apices and the entire adanal shield; females of this species are distinguished by having well-developed pygidial shields and a hysteronotal shield encompassing the bases of setae *c2*. Sequence data of the mitochondrial cytochrome *c* oxidase subunit I gene fragment (COI) are also obtained for the new species. An updated diagnosis of *Promegninia* and a key to the known species are provided.

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Introduction

The feather-mite genus *Promegninia* Gaud & Atyeo, 1967 (Analgoidea: Avenzoariidae) was originally established in the family Analgidae Trouessart & Mégnin, 1884 (see Gaud & Atyeo, 1967). Its only species, originally named *Megninia pedimana* Trouessart, 1898, was described from the wandering albatross *Diomedea exulans* Linnaeus (Procellariiformes: Diomedeidae) (Trouessart, 1899). Later, Atyeo & Gaud (1981) transferred *Promegninia* to the Avenzoariidae Oudemans, 1905 and placed it in the subfamily Bonnetellinae Atyeo & Gaud, 1981.

Within the Bonnetellinae, *Promegninia* and two other genera also associated with procellariiforms, *Zachvatkinia* Dubinin, 1949 and *Rhinozachvatkinia* Mironov, 1989, comprise the *Zachvatkinia* generic group (Mironov, 1989a, b; Mironov & Dabert, 1999; Stefan et al., 2014). In a phylogenetic study of the family Avenzoariidae, Mironov & Dabert (1999) have shown a close affinity of these three genera. Within the *Zachvatkinia* group, mites of the genera *Promegninia* and *Rhinozachvatkinia* are small-sized (adults 300–400 μm long) whereas mites of *Zachvatkinia* are large-sized (adults 500–800 μm long). Species of *Promegninia* and *Rhinozachvatkinia* are exclusively restricted to

procellariiforms and are known from birds of the families Diomedeidae, Procellariidae, Hydrobatidae and Pelecanoididae (see Gaud & Atyeo, 1967; Mironov, 1989b; Stefan et al., 2014). Representatives of the genus *Zachvatkinia* are known from birds of all procellariiform families, except for Pelecanoididae, and also are widely distributed on gulls, terns and crab plovers (Charadriiformes: Laridae and Dromadidae) (Dubinin, 1949; Gaud, 1976; Mironov, 1989a, 1992; Negm et al., 2013).

Here we describe two new species of the genus *Promegninia* found on birds of two procellariiform genera breeding on different islands in the northeastern Atlantic Ocean. Careful morphological investigation of the present material has shown that the authors of the genus *Promegninia* erroneously interpreted some diagnostic features of the genus (see Gaud & Atyeo, 1967). Therefore, we provide a revised diagnosis of the genus and a key to the known species.

Materials and methods

The material used in the present study was collected by Dr. Jacob González-Solís, Dr. Elena Gómez-Díaz, Dr. Jose Luis Roscales, Laura M. Stefan and Teresa Militão between 2003 and 2012 from living procellariiform birds breeding on different archipelagos in the northeastern Atlantic Ocean: Cape Verde, Azores, Madeira, Berlengas and Canary Islands. Bird capturing and mite sampling were carried out under permissions from the corresponding governmental authorities of Spain, Portugal and Cape Verde. All animals were handled in accordance with good animal practices as defined by the current European legislation. Feather mites were collected using the dust-ruffling method [for *Calonectris edwardsii* (Oustalet) and *Bulweia bulwerii* (Jardine and Selby) (see Walther & Clayton, 1997)] or direct sampling of barbs from primary feathers [for *Calonectris borealis* (Cory)], and all material was subsequently preserved in vials with absolute ethanol. For morphological identification, feather mites were cleared in lactic acid for 24 h and mounted on microscope slides in PVA medium (BioQuip Products, Rancho Dominguez, California).

The description and measuring technique of the new species follows the standards used for avenzoariid mites (Atyeo & Gaud, 1981; Mironov, 1989a; Mironov & Dabert, 1997; Mironov & Stefan, 2013). The distance between setae of the same pair is measured as the direct distance between their bases, and the distance between different pairs of setae is the shortest distance between the transverse levels formed by the setae of respective pairs. General morphological terms and leg chaetotaxy follow Gaud & Atyeo (1996), the idiosomal chaetotaxy also follows these authors with the corrections proposed by Norton (1998). All measurements are in micrometres. Drawings were made using a Leica DM 5000B light microscope with DIC illumination and camera lucida.

Prior to mounting on slides, six individual mites (five from *C. borealis* and one from *B. bulwerii*) were subjected to DNA extraction using the nondestructive method described by Dabert et al. (2008). A 600-bp fragment of the COI gene was amplified using the primers bcdF05 (5′-TTT TCT ACH AAY CAT AAA GAT ATT GC-3′) and bcdR04 (5′-TAT AAA CYT CDG GAT GNC CAA AAA A-3′) (Dabert et al., 2008). Polymerase chain reactions (PCRs) were carried out in a total volume of 25 µl containing 2 µl 10× reaction buffer with $MgCl_2$ (15 mM) (Roche Diagnostics), 1.5 mM $MgCl_2$, 0.15 mM of each dNTP, 0.4 µM of each primer, 1.25 U *Taq* DNA polymerase (Roche Diagnostics, Meylan, France) and 30–50 ng of DNA template. Amplification conditions consisted of an initial step of 5 min at 95°C, followed by 35 cycles of 30 sec at 95°C, 1 min 30 sec at 50°C, 1 min at 72°C, with a final step of 5 min at 72°C. PCR products were separated by electrophoresis in 2% agarose gel and visualised under UV light. Samples containing visible bands were sent for sequencing to Beckman Coulter Genomics (France). BioEdit version 7.0.5.3 (Hall, 1999) was used to assemble, edit and align sequences and all variable sites were confirmed by visual inspections of the chromatograms. Pairwise distances between sequences were computed with MEGA 4 (Tamura et al., 2007) using K2P distance model (Kimura, 1980).

The taxonomic system and scientific names of birds follow Clements et al. (2013) and Sangster et al. (2012). Type- and voucher material is deposited in the Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia (ZISP).

Family Avenzoariidae Oudemans, 1905
Subfamily Bonnetellinae Atyeo & Gaud, 1981
Genus *Promegninia* Gaud & Atyeo, 1967

Diagnosis

Both sexes. Small to medium-sized bonnetellines (300–500 µm). Subcapitulum roughly rectangular.

Chelicerae normal, basal segment not narrowed anteriorly. Prodorsal shield roughly pear-shaped, occupying entire median area of prodorsum; scapular and humeral shields well developed. Laterocoxal setae *scx* absent. Setae *vi* present, paired, minute. Subhumeral setae *c3* filiform, located at level of humeral setae *cp* or slightly anterior. Epimerites I fused into a Y-shape. Tarsi I, II without apical spine-like extension. Setae *ba* of tarsi I and II filiform. Famulus ε of tarsi I large, spine-like. Setae *mG* of genua I filiform or thickened, with filiform apex. *Male*. Coxal fields III closed. Opisthosoma with short or moderately elongated opisthosomal lobes. Terminal cleft short, triangular or semi-ovate. Interlobar membrane narrow, occupies only anterior part of terminal cleft. Lateral membrane absent. Terminal membranes on lobar apices short, semicircular or bidentate. Genital apparatus located approximately at level of bases of trochanters IV. Genital setae *g* located on tips of genital arch. Paragenital apodemes present, free from coxal fields IV. Adanal shield present, entire or split into several pieces. Adanal membranes present or absent. Corolla of anal suckers smooth. Cupules *ih* distinct. Legs III hypertrophied. Tarsus III with or without apical extension; seta *s* claw-like with bidentate apex; seta *w* strongly thickened at base and with filiform apex or lanceolate; remaining setae filiform. Tarsus IV with dorsobasal extension, modified setae *d* and *e* barrel-shaped, with discoid cap. *Female*. Hysteronotal shields represented by two large pieces spreading from level of humeral shields to postero-lateral margins of opisthosoma; median area of hysterosoma with longitudinally striated cuticle. Pygidial shield present, paired or entire. Setae *h3* represented by macrosetae, setae *h2* short, filiform. Epigynum large, bow-shaped, located at level of humeral shields. Copulatory opening dorsal on small nipple-like extension, anterior to setae *h1*.

Hosts: Procellariiformes: Diomedeidae and Procellariidae.

Type-species: *Megninia pedimana* Trouessart, 1899, by original designation.

Remarks

Gaud & Atyeo (1967, 1996) indicated the main diagnostic feature of *Promegninia* in the diagnosis and the key to the genera as follows: “seta *ba* dilated into short spine on tarsi I (sometimes also on tarsus II)”. Neither the type-specimens of *Promegninia pedimana* (Trouessart, 1898) nor any material collected subsequently from the type-host, *Diomedea exulans* Linnaeus, were available for examination. However, investigation of the two new species found in the course of the present study and of a few undescribed species deposited in the collection of the Zoological Institute (Saint Petersburg, Russia) indicates that the authors of the genus incorrectly interpreted the named morphological feature. In the specimens examined, only tarsi I have a spiniform structure of setal origin near the base of the solenidion *ω1*. Also, this spiniform structure is definitely not seta *ba*, because for certain, the short filiform setae sitting at the very bases of solenidia *ω1* on tarsi I and II (Figs. 3A, B) are true setae *ba*. Here it is necessary to add that in both of the closest genera, *Zachvatkinia* and *Rhinozachvatkinia*, setae *ba* of tarsi I, II are also filiform and occupy the same position. The only conclusion that can be drawn out is that the spine-like structure on tarsi I is a hypertrophied famulus ε. This setal structure exists only on tarsi I in Astigmata but is usually represented by an extremely tiny spine near solenidion *ω1*, or even can be just vaguely discerned as a short channel in the thick cuticle. As for the note that “seta *ba*” can also be dilated on tarsi II, the authors of the genus had apparently misinterpreted a small ledge anterior to the base of seta *d* (Fig. 3B) as a tip of “dilated seta *ba*” stretching along the tarsus, that can be inferred from the drawings in their papers (see figures 2A, B and 80C, D in Gaud & Atyeo, 1967, 1996).

***Promegninia bulweriae* n. sp.**

Type-host: Bulwer’s petrel *Bulweria bulwerii* (Jardine & Selby) (Procellariiformes: Procellariidae).

Type-locality: Roque Negro, La Palma Island, Canary Islands, Spain.

Type-material: Holotype male (ZISP 6031), 12.v.2006, col. J. L. Roscales. Paratypes: 2 females (ZISP 6032) from the same host species, Ilhéu de Cima Island, Cape Verde, 24.ii.2012, col. J. González-Solís; 1 female (ZISP 6033) from the same host species, Raso Island, Cape Verde, 4.vii.2006, col. E. Gómez-Díaz.

Representative sequence: 600 bp fragment of the COI gene; GenBank accession No. KM401844 (paratype ZISP 6034).

Etymology: The specific epithet is derived from the generic name of the type-host and is a noun in the genitive case.

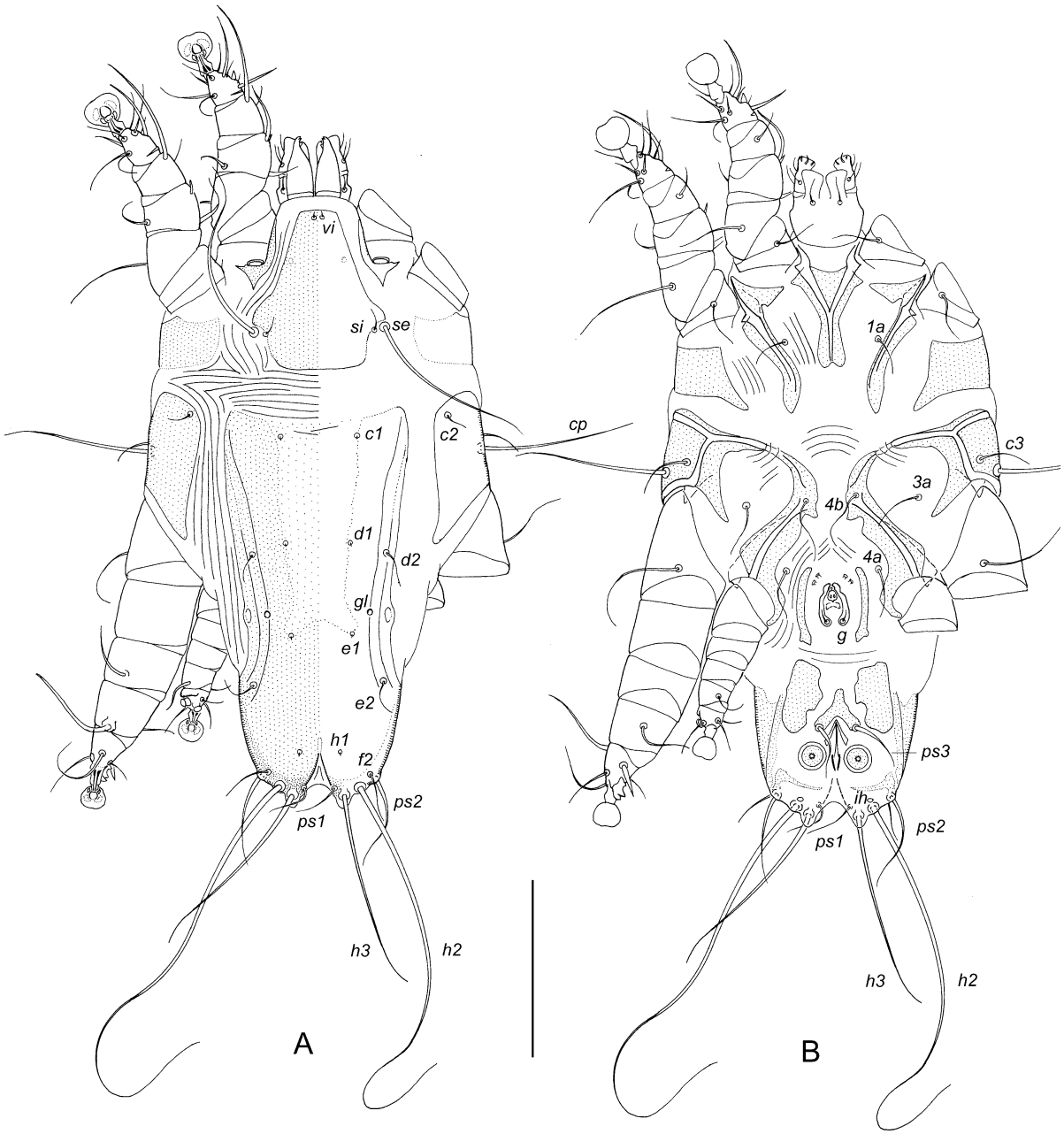

Fig. 1 *Promegninia bulweriae* n. sp. Male. A, Dorsal view; B, Ventral view. *Scale-bar*: 100 μm

Description (Figs. 1, 2, 3)

Male [Based on the holotype.] Length of idiosoma from anterior end to lobar apices 330, width at level of humeral shields 185. Subcapitulum roughly rectangular, with small ledges on lateral margins; length including palps 46, greatest width 40 (Fig. 3F). Prodorsal shield roughly pear-shaped, without median ridges; posterior margin straight, lateral margins with short angular extension anterior to bases of scapular setae; length along midline 88, width at level of lateral extensions 72 (Fig. 1A). Setae *si* located on lateral margins of prodorsal shield; setae *se* off this shield, separated by 75. Length of hysterosoma from level of sejugal furrow to lobar apices 225. Setae *c3* filiform, *c*.25 long. Hysteronotal shield with acute anterior

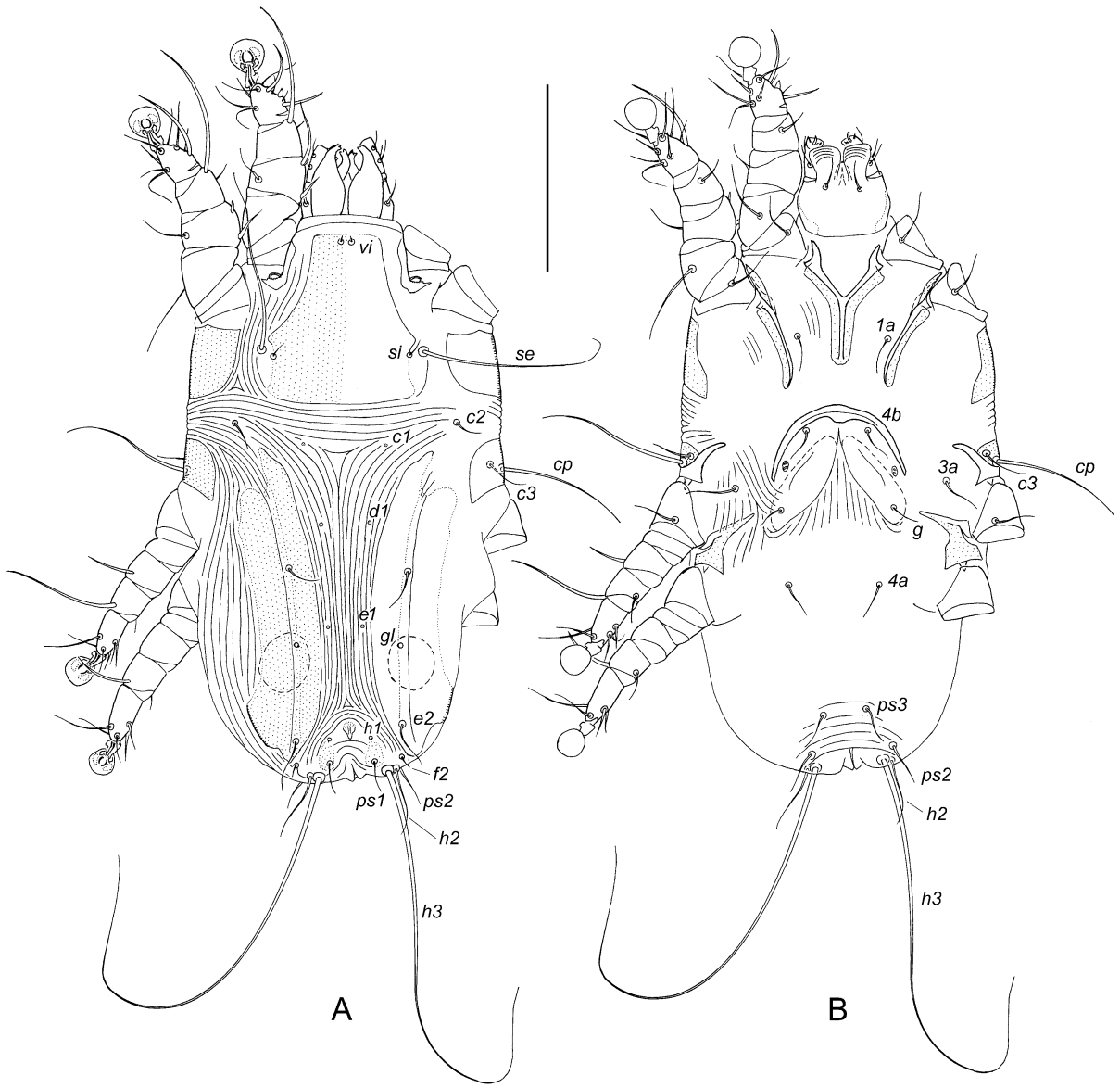

Fig. 2 *Promegninia bulweriae* n. sp. Female. A, Dorsal view; B, Ventral view. *Scale-bar*: 100 μm

angles; median area of anterior half poorly sclerotised, with indistinct concave anterior margin; greatest length from anterior margin to bases of setae *h3* 215, width at anterior margin 100. Opisthosomal lobes very short, bluntly-angular, lobar apices bearing setae *h3* with short, rounded terminal lamellae *c*.5 long. Terminal cleft small, triangular, extends to level of setae *h1*; length including supranal concavity 22. Lateral membranes not developed. Interlobar membrane occupies anterior half of terminal cleft, with free margin shallowly concave. Length from apices of terminal lamellae to free margin of interlobar membrane 13. Setae *ps1 c*.40 long, located at level of setae *h2*, extend beyond apices of lamellae. Distance between dorsal setae *c2:d2* 77, *d2:e2* 70, *e2:h3* 62, *d1:d2* 7, *e1:e2* 27, *h2:h2* 44, *h3:h3* 31, *ps1:ps1* 16, *ps2:ps2* 60.

Sternum length about half total length of epimerites I. Coxal fields III closed. Sclerotised areas of coxal fields IV narrow, widely separated from each other (Fig. 1B). Setae *3a* and *4b* approximately at same transverse level. Genital apparatus with slightly curved

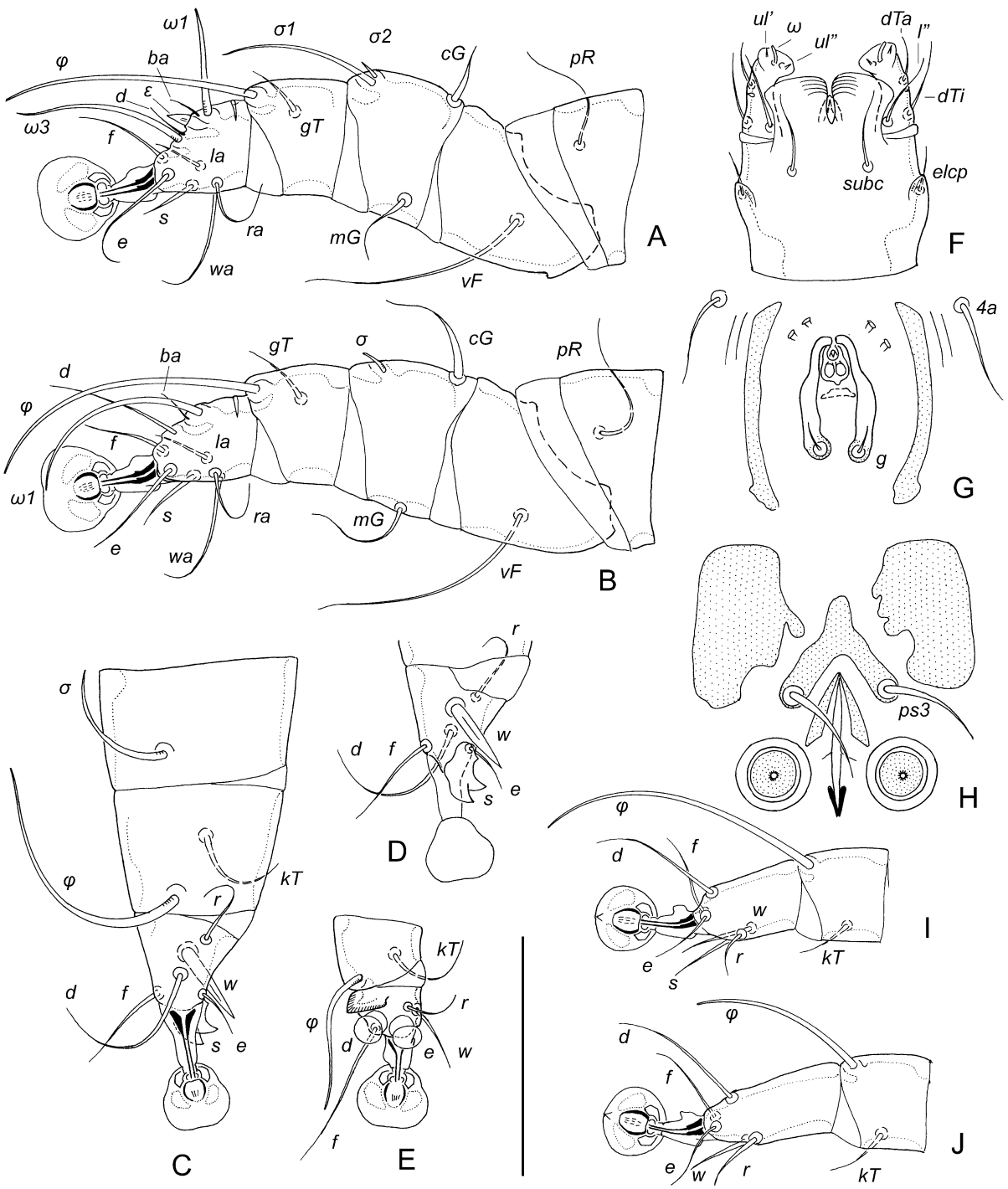

Fig. 3 *Promegninia bulweriae* n. sp. Details. A, Leg I of male, dorsal view; B, Leg II of male, dorsal view; C, Genu, tibia and tarsus III of male, dorsal view; D, Tarsus III of male, ventral view; E, Tarsus and tibia IV of male, dorsal view; F, Subcapitulum of male; G, Genital apparatus of male; H, Adanal shields of male; I, Tibia and tarsus III of female, dorsal view; J, Tibia and tarsus IV of female, dorsal view. *Scale-bar*: 50 μm

branches bearing setae *g* on tips; length of genital apparatus 23, width at base 15. Genital shield(s) absent. Paragenital apodemes represented by pair of bow-shaped sclerites flanking genital apparatus from lateral sides (Fig. 3G). Adanal shields split into 3 pieces: median part shaped as inverted Y-shape and 2 lateral pieces of uneven form. Setae *ps3* located on posterior tips of median fragment of adanal shield (Fig. 3H). Diameter of adanal suckers 14. Anal field posterior to adanal suckers with pair of transverse bow-shaped sclerites. Adanal apodemes and adanal membranes absent. Distance between ventral setae: *4b:4a* 42, *4a:g* 29, *g:ps3* 57, *4b:4b* 29, *g:g* 9, *ps3:ps3* 18.

Tarsi I, II without apical spine-like processes (Figs. 3A, B). Seta *mG* on genu I narrow, filiform, slightly thickened at base; seta *mG* on genu II filiform. Setae *cG* of genua I, II narrow, spine-like, with filiform apex. Legs III relatively short, with tips of ambulacra scarcely extending to level of lobar apices. Tarsus III conical, approximately as long as wide at base, 22 long excluding pretarsus; claw-like seta *s* with bidentate apex; seta *w* lanceolate, 16 long; remaining setae filiform (Figs. 3C, D). Tarsus IV with dorso-basal extension, 11 long (Fig. 3E).

Female [Based on 2 paratypes.] Length of idiosoma 285–300, width 160–170. Gnathosoma shaped as in male, but slightly wider, length of subcapitulum including palps 45–48, greatest width 48–50. Prodorsal shield shaped as in male, length along median line 85–88, width at level of lateral extensions 73–75 (Fig. 2A). Setae *si* located on lateral margins of prodorsal shield, setae *se* off this shield; distance between setae *se* 83–85. Length of hysterosoma from sejugal furrow to posterior margin of opisthosoma 185–200. Setae *c3* filiform, *c*.25 long. Hysteronotal shield represented by 2 longitudinal pieces, separated medially by wide area of striated tegument; anterior ends of shields extend beyond level of humeral setae *cp*; length of shields 160–170, shortest distance between their inner margins 28–35. Setae *d2, e2* and hysteronotal gland openings *gl* located on hysteronotal shields. Setae *c1, c2, d1, e1* located on striated tegument. Pygidial shield poorly developed, represented by pair of small sclerotised areas on posterior end of opisthosoma between bases of setae *h1* and *ps1*. Copulatory opening on small nipple-like extension, slightly anterior to level of setae *h1*. Distance between dorsal setae *c2:d2* 75–80, *d2:e2* 80–82, *e2:h3* 22–25, *h1:h3* 16–17, *h1:h1* 18–22, *h3:h3* 33–38, *d1:d2* 22–25, *e1:e2* 55–60.

Sternum length approximately half total length of epimerites I, bases of epimerites not thickened. Epigynum large, semicircular, thin, extends slightly beyond level of genital papillae (Fig. 2B), length 36–38, width 58–70. Rudimentary sclerites rEpIIa absent. Setae *g* situated posterior to setae *3a*. Distance between ventral setae: *4b:3a* 31:35, *4b:g* 40:42, *g:4a* 32–36.

Legs I, II as in male. Tarsi III, IV without apical spine-like extensions (Figs. 3I, J). Legs IV not extending to posterior end of the body.

Remarks

Promegninia bulweriae n. sp. differs from the type- and only known species, *P. pedimana*, in the following features. In males of *P. bulweriae*, legs III are short, with tips of ambulacra scarcely extending to the level of lobar apices; tarsus III is conical, approximately as long as wide at base; seta *w* of tarsus III is lanceolate; the median part of adanal shield is shaped as an inverted Y; and the paragenital apodemes are bow-shaped, not enlarged posteriorly. In females of the new species, additional sclerites at postero-lateral angles of the prodorsal shield are absent; the striated area between hysteronotal shields is not sclerotised; and the epigynum extends slightly beyond the level of genital papillae. In males of *P. pedimana*, legs III are long, with tarsus and distal half or tibia extending beyond the level of lobar apices; tarsus III is elongate and approximately three times longer than wide at base; seta *w* of tarsus III is spiculiform, with filiform apex; the median part of adanal shield has a shape of an inverted V, and the paragenital apodemes are enlarged posteriorly and with a shape of an inverted T. In females of this species, a pair of small rounded sclerites is present at postero-lateral angles of the prodorsal shield; the striated area between hysteronotal shields is sclerotised noticeably more strongly than remaining striated cuticle; and the epigynum does not extend beyond the level of genital papillae.

***Promegninia calonectris* n. sp.**

Type-host: Cory's shearwater *Calonectris borealis* (Cory) (Procellariiformes: Procellariidae).
Type-locality: Mogan, Gran Canaria Island, Canary Islands, Spain.

Type-material: Holotype male (ZISP 6034), 22.vi.2011, col. L. Stefan. Paratypes: 1 male (ZISP 6035) from *C. borealis*, same location, 7.vii.2011, col. L. Stefan; 2 females (ZISP 6036, 6037), same data as for the holotype; 1 female (ZISP 6038), same location, 5.vii.2011, col. L. Stefan; 2 females (ZISP 6039), same location, 5.vii.2011, col. L. Stefan.
Additional voucher material: 1 female (ZISP 6040) from *C. borealis*, Desertas Islands, Madeira, Portugal, 19.ix.2005, col. J. González-Solís; 1 female (ZISP 6041) from *C. borealis*, Poblet, Berlengas Islands, Portugal, 22.ix.2004, col. J. González-Solís; 1 female (ZISP 6042) from *C. borealis,* Pesqueiros, Corvo Island, Azores Archipelago, Portugal, 20.viii.2003, col. J. González-Solís; 1 female (ZISP 6043) from *C. edwardsii* (Oustalet), Raso Island, Cape Verde, 13.xi.2009, col. Teresa Militão.
Representative sequences: 600 bp fragment of the COI gene; GenBank accession nos KM401841 (holotype ZISP 6034), KM401839 (paratype ZISP 6038), KM401840 (paratype ZISP 6036), KM401842 (paratype ZISP 6035), and KM401843 (paratype ZISP 6037).
Etymology: The specific epithet is taken from the generic name of the type-host and is a noun in apposition.

Description (Figs. 4, 5, 6)

Male [Based on the holotype.] Length of idiosoma from anterior end to level of setae *h3* 478, greatest width at level of humeral shields 285. Subcapitulum roughly rectangular, with slightly convex lateral margins; length including palps 58, greatest width 54 (Fig. 6A). Prodorsal shield roughly pear-shaped, with pair of median ridges; posterior margin convex, lateral margins with short rectangular extension anterior to bases of scapular setae; length along midline 128, greatest width 115 (Fig. 4). Setae *se* located on lateral margins of prodorsal shield, separated by 108. Length of hysterosoma from level of sejugal furrow to lobar apices 345. Setae *c3* filiform, *c*.25 long. Hysteronotal shield with acute anterior angles; median area of anterior half poorly sclerotised with indistinct anterior margin medially; length from anterior margin to bases of setae *h3* 345, width at anterior margin 156. Opisthosomal lobes subtriangular, lobar apices with bidentate terminal membranes 13–15 long. Terminal cleft semi-ovate, extending beyond level of setae *h1*, length of cleft from anterior end to bases of setae *h3* 70. Lateral membranes not developed. Interlobar membrane occupies anterior part of terminal cleft, with strongly concave margin. Length from apices of terminal lamellae to free margin of interlobar membrane 42. Setae *ps1 c*.40 long, located at level of setae *h2*, extend far beyond apices of lamellae. Distance between dorsal setae *c2:d2* 117, *d2:e2* 122, *e2:h3* 100, *d1:d2* 35, *e1:e2* 55, *h2:h2* 75, *h3:h3* 42, *ps1:ps1* 30, *ps2:ps2* 104.

Sternum length about half length of epimerites I, surrounded by wide sclerotised area. Epimerites II with narrow sclerotised areas. Coxal fields III closed. Sclerotised areas of coxal fields IV wide, striated, not encompassing bases of setae *4a* (Fig. 4B). Setae *4b* anterior to level of setae *3a*. Genital apparatus with almost parallel-sided branches bearing setae *g*; tips of branches connected by narrow sclerotised bridge; length 29, width 22. Genital shield(s) absent. Paragenital apodemes represented by pair of bow-shaped sclerites, slightly enlarged anteriorly and flanking genital apparatus from lateral sides. Adanal shield entire, its posterior margin with pair of narrow, deep lateral incisions and short triangular median incision. Setae *ps3* located on posterior tips of Y-shaped median extension of adanal shield. Diameter of adanal suckers 26. Adanal membranes stretch along lateral margins of adanal shield, extend to bases of setae *ps2*. Anal field posterior to adanal suckers with pair of transverse bow-shaped sclerites. Adanal apodemes absent. Distance between ventral setae: *4b:3a* 26, *4b:4a* 62, *4a:g* 40, *g:ps3* 93,*4b:4b* 45, *g:g* 15, *ps3:ps3* 42.

Tarsi I, II without apical spine-like processes (Figs. 6C, D). Seta *mG* on genu I narrow, filiform, slightly thickened at base; seta *mG* on genu II filiform. Setae *cG* of genua I, II narrow, spine-like, with filiform apex. Legs III long, with tarsi and distal parts of tibia extending beyond lobar apices. Tarsus III convex dorso-basally, with finely-indented apical extension and pair of short crests on paraxial surface, 66 long excluding pretarsus; claw-like seta *s* with bidentate apex; seta *w* long, thickened in basal half, with minute additional spine at mid-length (Fig. 6E). Tarsus IV with acute dorso-basal extension, 16 long (Fig. 6F).

Female [Based on 6 paratypes.] Length of idiosoma 370–375, width 180–200. Subcapitulum shaped as in male, but slightly wider; length including palps 62–66, greatest width 62–65. Prodorsal shield roughly pear-shaped, without median ridges; lateral margins without

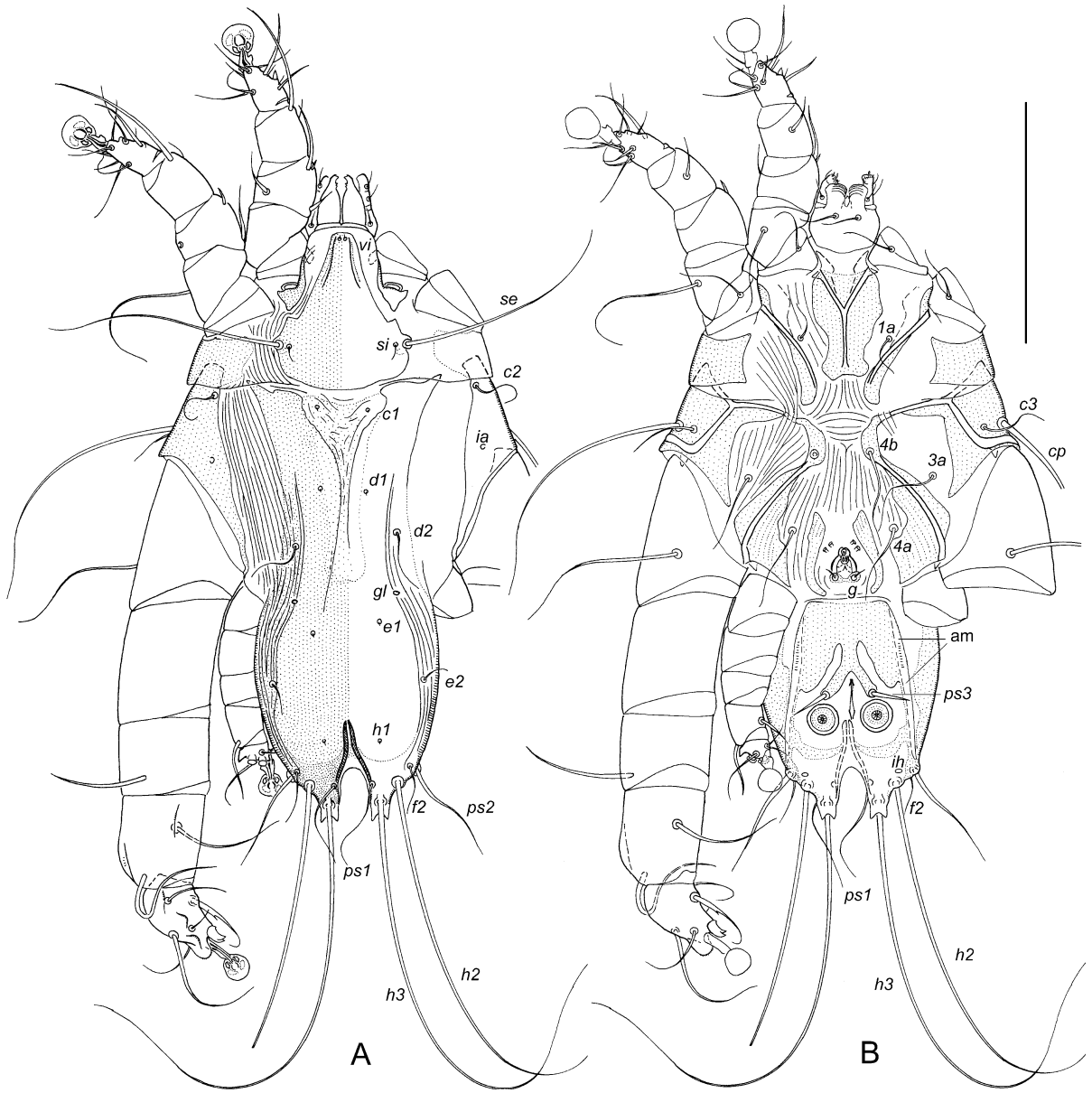

Fig. 4 *Promegninia calonectris* n. sp. Male. A, Dorsal view; B, Ventral view (am, adanal membrane). *Scale-bar*: 200 µm

rectangular ledge, with small incision posterior to base of setae *se*; posterior margin convex; length along midline 113–122, greatest width 73–75 (Fig. 5A). Two small additional sclerites located at postero-lateral angles of prodorsal shield. Distance between setae *se* 90–98. Length of hysterosoma from sejugal furrow to posterior margin of opisthosoma 245–255. Setae *c3* filiform, *c*.20 long. Hysteronotal shield represented by 2 longitudinal pieces, separated medially by wide area of striated tegument; anterior ends of these shields extending to bases of setae *c2*, length of shields 215–225, shortest distance between their inner margins 45–55 (Fig. 5A). Setae *c2, d2, e2* and hysteronotal gland openings *gl* located on hysteronotal shields. Setae *c1, d1, e1* located on striated tegument. Pygidial shield represented by pair of longitudinal sclerites, 40–50 long, bearing setae *h1, h2, h3* and *ps1*. Copulatory opening on small nipple-like extension between

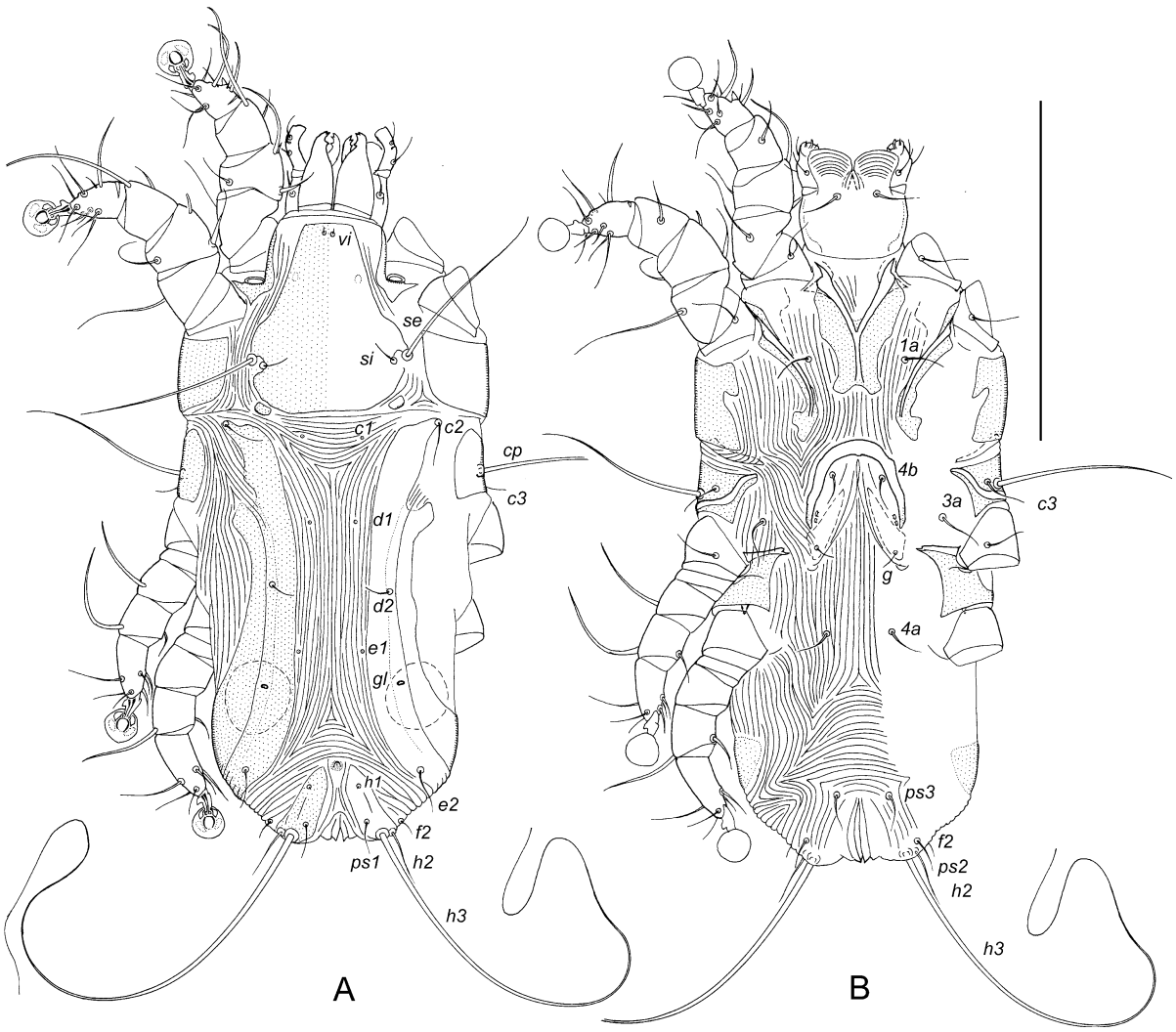

Fig. 5 *Promegninia calonectris* n. sp. Female. A, Dorsal view; B, Ventral view. *Scale-bar*: 200 μm

anterior tips of pygidial shields. Distance between dorsal setae *c2:d2* 100–105, *d2:e2* 102–108, *e2:h3* 33–40, *h1:h3* 30–33, *h1:h1* 28–30, *h2:h2* 50–55, *d1:d2* 25–30, *e1:e2* 70–75.

Sternum length approximately half length of epimerites I, surrounded by wide sclerotised area. Epigynum large, thin, extending to level of genital papillae (Fig. 5B), length 47–50, width 58–70. Rudimentary sclerites rEpIIa absent. Setae *g* situated posterior to setae *3a*. Distance between ventral setae: *4b:3a* 24–30, *4b:g* 44–48, *g:4a* 50–55.

Legs I, II as in male. Tarsi III, IV without apical extension (Figs. 6G, H). Legs IV extend to posterior end of the body.

Remarks

Promegninia calonectris n. sp. differs from *P. pedimana* and also from *P. bulweriae* n. sp. described above by the following features. In males of *P. calonectris*, the terminal lamellae on lobar apices are bidentate; the adanal shield is entire and has a pair of deep, narrow incisions on the posterior margin; the adanal membranes are present and heavily sclerotised; and the tips of the genital arch are connected by a narrow sclerotised bridge. In females of the new species, the hysteronotal shields bear the bases of setae *c2*; the pygidial shields are clearly outlined, *c*.40–50 μm long and bear bases of setae *h1, h2, h2*

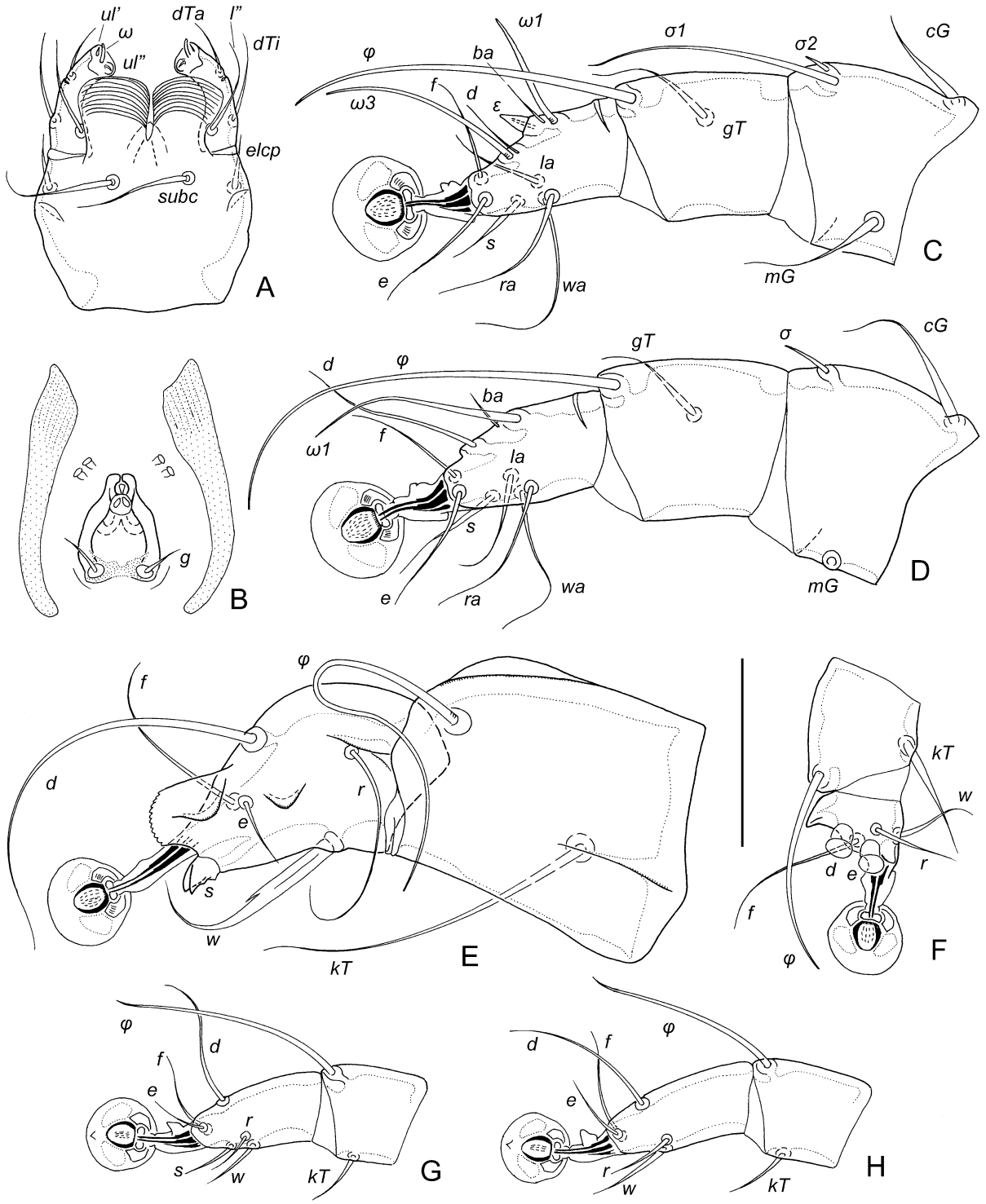

Fig. 6 *Promegninia calonectris* n. sp. Details. A, Subcapitulum of male; B, Genital apparatus of male; C, Genu, tibia and tarsus I of male, dorsal view; D, Genu, tibia and tarsus II of male, dorsal view; E, Tibia and tarsus III of male, dorsal view; F, Tibia and tarsus IV of male, dorsal view; G, Tibia and tarsus III of female, dorsal view; H, Tibia and tarsus IV of female, dorsal view. *Scale-bar*: 50 μm

and *ps1*. In males of *P. pedimana* and *P. bulweriae*, the terminal lamellae are short and rounded; the adanal shield is split into a medial and a pair of lateral pieces; adanal membranes are absent; and the tips of the genital arch are not connected by a sclerotised bridge. In females of these two species, the hysteronotal shields do not encompass the bases of setae *c2* and pygidial shields are absent (in *P. pedimana*) or represented by small patches between the bases of setae *h1* and *ps1* (in *P. bulweriae*).

DNA barcode

We sequenced a 600 bp fragment of the mitochondrial cytochrome *c* oxidase subunit I (COI) gene for two males (ZISP 6034, 6035; accession nos KM401841 and KM401842, respectively) and three females (ZISP 6036–6038; accession nos KM401840, KM401843 and KM401839, respectively) of *P. calonectris* collected from *C. borealis* and for one female (ZISP 6033; accession no. KM401844) of *P. bulweriae* collected from *B. bulwerii*. The average genetic distance (K2P) among the COI sequences for *P. calonectris* from *C. borealis* was 0.5% (SE 0.17). All nucleotide substitutions were synonymous, except one amino acid change (substitution of proline with serine) detected at position 71. The genetic divergence between the sequences for the two *Promegninia* species was 8.5% (SE 0.013).

Key to the species of *Promegninia*

1a *Male*: terminal lamellae on lobar apices bidentate; tarsus III with apical extension with fine indentations; adanal shield entire. *Female*: hysteronotal shields extend to bases of setae *c2*; pygidial shields represented by pair of sclerites 30–40 μm long, bearing setae *h1, h2, h2* and *ps1* ….. *P. calonectris* n. sp.

1b *Male*: terminal lamellae on lobar apices rounded; tarsus III without apical extension with indentations; adanal shield split into median piece, shaped as an inverted V or Y, and a pair of lateral plates of uneven form. *Female*: hysteronotal shields not extending to bases of setae *c2*; pygidial shields absent or scarcely developed between setae *ps1* and *h1* …….. 2

2a *Male*: tarsus and distal half or tibia III extend beyond level of lobar apices; tarsus III *c*. 3× longer than wide at base; seta *w* of tarsus III spiculiform with filiform apex; paragenital apodemes shaped as an inverted T. *Female*: pair of small rounded sclerites present postero-lateral to prodorsal shield; striated area between hysteronotal shields distinctly more sclerotised; epigynum not extending beyond level of genital papillae ……..... *P. pedimana* (Trouessart, 1899)

2b *Male*: legs III not extending beyond level of lobar apices; tarsus III conical, approximately as long as wide at base; seta *w* of tarsus III lanceolate; paragenital apodemes bow-shaped. *Female*: sclerites postero-lateral to prodorsal shield absent; striated area between hysteronotal shields similar to striated cuticle of other areas; epigynum slightly extending beyond genital papillae ……..... *P. bulweriae* n. sp.

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1.5 ON SPECIES IDENTIFICATION OF THE FEATHER MITE GENUS *LAMINALLOPTES* DUBININ, 1955 (ACARI: ALLOPTIDAE)

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Acarina, 24: 77-85, 2016

IDENTIFICACIÓN DE LAS ESPECIES DE ÁCAROS DE LA PLUMA DEL GÉNERO *LAMINALLOPTES* DUBININ, 1955 (ACARI: ALLOPTIDAE)

RESUMEN

En base a las secuencias parciales de dos genes mitocondriales, 12S rRNA (12S) y 16S rRNA (16S), se descubrió que los machos y las hembras de dos especies de ácaros muy cercanas, *Laminalloptes minor* (Trouessart, 1885) y *L. simplex* (Trouessart, 1885), se correlacionaron erróneamente el uno con el otro en la última revisión del género *Laminalloptes* Dubinin, 1955 (Analgoidea, Alloptidae). La investigación de los especímenes de referencia utilizados para los análisis moleculares y de varios materiales adicionales reveló características morfológicas que confirman este resultado y permiten identificar correctamente los machos y hembras de estas dos especies. Se propone una nueva clave de diagnóstico para las especies de *Laminalloptes*.

ON IDENTIFICATION OF SPECIES IN THE FEATHER MITE GENUS *LAMINALLOPTES* DUBININ, 1955 (ACARI: ALLOPTIDAE)

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ABSTRACT: Based on partial sequences of two mitochondrial genes, the ribosomal 12S rRNA (12S) and ribosomal 16S rRNA (16S), we found that males and females of the two closely related feather mite species, *Laminalloptes minor* (Trouessart, 1885) and *L. simplex* (Trouessart, 1885), have been erroneously associated in the revision of the genus *Laminalloptes* (Atyeo and Peterson 1967). Careful examination of the morphological features in voucher specimens used in the molecular study and additional museum specimens revealed characters confirming this finding and allowed us to unmistakably associate males and females for each of these two species. A new identification key to *Laminalloptes* species is proposed.

KEY WORDS: Alloptidae, Laminalloptes, systematics, morphology, mitochondrial genes, Phaethontidae.
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INTRODUCTION

The feather mite genus *Laminalloptes* Dubinin, 1955 (Alloptidae: Alloptinae) includes three species associated with tropicbirds, or phaetons, (Pelecaniformes: Phaethontidae) (Dubinin, 1955; Atyeo and Peterson 1967). In the plumage of their hosts, these mites occupy the flight and covert feathers of the wings where they are located in corridors of the ventral surface of the vanes. All three species have been recorded from three extant species of phaetons, *Phaethon aethereus* Linnaeus, *P. lepturus* Daudin and *P. rubricauda* Boddaert (Trouessart 1885; Dubinin 1955; Atyeo and Peterson 1967; Miller and Miller 1986; Swift 1997; Bishop and Heath 1998; Hernandes *et al.* 2015).

In the latest revision of the genus, Atyeo and Peterson (1967) provided seemingly exhaustive redescriptions and detailed illustrations of all included species, *Laminalloptes phaetontis* (Fabricius, 1775), *L. minor* (Trouessart, 1885), and *L. simplex* (Trouessart, 1885), and it seemed that there were left no problems in the systematics of these well discernible feather mite species. In the course of the PhD project "Diversity, ecology and evolution of feather mites in seabirds", the junior author found that the pairwise genetic distances between two species, *L. minor* and *L. simplex,* are unexpectedly low. We have come up to conclusion that DNA sequence data suggest wrong sex association by previous studies. A precise morphological study of the specimens used in the molecular study and morphological analysis of additional collection samples loaned from various museums has confirmed our assumption that males and females of *L. minor* and *L. simplex* were incorrectly associated in the revision of *Laminalloptes* (Atyeo and Peterson 1967).

This error can probably be explained by the fact that the sexual dimorphism in *Laminalloptes* species is greatly pronounced and from the first glance it seems impossible to find any morphological features characterizing simultaneously both the male and female of *L. minor* and *L. simplex*. Among the three species of the genus, *L. phaetontis* is an unmistakable species because of its giant size reaching nearly 1 mm so its sexes can be easily associated. The two other species, *L. minor* and *L. simplex,* are smaller and similar in size (males about 700 μm, females 500–600 μm). In the course of our study we found differences in the structure of the two anterior pairs of legs that can unambiguously correlate males and females of each *L. minor* and *L. simplex*. In the present work we discuss genetic data supporting our conclusion and provide detailed illustrations of the leg structures of all *Laminalloptes* species and give a new key to the species. Since the original descriptions of *L. minor* and *L. simplex* by Trouessart (1885) were only from males, the determination of these two species is stated here based on this sex.

MATERIAL AND METHODS

The main part of the material used in the presents study was collected by Drs. Elena Gómez-Díaz, Raül Ramos, and Samir Martins from live

red-billed tropicbirds, *Phaethon aethereus,* on Raso Island, Cape Verde in 2006–2008. Bird capturing and handling as well as mite sampling were made in accordance with good animal practice as defined by the current European legislation and under permissions from the corresponding governmental authorities of Cape Verde. Mites were collected using the dust-ruffling method (Walther and Clayton 1997) or direct sampling with fine tweezers. Collected material was preserved in vials with absolute ethanol.

Molecular study. We individually extracted DNA from eight specimens of *Laminalloptes* using DNeasy Tissue Kit (Qiagen, Valencia, CA, USA) and the nondestructive method described by Dabert *et al*. (2008). This method allows to maintain the feather mite exoskeleton intact for subsequent morphological identification. All mites subjected to molecular analyses were mounted and kept as reference vouchers for morphological examination. Initially, based on the old morphological criteria, three of these specimens were identified as *L. minor* (all females) and five specimens as *L. simplex* (four males and one female) (Table 1).

Partial sequences of two mitochondrial genes: the ribosomal 12S rRNA (12S) and the ribosomal 16S rRNA (16S) were amplified for each feather mite using the following primers: SR-J-14199 (5'-TACTATGTTACGACTTAT-3') and SR-N-14594 (5'-AAACTAGGATTAGATACCC-3') for 12S gene (Kambhampati and Smith 1995) and 16SA2 (5'-TTTAATTGGTTACTTGTATGAATG-3') and 16C2 (5'-CGCTGTTATCCCTAGAGTAT-3') for 16S gene (Dabert*et al*. 2001). Polymerase chain reactions (PCRs) were carried out in a total volume of 25 µl containing 2.5 µl 10x reaction buffer with 15 mM $MgCl_2$ (Roche Diagnostics), 2 mM $MgCl_2$, 0.2 mM of each dNTP, 0.4 µM of each primer, 1.25 U *Taq* DNA polymerase (Roche Diagnostics) and 2 µl of DNA template. Amplification conditions for the 12S rRNA gene consisted of an initial step of 2 min at 94°C, followed by 10 cycles of denaturation at 94°C for 30 sec, annealing at 40°C for 30 sec, and extension at 68°C for 1 min, and 35 cycles of denaturation at 94°C for 30 sec, annealing at 43°C for 30 sec, and extension at 68°C for 1 min, with a final step of 5 min at 72°C. For the 16S rRNA gene, the PCR conditions followed Black and Piesman (1994). Amplification products were separated by electrophoresis on 2% agarose gel and visualized under UV light. Samples containing visible bands were sent for sequencing to Beckman Coulter Genomics (France, GenBank Accession nos KX372354–KX372371).

DNA sequences were checked and edited using Bioedit version 7.0.5.3 (Hall 1999) and all variable sites were confirmed by visual inspection of the chromatograms. Sequences were aligned for each gene independently using MAFFT version 7, with default parameters. Basic genetic statistics and standard diversity estimates (number of polymorphic sites, number of haplotypes, nucleotide diversity and haplotype diversity) were calculated for each gene and for each mite species using DNASP v.5 (Librado and Rozas 2009). Mean genetic distances between mite species and between individuals within each mite species were calculated with MEGA 4.1 software using Kimura's 2-parameter (K2P) distance model (Tamura el al. 2007).

Morphological study. For species identifications and subsequent morphological study, cuticle skeletons of samples retained after the DNA extraction as well as the intact feather mite specimens from ethanol were cleared in lactic acid for 24 h at room temperature and mounted on microscope slides in PVA medium (BioQuip Products, Rancho Dominguez, California). Slide-mounted mites were studied using a Leica DM2500 microscope (Leica Microsystems Inc.) with differential interference contrast (DIC) and a camera lucida. General morphological terms, body and leg chaetotaxy follow those in Gaud and Atyeo (1996).

Abbreviations used in collection numbers of depositories, where additional materail was loaned: NU (collection of W.T Atyeo)—University of Michigan, Ann Arbor, USA; MNHN (collection of E.L. Trouessart)—Museum National de Histoire Naturelle, Paris, France; ZISP—Zoological Institute, Russian Academy of Sciences, Saint Pe-tersburg, Russia.

RESULTS

Based on the morphological determination of *Laminalloptes simplex* and *L. minor* given in the generic revision by Atyeo and Peterson (1967), the pairwise K2P genetic distances between the two species were 4.18% (SE = 0.006) for 12S gene and 4.87% (SE=0.009) for 16S gene. When morphological determination of *Laminalloptes* species presented by our morphological study is taken into account, the sequence divergences between these two species appeared significantly higher, 20.91% (SE = 0.029) for 12S gene and 22.57% (SE = 0.044) for 16S gene. Furthermore, average genetic divergences between individuals within species also differed depending on previous or our morphological determination of the species (Table 1).

When the old determination was considered, genetic distances between individuals within *L. simplex* ranged between 8.36% for 12S gene and 9.2% for 16S gene. When the new "correct" determination of these *Laminalloptes* species was used, sequence divergences were significantly lower for both genes (0 and 0.4%, respectively). Basic genetic statistics, such as the number of polymorphic sites, haplotype diversity, nucleotide diversity, and average number of nucleotide differences, for both mitochondrial genes for *L. minor* and *L. simplex* are also shown in Table 1.

SYSTEMATICS

Family Alloptidae Gaud, 1957
Subfamily Alloptinae Gaud, 1957
Genus *Laminalloptes* Dubinin, 1955

Laminalloptes phaetontis (Fabricius, 1775)

(Figs. 1, 4A)

Acarus phaetontis Fabricius 1775: 815, No. 25.

Gamasus phaetontis, Fabricius 1805, Syst. Antliat., p. 363, no 16 (cited after: Atyeo and Peterson 1967).

Dermaleichus phaetonis, Buchholz 1869: 52, figs. 39–45.

Alloptes phaetontis, Trouessart 1885: 67; Oudemans 1929: 694.

Laminalloptes phaetontis, Dubinin 1955: 270, figs. 8 (1, 2), 10; Atyeo and Peterson 1967: 449, figs. 1–8; Hernandes *et. al*. 2015: 82.

Type host: *Phaethon lepturus fulvus* von Brandt.

Material examined. From *Phaethon lepturus* Daudin: BERMUDA ISLANDS (British Overseas Territory)—3 males, 2 female (ZISP 19882; 19883), 5 May 1881, V.B. Dubinin. From *Phaethon lepturus dorotheae* Mathews: FEDERAL STATES OF MICRONESIA**,** Caroline Islands, Kusaie Island (now Korsae Island)—1 male, 1 female (NU 21300), April, 1931, N. Wilson.

From *Phaethon rubricauda* Boddaert: no location data—1 male, 3 females (ZISP 19884), 1843, V.B. Dubinin. From *Phaethon aethereus* Linnaeus: CAPE VERDE, Raso Island (16º36´N, 24º35´W) —1 male (ZISP 6900), (bird ring: 7500202), 4 April 2008, col. S. Martins; 1 female ZISP 6905 (bird ring: 7500201), 1 April 2008, col. R. Ramos; 1 female—(ZISP 6906) (bird ring: 7500203), 6 April 2008, col. R. Ramos; 1 female (ZISP 6907) (bird ring: 7500194), 24 March 2008, col. S. Martins.

Laminalloptes phaetontis is an unmistakable species among all feather mites mostly because of its really giant size reaching nearly 1 mm long. Among *Laminalloptes* species it is probably the most derived species because of the greatly modified tarsi I and II in males and females (Figs. 1A, E). Interestingly because of extremely large size of this species it is possible to distinguish minute rudiments of the proral setae *p* and *q* on all tarsi (Figs 1A–F). These setae are considered to be lost in all other Analgoidea.

Laminalloptes simplex (Trouessart, 1885)

(Figs. 2, 4B)

Alloptes phaetontis var. *simplex* Trouessart 1885: 67. (Syntypes, slides 40C7, 40C12 in MNHN, not studied.)

Laminalloptes microphaeton Dubinin 1955: 271 (part), figs. 8 (3, 5), 9 (2) (female of *L. minor*), 11.

Laminalloptes simplex, Atyeo and Peterson 1967: 457 (part), figs. 17 (male), 19 (female, not 18), 9, 10 (male tarsi), 15, 16 (female tarsi, not 11, 12); Hernandes *et. al*. 2015: 83.

Type host: *Phaethon aethereus* Linnaeus.

Material examined. From *Phaethon rubricauda melanorhynchus* Mathew: USA, Central Pacific, Midway Atoll, Eastern Island—2 males (NU 4006, 4812), 20 July 1962, col. H.I. Fisher.

From *Phaethon* sp.: USA, Central Pacific, Midway Island—1 female (NU 4002), 4 December 1959, col. J.C. Downey. From *Phaethon aethereus* from CAPE VERDE, Raso Island (16º36'N 24º35'W): 1 male (ZISP 6891*), (bird ring: 14.s.a), 13 January 2006, col. E. Gómez-Díaz; 2 males (ZISP 6900, ZISP 6895*) (bird ring: 7500202), 4 April 2008, col. S. Martins; 1 male (ZISP 6892*) and 1 female (ZISP 6896*) (bird ring: 7500201), 1 April 2008, col. R. Ramos; 1 male (ZISP 6893*) and 1 female (ZISP 6897*) (bird ring: 7500197), 30 March 2008, col. S. Martins; 1 male (ZISP 6894*) and 1 female (ZISP 6898*) (bird ring: 7500210), 8 April 2008, col. S. Martins.

Asterisk (*) indicates specimens used for extracting sequences.

Access numbers of molecular sequences (fragments 12S and 16S, respectively): ZISP 6891 (KX372358, KX372367), ZISP 6892 (KX372362, KX372371), ZISP 6893 (KX372359, KX372368), ZISP 6894 (KX372360, KX372369), ZISP 6895 (KX372361, KX372370), ZISP 6896 (KX372355, KX372364), ZISP 6897 (KX372356, KX372365), ZISP 6898 (KX372357, KX372366).

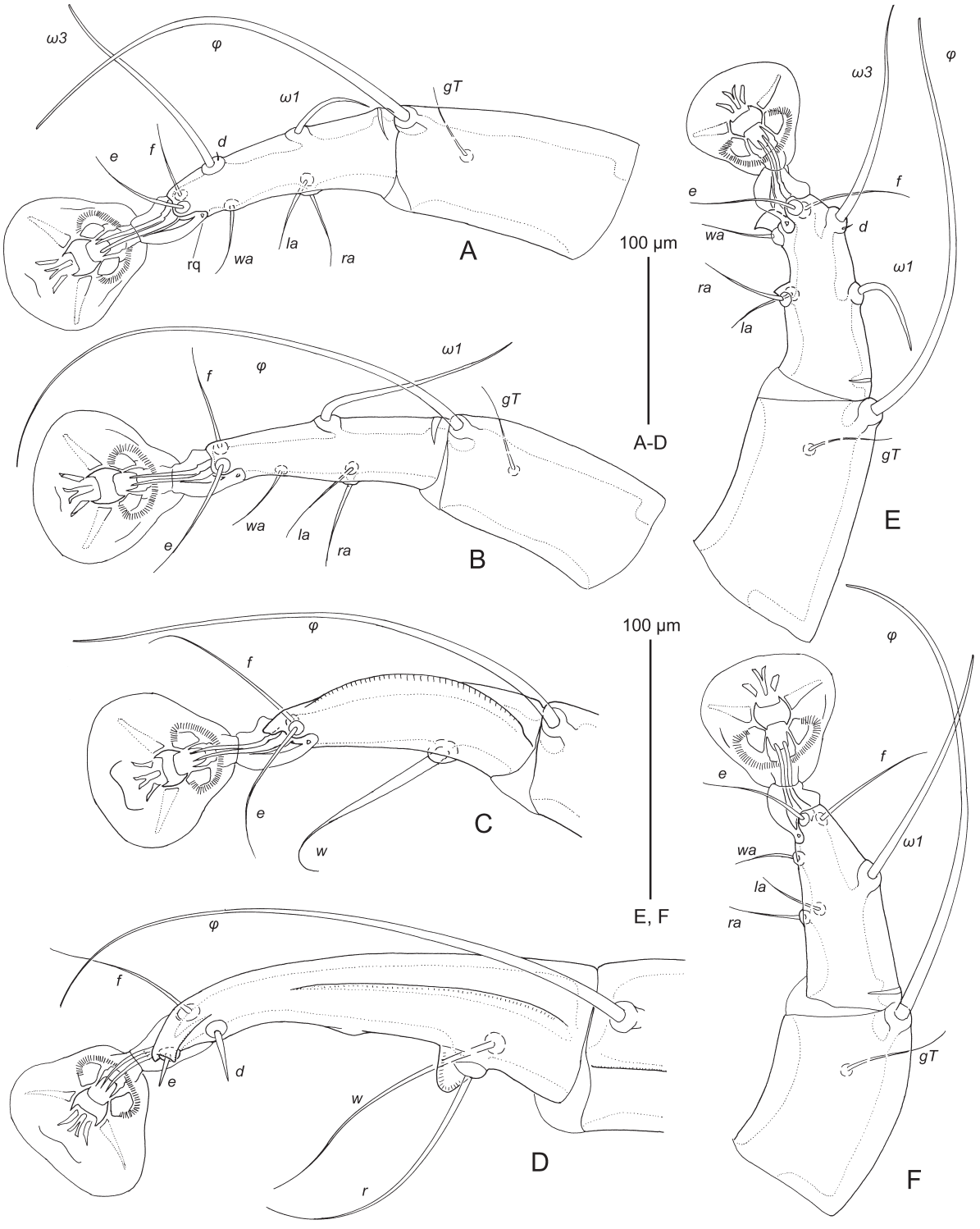

Fig. 1. *Laminalloptes phaetontis*, distal segments of legs. A—tarsus and tibia I of male, B—tarsus and tibia II of male, C—tarsus III of male, D—tarsus IV of male, E—tibia and tarsus I of female, F—tibia and tarsus II of female. rq—rudimentary proral seta *q*.

The only clear character of *Laminalloptes simplex* allowing to associate univocally its males and females and distinguish them from those of *L. minor* is the position of three ventral setae on tarsi I and II. In this species, bases of the setae *la, ra*, and *wa* are distinctly closer to each other (Fig. 2A, B, E, F), while in *L. minor*, the seta *wa* is situated distinctly anterior from the setae *la* and *ra* (Figs. 3A, B, E, F).

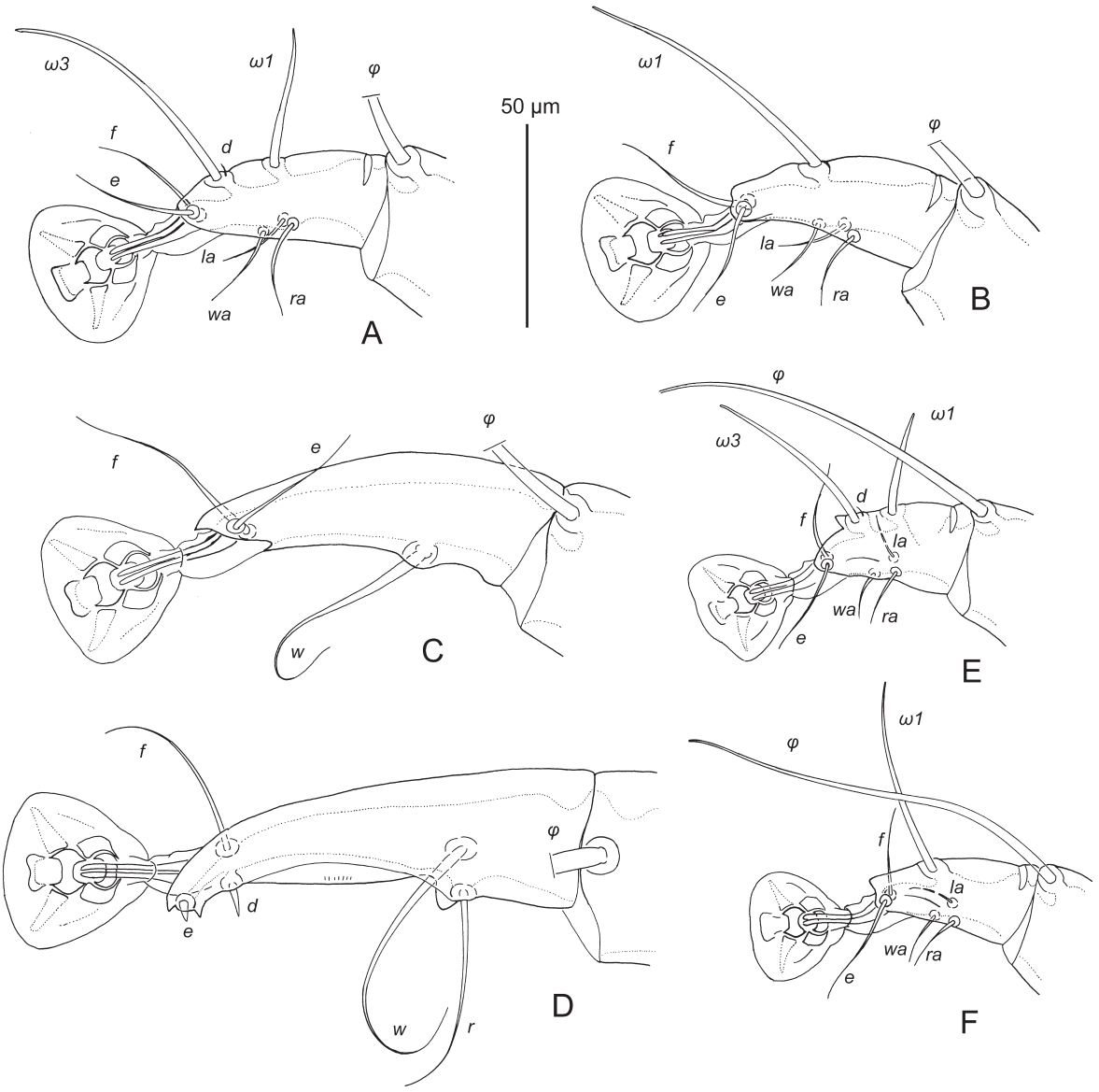

Fig. 2. *Laminalloptes simplex*, tarsi I–IV. A—tarsus I of male, B—tarsus II of male, C—tarsus III of male, D—tarsus IV of male, E—tarsus I of female, F—tarsus II of female.

Curiously Atyeo and Peterson (1967: Figs. 9–16) had actually illustrated these diagnostic features of the legs, but did not recognize them and associated males and females incorrectly. Thus, in their figures, it is clearly illustrated that three ventral setae of tarsi I and II in males of *L. simplex* are grouped near the center of the segment, while on tarsi of females of "*L. simplex*", the seta *wa* is situated distinctly anterior from the two others situated in the center.

***Laminalloptes minor* (Trouessart, 1885)**

(Fig. 3, 4C)

Alloptes phaetontis var. *minor* Trouessart 1885: 67. (Syntypes, slide 40C8 in MNHN, not studied.)

Alloptes longipes Ewing 1911, Psyche, 18:41–42, PI. 7, fig. 3.

Laminalloptes pseudophaetontis Dubinin 1955: 273, figs. 8 (4, 6), 9 (1).

Laminalloptes simplex, Atyeo and Peterson 1967: 457 (part), figs. 11, 12 (female tarsi, not 15, 16), 13, 14 (male tarsi), 18 (female, not 19), 20–22 (male); Hernandes *et al*. 2015: 83.

Type host: *Phaethon aethereus* Linnaeus.

Material examined. From *Phaethon rubricauda melanorhynchus* Mathew: USA, Central Pacific, Midway Atoll, Eastern Island—1 female (NU 4809), 20 July 1962, col. H.I. Fisher. From *Phaethon* sp.: USA, Central Pacific, Midway Island—2 males (NU 4002), 4 December 1959, col.

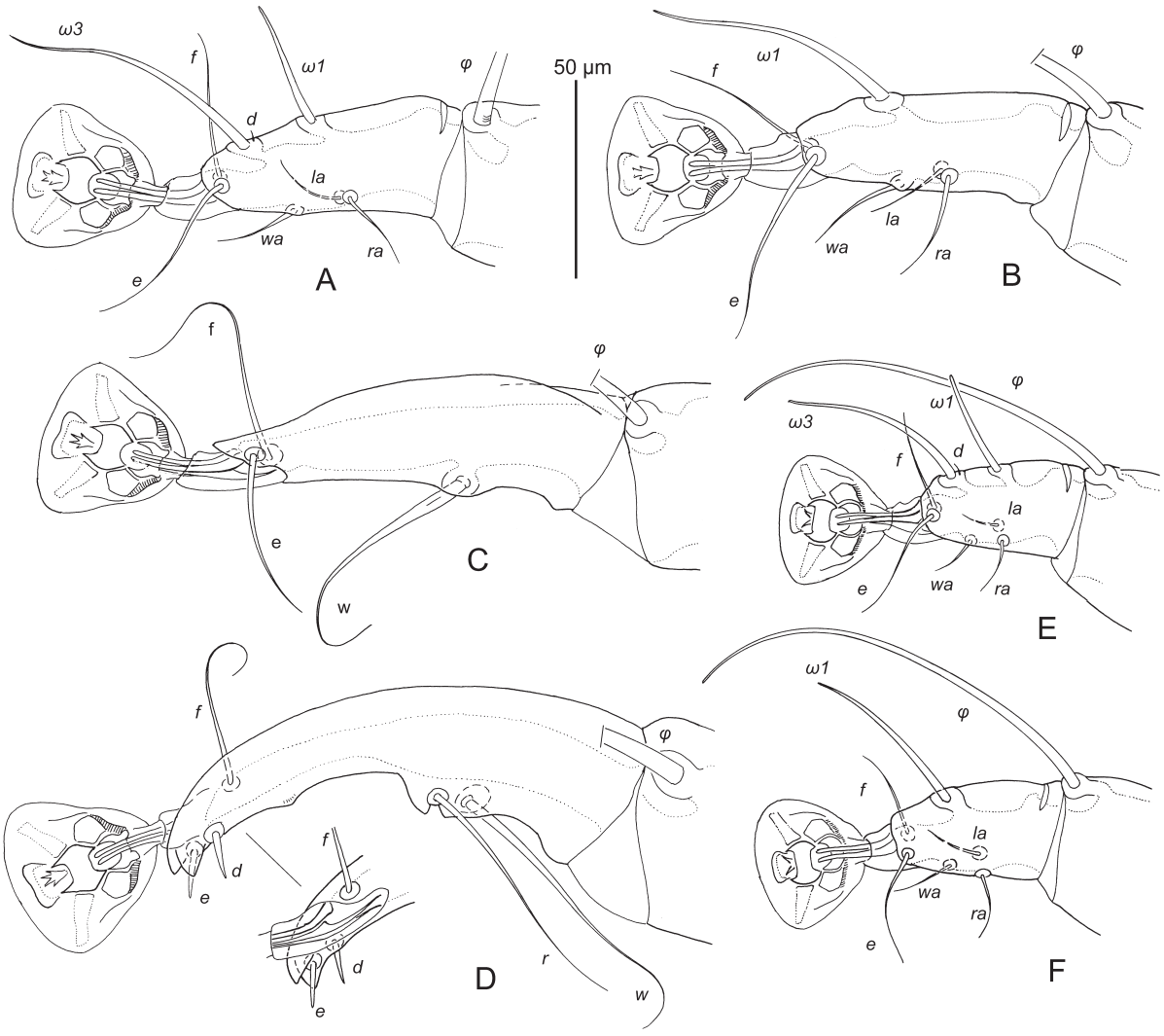

Fig. 3. *Laminalloptes minor*, tarsi I–IV. A—tarsus I of male, B—tarsus II of male, C—tarsus III of male, D—tarsus IV of male, E—tarsus I of female, F—tarsus II of female.

J.C. Downey. From *P. aethereus*: CAPE VERDE, Raso Island (16°36'N 24°35'W)—1 male (ZISP 6895), 2 females (ZISP 6889*, 6890), (bird ring: 7500202), 4 April 2008, col. S. Martins

Access numbers of molecular sequences (fragments 12S and 16S, respectively): ZISP 6889 (KX372354, KX372363).

The only character of *Laminalloptes minor* providing correct association of its males and females is the position of three ventral setae of tarsi I and II. In *L. minor*, the seta *wa* is situated distinctly anterior from the setae *la* and *ra*, i.e. almost at the midlength between these setae and the base of the ambulacral stalk (Figs 3A, B, E, F).

Key to *Laminalloptes* species

(Males and females)

1. In both sexes, sclerotized areas flanking bases of coxae I, II wide, with flame-shaped posterior margin, seta *wa* of tarsi I, II closer to base of ambulacral stalk than to seta *ra* (Figs. 1A, B, E, F). In males, length of idiosoma 900–1000 µm; tarsi I, II nearly 3 times longer than wide at base; femora III, IV each with long and acute paraxial spine directed backward, seta *d* on tarsus IV more distant from tarsal apex than seta *f* (Fig. 1D). In female, length of idiosoma 700–800 µm, tarsus I with apicoventral claw-like extension (Fig. 1E), tibia I nearly 2 times longer than wide at base .... *L. phaetontis* (Fabricius, 1775)
— In both sexes, sclerotized bands flanking bases of coxae I, II narrow, with smooth posterior margin;

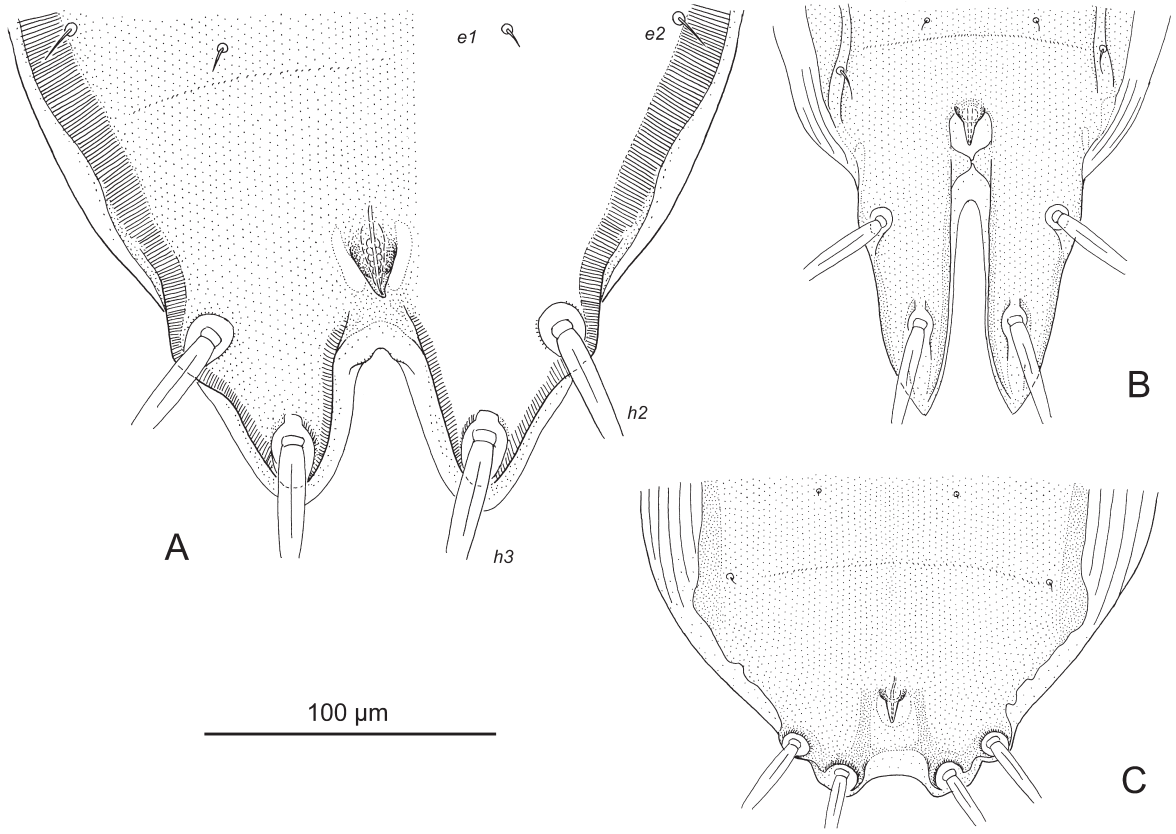

Fig. 4. Females of *Laminalloptes* species, posterior end opisthosoma. A—*Laminalloptes phaetontis*, B—*L. simplex*, C—*L. minor*.

seta *wa* of tarsi I, II situated approximately at mid-length between ambulacral stalk and seta *ra* or closer to the latter (Figs. 2E, 3E). In males, length of idiosoma about 700 µm; femora III, IV without acute paraxial spine, or small spine can present on femora IV, seta *d* on tarsus IV more distant from tarsal apex than seta *f* (Fig. 1D). In female, length of idiosoma 500–600 µm, tarsus I without apicoventral claw-like extension, tibia I less than 1.5 times longer than wide at base.....2

2. In both sexes, bases of ventral setae *ra, wa* and *la* of tarsi I, II grouped close to each other (Figs. 2E, F). In male, setae *h2* simple whip-like, coxal fields III without oblique sclerite running along central part of these fields; tarsus IV with one small blunt spine at level of setae *r* and *w*, seta *d* of tarsus IV twice longer than seta *e* and distinctly moved from tarsal apex (Fig. 2D). In females, idiosoma noticeably elongate, about 2.5 times longer than wide, opisthosomal lobes long and narrow, two times longer than wide at base, terminal cleft narrow U-shaped, tarsus I with small spine anterior to base of solenidion *ω3* (Figs. 3E, 4B).....
.....*L. simplex* (Trouessart, 1885)

— In both sexes, base of ventral seta *wa* of tarsi I, II not close to bases of setae *ra* and *la* (Figs. 3E, F). In male, setae *h2* with ovate-shaped enlargement in medial part; coxal fields III with narrow sclerite running obliquely along central part of these fields; tarsus IV with two blunt spines near bases of setae r and w (Fig. 3D); setae *d* and *e* of tarsus IV spiculiform, similar in length and both situated near its apex. In females, idiosoma robust, less than 2 times longer than wide; opisthosomal lobes short, scarcely expressed, terminal cleft shallow, tarsus I without spine near base of solenidion *ω3* (Figs. 3E, 4C).....*L. minor* (Trouessart, 1885)

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Table 1.

Basic genetic statistics based on two mitochondrial genes (12S and 16S) of the two mite species inhabiting *Phaeton aethereus*, considering the old morphological determination (A) and the new determination (B). Number of individuals sequenced (N), number of polymorphic sites (Np), number of haplotypes (Nh), haplotype diversity (h), nucleotide diversity (π), average number of nucleotide differences (k), and average genetic divergence between individuals within species (d) are shown.

Mite species	N	Np		Nh		h		π		k		d	
		12S	16S	12S	16S	12S	16S	12S	16S	12S	16S	12S	16S
(A) *L. simplex* (4M, 1F)	5	56/310	28/165	2	3	0.4	0.7	0.073	0.079	22.4	11.4	0.084 (SE=0.011)	0.092 (SE=0.018)
L. minor (3F)	3	0/308	1/143	1	2	0	0.667	0	0.005	0	0.667	0	0.005 (SE=0.004)
(B) *L. simplex* (4M, 3F)	7	0/308	2/143	1	3	0	0.524	0	0.004	0	0.571	0	0.004 (SE=0.003)
L. minor (1F)	1	-	-	-	-	-	-	-	-	-	-	-	-

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CHAPTER 2

DIVERSIFICATION PROCESSES. HOST VERSUS SPATIAL GENETIC STRUCTURE OF SEABIRD FEATHER MITE COMMUNITIES

2.1 HOST-SPECIFICITY AND CRYPTIC DIVERSITY OF SEABIRD FEATHER MITES: INTEGRATING MORPHOLOGICAL AND GENETIC DATA

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In preparation

ESPECIFICIDAD DE HUÉSPED Y DIVERSIDAD CRIPTICA EN ÁCAROS DE LAS PLUMAS DE AVES MARINAS: INTEGRACIÓN DE DATOS MORFOLÓGICOS Y GENÉTICOS

RESUMEN

Los ácaros de las plumas son modelos útiles para estudiar los patrones y procesos de diversificación y especiación debido a su gran diversidad y alto grado de especialización en microhábitats. Los procelariformes albergan una rica comunidad de ácaros de las plumas, pero la mayoría de los estudios se han centrado en la evolución de los taxones de rango superior y una diversidad mas oculta probablemente ocurre dentro de estas comunidades. En este estudio, hemos explorado la estructura morfológica y genética de la comunidad de ácaros de las plumas para testar la contribución de la especificidad del huésped y de la ecología en la estructuración de la comunidad y la diversidad en este grupo, en seis especies de aves marinas simpátricas de seis géneros diferentes que crían en el archipiélago de Cabo Verde. En base a los criterios morfológicos, se caracterizaron 32 especies de ácaros de diez géneros y tres familias, de los cuales nueve correspondieron a nuevas especies no descritas. Los datos moleculares se correlacionaron con las descripciones morfológicas, excepto por la presencia de dos especies cripticas en base a los datos genéticos. A pesar de que la mayoría de las especies de aves marinas eran simpátricas, hemos encontrado que cada especie de huésped albergaba una comunidad distinta de ácaros de las plumas. Los patrones de la estructura genética fueron variables entre los taxones de ácaros; 20 especies mostraron una fuerte estructura genética asociada al huésped, mientras que tres especies de ácaros (*Microspalax brevipes*, *Brephosceles puffini* and *Plicatalloptes sp.1*) fueron compartidas por dos especies de aves marinas que crían en simpatría en una isla. Nuestros resultados confirman la importancia de la especificidad de huésped en la conformación de la estructura genética y la diversificación de estos simbiontes y destaca la diversidad vasta y poco conocida de ácaros de las plumas en las aves marinas. Estudios detallados sobre los rasgos de los parásitos y de los huéspedes que influyen la especificidad son necesarios ahora para identificar los procesos y factores inmediatos implicados en la diversificación de los ácaros.

HOST-SPECIFICITY AND CRYPTIC DIVERSITY OF SEABIRD FEATHER MITES: INTEGRATING MORPHOLOGICAL AND GENETIC DATA

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ABSTRACT

Feather mites are useful modelsfor studying patterns and processesof diversification and speciation due to their high diversity and strongdegree of microhabitat specialization. Procellariiform birds harbour a particularly rich feather mite community, but most studies to date have focused on the evolution of higher-order taxa and much hidden diversity likely occurs within these communities. Here, we explore the morphological and genetic structure of the feather mite community of six sympatric seabird species of six different genera breeding in the Cape Verde archipelago to test the contribution of host specificity and ecology in driving the community structure and diversity in this group. Based on morphological criteria, 32 feather mite species from ten genera and three families were characterized, of which nine corresponded to new, undescribed species. Molecular data corroborated morphological species descriptions, except for the presence of two putative cryptic species based on genetic data. Although most of the seabird species were sympatric, we found that each host species harboured a distinct feather mite community. Patterns of genetic structure were variable among mite taxa; 20 species exhibited strong host-associated genetic structure, whereas three mite species (*Microspalax brevipes*, *Brephosceles puffini* and *Plicatalloptes sp.1*) were shared by two related seabird species breeding in sympatry on one island. Our findings confirm the importance of host specificity in shaping the genetic structure and diversification of these ectosymbionts, and highlight the vast and largely unrecognized diversity of avian feather mites on seabirds. Detailed studies of parasite and host traits that influence specificity are now called for to identify the processes and proximate factors involved in mite diversification.

Keywords: diversification, community structure, Procellariiformes, Phaethontiformes, Avenzoariidae, Alloptidae, Xolalgidae

INTRODUCTION

Parasites are amongst the most diverse functional groups on Earth. As they depend almost entirely on their host to complete their life cycle, these organisms have evolved intricate adaptations to optimize survival and transmission (de Meeûs et al. 1998, Criscione et al. 2005). As the intimacy of the interaction between a host and a parasite increases, we expect to find higher parasite diversity and stronger patterns of host specialization and a restriction of the range of host types used by a given parasite (Poulin and Morand 2000, Mouillot et al. 2006). High host specificity may be due to limited opportunities for parasite dispersal and thus, for the colonization of new hosts (Clayton et al. 1992, Johnson et al. 2002, Whiteman et al. 2004). However, it can also be determined by specific parasite adaptations to host structures (e.g. feather, hair, immune responses), such that parasites are incapable of surviving and reproducing on foreign hosts (Tompkins and Clayton 1999, Reed et al. 2000). The co-structure approach, that is, comparing population demographic or genetic structures between two or more species (host-parasite species, or multiple parasite species), has been shown to be useful in elucidating factors that shape genetic variation within and among different parasite populations (Criscione 2008). Such an approach has previously been used to evaluate the relationship between population structure and host specificity in avian ectoparasites. Johnson et al. (2002) showed that dove body lice of the genus *Physconelloides*, which are very host specific, have more pronounced population genetic structure than dove wing lice of the genus *Columbicola*, which exhibit low host specificity. Similar results have been also reported for pinworms parasitizing reptiles (Falk and Perkins 2013).

Multiple host and parasite factors can influence parasite population structure and dynamics (i.e. host and parasite dispersal, host abundance and behavior, host predictability, parasite life-cycle complexity, etc.) (Blouin et al. 1995, McCoy et al. 2003, Criscione and Blouin 2004, Bruyndonckx et al. 2009, Mazé-Guilmo et al. 2016). This can lead to conflicting predictions on parasite diversification rates, host-parasite associations and co-structure. In this context, model systems involving parasite communities exploiting a restricted range of ecologically similar and geographically overlapping host species provide the ideal framework to investigate the proximate factors and processes driving parasite diversification and speciation. Not surprisingly, few such studies exist (but see Johnson et al. 2002, Rivera-Parra et al. 2015).

Feather mites (Arachnida: Acari: Astigmata) are particularly useful models to study diversification and speciation in parasites. They are common obligate ectosymbionts of birds, with approximately 2 500 species reported from across extant avian orders (Gaud and Atyeo 1996, Proctor 2003, Mironov and Proctor 2008). Feather mites cannot survive in the off-host environment and tend to exploit specialized microhabitats on the bird host, such that host specificity may strongly shape their evolution, ecology (trophic and spatial) and community structure (Dabert and Mironov 1999, Doña et al. 2015a, Stefan et al. 2015). However, some feather mite groups have been reported to show varying degrees of host specialization and diversification (Gaud and Atyeo 1996, Proctor 2003), with some being restricted to one or a few closely-related host species and others being widely associated with hosts from different genera and families. Some mite genera even cross host ordinal boundaries, inhabiting different avian orders (e.g. *Brephosceles*, *Ingrassia*). These patterns in mite host specificity could be explained by either habitat or host-related factors; morphological adaptations to feather structure and/or the mode of transmission (vertical between parents and offspring or horizontal between mates) have all been considered to be important in shaping the close association between mites and their avian hosts (Gaud and Atyeo 1996, Dabert and Mironov 1999, Proctor and Owens 2000, Proctor 2003). However, comparative studies among multiple feather mite species co-occuring on different avian hosts are currently lacking.

One of the main limitations of studying feather mite evolution and host-specificity could be the presence of cryptic diversity. Often, feather mite identification is difficult and laborious work given that immature stages and females of many taxa are often indistinguishable and male morphological characterizations can be complicated even for experienced taxonomists (Doña et al. 2015b). Molecular studies on feather mite diversity are still scarce (but see Dabert et al. 2001, Klimov and OConnor 2008, Knowles and Klimov 2011, Stefka et al.

2011, Dabert et al. 2015, Doña et al. 2015b), but hold much promise for documenting and understanding diversity in this group.

In the present study, we explore the diversity and genetic structure of feather mite species co-occurring on colonial seabirds of the Cape Verde Islands. Colonial seabirds represent excellent hosts for investigating parasite community structure and the processes associated with parasite diversification and adaptation. Seabirds are highly pelagic and breed in large colonies on remote oceanic islands. Therefore, they represent spatially discrete, hierarchical habitats, with extremely high host densities, but relatively low host diversity compared to mainland ecosystems. Most seabird species show strong interannual fidelity and natal philopatry to their breeding sites, features that can favor parasite specialization and host specificity (Brooke 2004, McCoy et al. 2013). However, seabirds are also long distance migrants and frequently breed sympatrically in mixed species colonies, which in turn can promote long-distance dispersal and host switching in their parasites. Previous work examined the evolutionary relationships between feather mites and their seabird hosts, but these studies focused almost entirely on higher-order mite taxa and morphological characters (Mironov 1991a, b, 2005, 2007, Mironov and Dabert 1999, Dabert and Mironov 1999). Dabert et al. (2001) inferred the phylogeny of feather mite subfamily Avenzoariinae, associated exclusively with Charadriiformes, using both molecular and morphological data. In another study, authors also investigated the genetic structure of two feather mite species, *Zachvatkinia isolata* and *Alloptes stercorarii* inhabiting two sister species of skuas (Dabert et al. 2015). Other than these, no study has yet examined the genetic structure of mite communities and no systematic examination of host specialisation has been performed.

In this context, we had three specific aims in the present study: 1) characterize the diversity of feather mites within the seabird community of the Cape Verde archipelago; 2) explore congruence between morphological and molecular data and identify potential cryptic species; 3) examine the genetic structure of the feather mites at two different levels: by seabird host and by between island distance to make inferences about patterns and processes shaping mite community structure and diversity.

MATERIAL AND METHODS

STUDY SPECIES AND FEATHER MITE SAMPLING

The Cape Verde Archipelago is located in the mid-Atlantic Ocean (16^{o}N 24^{o}W) approximately 570 km off the west coast of Africa. Mite sampling was performed on six seabird species, five Procellariiformes (Cape Verde shearwater, *Calonectris edwardsii*; Boyd´s shearwater, *Puffinus boydi*; Bulwer´s petrel, *Bulweria bulwerii*; band-rumped storm-petrel, *Hydrobates castro*; Cape Verde petrel, *Pterodroma feae*) and one Phaethontiformes (the red-billed tropicbird, *Phaethon aethereus*), breeding on five islands and islets of the archipelago: Raso, Ilhéu Cima, Ilhéu Grande, Curral Velho and Fogo (Figure 1). All sampled islands harbor multiple seabird species, except Fogo, which is inhabited by a single species, the Cape Verde petrel. Bird captures and mite sampling were performed in accordance with good animal practices as defined by current European legislation and under permission from the government authorities of Cape Verde. From 2003 to 2012, feather mites were collected from captured adult birds using the dust-ruffling method (Walther and Clayton 1997) and stored in absolute ethanol for subsequent morphological identification and molecular analyses. A total of 453 birds were sampled; details on the geographic locations and sample sizes are described in Figure 1.

MORPHOLOGICAL IDENTIFICATIONS

Initial screening of feather mites used morphological criteria to evaluate species diversity and within-host species community composition. Mites were cleared in lactic acid for 24h and mounted on microscope slides in PVA medium (BioQuip Products, Rancho Dominguez, California). The slides were cured on a slide warmer at 40^{o}C for 4 days and then examined using a Leica DM 5000B light microscope with differential interference contrast (DIC) illumination. Mites were identified using the identification keys for bonnetelline mites (Mironov 1989a, b; 2000), xolalgid mites (Dabert and Ehrnsberger 1991; Mironov and Palma 2006) and alloptid mites (Peterson and Atyeo 1968, Peterson 1971, Atyeo and Gaud 1991, Mironov 1996, Mironov and

Stefan 2016). Feather mite specimens of each identified species were deposited in the Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia (ZISP).

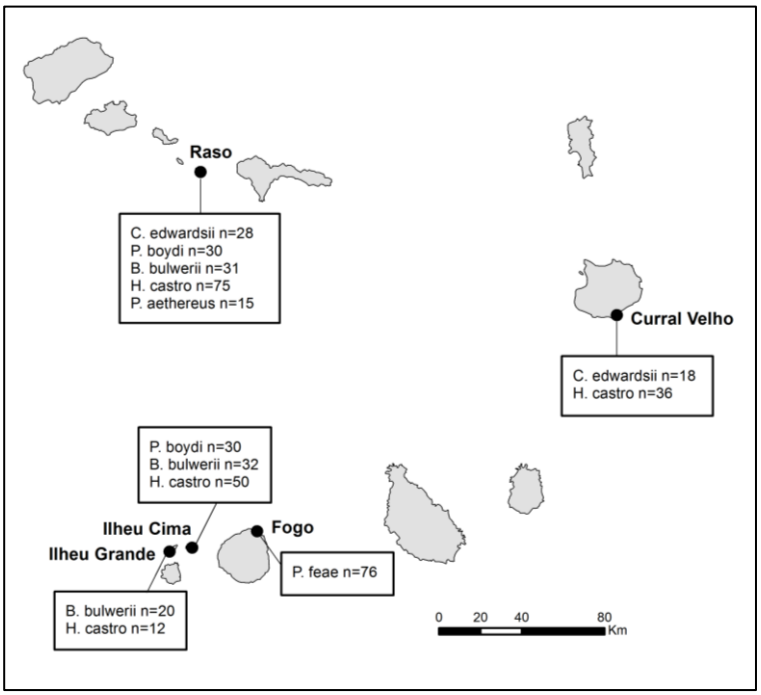


Figure 1. Map of the Cape Verde Archipelago showing the five islands where feather mites were sampled. The name of seabird species and the number of dust-ruffling samples examined per host species and locality are shown in boxes.

DNA ISOLATION, AMPLIFICATION AND SEQUENCING

After the initial morphological screening, the specimens included in the molecular analysis were selected from the remaining samples. We analyzed five individuals of each mite species from five host individuals per species per island, when possible. In total, we individually extracted DNA from 50 specimens from the genus *Zachvatkinia* (five species), 37 from the genus *Microspalax* (four species), 66 from the genus *Brephosceles* (nine species), 19 from the genus *Plicatalloptes* (one species), 13 from the genus *Laminalloptes* (three species) and five specimens from *Onychalloptes* (one species) (Supplementary Information: Table S1). Four mite genera (*Rhinozachvatkinia, Promegninia, Ingrassia* and *Opetiopoda*) that were also found in our samples (see results) were not included in the molecular analyses due to low sample sizeor failure to obtain DNA sequences.

Total genomic DNA was extracted from individual mites using a DNeasy Tissue Kit (Qiagen, Valencia, CA, USA) and the non-destructive method described by Dabert et al. (2008). This method allowed us to maintain the feather mite exoskeleton intact for subsequent morphological verification of species identifications and therefore match morphological and genetic data. Thus, following DNA extraction, mite exoskeletons were recovered, mounted, re-identified morphologically and kept as reference vouchers. Partial sequences of two mitochondrial genes, 12S rRNA (12S) and 16S rRNA (16S), were amplified for each feather mite using the following primers: SR-J-14199 (5'-TACTATGTTACGACTTAT-3') and SR-N-14594 (5'-AAACTAGGATTAGATACCC-3') for the 12S gene (Kambhampati and Smith 1995); and 16SA2 (5'-TTTAATTGGTTACTTGTATGAATG-3') and 16C2 (5'-CGCTGTTATCCCTAGAGTAT-3') for the 16S gene (Dabert et al. 2001). Polymerase chain reactions (PCRs) were carried out in a total volume of 25 µl containing 2.5 µl 10x reaction buffer containing 15mM $MgCl_2$ (Roche Diagnostics), 2 mM $MgCl_2$, 0.2mM of each dNTP, 0.4 µM of each primer, 1.25 U *Taq* DNA polymerase (Roche Diagnostics) and 2 µl of DNA template. Amplification conditions for the 12S rRNA gene consisted of an initial step of 2 min at 94°C, followed by 10 cycles of denaturation at 94°C for 30 sec, annealing at 40°C for 30 sec, and extension at 68°C for 1 min, and 35 cycles of denaturation at 94°C for 30 sec, annealing at 43°C for 30 sec, and extension at 68°C

for 1 min, with a final step of 5 min at 72°C. For the 16S rRNA gene, the PCR conditions followed Black and Piesman (1994). Amplification products were separated by electrophoresis in a 2% agarose gel and visualized under UV light. Successful amplifications were sent for sequencing to Beckman Coulter Genomics (France). Only mite specimens with complete sequence information for the two mitochondrial genes were included in the analyses. DNA sequences were checked and edited using Bioedit version 7.0.5.3 (Hall 1999) and all variable sites were confirmed by visual inspections of the chromatograms. Sequences were aligned for each gene independently using MAFFT version 7, with default parameters. We tested for neutrality for each mite genusbased on the Tajima´s D test included in DNASP v.5 software (Librado and Rozas 2009).

MOLECULAR DIVERSITY AND SPECIES DELIMITATION

Two different approaches were employed in order to delimit species within genera. First, we inferred haplotype networks using the statistical parsimony algorithm implemented in TCS version 1.21 based on the concatenated sequences of the two mitochondrial genes (Clement et al. 2000). Network approaches are being increasingly used for species delimitations and the discovery of new cryptic species (Criscione and Blouin 2004; Pons et al. 2006; Whiteman et al. 2006; Wiens and Penkrot 2002). Statistical parsimony analysis partitions the data into independent networks of haplotypes connected by changes that are non-homoplastic with a 95 % probability (Templeton 2001). Although this threshold does not necessarily correspond to species boundaries, this algorithm has been shown to be useful in separating independent lineages that in most cases correspond to good species (Hart and Sunday 2007).

Second, we applied the general mixed Yule-coalescent (GMYC) method in order to estimate species boundaries from mitochondrial data (Pons et al. 2006). This approach uses maximum-likelihood statistics and a time-calibrated gene tree and identifies a time in the tree when the branching rates shift from a Yule (species) to a coalescent (population) process. The GMYC analysis was conducted using the ´splits´ package (Species Limits by Threshold Statistics) in R version 3.0.3. The single threshold method was applied in order to find the ML solution of the GMYC model. An ultrametric tree was generated with BEAST v.1.6.2 (Drummond and Rambaut 2007) after removing identical sequences. In order to choose the most appropriate tree prior, we considered different parameter combinations: Yule vs. coalescent tree priors and strict clock vs. relaxed uncorrelated lognormal clock.

Genetic statistics (number of polymorphic sites, number of haplotypes, nucleotide and haplotype diversity) for each gene and for each morphospecies/genetic lineage identified as described above were assessed using DNASP v.5. Mean genetic distances between morphospecies/genetic lineages within genera and between individuals within species/lineages were calculated with MEGA 4.1 using Kimura's 2-parameter (K2P) distance model (Tamura el al. 2007).

GENETIC STRUCTURE OF FEATHER MITES

Once we characterized the interspecific diversity of seabird mites from Cape Verde, we went onto examine the contribution of host species and local geography to mite genetic structure. For this purpose, we first mapped host and geographic information onto the mitochondrial haplotype networks of each mite species.We then carried out analyses of molecular variance (AMOVA) as implemented in Arlequin v3.5 (Excoffier and Lischer 2010). In general, each host species harboured its own species of feather mite, except three mite species (*M. brevipes, B. puffini* and *P. sp.1*) shared by Cape Verde and Boyd´s shearwaters (see results). For these species, we quantified variation among hosts and within host populations. In a second set of AMOVA, we partitioned genetic variation among islands and among individuals within islands for each mite species that occurred on at least two islands.

RESULTS

MORPHOLOGICAL DIVERSITY OF FEATHER MITES

Thirty-two feather mite species belonging to ten genera and three families were found on the six studied seabird species based only on morphological criteria: *Zachvatkinia*, *Rhinozachvatkinia*, *Promegninia* (Avenzoariidae), *Microspalax*, *Brephosceles*, *Plicatalloptes*, *Laminalloptes*, *Onychalloptes* (Alloptidae), *Ingrassia* and *Opetiopoda* (Xolalgidae) (Supplementary Information Table S2). Many of these genera, such as *Zachvatkinia*, *Microspalax*, *Brephosceles* and *Ingrassia*, co-occurred in multiple seabird species in Cape Verde Islands, whereas *Rhinozachvatkinia*, *Promegninia*, *Opetiopoda*, *Plicatalloptes*, *Laminalloptes* and *Onychalloptes* were restricted to one or two host species (Figure 2).The procellariiform seabirds harboured distinct acarofauna compared to the phaethontiform bird, *Ingrassia* being the only genus shared by the two seabird orders. Nine of the recorded mite species correspond to new species and six others have only recently been described (*Rhinozachvatkinia calonectris*, *Promegninia calonectris*, *Promegninia bulweriae*, *Opetiopoda bulweriae*, *Ingrassia calonectris* and *Ingrassia micronota*) (Stefan et al. 2013, 2014, Mironov et al. 2015). The Cape Verde shearwater and Bulwer´s petrel hosted the greatest number of feather mite species (eight each) with the highest number of new species (three for the Cape Verde shearwater and four for Bulwer´s petrel), whereas Cape Verde petrel harboured the lowest with only three species found. Except for three feather mite species (*M. brevipes*, *B. puffini* and *Plicatalloptes sp.1*) which were shared by the two shearwater species (Cape Verde and Boyd´s shearwaters), each host species harboured its own feather mite species (Figure 2, Supplementary Information Table S2).

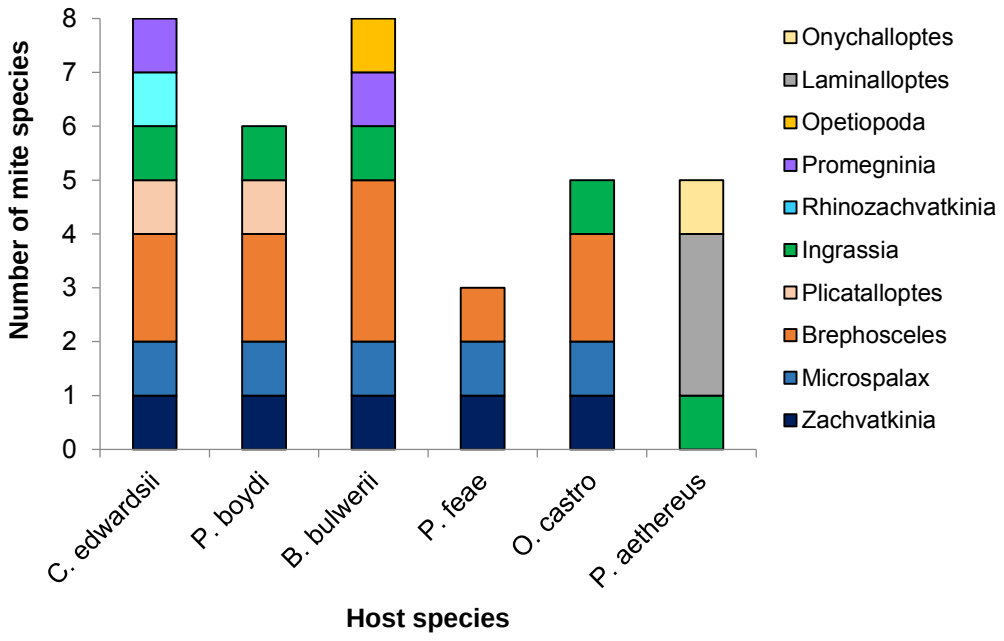


Figure 2. Feather mite richness for each seabird species. The size of each stacked bar indicates the number of species of each mite genus. Colors represent the ten feather mite genera hosted by the six seabirds breeding in the Cape Verde islands.

MOLECULAR DIVERSITY OF FEATHER MITES AND SPECIES DELIMITATION

In total, 190 sequences for each of the two mitochondrial genes were obtained for 23 of the 32 morphologically distinct species (GenBank Accession nos. XXXX - XXXX) (Supplementary material: Table S1). The remaining nine species, belonging to four mite genera (*Rhinozachvatkinia*, *Promegninia*, *Ingrassia* and *Opetiopoda*) could not be included in the molecular analyses because of low sample sizes or difficulties in the sequencing. Six specimens of four mite species found on two seabird species co-habiting in Raso were

considered to be natural or artificial contamination based on the host-range from the original species description and sampling method (i.e., mite collection from different host species in the same day using the same bird bags), and were not included in the molecular analyses. These exceptions corresponded to two specimens each of *M. brevipes* and *Plicatalloptes sp.1* (normally hosted by Cape Verde and Boyd´s shearwaters), and one specimen of *B. sp.1* (normally hosted by Bulwer´s petrel) all found on the band-rumped storm-petrel and one specimen of *B. lanceolatus* (normally found on the Madeiran storm petrel) isolated from the Bulwer´s petrel.

Standard genetic parameters for each gene and for each of the 23 mite species were analyzed and are indicated in Table 1. The number of haplotypes per mite species ranged from 1 to 11 for 12S gene and from 1 to 6 for 16S gene. Haplotype diversity ranged from 0 to 1 for both genes, while nucleotide diversity ranged from 0 to 0.0051 when cryptic lineages were accounted for. The neutrality test scores were not significant for any of the mite genes analyzed (12S and 16S) (all $P > 0.05$), except for 12S data of *Plicatalloptes sp.1*, which may indicate purifying selection or population expansion (Tajima´s $D = -1.87$; $P < 0.05$). A Tajima´s test could not be computed for the 16S data of *O. microphaeton* due to the lack of polymorphism in this species. Sequence divergence between feather mite morphospecies within each genus for the 12S gene were higher than 7.4 % for *Zachvatkinia*, 9 % for *Microspalax*, 3.6 % for *Brephosceles* and 20 % for *Laminalloptes*, whereas for the 16S gene genetic distances ranged from 6.6 % to 19.1 % for *Zachvatkinia*, 12.9 % to 20 % for *Microspalax*, 1.9 % to 28.2 % for *Brephosceles* and 21.9 % to 32.2 % for *Laminalloptes* (Table 2). Sequence divergence between genetic lineages *Z. oceanodromae* A and *Z. oceanodromae* B was 6.6 % for 12S gene and 7 % for 16S gene, whereas between *L. simplex* A and *L. simplex* B was 11.2 % and 16.4 %, respectively. Mean genetic distances between individuals within morphospecies ranged from 0 % to 0.7 % for all species from all genera and for both genes, except for *Z. oceanodromae* (1 %, SE=0.002 for 12S gene and 1.5 %, SE=0.006 for 16S gene; bootstrap 1000 replicates) and *L. simplex* (2.8 %, SE=0.005 for 12S gene and 4.4 %, SE=0.010 for 16S gene, respectively; bootstrap 1000 replicates) (Table 2). When cryptic lineages were considered, mean genetic distances between individuals within *Z. oceanodromae* A and *L. simplex* A were reduced to less than 0.6 % for both genes.

The mtDNA networks revealed high levels of haplotypic diversity, with 102 distinct haplotypes, based on the concatenated 12S and 16S sequences, and 25 different networks identified across specimens (Figures 3 A-F). We found a high degree of correspondence between morphological and molecular data. Feather mites of the genus *Zachvatkinia* displayed 31 haplotypes separated into six distinct sub-networks, each corresponding to one morphospecies of *Zachvatkinia*. The only exception was for *Z. oceanodromae* from band-rumped storm-petrel, where two different sub-networks were identified (*Z. oceanodromae* A and *Z. oceanodromae* B - Figure 3A) likely corresponding to cryptic species; however, only one specimen of *Z. oceanodromae* B was found. The 20 haplotypes found for *Microspalax* grouped into four sub-networks, in agreement with the four mite species identified based on morphological criteria (Figure 3B). The 29 haplotypes identified for feather mites of the genus *Brephosceles* grouped into nine distinct sub-networks that again were in clear agreement with morphological identifications (Figure 3C). Feather mites of the genus *Plicatalloptes* grouped into a single network containing 13 haplotypes, which corresponded with the only morphospecies identified (Figure 3D). Feather mites of the genus *Laminalloptes* displayed seven haplotypes grouped into four distinct sub-networks, which partially correlated with the described morphospecies. The exception was *L. simplex*, where two different sub-networks were found (*L. simplex* A and *L. simplex* B - Figure 3E) and again likely correspond to cryptic species; as for *Z. oceanodromae* B, only one specimen of *L. simplex* B was found. Finally, *Onychalloptes* represented by one morphospecies displayed a single network with two haplotypes (Figure 3F).

Table 1. Basic genetic statistics of 23 feather mite morphospecies (or 25 genetic lineages) from Cape Verde Islands analysed in this study based on two mitochondrial genes (12S and 16S). Number of individuals sequenced (N), number of polymorphic sites (Np), number of haplotypes (Nh), haplotype diversity (h), nucleotide diversity (π), average number of nucleotide differences (k) and average genetic divergence (d) are shown. Island abbreviations: Rs – Raso, CV – Curral Velho, IC – Ilhéu Cima, IG – Ilhéu Grande, Fg – Fogo.

Mite species	Host species	Locality	N	Np		Nh		h		Π		k		d	
				12S	16S	12S	16S	12S	16S	12S	16S	12S	16S	12S	16S
Z. ovata	*C. edwardsii*	Rs, CV	9	4/316	1/132	5	2	0.806	0.222	0.0033	0.0017	1.056	0.222	0.003 (SE=0.002)	0.002 (SE=0.002)
Z. sp.1	*P. boydi*	Rs, IC	10	0/319	1/133	1	2	0	0.200	0	0.0015	0	0.200	0	0.002 (SE=0.002)
Z. sp.2	*B. bulwerii*	Rs, IC, IG	13	6/320	2/134	5	3	0.538	0.295	0.0029	0.0048	0.923	0.308	0.003 (SE=0.001)	0.002 (SE=0.002)
Z. oceanodromae (morphospecies)	*H. castro*	Rs, CV, IC, IG	13	23/325	9/133	4	4	0.679	0.603	0.0123	0.0143	3.923	1.885	0.010 (SE=0.002)	0.015 (SE=0.006)
Z. oceanodromae A (genetic lineage)	*H. castro*	Rs, CV, IG	12	2/325	2/133	3	3	0.621	0.530	0.0022	0.0049	0.712	0.652	0	0.005 (SE=0.004)
Z. oceanodromae B (genetic lineage)	*H. castro*	IC	1	-	-	-	-	-	-	-	-	-	-	-	-
Z. sp.3	*P. feae*	Fg	5	3/324	0/136	3	1	0.700	0	0.0037	0	1.200	0	0.004 (SE=0.002)	0
M. brevipes	*C. edwardsii, P. boydi*	Rs, CV, IC	20	7/326	3/148	6	4	0.737	0.621	0.0051	0.0049	1.642	0.726	0.005 (SE=0.002)	0.005 (SE=0.004)
M. bulweriae	*B. bulwerii*	Rs, IC, IG	8	0/322	1/153	1	2	0	0.250	0	0.0016	0	0.250	0	0.002 (SE=0.002)
M. cymochoreae	*H. castro*	Rs, CV, IC	8	1/324	1/148	2	2	0.250	0.250	0.0008	0.0017	0.250	0.250	0.001 (SE=0.001)	0.002 (SE=0.002)
M. pterodromae	*P. feae*	Fg	1	-	-	-	-	-	-	-	-	-	-	-	-
B. puffini	*C. edwardsii, P. boydi*	Rs, CV, IC	20	3/312	1/145	4	2	0.432	0.189	0.0018	0.0013	0.558	0.189	0.002 (SE=0.001)	0
B. sp.1	*B. bulwerii*	Rs, IC, IG	15	1/315	1/151	2	2	0.248	0.133	0.0008	0.0009	0.248	0.133	0.001 (SE=0.001)	0.001 (SE=0.001)
B. sp.2	*B. bulwerii*	Rs, IC	2	1/311	0/148	2	1	1	0	0.003	0	1	0	0.003 (SE=0.003)	0
B. sp.3	*B. bulwerii*	IC	2	0/310	1/140	1	2	0	1	0	0.007	0	1	0	0.007 (SE=0.007)
B. sp.4	*C. edwardsii*	Rs	1	-	-	-	-	-	-	-	-	-	-	-	-
B. sp.5	*P. boydi*	Rs	1	-	-	-	-	-	-	-	-	-	-	-	-
B. decapus	*H. castro*	Rs, CV	15	1/310	2/141	2	3	0.248	0.362	0.0008	0.0027	0.248	0.381	0.001 (SE=0.001)	0.003 (SE=0.002)
B. lanceolatus	*H. castro*	Rs, CV, IC	6	0/310	2/141	1	3	0	0.600	0	0.0047	0	0.667	0	0.005 (SE=0.004)
B. disjunctus	*P. feae*	Fg	4	0/311	1/145	1	2	0	0.500	0	0.0034	0	0.500	0	0.004 (SE=0.004)
P. sp.1	*C. edwardsii, P. boydi*	Rs, CV, IC	19	10/322	5/139	11	6	0.830	0.538	0.0047	0.0045	1.509	0.620	0.005 (SE=0.002)	0.005 (SE=0.002)
L. phaetontis	*P. aethereus*	Rs	4	0/312	1/142	1	2	0	0.500	0	0.0035	0	0.500	0	0.004 (SE=0.003)
L. simplex (morphospecies)	*P. aethereus*	Rs	8	33/308	19/147	2	4	0.250	0.643	0.0268	0.0347	8.250	4.929	0.028 (SE=0.005)	0.044 (SE=0.010)
L. simplex A (genetic lineage)	*P. aethereus*	Rs	7	0/308	2/143	1	3	0	0.524	0	0.0040	0	0.571	0	0.004 (SE=0.003)
L. simplex B (genetic lineage)	*P. aethereus*	Rs	1	-	-	-	-	-	-	-	-	-	-	-	-
L. minor	*P. aethereus*	Rs	1	-	-	-	-	-	-	-	-	-	-	-	-
O. microphaeton	*P. aethereus*	Rs	5	1/310	0/152	2	1	0.400	0	0.0013	0	0.400	0	0.001 (SE=0.001)	0

Table 2. Mean genetic distances measured as Fst among feather mite species within four genera: *Zachvatkinia*, *Microspalax*, *Brephosceles* and *Laminalloptes* from Cape Verde Islands based on the 12S (A) and the 16S (B) genes. Two mite genera, *Plicatalloptes* and *Onychalloptes*, included only a single species and are therefore not shown.

(A – 12S gene)	*Z. sp.1*	*Z. ova*	*Z. sp.3*	*Z. sp.2*	*M. bre*	*M. cym*	*M. bul*	*B. dec*	*B. sp.1*	*B. puf*	*B. dis*	*B. sp.2*	*B. lan*	*B. sp.3*	*B. sp.4*	*L. min*	*L. pha*
Z. sp.1																	
Z. ovata	0.075																
Z. sp.3	0.127	0.131															
Z. sp.2	0.148	0.154	0.149														
Z. oceanodromae	0.111	0.129	0.106	0.156													
M. brevipes																	
M. cymochoreae					0.097												
M. bulweriae					0.092	0.119											
M. pterodromae					0.105	0.138	0.120										
B. decapus																	
B. sp.1								0.197									
B. puffini								0.233	0.169								
B. disjunctus								0.275	0.274	0.255							
B. sp.2								0.254	0.235	0.230	0.089						
B. lanceolatus								0.294	0.284	0.274	0.110	0.116					
B. sp.3								0.288	0.270	0.274	0.125	0.155	0.173				
B. sp.4								0.288	0.251	0.265	0.109	0.127	0.144	0.037			
B. sp.5								0.307	0.270	0.285	0.133	0.155	0.152	0.051	0.037		
L. minor																	
L. phaetontis																0.249	
L. simplex																0.205	0.233

Table 2. Continuation

(B – 16S gene)	*Z. sp.1*	*Z. ova*	*Z. sp.3*	*Z. sp.2*	*M. bre*	*M. cym*	*M. bul*	*B. dec*	*B. sp.1*	*B. puf*	*B. dis*	*B. sp.2*	*B. lan*	*B. sp.3*	*B. sp.4*	*L. min*	*L. pha*
Z. sp.1																	
Z. ovata	0.066																
Z. sp.3	0.142	0.170															
Z. sp.2	0.165	0.152	0.191														
Z. oceanodromae	0.185	0.176	0.167	0.165													
M. brevipes																	
M. cymochoreae					0.179												
M. bulweriae					0.129	0.156											
M. pterodromae					0.114	0.200	0.156										
B. decapus																	
B. sp.1								0.210									
B. puffini								0.219	0.218								
B. disjunctus								0.282	0.172	0.250							
B. sp.2								0.228	0.151	0.239	0.099						
B. lanceolatus								0.201	0.118	0.234	0.166	0.136					
B. sp.3								0.229	0.194	0.260	0.184	0.155	0.148				
B. sp.4								0.208	0.190	0.239	0.191	0.141	0.143	0.019			
B. sp.5								0.239	0.199	0.272	0.191	0.141	0.135	0.027	0.023		
L. minor																	
L. phaetontis																0.322	
L. simplex																0.219	0.317

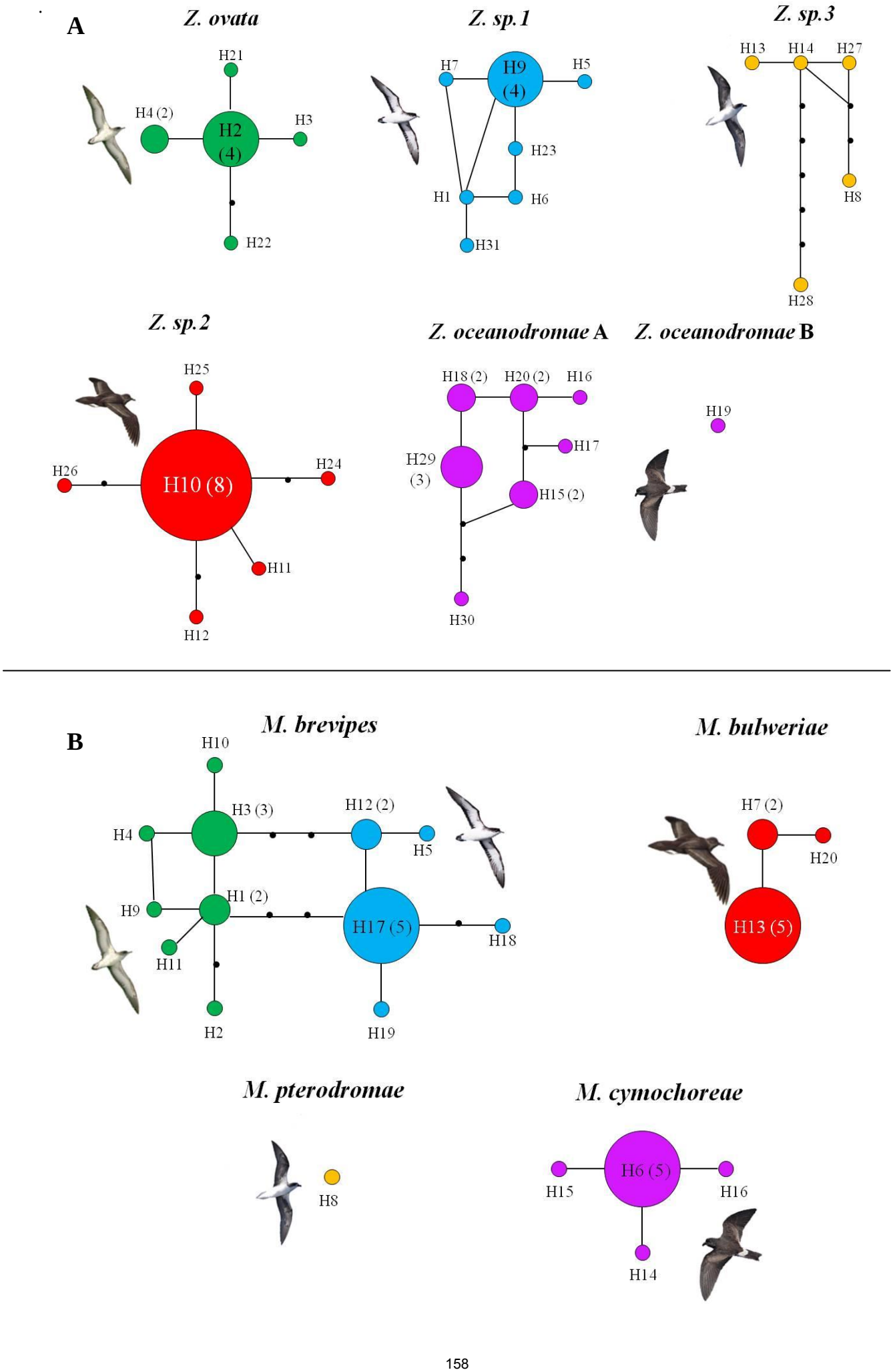
Table 3. Analysis of molecular variance for mitochondrial haplotypes from the three feather mite species sheared by Cape Verde shearwater and Boyd's shearwater partitioned by seabird host.

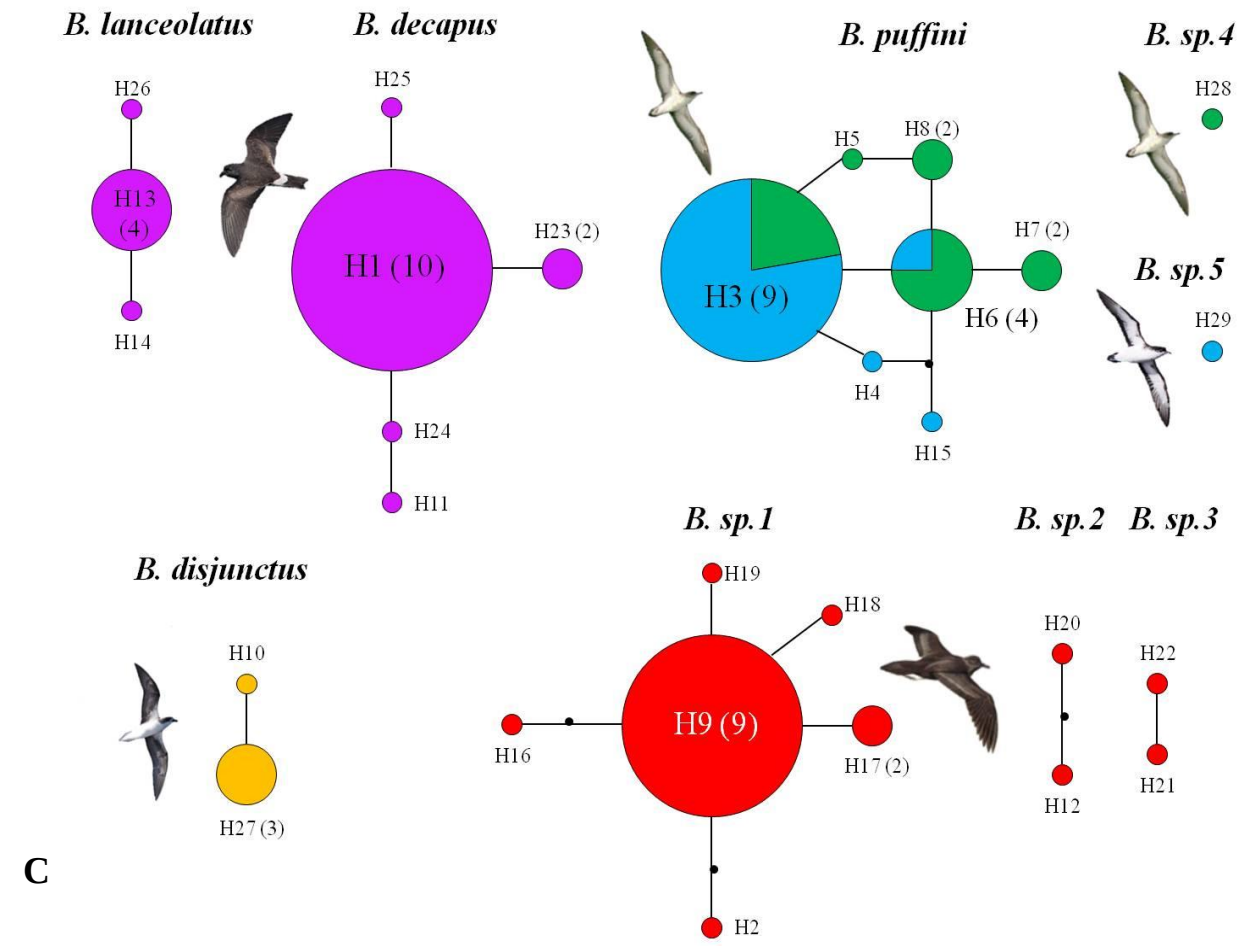
Species	Partition	d.f.	Sum of squares	% variation	Φ_{ST}	P
Microspalax brevipes	Among-host populations	1	15.800	66.91	0.669	0
	Within-host populations	18	13.400	33.09	-	-
Brephosceles puffini	Among-host populations	1	2.150	22.54	0.225	0.010
	Within-host populations	18	9.900	77.46	-	
Plicatalloptes sp.1	Among-host populations	1	1.503	4.82	0.048	0.069
	Within-host populations	17	17.655	95.18	-	-

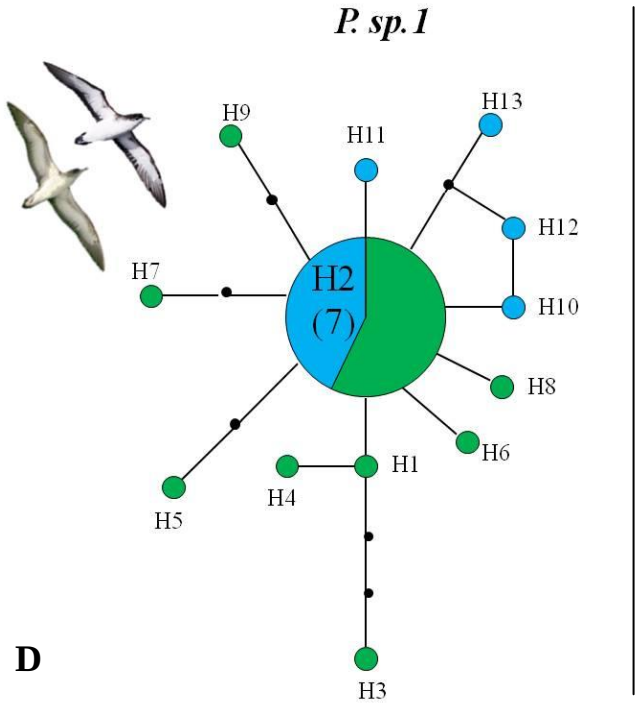
Table 4. Analysis of molecular variance for mitochondrial haplotypes from twelve feather mite species partitioned by geography

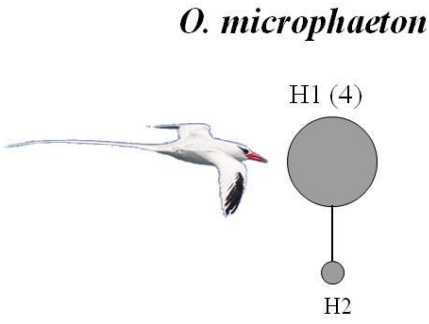
Species	Partition	d.f.	Sum of squares	% variation	Φ_{ST}	P
Zachvatkinia ovata	Among-island populations	1	0.961	12.26	0.122	0.122
	Within-island populations	7	4.150	87.74	-	-
Zachvatkinia sp.1	Among-island populations	1	1.500	24.34	0.243	0.053
	Within-island populations	8	4.600	75.66	-	-
Zachvatkinia sp.2	Among-island populations	2	1.251	0.47	0.005	0.597
	Within-island populations	10	6.133	99.53	-	-
Zachvatkinia oceanodromae A	Among-island populations	2	1.333	-23.17	-0.231	0.883
(genetic lineage)	Within-island populations	9	11.000	123.17	-	-
Microspalax brevipes	Among-island populations	1	1.700	20.21	0.202	0.071
(*C. edwardsii*)	Within-island populations	8	6.000	79.79	-	-
Microspalax brevipes	Among-island populations	1	0.500	-4.84	-0.048	1
(*P. boydi*)	Within-island populations	8	5.200	104.84	-	-
Microspalax bulweriae	Among-island populations	2	1.450	45.70	0.457	0.218
	Within-island populations	5	1.300	54.30	-	-
Microspalax cymochoreae	Among-island populations	2	0.825	6.42	0.064	0.473
	Within-island populations	5	1.800	93.58	-	-
Brephosceles puffini	Among-island populations	2	1.750	6.64	0.066	0.227
	Within-island populations	17	10.300	93.36	-	-
Brephosceles sp.1	Among-island populations	2	0.933	-2.56	-0.025	1
	Within-island populations	12	6.400	102.56	-	-
Brephosceles decapus	Among-island populations	1	0.220	-8.14	-0.081	0.944
	Within-island populations	13	5.114	108.14	-	-
Brephosceles lanceolatus	Among-island populations	2	1.000	40.54	0.405	0.325
	Within-island populations	3	0.667	59.46	-	-
Plicatalloptes sp.1	Among-island populations	2	2.682	4.92	0.049	0.132
	Within-island populations	16	16.476	95.08	-	-

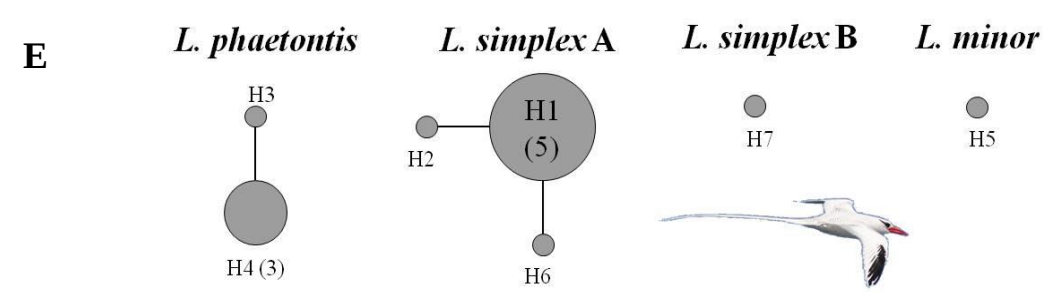
Figure 3. Statistical parsimony haplotype networks for seabird feather mites *Zachvatkinia* (A), *Microspalax* (B), *Brephosceles* (C), *Plicatalloptes* (D), *Laminalloptes* (E) and *Onychalloptes* (F) from the Cape Verde islands based on the concatenation of two mitochondrial genes (12S and 16S). Haplotypes are coloured according to the hosts harbouring the mites (green - *C. edwardsii*, blue - *P. boydi*, red - *B. bulwerii*, purple - *H. castro*, orange - *P. feae* and grey - *P. aethereus*). Circle sizes are proportional to the number of individuals possessing each haplotype, indicated in brackets. Black dots represent mutational steps.


A
Z. ovata
H21
H4 (2)
H2 (4)
H3
H22
Z. sp.1
H7
H9 (4)
H5
H23
H1
H6
H31
Z. sp.3
H13
H14
H27
H8
H28
Z. sp.2
H25
H26
H10 (8)
H24
H11
H12
Z. oceanodromae A
H18 (2)
H20 (2)
H16
H17
H29 (3)
H15 (2)
H30
Z. oceanodromae B
H19
B
M. brevipes
H10
H3 (3)
H12 (2)
H4
H5
H1 (2)
H9
H17 (5)
H18
H11
H2
H19
M. bulweriae
H7 (2)
H20
H13 (5)
M. pterodromae
H8
M. cymochoreae
H6 (5)
H15
H16
H14


B. lanceolatus
B. decapus
B. puffini
B. sp.4
H26
H13 (4)
H14
H25
H1 (10)
H23 (2)
H24
H11
H5
H8 (2)
H7 (2)
H3 (9)
H6 (4)
H4
H15
H28
B. sp.5
H29
B. disjunctus
H10
H27 (3)
B. sp.1
B. sp.2
B. sp.3
H19
H18
H9 (9)
H16
H17 (2)
H20
H22
H12
H21
H2
C


P. sp.1
H9
H11
H13
H12
H7
H2 (7)
H10
H8
H6
H1
H4
H5
H3
D


O. microphaeton
H1 (4)
H2
F


E
L. phaetontis
L. simplex A
L. simplex B
L. minor
H3
H4 (3)
H1 (5)
H2
H6
H7
H5

The bayes factors of the GMYC analysis indicated that a Yule prior with a strict clock gives a slightly better fit than a coalescent prior (Yule: -5755.31, coalescent: -5741.33). Similarly, the single threshold model of the GMYC analysis suggested the presence of 26 putative mite species within Cape Verde Islands when considering the Yule-strict clock combination (N_{GMYC} = 29 (CI 28-30) including the three outgroup species, L_{GMYC} = 732.49; where N = number of species and L = likelihood of GMYC model). For the coalescent strict clock, the GMYC analysis resulted in 25 putative mite species (N_{GMYC} = 28 (CI 28-30) including the three outgroup species, L_{GMYC} =738.21), which agrees with the 25 different networks identified by the TCS analysis (Supplementary Information: Figure S1). For both models (Yule and coalescent), the GMYC method indicated that there are two species within *Z. oceanodromae* and four within the *Laminalloptes* genus. The only difference consists in the partition of *M. brevipes* haplotypes into two distinct species (one species for each host: Cape Verde shearwater and Boyd´s shearwater) for the Yule-strict clock combination.

GENETIC STRUCTURE OF FEATHER MITES

Clear patterns of host-associated genetic structure are apparent in most of the feather mite genera analyzed (Figure 3). All mite species showed one-host one-mite species pattern, except *M. brevipes*, *B. puffini* and *Plicatalloptes sp.1*, which were shared between the two related shearwater species. In these mite species, however, AMOVA results with host as the grouping factor showed significant genetic differentiation among seabird species for *M. brevipes* (Φ = 0.669, P = 0) and *B. puffini* (Φ = 0.225, P = 0.010) suggesting some host-associated isolation (Table 3). This was not significant for *P. sp.1* (Φ = 0.048, P = 0.069), indicating shared populations, or a very recent host shift. When looking at the relationship between genetic diversity and geography, the TCS parsimony networks showed weak structuring of seabird feather mites with respect to their geographic location (Figures 4A-D). Almost all mite species shared haplotypes among islands when they occurred in more than one location and had reasonable sample sizes. AMOVA analyses with island as a grouping factor supported this conclusion, with only *Z.* sp.1 and *M. Brevipes* showing tendancies for island-related genetic structure. (Table 4).

DISCUSSION

In this study, we combined morphological and molecular data to investigate diversity and genetic structure of feather mite communities in the seabirds (Procellariiformes and Phaethontiformes) of the Cape Verde Islands. We found a high diversity of mites and evidence of cryptic species in two mite genera. In agreement with the predicted high level of specialization of this group, we also found strong host-dependent genetic structure for most feather mites. On the other hand, between island structure, after controlling for host, was weak or non-existent, suggesting that mixing readily occurs at the scale of the archipelago.

Procellariiform and phaenthontiform seabirds from Cape Verde harboured a diverse and unique mite fauna composed of 10 genera and 32 morphologically distinct species. The most common feather mite species belonged to the genera *Zachvatkinia*, *Microspalax* and *Brephosceles*. Most of these species have been previously reported from other seabird species and geographic locations (Atyeo and Gaud 1991, Mironov 1989a, Peterson 1971). However, diversity was very high at a local level, with five species inhabiting the red-billed tropicbird and 27 species reported from the five procellariiform hosts, of which 11 are new, undescribed species. Furthermore, four recently described species (Stefan et al. 2013, 2014) represent first records from procellariiform seabirds. Birds frequently harbour more than one feather mite species, with each species occupying a specific microhabitat in the plumage (Gaud and Atyeo 1996, Stefan et al. 2015). All seabirds examined in this study hosted at least three feather mite species, with Cape Verde shearwaters and Bulwer´s petrels presenting the richest mite communities (eight species each). Our results highlight the vast and largely unrecognized diversity of feather mites harboured by seabirds.

The host-feather mite associations found in the present study are largely in agreement with previous species descriptions in the literature, although inconsistencies concerning some feather mite species were detected.

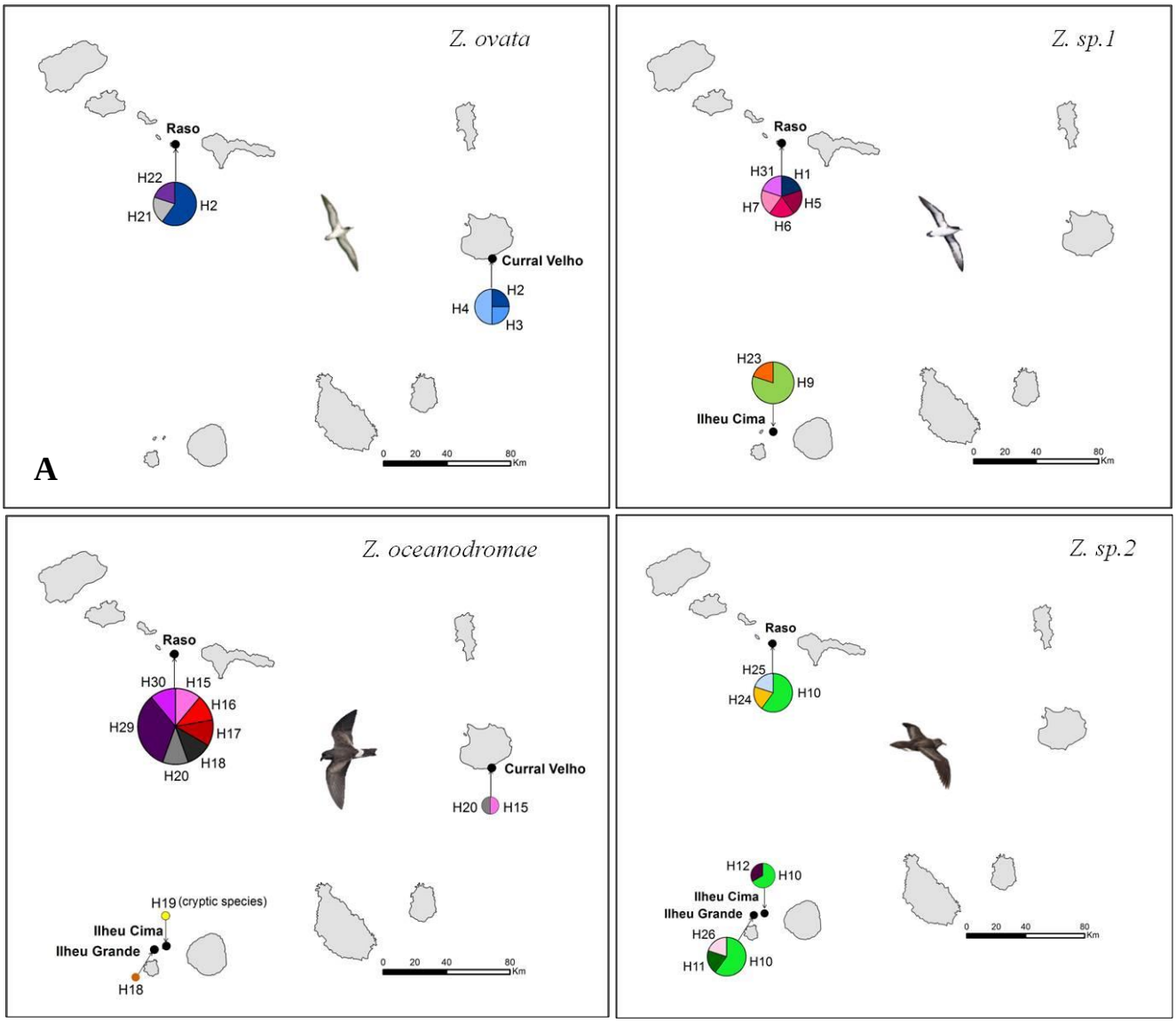


Figure 4. Geographic distribution of haplotypes for seabird feather mites *Zachvatkinia* (A), *Microspalax* (B), *Brephosceles* (C) and *Plicatalloptes* (D) from Cape Verde islands. Each colour represents a different haplotype and the size of each haplotype is proportional to the number of individuals possessing that haplotype.

First, *Z. ovata* was previously reported from *Calonectris diomedea borealis* and different species of *Puffinus* shearwaters (Mironov 1989a). Our study clearly shows that these two host genera harbour distinct species of *Zachvatkinia*. The previous description of *Z. ovata* on a range of hosts could have been due to the non-detection of novel species or contamination, as the material was collected from dry museum skins. Another disagreement concerns *Brephosceles puffini*, currently known only from *Puffinus* hosts (Peterson 1971); the present study revealed that *B. puffini* also inhabits *Calonectris* shearwaters. This does not seem to be a spurious result. *Brephosceles puffini* specimens were found in one locality (Raso) on both seabird species, but were also found in two independent localities where the seabird hosts are not sympatric (e.g. in Curral Velho on *Calonectris* shearwaters and Ilheu de Cima on *Puffinus* shearwaters).

In the present study, a strong correlation between morphological observations and molecular data was observed. However, based on genetic evidence we detected the presence of two putative cryptic species. Thus, of the 23 species identified morphologically and examined using genetic markers, the haplotype network analysis found 25 different genetic lineages and the GMYC analysis 26. *Zachvatkinia oceanodromae*, found exclusively on the band-rumped storm-petrel, included a potentially cryptic species (*Z. oceanodromae* B) restricted to Ilheu de Cima. Although some small morphological differences could be detected on secondary examination (ie., slightly shorter incision in the interlobar membrane; S. Mironov personal observation), this

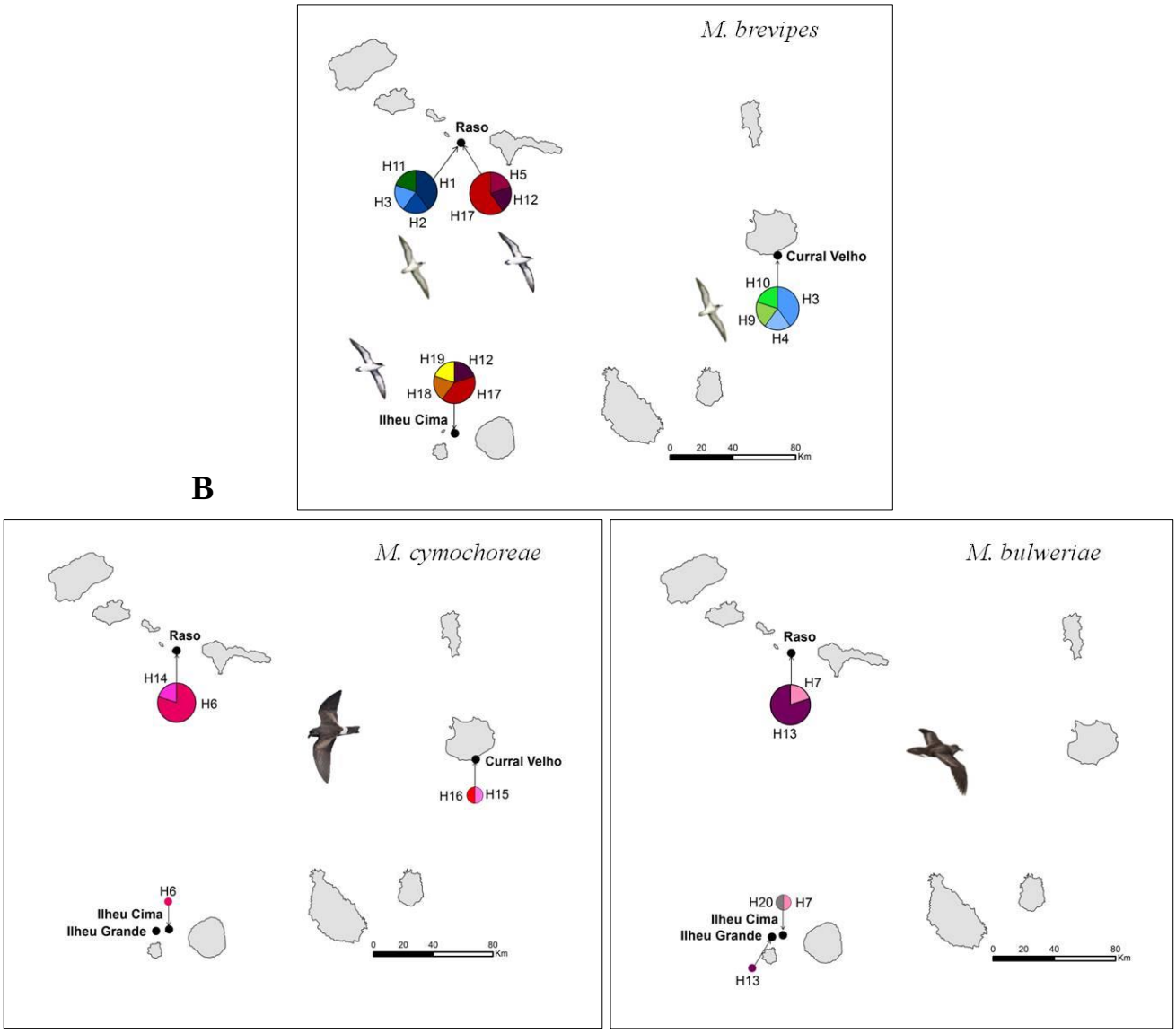


Figure 4. Continuation

characteristic is not enough to treat this new lineage as a distinct species based on morphological criteria only. Furthermore, we collected only a single specimen of this novel lineage and therefore, do not yet know how much variation in morphology and genetics may be present in *Z. oceanodromae*. A similar case was found within the genus *Laminalloptes* with the presence of *L. simplex* B. The only specimen belonging to this lineage is a strange male with an enormously widened opisthosoma (the posterior part of the mite body). The only disagreement between the two molecular analyses used to delimit species concerned *M. brevipes*, which was partitioned into two distinct species by the GMYC analysis only.

Cryptic speciation appears to be common in many parasitic groups, such as trematodes, due to the lack of distinguishing morphological characters (Miura et al. 2005, Saijuntha et al. 2007, Leung et al. 2009), feather lice (Malenke et al. 2009) or eriophyoid mites (Miller et al. 2013). This phenomenon also seems to be present in feather mites (Whiteman et al. 2006, Dabert et al. 2008, Doña et al. 2015b) particularly given that females of some taxa are often indistinguishable and male morphological identifications can be difficult even for experienced taxonomists. For example, the generalist and widely-distributed avian skin mite *Myialges caulotoon*, vectored by hippoboscid flies, exhibits cryptic host specificity, with one lineage associated with Galápagos hawks and another associated with flightless cormorants (Whiteman et al. 2006). In addition, strong host-associated adaptive pressures on parasite species may promote convergence in morphology, rendering traditional morphological methods inadequate for species identification. In order to confirm the two potential cryptic species found in the present study, more specimens belonging to each species will therefore need to be

collected and redescribed using multiloci genetic data and more quantitative morphological methods (ex., geometric morphometrics).

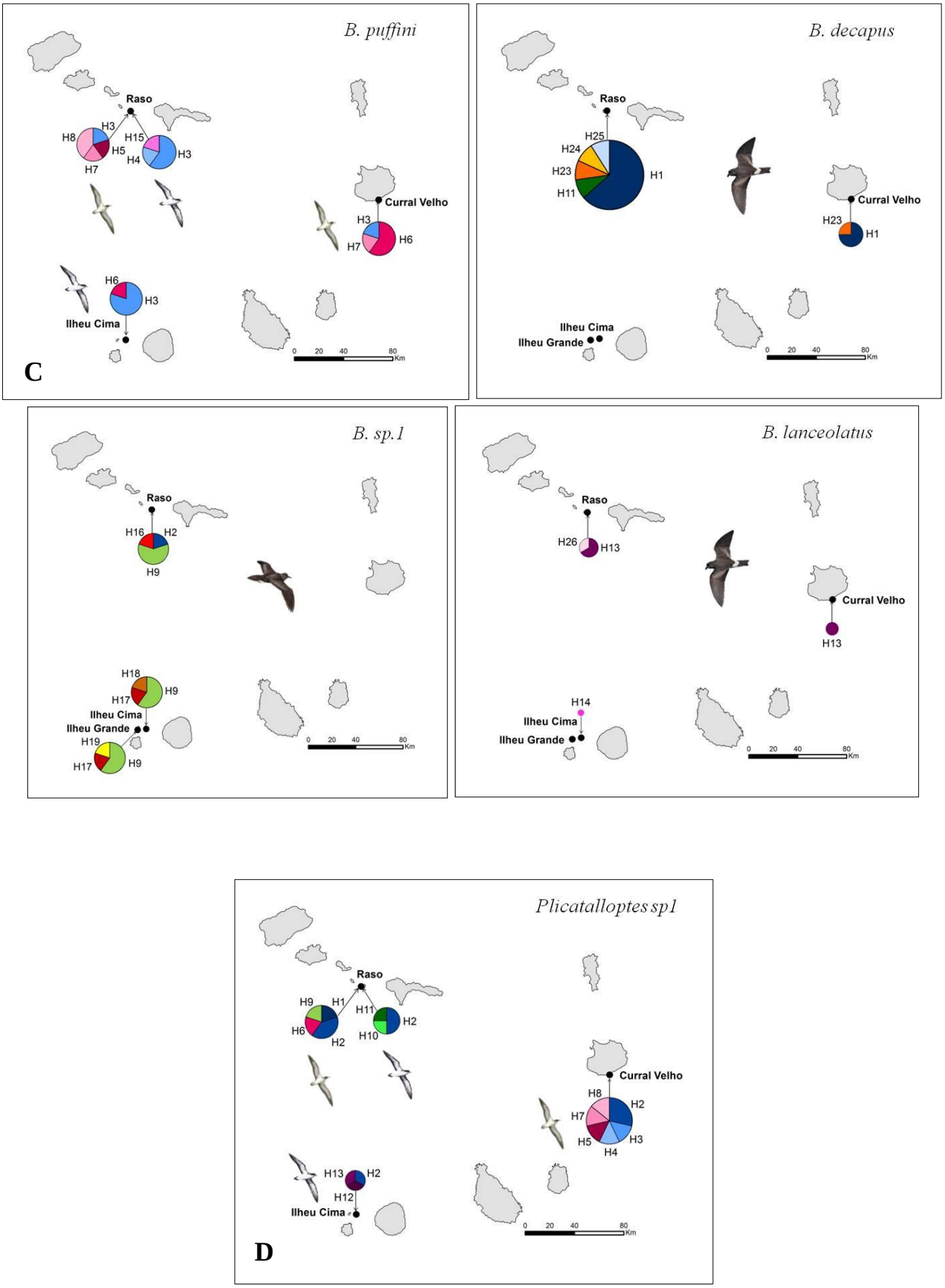


Figure 4. Continuation

Feather mites are highly specialized ectosymbionts that are adapted to inhabit well-defined host microhabitats including the vane surface of contour feathers, soft down feathers, the surface of the skin or subcutaneous layers and the interior of feather quills (Gaud and Atyeo 1996, Dabert and Mironov 1999, Proctor 2003). While large vane-dwelling mites with dorso ventrally flattened and heavily sclerotized bodies (e.g. *Z. ovata* and *M. brevipes*) are specialized to inhabit the ventral surfaces of flight feathers (primary and tail feathers) and withstand the strong air turbulence during flight (Stefan et al. 2015), other mite genera, such as *Brephosceles* and *Plicatalloptes*, include small and weakly sclerotized mites which occupy more protected areas of the plumage (e.g. wing coverts and soft body feathers) (Peterson 1971, Bourgeois and Threlfall 1979, Dabert et al. 2015, L. Stefan personal observations). In our study, most seabird species hosted different mite species, even under sympatry, suggesting that the selective pressure imposed by the host environment has resulted in host adaptation, which, in turn, has promoted parasite specialization and diversification (Lajeunesse and Forbes 2002, Gandon and Michalakis 2002, Malenke et al. 2009). However, three mite species (*M. brevipes, B. puffini* and *Plicatalloptes sp.1*) showed a more generalist pattern, inhabiting related shearwater species, Cape Verde and Boyd´s shearwaters. While *Plicatalloptes sp.1* showed no significant genetic differentiation among host species, some genetic structure was evident among host populations for *M. brevipes* and *B. puffini*. Differences in the habitat preferences of these mite species could explain the variation in the genetic differentiation and host-specificity observed. For example, M. brevipes is a large vane-dwelling mite with dorso ventrally flattened and heavily sclerotized body that inhabit the ventral surfaces of flight feathers, features that may favour dispersal. In addition, the fact that the seabird host species breed sympatrically and may even share nest sites could decrease dispersal barriers and promote host switching. It remains to be tested whether the two seabird hosts offer similar habitats and resources to these mites; a field-based transplantation experiment could provide a lot of insight for answering this question (Tompkins and Clayton 1999, Bridge 2002).

In contrast to strong host-associated genetic structure, we found almost no genetic differentiation among islands after controlling for host, suggesting that mite dispersal regularly occurs among host populations. For this, direct physical contact among hosts is required. This can logically occurring during mating and chick rearing, but it more difficult to explain at broader scales. Indeed, procellariiform seabirds spend most of their life in the open ocean and breed on remote oceanic islands, features that should limit mite dispersal in time and space. However, studies have shown that different seabird populations can mix in specific and restricted foraging areas during the non-breeding period (González-Solís et al. 2007). These periods may provide opportunities for feather mites to switch among individual hosts if there are repeated contacts at sea. Indeed, this hypothesis has been evoked to explain the surprising homogeneity of populations of three louse species exploiting three *Calonectris* taxa (Gómez-Díaz et al. 2007). Mite dispersal between host populations could also be favoured by juvenile birds that prospect among breeding colonies, or adult birds that change their breeding locality (Boulinier et al. 2016), or even by phoresy (Harbison et al. 2009), but all these potential mechanisms require more in-depth investigation.

In conclusion, this study revealed a vast diversity of avian feather mites within the Cape Verde seabird community, highlighting the importance of host species in shaping the genetic structure of these ectosymbionts. Host specialization is considered an important driver of parasite diversification, through either host switching or cospeciation (Malenke et al. 2009). The morphological and molecular data in the present work support the presence of 11 new species and suggest the existence of at least two putative cryptic species in these seabird feather mite communities. However, two of these cryptic lineages were described based on a single specimen, and future investigations that integrate biogeography and ecology are now required to confirm that the new molecular lineages found correspond to good species associated with the specific seabird host. Although most feather mite species exhibited strong host-associated genetic structure, others were more generalists. Different degrees of host specificity may reflect, at least partially, particular microhabitat preferences of feather mites on the host body (e.g. flight feathers vs body feathers), along with more or less favourable zones for dispersal. Detailed examination of specific host and parasite traits associated with host specificity and studies of co-phylogenies comparing patterns of mite-host diversification are now called for to identify the relative roles of isolation and adaptation in generating mite diversity.

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SUPPLEMENTARY INFORMATION

Table S1. Details of the 190 feather mites collected from five seabird species breeding in Cape Verde Archipelago included in the genetic analyses of this study (50 *Zachvatkinia*, 37 *Microspalax*, 66 *Brephosceles*, 19 *Laminalloptes*, 13 *Plicatalloptes* and 5 *Onychalloptes*). Specimen codes, host species, sampling locations and the genes amplified per individual with their corresponding GenBank Accession numbers are indicated. Haplotypes for concatenated mitochondrial data corresponding to those in Figure 3 are indicated. Intraspecific lineages are defined based on general mixed Yule-coalescent method (GMYC).

Mite ID	Mite species	Mite sex	Host species	Locality	Haplotype	Species delimitation (TCS)	Species delimitation (GMYC)
Z143	*Z. ovata*	F	*Calonectris edwardsii*	Raso (Rs)	H2	Z. ovata	Z. ovata
Z164	*Z. ovata*	M	*Calonectris edwardsii*	Raso (Rs)	H2	Z. ovata	Z. ovata
Z215	*Z. ovata*	M	*Calonectris edwardsii*	Raso (Rs)	H21	Z. ovata	Z. ovata
Z216	*Z. ovata*	F	*Calonectris edwardsii*	Raso (Rs)	H22	Z. ovata	Z. ovata
Z243	*Z. ovata*	M	*Calonectris edwardsii*	Raso (Rs)	H2	Z. ovata	Z. ovata
Z136	*Z. ovata*	F	*Calonectris edwardsii*	Curral Velho (CV)	H2	Z. ovata	Z. ovata
Z139	*Z. ovata*	F	*Calonectris edwardsii*	Curral Velho (CV)	H3	Z. ovata	Z. ovata
Z142	*Z. ovata*	F	*Calonectris edwardsii*	Curral Velho (CV)	H4	Z. ovata	Z. ovata
Z217	*Z. ovata*	M	*Calonectris edwardsii*	Curral Velho (CV)	H4	Z. ovata	Z. ovata
Z69	*Z. sp.1*	F	*Puffinus boydi*	Raso (Rs)	H1	Z. sp1	Z. sp1
Z146	*Z. sp.1*	F	*Puffinus boydi*	Raso (Rs)	H5	Z. sp1	Z. sp1
Z147	*Z. sp.1*	F	*Puffinus boydi*	Raso (Rs)	H6	Z. sp1	Z. sp1
Z150	*Z. sp.1*	F	*Puffinus boydi*	Raso (Rs)	H7	Z. sp1	Z. sp1
Z244	*Z. sp.1*	F	*Puffinus boydi*	Raso (Rs)	H31	Z. sp1	Z. sp1
Z168	*Z. sp.1*	F	*Puffinus boydi*	Ilheu Cima (IC)	H9	Z. sp1	Z. sp1
Z218	*Z. sp.1*	M	*Puffinus boydi*	Ilheu Cima (IC)	H9	Z. sp1	Z. sp1
Z219	*Z. sp.1*	F	*Puffinus boydi*	Ilheu Cima (IC)	H9	Z. sp1	Z. sp1
Z220	*Z. sp.1*	M	*Puffinus boydi*	Ilheu Cima (IC)	H23	Z. sp1	Z. sp1
Z221	*Z. sp.1*	F	*Puffinus boydi*	Ilheu Cima (IC)	H9	Z. sp1	Z. sp1
Z169	*Z. sp.2*	M	*Bulweria bulwerii*	Raso (Rs)	H10	Z. sp2	Z. sp2
Z222	*Z. sp.2*	F	*Bulweria bulwerii*	Raso (Rs)	H10	Z. sp2	Z. sp2
Z223	*Z. sp.2*	F	*Bulweria bulwerii*	Raso (Rs)	H24	Z. sp2	Z. sp2
Z224	*Z. sp.2*	F	*Bulweria bulwerii*	Raso (Rs)	H10	Z. sp2	Z. sp2
Z225	*Z. sp.2*	M	*Bulweria bulwerii*	Raso (Rs)	H25	Z. sp2	Z. sp2
Z173	*Z. sp.2*	M	*Bulweria bulwerii*	Ilheu Cima (IC)	H12	Z. sp2	Z. sp2
Z226	*Z. sp.2*	F	*Bulweria bulwerii*	Ilheu Cima (IC)	H10	Z. sp2	Z. sp2
Z227	*Z. sp.2*	F	*Bulweria bulwerii*	Ilheu Cima (IC)	H10	Z. sp2	Z. sp2
Z171	*Z. sp.2*	M	*Bulweria bulwerii*	Ilheu Grande (IG)	H11	Z. sp2	Z. sp2
Z228	*Z. sp.2*	F	*Bulweria bulwerii*	Ilheu Grande (IG)	H10	Z. sp2	Z. sp2
Z229	*Z. sp.2*	M	*Bulweria bulwerii*	Ilheu Grande (IG)	H10	Z. sp2	Z. sp2

Mite ID	Mite species	Mite sex	Host species	Locality	Haplotype	Species delimitation (TCS)	Species delimitation (GMYC)
Z230	*Z. sp.2*	F	*Bulweria bulwerii*	Ilheu Grande (IG)	H26	Z. sp2	Z. sp2
Z231	*Z. sp.2*	F	*Bulweria bulwerii*	Ilheu Grande (IG)	H10	Z. sp2	Z. sp2
Z177	*Z. oceanodromae*	M	*Hidrobates castro*	Raso (Rs)	H15	Z. oceanodromae A	Z. oceanodromae A
Z178	*Z. oceanodromae*	F	*Hidrobates castro*	Raso (Rs)	H16	Z. oceanodromae A	Z. oceanodromae A
Z179	*Z. oceanodromae*	M	*Hidrobates castro*	Raso (Rs)	H17	Z. oceanodromae A	Z. oceanodromae A
Z234	*Z. oceanodromae*	F	*Hidrobates castro*	Raso (Rs)	H29	Z. oceanodromae A	Z. oceanodromae A
Z235	*Z. oceanodromae*	F	*Hidrobates castro*	Raso (Rs)	H30	Z. oceanodromae A	Z. oceanodromae A
Z237	*Z. oceanodromae*	M	*Hidrobates castro*	Raso (Rs)	H29	Z. oceanodromae A	Z. oceanodromae A
Z238	*Z. oceanodromae*	M	*Hidrobates castro*	Raso (Rs)	H29	Z. oceanodromae A	Z. oceanodromae A
Z239	*Z. oceanodromae*	F	*Hidrobates castro*	Raso (Rs)	H18	Z. oceanodromae A	Z. oceanodromae A
Z242	*Z. oceanodromae*	M	*Hidrobates castro*	Raso (Rs)	H20	Z. oceanodromae A	Z. oceanodromae A
Z183	*Z. oceanodromae*	M	*Hidrobates castro*	Curral Velho (CV)	H15	Z. oceanodromae A	Z. oceanodromae A
Z184	*Z. oceanodromae*	F	*Hidrobates castro*	Curral Velho (CV)	H20	Z. oceanodromae A	Z. oceanodromae A
Z181	*Z. oceanodromae*	M	*Hidrobates castro*	Ilheu Grande (IG)	H18	Z. oceanodromae A	Z. oceanodromae A
Z182	*Z. oceanodromae*	M	*Hidrobates castro*	Ilheu Cima (IC)	H19	Z. oceanodromae B	Z. oceanodromae B
Z153	*Z. sp.3*	F	*Pterodroma feae*	Fogo (Fg)	H8	Z. sp3	Z. sp3
Z175	*Z. sp.3*	M	*Pterodroma feae*	Fogo (Fg)	H13	Z. sp3	Z. sp3
Z176	*Z. sp.3*	F	*Pterodroma feae*	Fogo (Fg)	H14	Z. sp3	Z. sp3
Z232	*Z. sp.3*	M	*Pterodroma feae*	Fogo (Fg)	H27	Z. sp3	Z. sp3
Z233	*Z. sp.3*	F	*Pterodroma feae*	Fogo (Fg)	H28	Z. sp3	Z. sp3
M42	*M. brevipes*	F	*Calonectris edwardsii*	Raso (Rs)	H1	M. brevipes	M. brevipes A
M43	*M. brevipes*	F	*Calonectris edwardsii*	Raso (Rs)	H2	M. brevipes	M. brevipes A
M44	*M. brevipes*	F	*Calonectris edwardsii*	Raso (Rs)	H3	M. brevipes	M. brevipes A
M45	*M. brevipes*	F	*Calonectris edwardsii*	Raso (Rs)	H1	M. brevipes	M. brevipes A
M97	*M. brevipes*	F	*Calonectris edwardsii*	Raso (Rs)	H11	M. brevipes	M. brevipes A
M46	*M. brevipes*	F	*Calonectris edwardsii*	Curral Velho (CV)	H3	M. brevipes	M. brevipes A
M47	*M. brevipes*	F	*Calonectris edwardsii*	Curral Velho (CV)	H4	M. brevipes	M. brevipes A
M89	*M. brevipes*	F	*Calonectris edwardsii*	Curral Velho (CV)	H9	M. brevipes	M. brevipes A
M90	*M. brevipes*	F	*Calonectris edwardsii*	Curral Velho (CV)	H3	M. brevipes	M. brevipes A
M91	*M. brevipes*	F	*Calonectris edwardsii*	Curral Velho (CV)	H10	M. brevipes	M. brevipes A
M53	*M. brevipes*	F	*Puffinus boydi*	Raso (Rs)	H5	M. brevipes	M. brevipes B
M120	*M. brevipes*	M	*Puffinus boydi*	Raso (Rs)	H12	M. brevipes	M. brevipes B
M173	*M. brevipes*	M	*Puffinus boydi*	Raso (Rs)	H17	M. brevipes	M. brevipes B
M174	*M. brevipes*	F	*Puffinus boydi*	Raso (Rs)	H17	M. brevipes	M. brevipes B
M175	*M. brevipes*	M	*Puffinus boydi*	Raso (Rs)	H17	M. brevipes	M. brevipes B
M121	*M. brevipes*	M	*Puffinus boydi*	Ilheu Cima (IC)	H12	M. brevipes	M. brevipes B
M176	*M. brevipes*	M	*Puffinus boydi*	Ilheu Cima (IC)	H17	M. brevipes	M. brevipes B
M177	*M. brevipes*	F	*Puffinus boydi*	Ilheu Cima (IC)	H18	M. brevipes	M. brevipes B

Mite ID	Mite species	Mite sex	Host species	Locality	Haplotype	Species delimitation (TCS)	Species delimitation (GMYC)
M178	*M. brevipes*	F	*Puffinus boydi*	Ilheu Cima (IC)	H17	M. brevipes	M. brevipes B
M179	*M. brevipes*	F	*Puffinus boydi*	Ilheu Cima (IC)	H19	M. brevipes	M. brevipes B
M55	*M. bulweriae*	F	*Bulweria bulwerii*	Raso (Rs)	H7	M. bulweriae	M. bulweriae
M123	*M. bulweriae*	M	*Bulweria bulwerii*	Raso (Rs)	H13	M. bulweriae	M. bulweriae
M181	*M. bulweriae*	F	*Bulweria bulwerii*	Raso (Rs)	H13	M. bulweriae	M. bulweriae
M182	*M. bulweriae*	F	*Bulweria bulwerii*	Raso (Rs)	H13	M. bulweriae	M. bulweriae
M183	*M. bulweriae*	F	*Bulweria bulwerii*	Raso (Rs)	H13	M. bulweriae	M. bulweriae
M128	*M. bulweriae*	F	*Bulweria bulwerii*	Ilheu Cima (IC)	H7	M. bulweriae	M. bulweriae
M180	*M. bulweriae*	F	*Bulweria bulwerii*	Ilheu Cima (IC)	H20	M. bulweriae	M. bulweriae
M125	*M. bulweriae*	M	*Bulweria bulwerii*	Ilheu Grande (IG)	H13	M. bulweriae	M. bulweriae
M54	*M. cymochoreae*	F	*Hidrobates castro*	Raso (Rs)	H6	M. cymochoreae	M. cymochoreae
M129	*M. cymochoreae*	F	*Hidrobates castro*	Raso (Rs)	H14	M. cymochoreae	M. cymochoreae
M184	*M. cymochoreae*	F	*Hidrobates castro*	Raso (Rs)	H6	M. cymochoreae	M. cymochoreae
M185	*M. cymochoreae*	F	*Hidrobates castro*	Raso (Rs)	H6	M. cymochoreae	M. cymochoreae
M186	*M. cymochoreae*	F	*Hidrobates castro*	Raso (Rs)	H6	M. cymochoreae	M. cymochoreae
M132	*M. cymochoreae*	M	*Hidrobates castro*	Curral Velho (CV)	H15	M. cymochoreae	M. cymochoreae
M133	*M. cymochoreae*	F	*Hidrobates castro*	Curral Velho (CV)	H16	M. cymochoreae	M. cymochoreae
M134	*M. cymochoreae*	M	*Hidrobates castro*	Ilheu Cima (IC)	H6	M. cymochoreae	M. cymochoreae
M56	*M. pterodromae*	F	*Pterodroma feae*	Fogo (Fg)	H8	M. pterodromae	M. pterodromae
B47	*B. puffini*	F	*Calonectris edwardsii*	Raso (Rs)	H5	B. puffini	B. puffini
B61	*B. puffini*	F	*Calonectris edwardsii*	Raso (Rs)	H8	B. puffini	B. puffini
B62	*B. puffini*	F	*Calonectris edwardsii*	Raso (Rs)	H8	B. puffini	B. puffini
B63	*B. puffini*	F	*Calonectris edwardsii*	Raso (Rs)	H3	B. puffini	B. puffini
B156	*B. puffini*	M	*Calonectris edwardsii*	Raso (Rs)	H7	B. puffini	B. puffini
B50	*B. puffini*	F	*Calonectris edwardsii*	Curral Velho (CV)	H6	B. puffini	B. puffini
B53	*B. puffini*	F	*Calonectris edwardsii*	Curral Velho (CV)	H6	B. puffini	B. puffini
B58	*B. puffini*	F	*Calonectris edwardsii*	Curral Velho (CV)	H3	B. puffini	B. puffini
B59	*B. puffini*	F	*Calonectris edwardsii*	Curral Velho (CV)	H6	B. puffini	B. puffini
B60	*B. puffini*	F	*Calonectris edwardsii*	Curral Velho (CV)	H7	B. puffini	B. puffini
B35	*B. puffini*	F	*Puffinus boydi*	Raso (Rs)	H3	B. puffini	B. puffini
B36	*B. puffini*	F	*Puffinus boydi*	Raso (Rs)	H4	B. puffini	B. puffini
B56	*B. puffini*	F	*Puffinus boydi*	Raso (Rs)	H3	B. puffini	B. puffini
B57	*B. puffini*	F	*Puffinus boydi*	Raso (Rs)	H3	B. puffini	B. puffini
B157	*B. puffini*	M	*Puffinus boydi*	Raso (Rs)	H15	B. puffini	B. puffini
B100	*B. puffini*	M	*Puffinus boydi*	Ilheu Cima (IC)	H3	B. puffini	B. puffini
B158	*B. puffini*	F	*Puffinus boydi*	Ilheu Cima (IC)	H3	B. puffini	B. puffini
B159	*B. puffini*	M	*Puffinus boydi*	Ilheu Cima (IC)	H3	B. puffini	B. puffini
B160	*B. puffini*	F	*Puffinus boydi*	Ilheu Cima (IC)	H6	B. puffini	B. puffini

Mite ID	Mite species	Mite sex	Host species	Locality	Haplotype	Species delimitation (TCS)	Species delimitation (GMYC)
B161	*B. puffini*	F	*Puffinus boydi*	Ilheu Cima (IC)	H3	B. puffini	B. puffini
B31	*B. sp.1*	F	*Bulweria bulwerii*	Raso (Rs)	H2	B. sp1	B. sp1
B102	*B. sp.1*	M	*Bulweria bulwerii*	Raso (Rs)	H9	B. sp1	B. sp1
B162	*B. sp.1*	F	*Bulweria bulwerii*	Raso (Rs)	H9	B. sp1	B. sp1
B163	*B. sp.1*	F	*Bulweria bulwerii*	Raso (Rs)	H16	B. sp1	B. sp1
B164	*B. sp.1*	M	*Bulweria bulwerii*	Raso (Rs)	H9	B. sp1	B. sp1
B107	*B. sp.1*	F	*Bulweria bulwerii*	Ilheu Cima (IC)	H9	B. sp1	B. sp1
B165	*B. sp.1*	F	*Bulweria bulwerii*	Ilheu Cima (IC)	H17	B. sp1	B. sp1
B166	*B. sp.1*	M	*Bulweria bulwerii*	Ilheu Cima (IC)	H18	B. sp1	B. sp1
B167	*B. sp.1*	F	*Bulweria bulwerii*	Ilheu Cima (IC)	H9	B. sp1	B. sp1
B168	*B. sp.1*	M	*Bulweria bulwerii*	Ilheu Cima (IC)	H9	B. sp1	B. sp1
B104	*B. sp.1*	M	*Bulweria bulwerii*	Ilheu Grande (IG)	H9	B. sp1	B. sp1
B169	*B. sp.1*	F	*Bulweria bulwerii*	Ilheu Grande (IG)	H17	B. sp1	B. sp1
B170	*B. sp.1*	M	*Bulweria bulwerii*	Ilheu Grande (IG)	H19	B. sp1	B. sp1
B171	*B. sp.1*	F	*Bulweria bulwerii*	Ilheu Grande (IG)	H9	B. sp1	B. sp1
B172	*B. sp.1*	F	*Bulweria bulwerii*	Ilheu Grande (IG)	H9	B. sp1	B. sp1
B173	*B. sp.2*	M	*Bulweria bulwerii*	Raso (Rs)	H20	B. sp2	B. sp2
B116	*B. sp.2*	M	*Bulweria bulwerii*	Ilheu Cima (IC)	H12	B. sp2	B. sp2
B174	*B. sp.3*	M	*Bulweria bulwerii*	Ilheu Cima (IC)	H21	B. sp3	B. sp3
B175	*B. sp.3*	M	*Bulweria bulwerii*	Ilheu Cima (IC)	H22	B. sp3	B. sp3
B 193	*B. sp.4*	M	*Calonectris edwardsii*	Raso (Rs)	H28	B. sp4	B. sp4
B194	*B. sp.5*	M	*Puffinus boydi*	Raso (Rs)	H29	B. sp5	B. sp5
B30	*B. decapus*	F	*Hidrobates castro*	Raso (Rs)	H1	B. decapus	B. decapus
B110	*B. decapus*	M	*Hidrobates castro*	Raso (Rs)	H1	B. decapus	B. decapus
B111	*B. decapus*	F	*Hidrobates castro*	Raso (Rs)	H11	B. decapus	B. decapus
B112	*B. decapus*	M	*Hidrobates castro*	Raso (Rs)	H1	B. decapus	B. decapus
B177	*B. decapus*	M	*Hidrobates castro*	Raso (Rs)	H23	B. decapus	B. decapus
B178	*B. decapus*	F	*Hidrobates castro*	Raso (Rs)	H1	B. decapus	B. decapus
B179	*B. decapus*	F	*Hidrobates castro*	Raso (Rs)	H1	B. decapus	B. decapus
B180	*B. decapus*	F	*Hidrobates castro*	Raso (Rs)	H1	B. decapus	B. decapus
B181	*B. decapus*	M	*Hidrobates castro*	Raso (Rs)	H24	B. decapus	B. decapus
B185	*B. decapus*	M	*Hidrobates castro*	Raso (Rs)	H1	B. decapus	B. decapus
B186	*B. decapus*	M	*Hidrobates castro*	Raso (Rs)	H25	B. decapus	B. decapus
B114	*B. decapus*	M	*Hidrobates castro*	Curral Velho (CV)	H1	B. decapus	B. decapus
B182	*B. decapus*	F	*Hidrobates castro*	Curral Velho (CV)	H1	B. decapus	B. decapus
B183	*B. decapus*	M	*Hidrobates castro*	Curral Velho (CV)	H23	B. decapus	B. decapus
B184	*B. decapus*	F	*Hidrobates castro*	Curral Velho (CV)	H1	B. decapus	B. decapus
B122	*B. lanceolatus*	M	*Hidrobates castro*	Raso (Rs)	H13	B. lanceolatus	B. lanceolatus

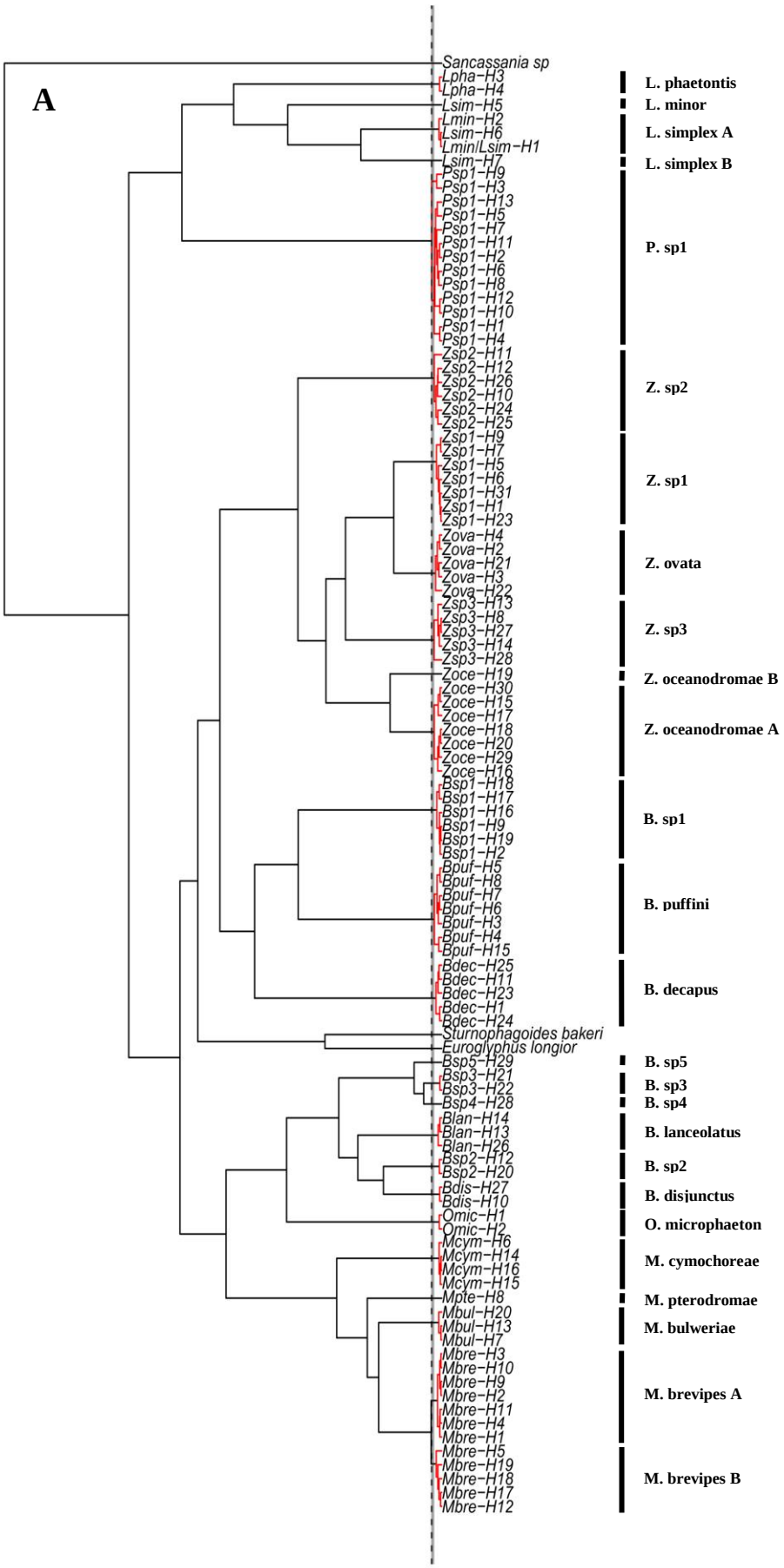
Mite ID	Mite species	Mite sex	Host species	Locality	Haplotype	Species delimitation (TCS)	Species delimitation (GMYC)
B187	*B. lanceolatus*	M	*Hidrobates castro*	Raso (Rs)	H13	B. lanceolatus	B. lanceolatus
B188	*B. lanceolatus*	M	*Hidrobates castro*	Raso (Rs)	H26	B. lanceolatus	B. lanceolatus
B119	*B. lanceolatus*	M	*Hidrobates castro*	Curral Velho (CV)	H13	B. lanceolatus	B. lanceolatus
B120	*B. lanceolatus*	F	*Hidrobates castro*	Curral Velho (CV)	H13	B. lanceolatus	B. lanceolatus
B121	*B. lanceolatus*	F	*Hidrobates castro*	Ilheu Cima (IC)	H14	B. lanceolatus	B. lanceolatus
B109	*B. disjunctus*	F	*Pterodroma feae*	Fogo (Fg)	H10	B. disjunctus	B. disjunctus
B189	*B. disjunctus*	F	*Pterodroma feae*	Fogo (Fg)	H27	B. disjunctus	B. disjunctus
B190	*B. disjunctus*	M	*Pterodroma feae*	Fogo (Fg)	H27	B. disjunctus	B. disjunctus
B192	*B. disjunctus*	F	*Pterodroma feae*	Fogo (Fg)	H27	B. disjunctus	B. disjunctus
P12	*P. sp.1*	F	*Calonectris edwardsii*	Raso (Rs)	H1	P. sp1	P. sp1
P27	*P. sp.1*	F	*Calonectris edwardsii*	Raso (Rs)	H6	P. sp1	P. sp1
P48	*P. sp.1*	M	*Calonectris edwardsii*	Raso (Rs)	H9	P. sp1	P. sp1
P57	*P. sp.1*	M	*Calonectris edwardsii*	Raso (Rs)	H2	P. sp1	P. sp1
P58	*P. sp.1*	F	*Calonectris edwardsii*	Raso (Rs)	H2	P. sp1	P. sp1
P13	*P. sp.1*	F	*Calonectris edwardsii*	Curral Velho (CV)	H2	P. sp1	P. sp1
P14	*P. sp.1*	F	*Calonectris edwardsii*	Curral Velho (CV)	H3	P. sp1	P. sp1
P15	*P. sp.1*	F	*Calonectris edwardsii*	Curral Velho (CV)	H4	P. sp1	P. sp1
P16	*P. sp.1*	F	*Calonectris edwardsii*	Curral Velho (CV)	H5	P. sp1	P. sp1
P28	*P. sp.1*	F	*Calonectris edwardsii*	Curral Velho (CV)	H7	P. sp1	P. sp1
P29	*P. sp.1*	F	*Calonectris edwardsii*	Curral Velho (CV)	H2	P. sp1	P. sp1
P30	*P. sp.1*	F	*Calonectris edwardsii*	Curral Velho (CV)	H8	P. sp1	P. sp1
P54	*P. sp.1*	F	*Puffinus boydi*	Raso (Rs)	H10	P. sp1	P. sp1
P60	*P. sp.1*	M	*Puffinus boydi*	Raso (Rs)	H2	P. sp1	P. sp1
P61	*P. sp.1*	M	*Puffinus boydi*	Raso (Rs)	H11	P. sp1	P. sp1
P62	*P. sp.1*	F	*Puffinus boydi*	Raso (Rs)	H2	P. sp1	P. sp1
P52	*P. sp.1*	F	*Puffinus boydi*	Ilheu Cima (IC)	H2	P. sp1	P. sp1
P63	*P. sp.1*	M	*Puffinus boydi*	Ilheu Cima (IC)	H12	P. sp1	P. sp1
P64	*P. sp.1*	F	*Puffinus boydi*	Ilheu Cima (IC)	H13	P. sp1	P. sp1
L1	*L. phaetontis*	F	*Phaeton aethereus*	Raso (Rs)	H3	L. phaetontis	L. phaetontis
L8	*L. phaetontis*	F	*Phaeton aethereus*	Raso (Rs)	H4	L. phaetontis	L. phaetontis
L10	*L. phaetontis*	F	*Phaeton aethereus*	Raso (Rs)	H4	L. phaetontis	L. phaetontis
L12	*L. phaetontis*	M	*Phaeton aethereus*	Raso (Rs)	H4	L. phaetontis	L. phaetontis
L19	*L. simplex*	F	*Phaeton aethereus*	Raso (Rs)	H1	L. simplex A	L. simplex A
L21	*L. simplex*	F	*Phaeton aethereus*	Raso (Rs)	H1	L. simplex A	L. simplex A
L24	*L. simplex*	F	*Phaeton aethereus*	Raso (Rs)	H2	L. simplex A	L. simplex A
L15	*L. simplex*	M	*Phaeton aethereus*	Raso (Rs)	H6	L. simplex A	L. simplex A
L17	*L. simplex*	M	*Phaeton aethereus*	Raso (Rs)	H1	L. simplex A	L. simplex A
L18	*L. simplex*	M	*Phaeton aethereus*	Raso (Rs)	H1	L. simplex A	L. simplex A

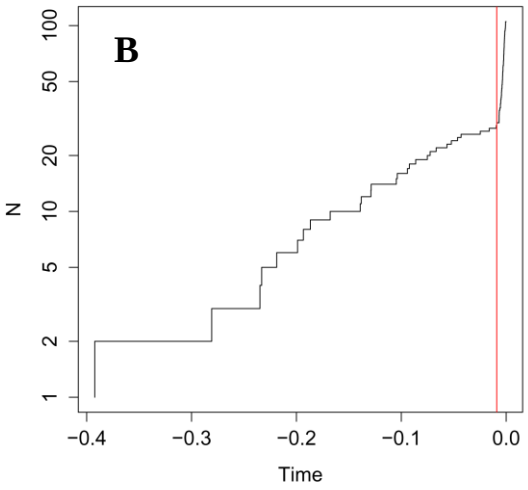
Mite ID	Mite species	Mite sex	Host species	Locality	Haplotype	Species delimitation (TCS)	Species delimitation (GMYC)
L28	*L. simplex*	M	*Phaeton aethereus*	Raso (Rs)	H1	L. simplex A	L. simplex A
L16	*L. simplex*	M	*Phaeton aethereus*	Raso (Rs)	H7	L. simplex B	L. simplex B
L13	*L. minor*	F	*Phaeton aethereus*	Raso (Rs)	H5	L. minor	L. minor
O1	*O. microphaeton*	F	*Phaeton aethereus*	Raso (Rs)	H1	O. microphaeton	O. microphaeton
O2	*O. microphaeton*	F	*Phaeton aethereus*	Raso (Rs)	H1	O. microphaeton	O. microphaeton
O3	*O. microphaeton*	F	*Phaeton aethereus*	Raso (Rs)	H1	O. microphaeton	O. microphaeton
O4	*O. microphaeton*	F	*Phaeton aethereus*	Raso (Rs)	H1	O. microphaeton	O. microphaeton
O5	*O. microphaeton*	F	*Phaeton aethereus*	Raso (Rs)	H2	O. microphaeton	O. microphaeton

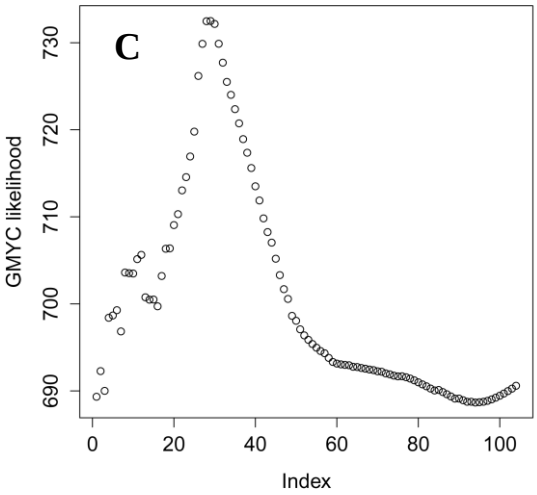
Table S2. Feather mite morphological diversity found on the six seabird species breeding in Cape Verde Islands. The feather mite species shared by different seabird species are shown in bold.

Feather mite species	Host species	Locality
Zachvatkinia ovata	*C. edwardsii*	Raso, Curral Velho
Z. sp.1	*P. boydi*	Raso, Ilhéu Cima
Z. sp.2	*B. bulwerii*	Raso, Ilhéu Cima, Ilhéu Grande
Z. oceanodromae	*H. castro*	Raso, Curral Velho, Ilhéu Cima, Ilhéu Grande
Z. sp.3	*P. feae*	Fogo
Rhinozachvatkinia calonectris	*C. edwardsii*	Raso, Curral Velho
Promegninia calonectris	*C. edwardsii*	Raso
P. bulweriae	*B. bulwerii*	Raso, Ilhéu Cima
Microspalax brevipes	***C. edwardsii***	**Raso, Curral Velho**
	P. boydi	**Raso, Ilhéu Cima**
M. bulweriae	*B. bulwerii*	Raso, Ilhéu Cima, Ilhéu Grande
M. cymochoreae	*H. castro*	Raso, Curral Velho, Ilhéu Cima
M. pterodromae	*P. feae*	Fogo
Brephosceles puffini	***C. edwardsii***	**Raso, Curral Velho**
	P. boydi	**Raso, Ilhéu Cima**
B. sp.1	*B. bulwerii*	Raso, Ilhéu Cima, Ilhéu Grande
B. sp.2	*B. bulwerii*	Raso, Ilhéu Cima
B. sp.3	*B. bulwerii*	Ilhéu Cima
B. sp.4	*C. edwardsii*	Raso
B. sp.5	*P. boydi*	Raso
B. decapus	*H. castro*	Raso, Curral Velho
B. lanceolatus	*H. castro*	Raso, Curral Velho, Ilhéu Cima
B. disjunctus	*P. feae*	Fogo
Plicatalloptes sp.1	***C. edwardsii***	**Raso, Curral Velho**
	P. boydi	**Raso, Ilhéu Cima**
Opetiopoda bulweriae	*B. bulwerii*	Raso
Ingrassia calonectris	*C. edwardsii*	Raso, Curral Velho
I. dubinini	*P. boydi*	Raso, Ilhéu Cima
I. micronota	*B. bulwerii*	Raso, Ilhéu Cima, Ilhéu Grande
I. oceanodromae	*H. castro*	Raso, Curral Velho, Ilhéu Cima
I. aequinoctialis	*P. aethereus*	Raso
Laminalloptes phaetontis	*P. aethereus*	Raso
L. minor	*P. aethereus*	Raso
L. simplex	*P. aethereus*	Raso
Onychalloptes microphaeton	*P. aethereus*	Raso

Figure S1. Ultrametric gene tree (A) based on concatenated mitochondrial data from six feather mite genera from the Cape Verde Archipelago. Species entities obtained by the GMYC algorithm are labeled with abbreviations following the species morphological identifications as in Table S1. The dotted vertical line shows the maximum likelihood transition point from a Yule to a coalescent branching process ("between inter and intraspecific branching" or "of the switch in branching rates") and the grey shading indicates the confidence interval of 2logL units of the maximum likelihood. The graphs below represent the lineage through time plot (B) and the single-threshold likelihood solution (C) to the GMYC model.


A
Sancassania sp
Lpha−H3
Lpha−H4
Lsim−H5
Lmin−H2
Lsim−H6
Lmin/Lsim−H1
Lsim−H7
Psp1−H9
Psp1−H3
Psp1−H13
Psp1−H5
Psp1−H7
Psp1−H11
Psp1−H2
Psp1−H6
Psp1−H8
Psp1−H12
Psp1−H10
Psp1−H1
Psp1−H4
Zsp2−H11
Zsp2−H12
Zsp2−H26
Zsp2−H10
Zsp2−H24
Zsp2−H25
Zsp1−H9
Zsp1−H7
Zsp1−H5
Zsp1−H6
Zsp1−H31
Zsp1−H1
Zsp1−H23
Zova−H4
Zova−H2
Zova−H21
Zova−H3
Zova−H22
Zsp3−H13
Zsp3−H8
Zsp3−H27
Zsp3−H14
Zsp3−H28
Zoce−H19
Zoce−H30
Zoce−H15
Zoce−H17
Zoce−H18
Zoce−H20
Zoce−H29
Zoce−H16
Bsp1−H18
Bsp1−H17
Bsp1−H16
Bsp1−H9
Bsp1−H19
Bsp1−H2
Bpuf−H5
Bpuf−H8
Bpuf−H7
Bpuf−H6
Bpuf−H3
Bpuf−H4
Bpuf−H15
Bdec−H25
Bdec−H11
Bdec−H23
Bdec−H1
Bdec−H24
Sturnophagoides bakeri
Euroglyphus longior
Bsp5−H29
Bsp3−H21
Bsp3−H22
Bsp4−H28
Blan−H14
Blan−H13
Blan−H26
Bsp2−H12
Bsp2−H20
Bdis−H27
Bdis−H10
Omic−H1
Omic−H2
Mcym−H6
Mcym−H14
Mcym−H16
Mcym−H15
Mpte−H8
Mbul−H20
Mbul−H13
Mbul−H7
Mbre−H3
Mbre−H10
Mbre−H9
Mbre−H2
Mbre−H11
Mbre−H4
Mbre−H1
Mbre−H5
Mbre−H19
Mbre−H18
Mbre−H17
Mbre−H12
L. phaetontis
L. minor
L. simplex A
L. simplex B
P. sp1
Z. sp2
Z. sp1
Z. ovata
Z. sp3
Z. oceanodromae B
Z. oceanodromae A
B. sp1
B. puffini
B. decapus
B. sp5
B. sp3
B. sp4
B. lanceolatus
B. sp2
B. disjunctus
O. microphaeton
M. cymochoreae
M. pterodromae
M. bulweriae
M. brevipes A
M. brevipes B


B
N
100
50
20
10
5
2
1
−0.4
−0.3
−0.2
−0.1
0.0
Time


C
GMYC likelihood
730
720
710
700
690
0
20
40
60
80
100
Index

2.2 CONTRASTING PATTERNS OF DIVERSITY AND GENETIC STRUCTURE IN ECTOFAUNAL COMMUNITIES OF LONG-LIVED SEABIRDS

Laura M. Stefan, Elena Gómez-Díaz, Jacob González-Solís, Karen D. McCoy

In preparation

PATRONES CONTRASTANTES DE DIVERSIDAD Y ESTRUCTURA GENÉTICA EN LAS COMUNIDADES DE ÁCAROS DE LAS AVES MARINAS DE VIDA LARGA

RESUMEN

La distribución espacial y las características de vida de los huéspedes son consideradas factores esenciales que determinan la estructura poblacional y las tasas de diversificación de sus parásitos. Sin embargo, los estudios de los ectoparásitos de las aves sin capacidad de dispersión independiente han revelado grados reducidos de especificidad de huésped y tasas altas de dispersión que contrastan con las expectativas teoréticas. En este estudio, hemos comparado la diversidad morfológica y genética de los ácaros de las plumas que habitan tres especies muy cercanas de pardelas del genero *Calonectris* para inferir si la transmisión de los ácaros se puede producir durante las interacciones transitorias entre hospedadores y examinar los factores que pueden condicionar este intercambio. Sabiendo que los ácaros de las plumas se encuentran entre los ectosimbiontes más diversos y abundantes de las aves y considerando que se cree que evolucionan en asociación estrecha con sus huéspedes, esperamos encontrar comunidades altamente divergentes en diferentes especies de huéspedes y una fuerte estructura de la población entre las distintas localidades geográficas. Nuestros resultados apoyan solo parcialmente estas predicciones. Las tres especies de pardelas albergaron una rica fauna de ácaros compuesta por nueve especies morfológicamente diferentes, de los cuales cinco (*Microspalax brevipes*, *Zachvatkinia ovata*, *Brephosceles puffini*, *B. sp.1*, *Plicatalloptes* sp.) fueron compartidas por los tres huéspedes. La diversidad molecular de dos genes mitocondriales se correlacionó bien con las descripciones morfológicas, pero revelaron la presencia de cuatro linajes crípticos adicionales dentro de los géneros *Brephosceles* y *Plicatalloptes*. Los análisis genéticos de la población para cada especie de ácaros revelaron patrones variables de estructura que se correlacionaron bien con el uso de microhábitat por el ácaro; las especies que habitan en las plumas de vuelo (*Microspalax brevipes* and *Zachvatkinia ovata*) mostraron una baja diversidad genética y alto flujo génico entre los huéspedes y localidades, mientras que las especies que viven en microhábitats de las plumas más protegidos (*Brephosceles puffini*, *Plicatalloptes* sp.) presentaron el revés. Nuestros resultados apoyan la hipótesis de que las breves interacciones inter- e intra-específicas entre huéspedes son de importancia clave para el intercambio y la diseminación de la ectofauna aviar, pero que la importancia de este mecanismo y sus implicaciones para la evolución de la diversidad de los parásitos está condicionada por las características de historia natural específica para cada especies.

CONTRASTING PATTERNS OF DIVERSITY AND GENETIC STRUCTURE IN ECTOFAUNAL COMMUNITIES OF LONG-LIVED SEABIRDS

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ABSTRACT

The spatial distribution and life history traits of hosts are considered to be essential factors determining the population structure and diversification rates of their parasites. However, studies of avian ectoparasites with no independent dispersal abilities have sometimes revealed surprisingly low degrees of host specificity and high dispersal rates that contrast theoretical expectations. Here, we compared morphological and genetic diversity of feather mites inhabiting three closely-related species of *Calonectris* shearwaters to infer whether feather mite transmission may occur during transient interactions among host individuals and examine the factors that may condition this exchange. Knowing that feather mites are among the most diverse and abundant avian ectosymbionts and are thought to evolve in close association with their hosts, we expected to find highly divergent communities on different host species and strong population structure among distinct geographic locations. Our findings only partially support these predictions. The three shearwater species were found to harbour a rich mite fauna composed of nine morphologicallydistinguishable species, of which five (*Microspalax brevipes*, *Zachvatkinia ovata*, *Brephosceles puffini*, *B. sp.1*, *Plicatalloptes* sp.) were shared by the three hosts. Molecular diversity at two mitochondrial genes correlated well with morphological descriptions, but revealed the presence of four additional cryptic lineages within the mite genera *Brephosceles* and *Plicatalloptes*. Population genetic analyses of each species revealed variable patterns of structure that correlated well with mite microhabitat use; species inhabiting flight feathers (*Microspalax brevipes* and *Zachvatkinia ovata)* exhibited low genetic diversity and high gene flow among hosts and localities, whereasthose living in more protected feather microhabitats (*Brephosceles puffini*, *Plicatalloptes* sp.) showed the reverse. Our results therefore support the hypothesis that brief inter- and intra-specific interactions among hosts are of key importance for the exchange and dissemination of avian ectofauna, but that the importance of this mechanism and its implications for the evolution of parasite diversity is conditioned by species-specific life history traits.

Keywords: dispersal, community richness, population genetic structure, colonial seabirds, Astigmata

INTRODUCTION

Hosts represent a variable and changing environment to which parasitic organisms must continuously adapt. Transmission mode, dispersal ability, mode of reproduction, life cycle complexity and host specificity are considered to be key parasite features that shape the outcome of host-parasite interactions and, ultimately, patterns of genetic diversity (Criscione et al. 2005). For obligate parasites with limited dispersal ability, the spatial distribution and social system of their hosts can be essential factors determining parasite population structure (Whiteman and Parker 2005, Criscione 2008, van Schaik et al. 2014). Host movements represent the principal means for these parasites to disperse among remote locations and diverse host types. Information on the genetic structure of parasites can provide an indication of the types of host movements that are involved and their relative importancein driving parasite diversity. The link between different types of host movements and parasite population structure has now been addressed for many parasite taxa (Mazé-Guilmo et al. 2016, Boulinier et al. 2016), including blood parasites (Witsenburg et al. 2015), trematodes (Criscione and Blouin 2004), seabird ticks (McCoy et al. 2005) and bat mites (Bruyndonckx et al. 2010), but results among different parasite groups exploiting the same host have lead to contrasting conclusions (Gómez-Díaz et al. 2007).

Seabirds and their ectofauna (parasites and symbionts) represent particularly good models to investigate mechanisms of parasite structure and diversification. Seabirds are pelagic species, widely distributed and breeding in dense colonies on isolated land masses. They harbour a rich ectofaunal community, including ticks, fleas, lice and mites (Clayton et al. 1992, Clayton and Price 1999, Adams et al. 2005, Proctor 2003, Dietrich et al. 2011). Most seabird species show strong interannual fidelity and natal philopatry to their breeding sites, features that can limit parasite dispersal in time and space and favor host specialization (Brooke 2004, McCoy et al. 2013). Seabirds from different breeding colonies tend to have particular, and often isolated, foraging and wintering areas, limiting parasite exchanges among different populations (González-Solís et al. 2007, Navarro et al. 2009). However, they also can breed in interspecific colonies, where phylogenetically diverse species reproduce in sympatry, which may promote parasite exchange and host switching (Gómez-Díaz et al. 2012, McCoy et al. 2016).

Among seabird ectofauna, feather mites (Astigmata: Analgoidea and Pterolichoidea) show the greatest species richness. They are obligate ectosymbionts highly specialized and adapted to inhabit well-defined host microhabitats including flight feathers, soft down feathers, skin and even feather quills (Gaud and Atyeo 1996, Dabert and Mironov 1999, Proctor 2003). Given the close association of feather mites with their seabird hosts, transmission of these species is expected to be limited to vertical transfers from parents to fledglings or horizontal transfers between adults during courtship and mating (Proctor 2003). These features, together with high diversity (more than 2 500 species described) and strong host specificity, make feather mites good candidates for host-parasite co-evolutionary studies (Dabert 2004, Proctor and Owens 2000). Indeed, morphological data has indicated that almost all extant avian orders have their own specific feather mite fauna and feather mite families are considered to be restricted to a single host genus or species (Gaud and Atyeo 1996, Dabert and Mironov 1999). As a consequence, these ectosymbionts often display congruent phylogenies with their hosts (Dabert and Mironov 1999, Dabert et al. 2001, Ehrnsberger et al. 2001, Mironov and Dabert 1999, Mironov and Wauthy 2006, Mironov 2005, 2007, 2009). Based on these macroevolutionary patterns, we expect mites should also show important community and population level structure among isolated host populations within host genera. However, no study has yet explored the degree of congruence in the population structure among different species of feather mites infesting the same hosts. Such studies can add important insight into the host and parasite traits driving genetic structure and, ultimately, speciation (Clayton et al. 2004).

In the present study, we focus on thefeather mite community of the Cory´s shearwater species complex, which includes three closely-related species with largely peripatric breeding distributions: Scopoli´s shearwater (*Calonectris diomedea*), Cory´s shearwater (*Calonectris borealis*) and Cape Verde shearwater (*Calonectris edwardsii*). Previous work investigated genetic structure in other ectoparasite taxa parasitizing these hosts. In

particular, Gómez-Díaz et al. (2007) compared the population structure of three louse species (*Halipeurus abnormis*, *Austromenopon echinatum* and *Saemundssonia peusi*) and one flea species (*Xenopsylla gratiosa)*. In direct contrast to general predictions, they found that the lice species were genetically undifferentiated among the three *Calonectris* taxa, whereas the more mobile flea species displayed significant levels of host-associated and population differentiation. Suggested hypotheses to explain these results were higher at-sea dispersal rates of lice compared to fleasand/or higher host specificity in fleas. As feather mites and lice have similar life history traits with limited dispersal, we could expect similar patterns of structure and genetic differentiation in the feather mites, if transient at sea interactions of hosts represent important periods of parasite exchange. We tested this prediction by: 1) evaluatingthe morphologicaland genetic diversity of feather mites in different populations of each of the three host species; 2) determining the genetic structure of each mite species with respect to host species and geographic location, and 3) linking mite diversity and structure with microhabitat use on the host, and thus dispersal propensity.

MATERIAL AND METHODS

STUDY SPECIES AND FEATHER MITE SAMPLING

The members of the Cory´s shearwater complex breed on islands distributed across the Mediterranean Sea and the northeastern Atlantic Ocean. Although still controversal, Sangster et al. (2012) recommended treating this complex as three full species: Scopoli´s shearwater, *Calonectris diomedea*, breeding mainly from the Iberian coast to the Adriatic and Aegean Seas, Cory´s shearwater, *Calonectris borealis*, breeding mainly in the northeast Atlantic from the Canary to the Azores Archipelagos, and Cape Verde shearwater, *Calonectris edwardsii*, breeding on the Cape Verde Archipelago. Recently, one Mediterranean population belonging to the Atlantic Cory´s shearwater was also discovered on Terreros Island (Almeria) (Gómez-Díaz et al. 2006). Most populations of Scopoli´s and Cory´s shearwaters exploit four main wintering areas: eastern South Atlantic associated with the Benguela Current, the western Indian Ocean associated with the Agulhas Currents, western South Atlantic associated with the Brazilian Current, and northeast tropical Atlantic associated with the Canary Current (González-Solís et al. 2007). Although breeding populations clearly differ in their preferences amongst these wintering grounds, certain degree of mixing among different populations has been observed. In contrast, the main wintering area for the Cape Verde shearwater is the Brasil and Falklands/Malvinas confluence in front of the Uruguay coast (González-Solís et al. 2009). Furthermore, some cases of hybridization between Scopoli´s and Cory´s shearwaters have also been reported in Chafarinas and Columbretes Islands (Mediterranean Sea) (Martinez-Abrain et al. 2002, Navarro et al. 2009). The three *Calonectris* shearwater species are known to harbor a rich feather mite community, including at least six described species: *Microspalax brevipes*, *Microspalax ardennae* (Alloptidae), *Zachvatkinia ovata*, *Rhinozachvatkinia calonectris* (Avenzoariidae), *Promegninia calonectris* and *Ingrassia calonectris* (Xolalgidae) (Atyeo and Gaud 1991, Mironov 1989a, Mironov et al. 2015, Stefan et al. 2013, 2014).

From 2003 to 2011, we collected feather mites from adult birds on seven breeding colonies of Scopoli´s shearwater across the Mediterranean, 12 breeding colonies of Cory´s shearwater within the Atlantic region and at one Mediterranean location (Terreros Is.), and two breeding colonies of the Cape Verde shearwater from the Cape Verde islands (Figure 1). Bird captures and mite sampling were performed in accordance with good animal practices as defined by the current European legislation and under permission from the corresponding governmental authorities of Spain, Portugal, France, Greece, Tunisia and Cape Verde. Feather mites were collected using the dust-ruffling method for Cape Verde shearwaters (Walther and Clayton 1997) or by direct sampling of feather barbs for the other two shearwater species. Collected material was preserved in absolute ethanol at -20^{o}C for subsequent morphological and molecular analyses. In total, mites were collected from 345 individual host birds across the different localities (Table 1).

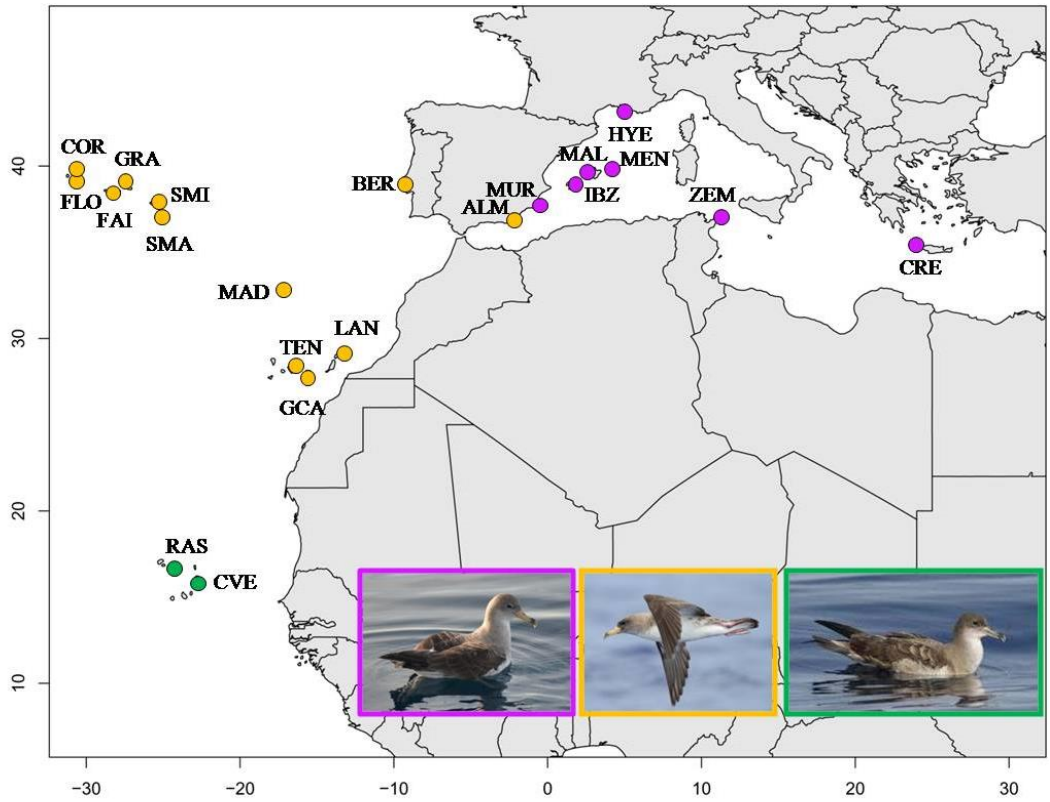

Figure 1. Breeding colonies of Scopoli´s (purple circles), Cory´s (orange circles) and Cape Verde shearwaters (green circles) sampled across their geographic distribution. Complete information on colony abbreviations are given in Table 1.

MORPHOLOGICAL IDENTIFICATIONS

For morphological identifications, mites from each seabird host were sorted into groups by general morphology and representative samples (at least 10 specimens per group when possible) were cleared in lactic acid for 24h and mounted on microscope slides in PVA medium (BioQuip Products, Rancho Dominguez, California). The slides were cured on slide warmers at 40^{o}C for 4 days and then examined using a Leica DM 5000B light microscope with differential interference contrast (DIC) illumination. Mites were identified in collaboration with Sergey Mironov using the standards for bonnetelline mites (Mironov 1989a, b), xolalgid mites (Dabert and Ehrnsberger 1991, Mironov and Palma 2006) and alloptid mites (Atyeo and Gaud 1991, Mironov 1996, Peterson 1971, Peterson and Atyeo 1968). Feather mite specimens of each species were deposited in the Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia (ZISP).

MOLECULAR METHODS

After the initial morphological screening, specimens were selected from the remaining samples for molecular analysis.We analyzed at least five individuals of each presumed mite species per host population taken from five different host birds when possible. A total of 295 specimens belonging to five presumed mite species, *Zachvatkinia ovata, Microspalax brevipes, Brephosceles puffini, Brephosceles sp.1* and *Plicatalloptes sp.1* (a new genus and species for these hosts, see results), were included in the molecular analysis: 84 specimens of *Z. ovata,* 89 of *M. brevipes*, 61 of *B. puffini*, 11 of *B. sp.1* and 50 of *P. sp.1*. Three mite genera (*Rhinozachvatkinia, Promegninia* and *Ingrassia*) were also identified in our samples, but were not included in the molecular analysis due to the small number of specimens found (see results). We also limited the analyses to those species sampled on all three host species. Therefore, specimens identified as *M. ardennae* were not included in the analyses because it was only found on Cory´s shearwaters (see results). All mites subjected to molecular analyses were mounted after DNA extraction and kept as reference vouchers for morphological examination.

Table 1. Sampling details of feather mites. For each locality, we indicate the number of birds sampled for feather mites. All sampled birds were infected with feather mites, except 5 individuals of Cape Verde shearwater *Calonectris edwardsii* breeding in Raso. The following abbreviations were used for the host species: CD – *Calonectris diomedea* (Scopoli´s shearwater), CB – *Calonectris borealis* (Cory´s shearwater) and CE – *Calonectris edwardsii* (Cape Verde shearwater).

Locality	Code	Region	Lat/Long	Host species	Number of sampled birds
Murcia (Spain)	MUR	Mediterranean	37°34'59"N/00°58'59"W	CD	9
Ibiza (Balearic Is.)	IBZ	Mediterranean	38°57'42"N/01°11'53"E	CD	21
Mallorca (Balearic Is.)	MAL	Mediterranean	39°39'58"N/02°34'53"E	CD	9
Menorca (Balearic Is.)	MEN	Mediterranean	39°48'07"N/04°17'16"E	CD	7
Hyeres (France)	HYE	Mediterranean	43°00'32"N/06°12'38"E	CD	4
Crete (Greece)	CRE	Mediterranean	35°36'38"N/23°34'49"E	CD	5
Zembra (Tunisia)	ZEM	Mediterranean	37°07'33"N/10°48'10"E	CD	15
Almeria (Spain)	ALM	Mediterranean	37°20'56"N/01°39'02"W	CB	12
Madeira (Portugal)	MAD	NE Atlantic	32°20'40"N/16°29'08"W	CB	34
Berlengas (Portugal)	BER	NE Atlantic	39°24'32"N/09°29'38"W	CB	16
Gran Canaria (Canary Is.)	GCA	NE Atlantic	27°50'40"N/15°47'19"W	CB	30
Lanzarote (Canary Is.)	LAN	NE Atlantic	29°17'29"N/13°31'57"W	CB	12
Tenerife (Canary Is.)	TEN	NE Atlantic	28°26'59"N/16°13'59"W	CB	8
Corvo (Azores Is.)	COR	NE Atlantic	39°40'28"N/31°06'21"W	CB	15
Flores (Azores Is.)	FLO	NE Atlantic	39°22'29"N/31°11'50"W	CB	14
Faial (Azores Is.)	FAI	NE Atlantic	38°31'27"N/28°44'48"W	CB	12
Graciosa (Azores Is.)	GRA	NE Atlantic	39°03'20"N/27°57'17"W	CB	23
Sao Miguel (Azores Is.)	SMI	NE Atlantic	37°43'02"N/25°25'59"W	CB	5
Santa Maria (Azores Is.)	SMA	NE Atlantic	36°56'31"N/25°10'17"W	CB	29
Raso (Cape Verde Is.)	RAS	NE Atlantic	16°36'36"N/24°36'00"W	CE	44
Curral Velho (Cape Verde Is.)	CVE	NE Atlantic	15°58'10"N/22°47'22"W	CE	20

Total genomic DNA was extracted from individual specimens using the DNeasy Tissue Kit (Qiagen, Valencia, CA, USA) and the nondestructive method described by Dabert et al. (2008). This method allows one to maintain the feather mite exoskeleton intact for subsequent morphological identification. Partial sequences of two mitochondrial genes: the ribosomal 12S rRNA (12S) and the ribosomal 16S rRNA (16S) were amplified for each feather mite using the following primers: SR-J-14199 (5'-TACTATGTTACGACTTAT-3') and SR-N-14594 (5'-AAACTAGGATTAGATACCC-3') for 12S gene (Kambhampati and Smith 1995) and 16SA2 (5'-TTTAATTGGTTACTTGTATGAATG-3') and 16C2 (5'-CGCTGTTATCCCTAGAGTAT-3') for 16S gene (Dabert et al. 2001). Polymerase chain reactions (PCRs) were carried out in a total volume of 25 µl containing 2.5 µl 10x reaction buffer with 15mM $MgCl_2$ (Roche Diagnostics), 2 mM $MgCl_2$, 0.2mM of each dNTP, 0.4 µM of each primer, 1.25 U *Taq* DNA polymerase (Roche Diagnostics) and 2 µl of DNA template. Amplification conditions for the 12S rRNA gene consisted of an initial step of 2 min at 94°C, followed by 10 cycles of denaturation at 94°C for 30 sec, annealing at 40°C for 30 sec, and extension at 68°C for 1 min, and 35 cycles of denaturation at 94°C for 30 sec, annealing at 43°C for 30 sec, and extension at 68°C for 1 min, with a final step of 5 min at 72°C. For the 16S rRNA gene, the PCR conditions followed Black and Piesman (1994). Amplification products were separated by electrophoresis on 2% agarose gel and visualized under UV light. Samples containing visible bands were sent for sequencing to Beckman Coulter Genomics (France; GenBank Accession nos. XXXX - XXXX).

GENETIC ANALYSES

Only mite specimens with complete sequence information for the two mitochondrial genes were included in the analyses. DNA sequences were checked and edited using Bioedit version 7.0.5.3 (Hall 1999) and all variable sites were confirmed by visual inspection of the chromatograms. Sequences were aligned for each gene independently using MAFFT version 7, with default parameters (Katoh and Standley 2013). We tested for neutrality for each mite species using two statistical tests, Tajima´s D test and Fu´s Fs test, implemented in the DNASP package (Librado and Rozas 2009). Tajima´s D test is based on the frequency of segregating nucleotide sites (Tajima 1989), while Fu´s Fs test uses the distribution of alleles or haplotypes (Fu 1997). Basic genetic statistics and standard diversity estimates (number of polymorphic sites, number of haplotypes, nucleotide diversity and haplotype diversity) were calculated for each gene and for each mite species using DNASP v.5. Mean genetic distances between individuals and between populations within each mite species were calculated for each gene with MEGA 4.1 using Kimura's 2-parameter (K2P) distance model (Tamura el al. 2007).

To visualize intraspecific genealogies of feather mite morpho-species, we used the statistical parsimony algorithm implemented in TCS version 1.21 (Clement et al. 2000) to create haplotype networks. The statistical parsimony analysis partitions the data into independent haplotype networks connected by changes that are non-homoplastic with a 95% probability (Templeton 2001). Although this threshold does not necessary correspond to a species boundary, it often separates independent lineages, which in most cases correspond to good species (Hart and Sunday 2007). This approach therefore enabled us to verify species delimitations and facilitated the discovery of new cryptic species (Criscione and Blouin 2004, Pons et al. 2006, Whiteman et al. 2006, Wiens and Penkrot 2002).

We investigated the genetic structure of different feather mite species both by host and by geographic location. Some breeding colonies were grouped by archipelago due to the small number of samples obtained from individual colonies and because no genetic structure was found among the mite populations at this spatial scale (see results): Mallorca, Menorca and Ibiza were grouped into Balearic Islands; Tenerife, Gran Canaria and Lanzarote were grouped into Canary Islands; Corvo, Flores, Faial, Graciosa, Sao Miguel and Santa Maria were grouped into Azores Islands; Raso and Curral Velho were grouped into Cape Verde. A hierarchical analysis of molecular variance (AMOVA), partitioning the genetic variance among hosts, among populations within hosts and within populations was performed using Arlequin 3.5 (Excoffier and Lischer 2010). The sequences belonging to the cryptic lineages were excluded from these analyses as was *B. sp.1* due to the small number of available sequences (see results). Isolation by distance was tested for each species using the correlation between genetic distance (Slatkin's index) and by-sea geographic distances (log transformed) among colony

pairs. Correlations were tested for significance using a Mantel test with 10000 permutations as implemented in Arlequin 3.5 (Mantel 1967, Smouse et al. 1986, Slatkin1993).

FEATHER MITE COMMUNITY STRUCTURE

Overall mite prevalence (number of birds infested/number of birds examined: Bush et al. 1997) and the prevalence of each individual feather mite species were calculated for each host species. Data on mite species richness were analysed for the assumption of normality and homogeneity of variance (Shapiro-Wilk's test; Kolmogorov-Smirnov test and Levene's test). These analyses were followed by the use of non-parametric tests (Kruskal Wallis, Mann Whitney U test) to test for differences in the mite species number found in the different host species. These analyses were conducted with SPSS 17.0. All analyses were conducted by removing rare mite species, occurring at a prevalence of < 5%. However, similar results were obtained when all mite species were included in the analyses.

Similarity in mite communities both among populations of a given host species and among host species was examined using the mite infracommunity as replicate samples, the infracommunity being all mite infrapopulations on an individual bird. Using the PRIMER v6 package (Anderson et al. 2008), we performed non-metric multi-dimensional scaling (NMDS) based on Jaccard similarities to obtain an ordination of mite infracommunities. To assess the effect of host species on the composition and structure of mite communities we used a permutational multivariate analysis of variance (PERMANOVA) with host species as a fixed factor. *P*-values were obtained using 9999 permutations of the raw data and represent the Type I (sequential) Sum of Squares. To identify key discriminating taxa on the basis of the overall percent contribution of each mite species to the average dissimilarity between host species, we used the SIMPER procedure. For these analyses we did not transform the data and added a dummy species with value 1 for all host individuals in order to include those seabirds harbouring no feather mites.

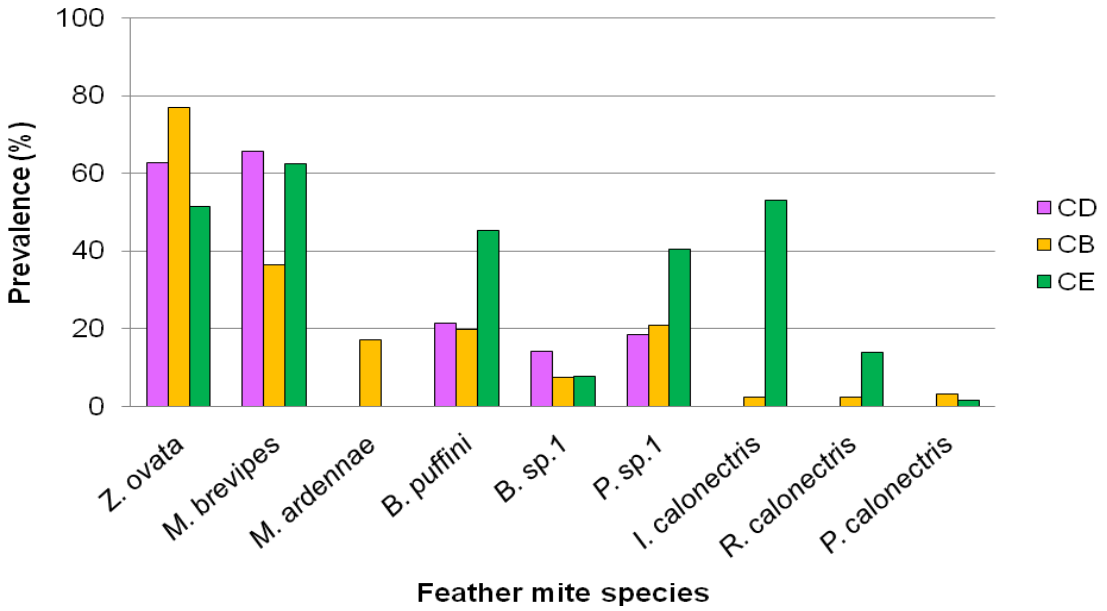

Figure 2. Prevalence of nine mite species identified morphologically on the three *Calonectris* hosts. The following abbreviations and colours were used for the different host species: Scopoli´s shearwater *C. diomedea* – CD (purple), Cory´s shearwater *C. borealis* – CB (orange) and Cape Verde shearwater *C. edwardsii* - CE (green).

RESULTS

MORPHOLOGICAL AND MOLECULAR DIVERSITY OF FEATHER MITES

On the three shearwater sister species studied, we found nine morphologically different species of feather mite belonging to seven genera: *Zachvatkinia*, *Rhinozachvatkinia*, *Promegninia* (Avenzoariidae), *Microspalax*, *Brephosceles*, *Plicatalloptes* (Alloptidae) and *Ingrassia* (Xolalgidae) (Figure 2, Supplementary Information

Table S1). Two of these species were undescribed (*B. sp. 1* and *Plicatalloptes sp.1*). Five feather mite species - *Z. ovata, M. brevipes, B. puffini, B. sp.1* and *Plicatalloptes sp.1*, were found on all three host species. Three mite species, *R. calonectris, I. calonectris* and *P. calonectris*, were shared by Cory´s and Cape Verde shearwaters and one mite species, *M. ardennae*, was found only on Cory´s shearwaters. Three feather mite species (*Z. ovata, M. brevipes* and *B. puffini*) were widely distributed, being found in all 21 sampled breeding colonies (Supplementary Information Table S1). *Brephosceles sp.1* was prevalent in Atlantic areas, but scarce in the Mediterranean Sea, whereas *Plicatalloptes sp.1* was found in 18 breeding colonies across the Atlantic and the Mediterranean. Finally, *M. ardennae*, *R.calonectris*, *I.calonectris* and *P. calonectris* were restricted to a few NE Atlantic colonies.

TCS network analyses on the combined mitochondrial genes indicated a high level of haplotypic diversity, with 112 distinct haplotypes and nine networks for the five identified morphospecies. The only morphospecies of the genus *Zachvatkinia,* identified as *Z. ovata,* presented a single network with three common dominant haplotypes shared by the three *Calonectris* host species (Figure 3A) and spread across all geographic locations (Figure 4A). Likewise, all feather mites identified as *Microspalax brevipes* grouped into a single network with three common haplotypes shared by the three host species and many rare, private haplotypes (Figure 3B); no geographic structure was visible in this network (Figure 4B). The 24 haplotypes obtained for the feather mites of the genus *Brephosceles* grouped into four sub-networks, disagreeing with morphological identifications which distinguished only two morphospecies. Two sub-networks were found for each morphospecies (Figures 3C and D) suggesting the existence of two putative cryptic species. In the case of *B. puffini*, one sub-network included only mites from Cory´s shearwater across its range (*B. puffini* B), whereas the second presented a single dominant haplotype shared by the three host species, and five private haplotypes, one corresponding to Scopoli´s shearwater and four to Cape Verde shearwater (*B. puffini* A). For *B. sp.1,* one sub-network was also restricted to Cory´s shearwaters breeding in the most northern colonies (Berlengas and Azores Islands) (*B. sp.1* B) (see Figures 4C and D), while the other was shared by the three *Calonectris* species (*B. sp.1* A). Feather mites of the genus *Plicatalloptes* presented 20 haplotypes grouped into three sub-networks (Figure 3E), indicating the potential presence of three species rather than a single one as suggested by morphology. Two sub-networks, one with a single haplotype (*P. sp.1* C) and the other with six haplotypes (*P. sp.1 B*), belonged exclusively to Cory´s shearwaters breeding in the most northern colonies of Madeira, Berlengas and Azores Islands (Figure 4E). The most complex sub-network (*P. sp.1* A) included a common dominant haplotype,shared by the three *Calonectris* species, and 12 private haplotypes, four corresponding to Cory´s shearwaters breeding in Azores and Canary Islands and eight to Cape Verde shearwaters; some geographic structure was also obvious in this network.

POPULATION GENETIC ANALYSES

In total, 295 sequences for each of the two mitochondrial genes were obtained for the five most widely abundant feather mite species. *Plicatalloptes sp.1* sequences were the most variable across indices of genetic diversity, followed by *B. sp.1* and *B. puffini*, whereas *M. brevipes* and *Z. ovata* showed the lowest overall diversity (Table 2). The number of feather mites sequenced per species, along with information on the host species and locality can be found in Supplementary Information Table S2. The results of Tajima´s D test were negative and significant for *Zachvatkinia ovata* for both genes and for *Microspalax brevipes* for the 16S gene (all $P < 0.05$), indicating an excess of rare nucleotide sites compared to neutral expectations. Fu´s Fs values also indicated significant deviations from neutrality for both feather mite species (*Z. ovata* and *M. brevipes*) and for both genes (all $P < 0.02$). In contrast, the Tajima´s D scores were positive and significant for *B. puffini* for 16S gene ($D = 2.1106$, $P < 0.05$) and for *P. sp.1* for 12S gene ($D = 2.2154$, $P < 0.05$), whereas Fu´s Fs values were positive and significant for *B. sp.1* and *P. sp.1* for 12S gene ($P < 0.05$); neutrality could not be rejected for the remaining mite speciesand genes (all $P > 0.05$). The values for *Z. ovata* and *M. brevipes* may indicate either recent population expansions of these mites and/or purifying selection on the mitochondrial genome. The positive values for *Brephosceles* and *Plicatalloptes* mites, although not found for both genes, may indicate balancing selection or a recent population bottleneck.

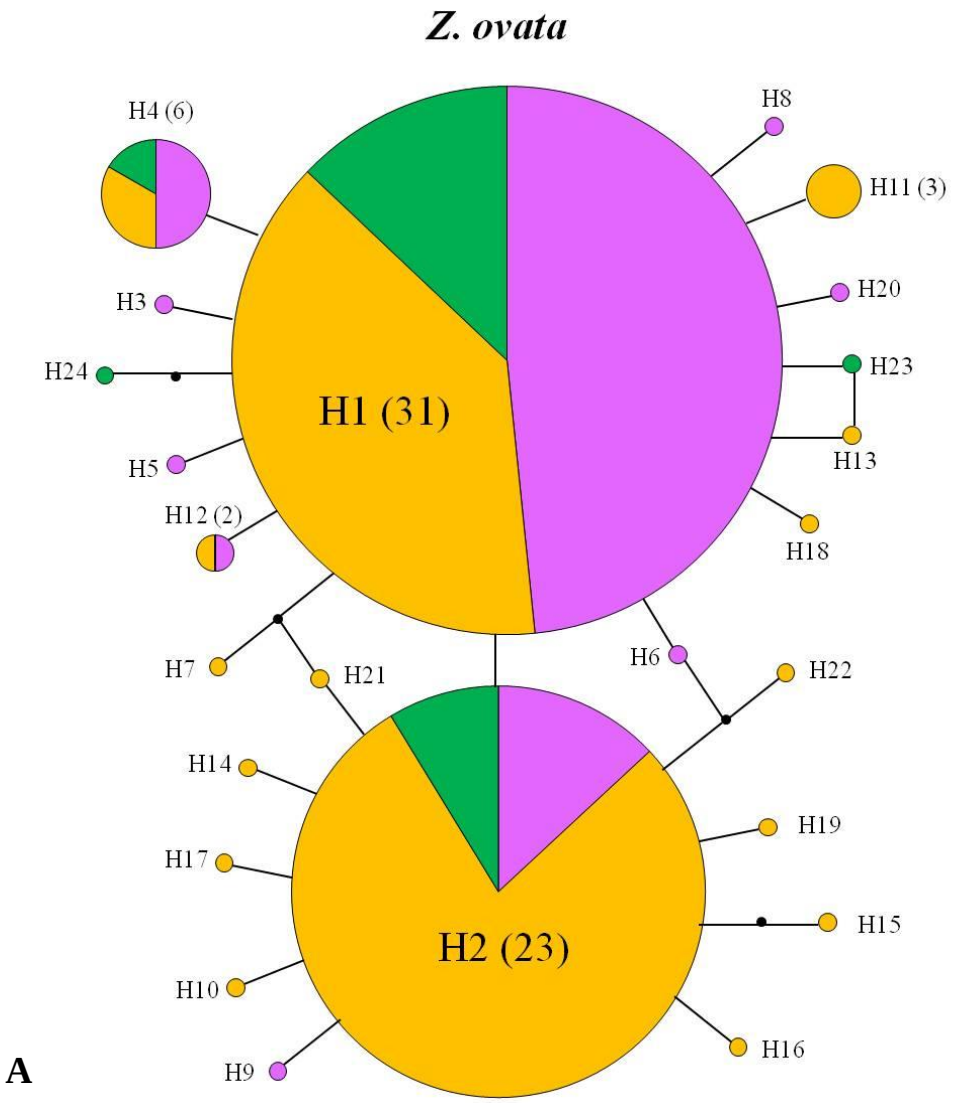

Figure 3. Haplotype networks for feather mite species *Zachvatkinia ovata* (A), *Microspalax brevipes* (B), *Brephosceles puffini* (C), *Brephosceles sp.1* (D) and *Plicatalloptes sp.1* (E) based on the concatenation of two mitochondrial genes (12S and 16S). Haplotypes corresponding to Scopoli´s, Cory´s and Cape Verde shearwaters are indicated in purple, orange and green, respectively. The size of the circles is proportional to the number of individuals sharing that haplotype, indicated in brackets. Black dots represent mutational steps.

Pairwise genetic distances between colonies within the four archipelagos (Balearic, Azores, Canary and Cape Verde Islands) were very low for the two genes and for all feather mite species analyzed (average Fst = 0.00276, SE = 0.00178 for 12S gene; average Fst = 0.00166; SE = 0.00140 for 16S gene). Based on this finding, different populations within an archipelago were regrouped and considered as a single population in all subsequent molecular analyses. Genetic divergences among populations differed greatly among mite species (Supplementary Information Tables S3-S7). Mean genetic distances between populations were low at both genes for *Z. ovata* and *M. brevipes* (Supplementary Information Tables S3 and S4). However, for *B.puffini*, there was a clear division among the populations of different regions with differences ranging from 2.34 % to 3.03 % for both genes between the populations of Almeria, Madeira, Berlengas, Azores Is. and Canary Is., and the other populations (Creta, Murcia, Zembra, Hyeres, Balearic Is.and Cape Verde) (Supplementary Information Table S5). However, within each group, differences were much lower and in line with values seen for *Z. ovata* and *M. brevipes*. These results support the TCS network results and indicate the presence of a cryptic species within the specimens identified morphologically as *B. puffini*. For *B. sp.1*, genetic distances also supported the presence of cryptic species, with two identifiable groups, one including the Atlantic populations of Berlengas and Azores Is. and the other in the populations of Zembra, Balearic Is., Canary Is. and Cape Verde. As for *B. puffini*, sequence differences were high between the two groups at both

genes (> 6%) and low within groups (< 0.7%) (Supplementary Information Table S6). Finally, for *P. sp.1*, two distinct groups could also be identified: one found in the colonies of Madeira, Berlengas and Azores Is., which differed from the other populations by more than 11 % sequence divergence. However, for this species, genetic distances remained relatively high among Berlengas, Madeira and Azores Is. populations (> 6%), but was low and homogeneous among the other six populations (< 0.95%) (Supplementary Information Table S7). These results also support the TCS network analysis, indicating the presence of two cryptic species.

AMOVA results showed significant genetic differentiation among hosts for *P. sp.1* (Φ = 0.642, P = 0.010), whereas *Z. ovata*, *M. brevipes* and *B. puffini* appeared undifferentiated among hosts (Table 3). Populations within each host species were not significantly differentiated for any mite species tested (*Z. ovata*, *M. brevipes*, *B.puffini* and *P. sp.1*) (Table 3). Furthermore, the Mantel tests indicated a significant correlation between genetic and geographic distance only for *B. puffini* (r = 0.554, P = 0.005; *Z. ovata*: r = 0.1113, P = 0.301*; M. brevipes*: r = -0.3132, P = 0.950; *P. sp.1*: r = 0.3138, P = 0.096), suggesting that mite dispersal does not depend on the geographic proximity of the seabird colonies.

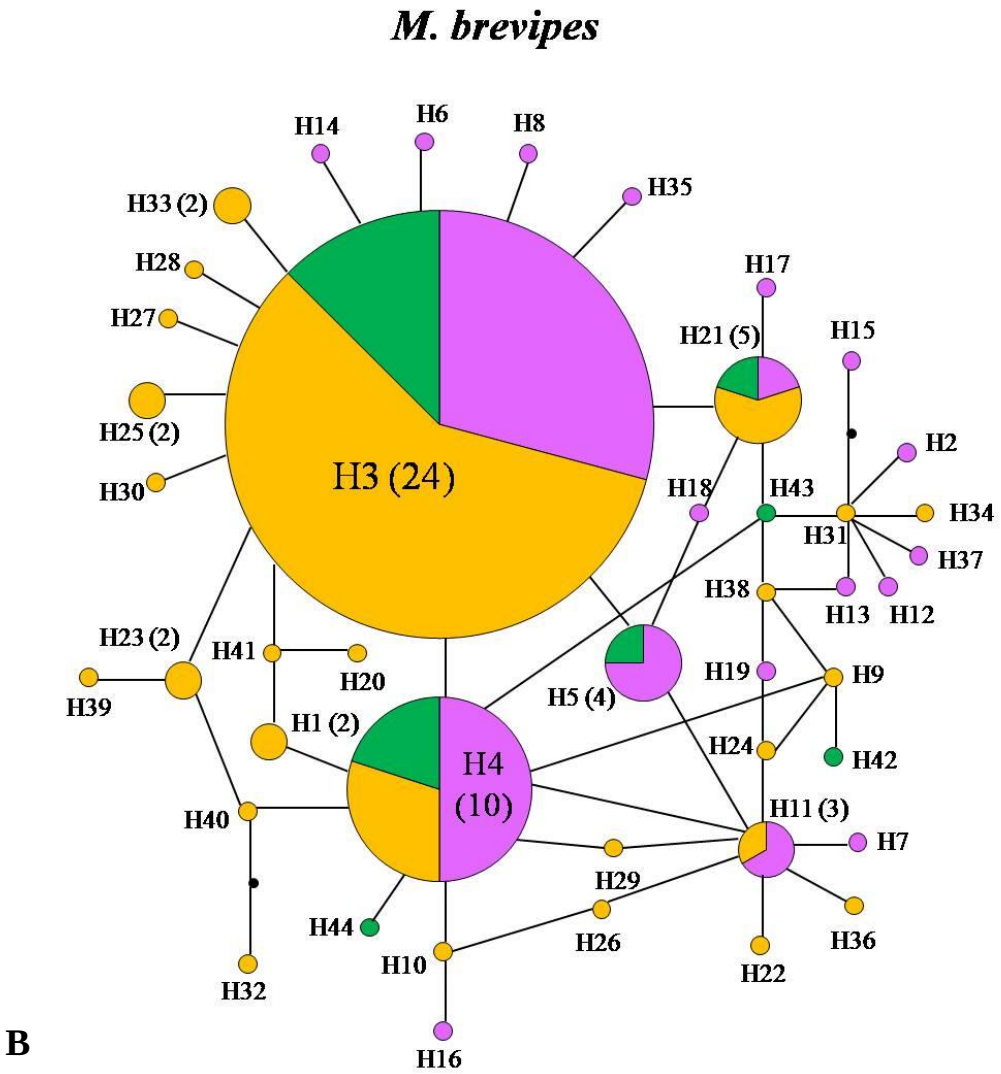

Figure 3. Continuation

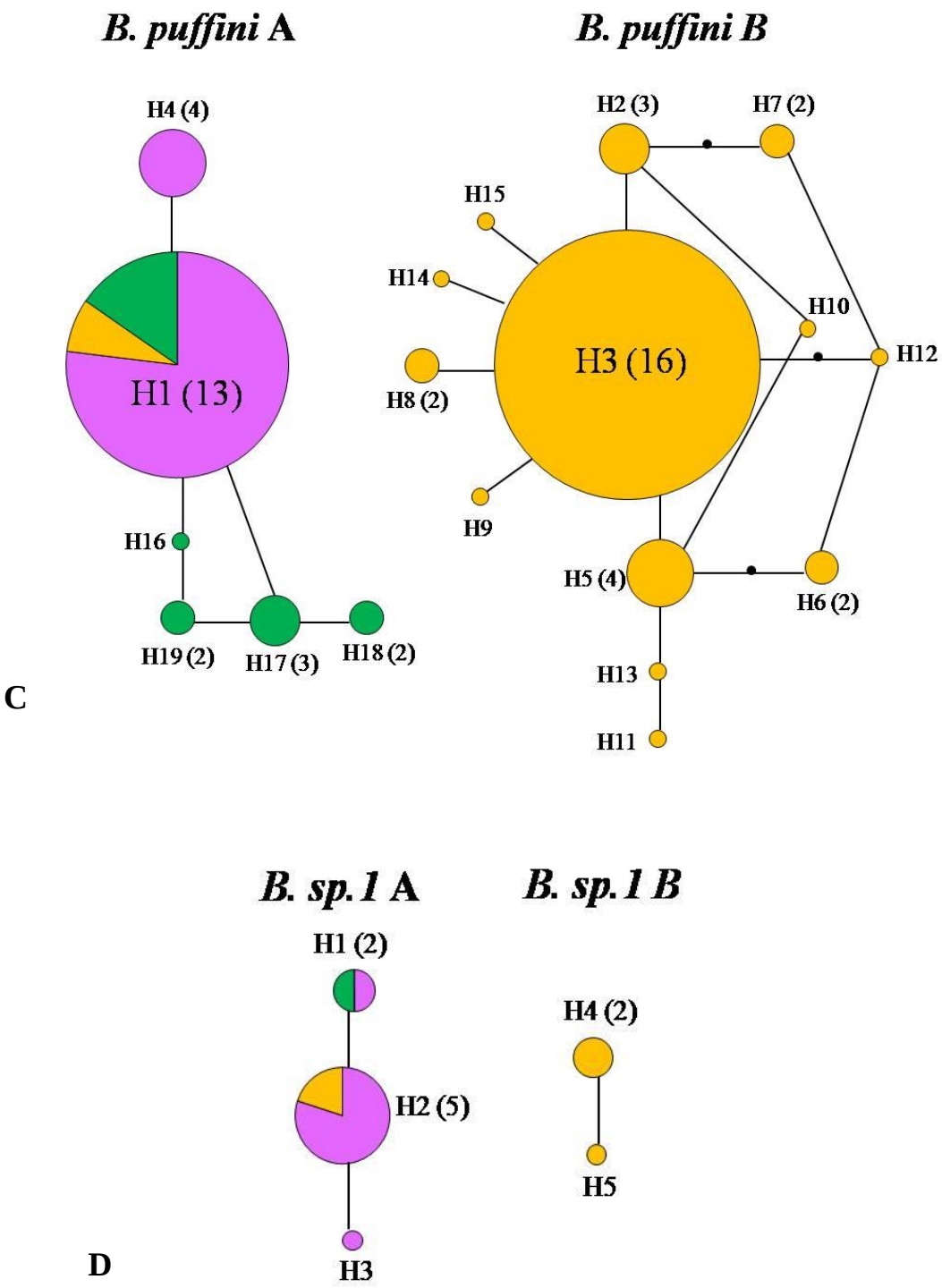

Figure 3. Continuation

FEATHER MITE COMMUNITY STRUCTURE

Almost all sampled birds were infested with feather mites (100 % for Cory´s and Scopoli´s shearwaters and 92.2 % for the Cape Verde shearwater). The prevalence of each mite species per host species is shown in Figure 2. Five mite species (*Z. ovata*, *M. brevipes*, *B. puffini*, *B. sp. 1* and *P. sp.1*) were found on all three host species with variable prevalence. Three species were only found in two of the three host species and only one species (*M. ardennae*) was restricted to a single host species. Although mite species may have been missed during sampling, these values provide a general idea of the host range of each species.

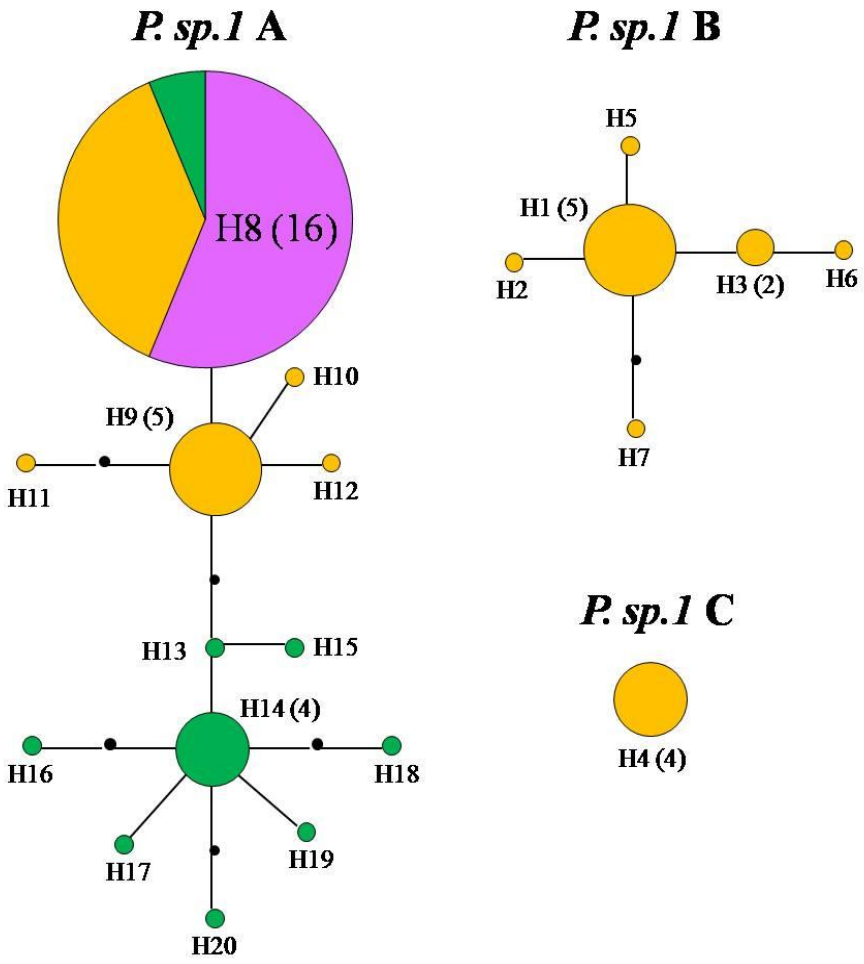

Figure 3. Continuation

Mean mite species richness in *Calonectris* species showed no significant difference between Cory´s shearwater (1.9 ± 1.0) and Scopoli´s shearwater (1.8 ± 0.9) (Mann Whitney test Z:-0.42; P > 0.05), while the value for the Cape Verde shearwater was higher (2.8 ± 1.7) but we decided not to test these difference because sampling methods for Cory's and Scopoli's shearwaters differed from those for Cape Verde shearwaters (see methods).

The visual inspection of NMDS ordination does not suggest a clear structure of mite infracommunities by host species, but the permutational MANOVA indicated significant differences in feather mite infracommunity composition among the three *Calonectris* species (Pseudo-$F_{2, 341}$ = 15.8; $P_{(perm)}$ = 0.0001) (Figure 5); the host species factor explained 15.1 % of the observed variation. Similarity in the composition of mite fauna was 42.97 % between Scopoli´s and Cory´s shearwaters, 36.11 % between Scopoli´s and Cape Verde shearwaters and 32.42 % between Cory´s and Cape Verde shearwaters. Similarity in the mite community composition among individuals of a given host species was less than 50 % for all three shearwater species (46.70 % for Scopoli´s shearwaters, 46.43 % for Cory´s shearwaters and 40.09 % for Cape Verde shearwaters). Furthermore, for Scopoli´s and Cory´s shearwaters, 90 % of the similarity among individual birds was explained by only two mite species, *Z. ovata* and *M. brevipes*, whereas four mite species (*Z. ovata*, *M. brevipes*, *B. puffini* and *I. calonectris*) contributed 88.23 % to the similarity in feather mite community composition among individuals of Cape Verde shearwaters.

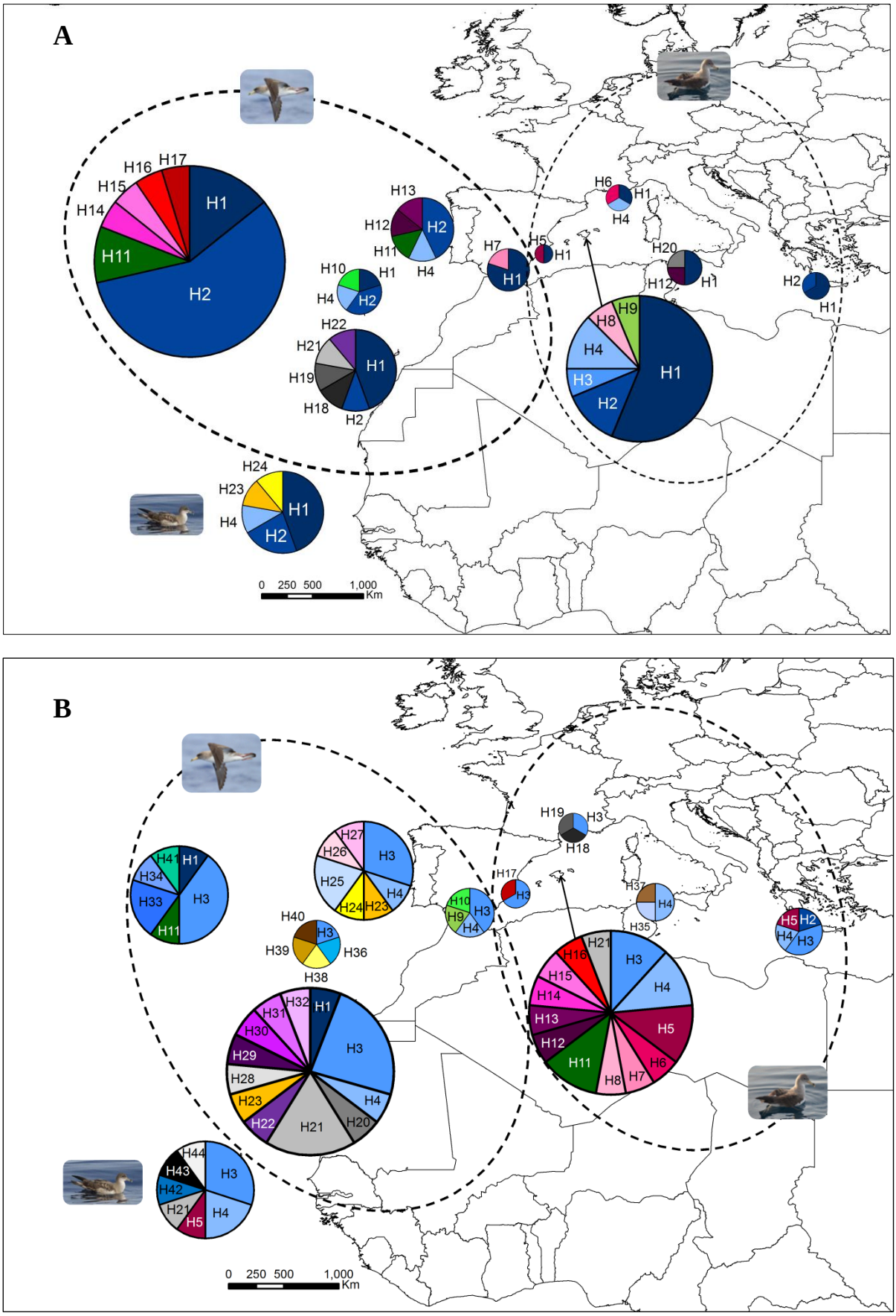

Figure 4. Geographic distribution of haplotypes for feather mite species *Zachvatkinia ovata* (A), *Microspalax brevipes* (B), *Brephosceles puffini* (C), *Brephosceles sp.1* (D) and *Plicatalloptes sp.1* (E) based on the concatenation of two mitochondrial genes (12S and 16S). The colours within the pie-diagram represent relative frequency of different haplotypes and the overall size is proportional to the number sampled mites.

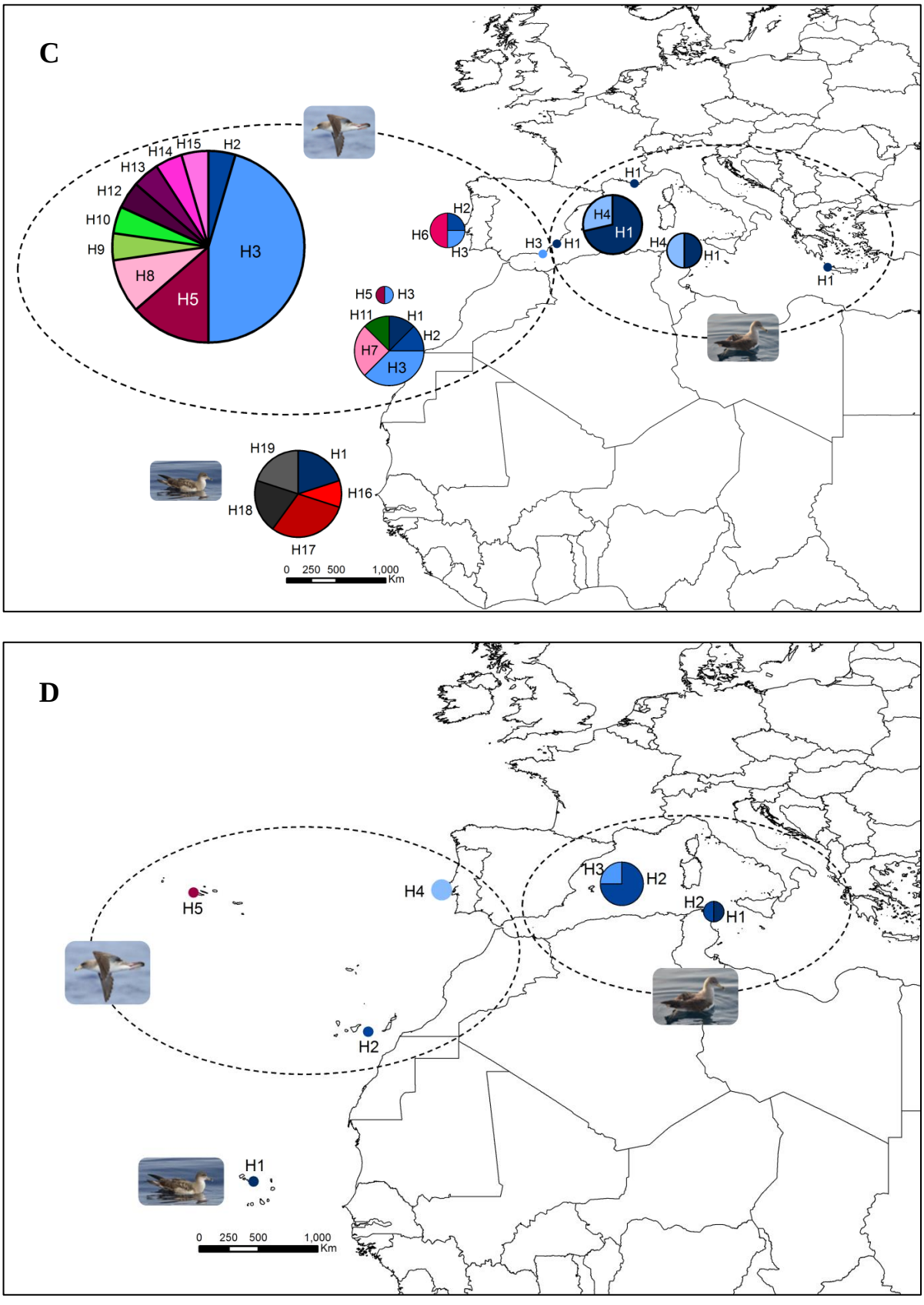

Figure 4. Continuation

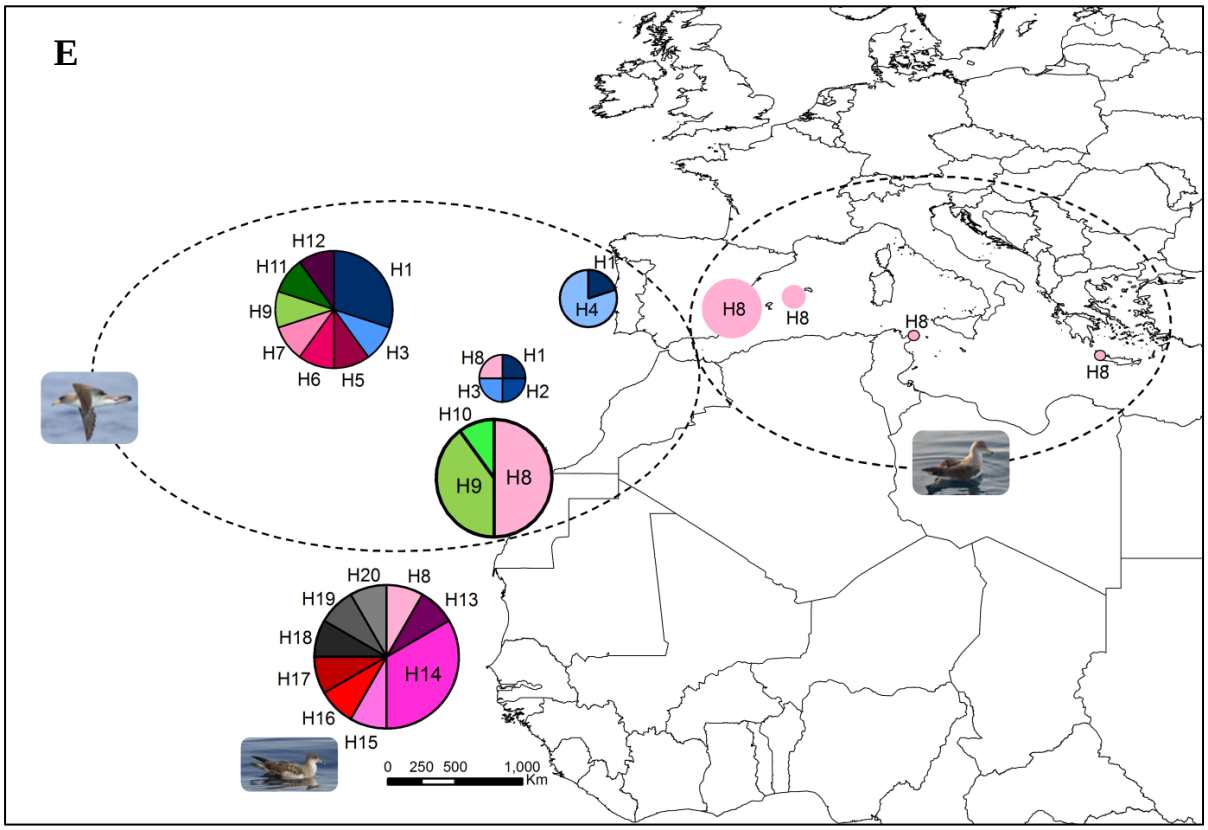

Figure 4. Continuation

DISCUSSION

In the present study, we examined the diversity and genetic structure of feather mites from *Calonectris* shearwaters in order to test the degree to which host traits shape these patterns in obligate ectofauna.As expected, ourresults revealeda high diversity of feather mites harboured by the three host species, with the presence of several morphologically cryptic lineages. We found significant differences in the composition of the communities infesting each host species. However, for those mite species which were shared among hosts, molecular analysesrevealed contrasting patterns of genetic structure in relation to the microhabitat used on the host, suggesting that dispersal propensitycan vary strongly among mites species exploiting a given host.

At the morphological level, we distinguished ninemorphospecies, of which five (*Z. ovata, M. brevipes, B. puffini, B. sp.1* and *P. sp.1*) wereshared by all three host species.Three mite species (*R.calonectris, P.calonectris*and *I.calonectris*) were found on two hosts (Cory´s and Cape Verde shearwaters), and only one species, *M. ardennae*, was restricted to a single host species (Cory´s shearwaters). The different mite species therefore seem to show different levels of host specificity. However, it is also possible that mite species may have been missed during sampling, and particularly for the Scopoli´s shearwater which showed the lowest mite species richness among the three host species. However, the sampling strategy used for this species was identicial to that used for the Cory´s shearwater (see methods) and overall sample sizes were greater for Scopoli´s shearwaters than for Cape Verde shearwaters. Observations of feather mites of the genus *Plicatalloptes* and of *B. puffini* represent first reports for *Calonectris* shearwaters. To date, the genus *Plicatalloptes* Dubinin, 1955 was known exclusively from ciconiiform and pelecaniform hosts (Mironov 1996), whereas *B. puffini* was described only from *Puffinus* hosts (Peterson 1971). Our morphological results also revealed higher mite species richness on the three *Calonectris* shearwaters than was previously reported (Mironov 1989a, Atyeo and Gaud 1991), with three species recently described by our team (Stefan et al. 2013, 2014, Mironov et al. 2015) and two new species requiring official descriptions.

Table 2. Basic genetic statistics of five feather mite species inhabiting *Calonectris* shearwaters based on two mitochondrial genes (12S and 16S). Number of individuals sequenced (N), number of polymorphic sites (Np), number of haplotypes (Nh), haplotype diversity (h), nucleotide diversity (π), average number of nucleotide differences (k) and average genetic divergence between individuals within species (d) are shown. * cryptic lineages included.

Mite species	N	Np		Nh		h		π		k		d	
		12S	16S	12S	16S	12S	16S	12S	16S	12S	16S	12S	16S
Z. ovata	84	14/307	6/135	16	7	0.725	0.139	0.0032	0.0011	0.990	0.143	0.0032 (SE=0.0016)	0.0011 (SE=0.0004)
M. brevipes	89	13/329	9/149	14	10	0.519	0.271	0.0025	0.0020	0.813	0.290	0.0025 (SE=0.001)	0.0019 (SE=0.0007)
*B. puffini**	61	13/314	5/146	7	4	0.660	0.536	0.0138	0.0143	4.297	2.037	0.0143 (SE=0.005)	0.0148 (SE=0.007)
*B. sp.1**	11	20/311	12/142	3	3	0.655	0.473	0.0286	0.0351	8.836	4.982	0.0303 (SE=0.006)	0.0373 (SE=0.011)
*P. sp.1**	50	66/326	26/143	18	8	0.871	0.696	0.0794	0.0674	25.493	9.367	0.0909 (SE=0.012)	0.075 (SE=0.016)

Table 3. Hierarchical analysis of molecular variance for mitochondrial haplotypes from four feather mite species partitioned among seabird hosts, among populations within hosts and within populations. The sequences belonging to the cryptic lineages were not included for *B. puffini* and *P. sp.1*. *Brephosceles sp.1* was also excluded due to the small number of available sequences.

Species	Partition	d.f.	Sum of squares	% variation	Φ_{ST}	P
Zachvatkinia ovata	Among hosts	2	3.946	6.83	0.068	0.185
	Among populations within hosts	8	6.245	4.62	0.049	0.051
	Within populations	73	42.702	88.55	0.114	0.006
Microspalax brevipes	Among hosts	2	2.594	1.22	0.012	0.185
	Among populations within hosts	8	8.043	-1.58	-0.016	0.795
	Within populations	78	88.262	100.36	-0.004	0.628
Brephosceles puffini	Among hosts	2	4.223	54.10	0.541	0.287
	Among populations within hosts	4	0.429	-23.12	-0.503	0.856
	Within populations	18	8.229	69.02	0.309	0.067
Plicatalloptes sp.1	Among hosts	2	21.488	64.21	0.642	0.010
	Among populations within hosts	5	1.743	-9.50	-0.265	0.179
	Within populations	27	18.483	45.29	0.547	0

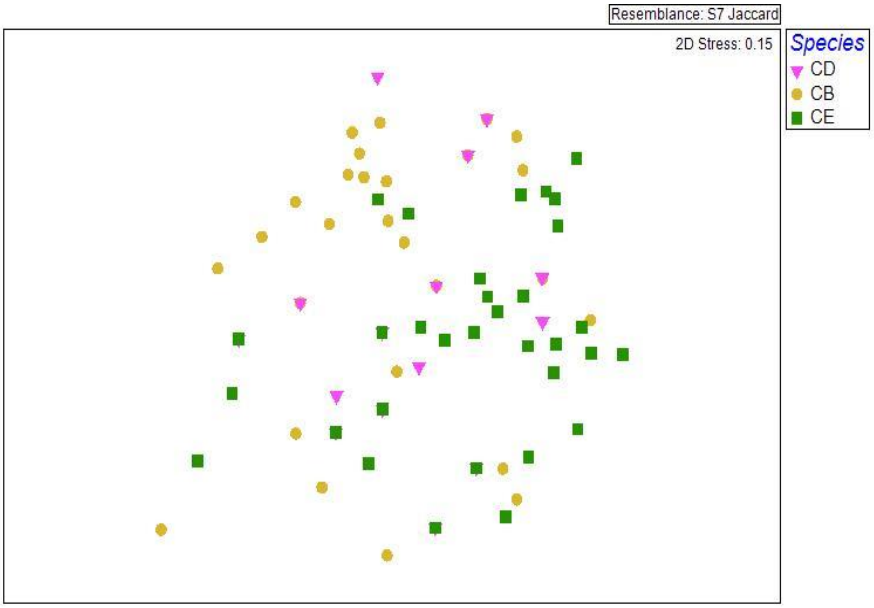

Figure 5. Non-metric multidimensional scaling ordination plot based on Jaccard similarities in mite species occurrence (non- transformed data) for *C. diomedea* (CD), *C. borealis* (CB) and *C. edwardsii* (CE), revealing no clear separation of mite infracommunities at host species level. Data were pooled when host species were sampled in different areas (see Table 1). 2D stress indicates how faithfully the high dimensional relationships among the samples are represented in the 2D ordination plot (stress > 2 is not reliable).

In addition to morphological data, the analysis of mitochondrial genes revealed the presence of several cryptic lineages in these seabird feather mites that likely represent distinct species. Advances in molecular taxonomy have lead to the discovery of cryptic species in different parasite taxa, such as nematodes (Grillo et al. 2007), trematodes (Criscione and Bouin 2004, Leung et al. 2009), cestodes (Lavikainen et al. 2010) and lice (Malenke et al. 2009). More recently, this phenomenon has been also reported for feather mites in passerine birds (Whiteman et al. 2006, Dabert et al. 2008, Hendricks et al. 2013, Doña et al. 2015a). In our study, three morphologically-identified feather mite species, *B. puffini*, *B. sp.1* and *P. sp.1*, appeared to contain cryptic species. Their mtDNA sequences revealed high levels of genetic divergence and network analyses identified separate lineages within each morphospecies. Interestingly, these cryptic complexes were found exclusively on Cory´s shearwaters. Of these cryptic lineages, *B puffini* B and *P.sp.1* B were found to be widely distributed across colonies, whereas *B. sp.1* B was limited to two islands (Berlengas and Azores) and *P. sp.1* C was only found in Berlengas. A recent duplication event (i.e. speciation of the parasite in absence of host speciation), which has not yet been followed by the expression of specific morphological characters, could explain the presence of these cryptic species (Johnson et al. 2003). However, as it is widely accepted that a single molecular marker can not be used as a unique criterion to define species (Nadler and Pérez-Ponce de León 2011), future studies should now examine nuclear molecular markers and integrate results with more detailed behavioural, morphological and ecological data in order to confirm that these new cryptic lineages represent "good" species and not simply strong intraspecific divergences.

Due to faster generation times and more limited dispersal, it has often suggested that parasites should be more strongly structured than their hosts (e.g., Mazé-Guilmo et al. 2016). Contrary to these general expectations, we observed contrasting patterns of genetic differentiation among host types for the feather mite species examined and no population genetic structure within a given host species. Two mite species, *M. brevipes* and *Z. ovata*, were genetic undifferentiated among both hosts and colonies. In a recent study, Dabert et al. (2015) reported low genetic diversity and structure in *Zachvatkinia isolata* and linked it to the dispersal strategy of mites; feather mites are considered to be transmitted by direct physical contact between parents and offspring or between conspecifics during mating or other social interactions (e.g. fighting, flock feeding, grooming) (Dabert and Mironov 1999, Proctor 2003). Our findings are therefore surprising because our three shearwater host

species are strongly structured both genetically and spatially (Gómez-Díaz et al. 2006, 2009), traits which should promote parasite isolation and differentiation. Indeed, the estimated divergence time between Cory´s and Scopoli´s shearwaters dates back to 1 MYA, and the separation of the Cape Verde shearwater from the Scopoli´s shearwater probability occurred about 700,000 years ago.The wide-scale presence of *M. brevipes* and *Z. ovata* on these hosts could suggest that these species evolve at lower rates than their hosts and that divergence by isolation may still be building up. However, in this case, we would still expect to see significant variation in haplotype frequencies among the host types. A more parsimonious explanation is therefore that these ecofauna have failed to speciate in response to host divergence. Failure to speciate can occur when gene flow among parasite populations is higher than that of their hosts (Johnson et al. 2003). As feather mites develop their entire life cycle on the host body and are incapable of surviving off the host, gene flow among mites from different shearwater species and distant colony locations seems unlikely to occur during the breeding period. However, a previous study has shown some mixing among populations of *Calonectris* taxa in the wintering areas (González-Solís et al. 2007), findings which may favor the dispersal of mites among host populations, and different host species during transient interactions at sea. In addition, *Calonectris* shearwaters may breed in sympatry with other seabird species, which could favor occasional host switches among different breeding populations. For example, in Raso island (Cape Verde), *M. brevipes*, *B. puffini* and *P. sp.1* have also been found inhabiting the Boyd's shearwater (*Puffinus boydi*) (Stefan et al. unpublished). Contacts with these additional host species may play an important role in mixing mites from different geographic areas.

In contrast to *M. brevipes* and *Z. ovata*, *Brephosceles* and *Plicatalloptes* feather mites showed high genetic diversity and significant structure among hosts/localities. Indeed both *B. puffini* and *P. sp.1* shared only a single haplotype among the three *Calonectris* taxa, with cryptic lineages present on select host species/geographic locations. These patterns suggest that specific mechanisms drive divergence in these species. Genetic divergence may result, for example, from adaptation to the different host species. Host race formation, or specialization after a host shift, has been documented for several ectoparasites (i.e. lice and ticks) infesting sympatric avian hosts (Johnson et al. 2002, McCoy et al. 2001, 2003), and surely represent an important mechanism driving parasite diversification. However, why these mite genera specialize and not the others remain an open question. In their study, Dabert et al. (2015) suggested that patterns of diversification and population structure in two feather mite species (*Zachvatkinia isolata* and *Alloptes stercorarii)* inhabiting the plumage of arctic and long-tailed skuas, were shaped by different rates of inter-host transmission conditioned by microhabitat use on the host. Our results support this hypothesis. *Microspalax brevipes* and *Z. ovata* are large vane-dwelling mites with dorso-ventrally flattened and heavily sclerotized bodies. They are specialized to inhabit the ventral surfaces of flight feathers (primary and tail feathers) and adapted to withstand the strong air turbulence during flight (Mironov 1989a, Stefan et al. 2015). In contrast, *Brephosceles* and *Plicatalloptes* are small and weakly sclerotized mites which occupy the more inaccessible areas of the plumage (e.g. wing coverts and soft downy feathers) and are only occasionally found on flight feathers (Peterson 1971, Fitzpatrick and Threlfall 1977, Bourgeois and Threlfall 1979, Dabert et al. 2015, personal observations). Mite exchange is more likely to occur for the more exposed vane-dwelling mites, such as *Zachvatkinia* and *Microspalax*, than for smaller feather mites (*Brephosceles* and *Plicatalloptes*) living within more protected microhabitats, increasing dispersal potential and thus, reducing the role of genetic drift in generating divergence and altering population dynamics. The relatively high haplotype diversity combined with low nucleotide diversity and the star-like haplotype network structure for both species suggest that these species have have undergone a recent demographic expansion or selective sweep (Bensch et al. 2006, de Jong et al. 2011). Similar findings have been recently reported for other feather mite species (Dabert et al. 2015, Doña et al. 2015b) suggesting that contraction/expansion dynamics may be common to many mites, and particularly those living in exposed microhabitats. The other feather mite species found in our study with more limited host and colony distributions also tend to live in more protected microhabitats on the host: *Ingrassia* mites mainly inhabit the body covert feathers (Mironov and Palma 2006), whereas *Rhinozachvatkinia* and *Promegninia* mites can be found on smaller coverts of the wing (Dabert and Mironov 1999). The only exception to this pattern is *M. ardennae*, which normally inhabits the vane of flight feathers (personal observations), but who's distribution was entirely restricted to Cory´s shearwaters. A role for selection in determining host species range may therefore be occurring in this species and more research into its particular biology is warrented.

In conclusion, although our study revealed differences in the feather mite ectofauna inhabiting sister-species of *Calonectris* shearwaters, several species were widely shared with almost no genetic differentiation among populations despite intercolony distances of several thousand kilometers. As for lice ectoparasites (Gómez-Díaz et al. 2007), we propose that mite exchange is favored by *Calonectris* shearwaters mixing in wintering areas at sea or by host switching between seabird species within heterospecific colonies. These mechanisms could maintain largely homogeneous communities, despite limited gene flow among hosts. However, this mechanism of parasite exchange is conditioned by the life history traits of the different species. Mite species living in highly exposed microhabitats may be more prone to dispersal than those using more protected environments. However, higher dispersal may trade-off with higher variation in population demographics, leading to higher probabilities of population extinction. Population genetic studies of these pervasive mite species using highly variable nuclear markers (microsatellite or SNPs) will now be required to test these predictions. More generally, our findings support the hypothesis host behaviour, and notably inter- and intra-specific interactions, are of key importance for the exchange and dissemination of avian ectofauna.

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SUPPLEMENTARY INFORMATION

Table S1. Diversity of feather mites found on the three *Calonectris* shearwater species based on morphological criteria. The sampling location where each species was found is listed.

Feather mite species	Host species	Locality
Zachvatkinia ovata	*C. diomedea*	Murcia-Spain
		Balearic Is. (Ibiza, Mallorca, Menorca)
		Hyeres-France
		Crete-Greece
		Zembra-Tunis
	C. borealis	Almeria-Spain
		Madeira
		Berlengas
		Canary Is. (Gran Canaria, Lanzarote, Tenerife)
		Azores Is. (Corvo, Flores, Faial, Graciosa, Sao Miguel, Santa Maria)
	C. edwardsii	Cape Verde (Raso, Curral Velho)
Microspalax brevipes	*C. diomedea*	Murcia-Spain
		Balearic Is. (Ibiza, Mallorca, Menorca)
		Hyeres-France
		Crete-Greece
		Zembra-Tunis
	C. borealis	Almeria-Spain
		Madeira
		Berlengas
		Canary Is. (Gran Canaria, Lanzarote, Tenerife)
		Azores Is. (Corvo, Flores, Faial, Graciosa, Sao Miguel, Santa Maria)
	C. edwardsii	Cape Verde (Raso, Curral Velho)
Microspalax ardennae	*C. borealis*	Madeira
		Berlengas
		Azores Is. (Corvo, Flores, Graciosa, Santa Maria)
Brephosceles puffini	*C. diomedea*	Murcia-Spain
		Balearic Is. (Ibiza, Menorca)
		Hyeres-France
		Crete-Greece
		Zembra-Tunis
	C. borealis	Almeria-Spain
		Madeira
		Berlengas
		Canary Is. (Gran Canaria, Lanzarote, Tenerife)
		Azores Is. (Corvo, Flores, Faial, Graciosa, Sao Miguel, Santa Maria)
	C. edwardsii	Cape Verde (Raso, Curral Velho)
Brephosceles sp1	*C. diomedea*	Balearic Is. (Ibiza)
		Zembra-Tunis
	C. borealis	Madeira
		Berlengas
		Canary Is. (Gran Canaria, Lanzarote)
		Azores Is. (Corvo, Flores, Faial, Graciosa, Sao Miguel)
	C. edwardsii	Cape Verde (Raso, Curral Velho)
Plicatalloptes sp.1	*C. diomedea*	Murcia-Spain
		Balearic Is. (Ibiza, Mallorca, Menorca)
		Crete-Greece
		Zembra-Tunis
	C. borealis	Madeira

Feather mite species	Host species	Locality
		Berlengas
		Canary Is. (Gran Canaria, Lanzarote, Tenerife)
		Azores Is. (Corvo, Flores, Faial, Graciosa, Santa Maria)
	C. edwardsii	Cape Verde (Raso, Curral Velho)
Rhinozachvatkinia calonectris	*C. borealis*	Azores Is. (Corvo, Flores, Graciosa, Santa Maria)
	C. edwardsii	Cape Verde (Raso, Curral Velho)
Promegninia calonectris	*C. borealis*	Madeira
		Berlengas
		Canary Is. (Gran Canaria)
		Azores Is. (Corvo)
	C. edwardsii	Cape Verde (Raso)
Ingrassia calonectris	*C. borealis*	Madeira
		Canary Is. (Lanzarote)
		Azores Is. (Flores, Santa Maria)
	C. edwardsii	Cape Verde (Raso, Curral Velho)

Table S2. Details of the 295 feather mites collected from three *Calonectris* species breeding in the Mediterranean Sea and the northeastern Atlantic Ocean included in the genetic analyses of this study (84 *Zachvatkinia*, 110 *Microspalax*, 72 *Brephosceles* and 50 *Plicatalloptes*). Specimen codes, mite species, host species, sampling locations and the genes amplified per individual with their corresponding GenBank Accession numbers are indicated. Haplotypes for concatenated mitochondrial data corresponding to those in Figure 2 and 3 are indicated.

Mite ID	Mite species	Host species	Locality	Haplotype
Z14	*Z. ovata*	*Calonectris diomedea* (Cd)	Palomas Is.-Murcia-NE coast Spain	H1
Z16	*Z. ovata*	*Calonectris diomedea* (Cd)	Palomas Is.-Murcia-NE coast Spain	H5
Z40	*Z. ovata*	*Calonectris diomedea* (Cd)	Malvins-Ibiza-Balearic Is.	H2
Z42	*Z. ovata*	*Calonectris diomedea* (Cd)	Malvins-Ibiza-Balearic Is.	H1
Z44	*Z. ovata*	*Calonectris diomedea* (Cd)	Malvins-Ibiza-Balearic Is.	H1
Z46	*Z. ovata*	*Calonectris diomedea* (Cd)	Malvins-Ibiza-Balearic Is.	H1
Z48	*Z. ovata*	*Calonectris diomedea* (Cd)	Malvins-Ibiza-Balearic Is.	H1
Z31	*Z. ovata*	*Calonectris diomedea* (Cd)	S'Esparta-Ibiza-Balearic Is.	H2
Z33	*Z. ovata*	*Calonectris diomedea* (Cd)	S'Esparta-Ibiza-Balearic Is.	H8
Z34	*Z. ovata*	*Calonectris diomedea* (Cd)	S'Esparta-Ibiza-Balearic Is.	H9
Z36	*Z. ovata*	*Calonectris diomedea* (Cd)	S'Esparta-Ibiza-Balearic Is.	H1
Z38	*Z. ovata*	*Calonectris diomedea* (Cd)	S'Esparta-Ibiza-Balearic Is.	H1
Z11	*Z. ovata*	*Calonectris diomedea* (Cd)	Pantaleu-Mallorca-Balearic Is.	H4
Z12	*Z. ovata*	*Calonectris diomedea* (Cd)	Pantaleu-Mallorca-Balearic Is.	H1
Z13	*Z. ovata*	*Calonectris diomedea* (Cd)	Pantaleu-Mallorca-Balearic Is.	H1
Z6	*Z. ovata*	*Calonectris diomedea* (Cd)	Ciutadella-Menorca-Balearic Is.	H3
Z8	*Z. ovata*	*Calonectris diomedea* (Cd)	Ciutadella-Menorca-Balearic Is.	H1
Z10	*Z. ovata*	*Calonectris diomedea* (Cd)	Ciutadella-Menorca-Balearic Is.	H4
Z18	*Z. ovata*	*Calonectris diomedea* (Cd)	PortCros-Hyeres-France	H1
Z19	*Z. ovata*	*Calonectris diomedea* (Cd)	PortCros-Hyeres-France	H6
Z21	*Z. ovata*	*Calonectris diomedea* (Cd)	PortCros-Hyeres-France	H4
Z1	*Z. ovata*	*Calonectris diomedea* (Cd)	Grambusa-Crete-Greece	H1
Z3	*Z. ovata*	*Calonectris diomedea* (Cd)	Grambusa-Crete-Greece	H2
Z4	*Z. ovata*	*Calonectris diomedea* (Cd)	Grambusa-Crete-Greece	H1
Z157	*Z. ovata*	*Calonectris diomedea* (Cd)	Zembra-Tunis	H1
Z207	*Z. ovata*	*Calonectris diomedea* (Cd)	Zembra-Tunis	H20
Z208	*Z. ovata*	*Calonectris diomedea* (Cd)	Zembra-Tunis	H1
Z209	*Z. ovata*	*Calonectris diomedea* (Cd)	Zembra-Tunis	H12
Z23	*Z. ovata*	*Calonectris borealis* (Cb)	Terreros Is.-Almeria-NE coast Spain	H1
Z24	*Z. ovata*	*Calonectris borealis* (Cb)	Terreros Is.-Almeria-NE coast Spain	H1
Z25	*Z. ovata*	*Calonectris borealis* (Cb)	Terreros Is.-Almeria-NE coast Spain	H7
Z27	*Z. ovata*	*Calonectris borealis* (Cb)	Terreros Is.-Almeria-NE coast Spain	H1
Z29	*Z. ovata*	*Calonectris borealis* (Cb)	Terreros Is.-Almeria-NE coast Spain	H1
Z51	*Z. ovata*	*Calonectris borealis* (Cb)	Desertas-Madeira	H2
Z54	*Z. ovata*	*Calonectris borealis* (Cb)	Desertas-Madeira	H4
Z56	*Z. ovata*	*Calonectris borealis* (Cb)	Desertas-Madeira	H2
Z58	*Z. ovata*	*Calonectris borealis* (Cb)	Desertas-Madeira	H10
Z60	*Z. ovata*	*Calonectris borealis* (Cb)	Desertas-Madeira	H1
Z81	*Z. ovata*	*Calonectris borealis* (Cb)	Cova-Berlengas	H12
Z82	*Z. ovata*	*Calonectris borealis* (Cb)	Cova-Berlengas	H2
Z84	*Z. ovata*	*Calonectris borealis* (Cb)	Cova-Berlengas	H13
Z76	*Z. ovata*	*Calonectris borealis* (Cb)	Poblet-Berlengas	H2
Z77	*Z. ovata*	*Calonectris borealis* (Cb)	Poblet-Berlengas	H4
Z78	*Z. ovata*	*Calonectris borealis* (Cb)	Poblet-Berlengas	H11
Z80	*Z. ovata*	*Calonectris borealis* (Cb)	Poblet-Berlengas	H2
Z94	*Z. ovata*	*Calonectris borealis* (Cb)	Caldeira-Corvo-Azores	H11
Z95	*Z. ovata*	*Calonectris borealis* (Cb)	Caldeira-Corvo-Azores	H2
Z86	*Z. ovata*	*Calonectris borealis* (Cb)	Pesqueiros-Corvo-Azores	H2
Z88	*Z. ovata*	*Calonectris borealis* (Cb)	Pesqueiros-Corvo-Azores	H14
Z91	*Z. ovata*	*Calonectris borealis* (Cb)	Pesqueiros-Corvo-Azores	H2
Z110	*Z. ovata*	*Calonectris borealis* (Cb)	Baixo du Moiño-Flores-Azores	H2
Z111	*Z. ovata*	*Calonectris borealis* (Cb)	Baixo du Moiño-Flores-Azores	H2
Z113	*Z. ovata*	*Calonectris borealis* (Cb)	Faja Lopo Vaz-Flores-Azores	H2

Mite ID	Mite species	Host species	Locality	Haplotype
Z115	*Z. ovata*	*Calonectris borealis* (Cb)	Faja Lopo Vaz-Flores-Azores	H16
Z116	*Z. ovata*	*Calonectris borealis* (Cb)	Faja Lopo Vaz-Flores-Azores	H2
Z98	*Z. ovata*	*Calonectris borealis* (Cb)	Castelo Branco-Faial-Azores	H2
Z101	*Z. ovata*	*Calonectris borealis* (Cb)	Castelo Branco-Faial-Azores	H1
Z104	*Z. ovata*	*Calonectris borealis* (Cb)	Praia-Graciosa-Azores	H11
Z107	*Z. ovata*	*Calonectris borealis* (Cb)	Praia-Graciosa-Azores	H15
Z109	*Z. ovata*	*Calonectris borealis* (Cb)	Praia-Graciosa-Azores	H2
Z118	*Z. ovata*	*Calonectris borealis* (Cb)	Vilafranca-Sao Miguel-Azores	H17
Z120	*Z. ovata*	*Calonectris borealis* (Cb)	Vilafranca-Sao Miguel-Azores	H1
Z122	*Z. ovata*	*Calonectris borealis* (Cb)	Vilafranca-Sao Miguel-Azores	H1
Z124	*Z. ovata*	*Calonectris borealis* (Cb)	Vila-Santa Maria-Azores	H2
Z127	*Z. ovata*	*Calonectris borealis* (Cb)	Vila-Santa Maria-Azores	H2
Z130	*Z. ovata*	*Calonectris borealis* (Cb)	Vila-Santa Maria-Azores	H2
Z132	*Z. ovata*	*Calonectris borealis* (Cb)	Veneguera-GCanaria-Canary Is.	H1
Z134	*Z. ovata*	*Calonectris borealis* (Cb)	Veneguera-GCanaria-Canary Is.	H2
Z160	*Z. ovata*	*Calonectris borealis* (Cb)	Veneguera-GCanaria-Canary Is.	H18
Z162	*Z. ovata*	*Calonectris borealis* (Cb)	MClara-Lanzarote-Canary Is.	H19
Z211	*Z. ovata*	*Calonectris borealis* (Cb)	MClara-Lanzarote-Canary Is.	H21
Z212	*Z. ovata*	*Calonectris borealis* (Cb)	MClara-Lanzarote-Canary Is.	H22
Z213	*Z. ovata*	*Calonectris borealis* (Cb)	MClara-Lanzarote-Canary Is.	H1
Z214	*Z. ovata*	*Calonectris borealis* (Cb)	MClara-Lanzarote-Canary Is.	H1
Z85	*Z. ovata*	*Calonectris borealis* (Cb)	Adeje-Tenerife-Canary Is.	H1
Z143	*Z. ovata*	*Calonectris edwardsii* (Ce)	Raso-Cape Verde	H1
Z164	*Z. ovata*	*Calonectris edwardsii* (Ce)	Raso-Cape Verde	H1
Z215	*Z. ovata*	*Calonectris edwardsii* (Ce)	Raso-Cape Verde	H4
Z216	*Z. ovata*	*Calonectris edwardsii* (Ce)	Raso-Cape Verde	H24
Z243	*Z. ovata*	*Calonectris edwardsii* (Ce)	Raso-Cape Verde	H1
Z136	*Z. ovata*	*Calonectris edwardsii* (Ce)	Curral Velho-Boavista-Cape Verde	H1
Z139	*Z. ovata*	*Calonectris edwardsii* (Ce)	Curral Velho-Boavista-Cape Verde	H23
Z142	*Z. ovata*	*Calonectris edwardsii* (Ce)	Curral Velho-Boavista-Cape Verde	H2
Z217	*Z. ovata*	*Calonectris edwardsii* (Ce)	Curral Velho-Boavista-Cape Verde	H2
M28	*M. brevipes*	*Calonectris diomedea* (Cd)	Palomas Is.-Murcia-NE coast Spain	H17
M147	*M. brevipes*	*Calonectris diomedea* (Cd)	Palomas Is.-Murcia-NE coast Spain	H3
M149	*M. brevipes*	*Calonectris diomedea* (Cd)	Palomas Is.-Murcia-NE coast Spain	H3
M23	*M. brevipes*	*Calonectris diomedea* (Cd)	Malvins-Ibiza-Balearic Is.	H13
M24	*M. brevipes*	*Calonectris diomedea* (Cd)	Malvins-Ibiza-Balearic Is.	H14
M25	*M. brevipes*	*Calonectris diomedea* (Cd)	Malvins-Ibiza-Balearic Is.	H5
M26	*M. brevipes*	*Calonectris diomedea* (Cd)	Malvins-Ibiza-Balearic Is.	H15
M27	*M. brevipes*	*Calonectris diomedea* (Cd)	Malvins-Ibiza-Balearic Is.	H16
M18	*M. brevipes*	*Calonectris diomedea* (Cd)	S'Esparta-Ibiza-Balearic Is.	H11
M19	*M. brevipes*	*Calonectris diomedea* (Cd)	S'Esparta-Ibiza-Balearic Is.	H4
M20	*M. brevipes*	*Calonectris diomedea* (Cd)	S'Esparta-Ibiza-Balearic Is.	H5
M21	*M. brevipes*	*Calonectris diomedea* (Cd)	S'Esparta-Ibiza-Balearic Is.	H12
M22	*M. brevipes*	*Calonectris diomedea* (Cd)	S'Esparta-Ibiza-Balearic Is.	H11
M8	*M. brevipes*	*Calonectris diomedea* (Cd)	Pantaleu-Mallorca-Balearic Is.	H7
M9	*M. brevipes*	*Calonectris diomedea* (Cd)	Pantaleu-Mallorca-Balearic Is.	H3
M11	*M. brevipes*	*Calonectris diomedea* (Cd)	Pantaleu-Mallorca-Balearic Is.	H8
M12	*M. brevipes*	*Calonectris diomedea* (Cd)	Pantaleu-Mallorca-Balearic Is.	H3
M103	*M. brevipes*	*Calonectris diomedea* (Cd)	Pantaleu-Mallorca-Balearic Is.	H21
M6	*M. brevipes*	*Calonectris diomedea* (Cd)	Ciutadella-Menorca-Balearic Is.	H4
M7	*M. brevipes*	*Calonectris diomedea* (Cd)	Ciutadella-Menorca-Balearic Is.	H6
M29	*M. brevipes*	*Calonectris diomedea* (Cd)	PortCros-Hyeres-France	H3
M30	*M. brevipes*	*Calonectris diomedea* (Cd)	PortCros-Hyeres-France	H18
M31	*M. brevipes*	*Calonectris diomedea* (Cd)	PortCros-Hyeres-France	H19
M1	*M. brevipes*	*Calonectris diomedea* (Cd)	Grambusa-Crete-Greece	H2
M2	*M. brevipes*	*Calonectris diomedea* (Cd)	Grambusa-Crete-Greece	H3
M3	*M. brevipes*	*Calonectris diomedea* (Cd)	Grambusa-Crete-Greece	H4
M4	*M. brevipes*	*Calonectris diomedea* (Cd)	Grambusa-Crete-Greece	H3
M5	*M. brevipes*	*Calonectris diomedea* (Cd)	Grambusa-Crete-Greece	H5
M106	*M. brevipes*	*Calonectris diomedea* (Cd)	Zembra-Tunis	H35
M150	*M. brevipes*	*Calonectris diomedea* (Cd)	Zembra-Tunis	H4
M151	*M. brevipes*	*Calonectris diomedea* (Cd)	Zembra-Tunis	H4

Mite ID	Mite species	Host species	Locality	Haplotype
M152	*M. brevipes*	*Calonectris diomedea* (Cd)	Zembra-Tunis	H37
M13	*M. brevipes*	*Calonectris borealis* (Cb)	Terreros Is.-Almeria-NE coast Spain	H3
M14	*M. brevipes*	*Calonectris borealis* (Cb)	Terreros Is.-Almeria-NE coast Spain	H9
M15	*M. brevipes*	*Calonectris borealis* (Cb)	Terreros Is.-Almeria-NE coast Spain	H3
M16	*M. brevipes*	*Calonectris borealis* (Cb)	Terreros Is.-Almeria-NE coast Spain	H4
M17	*M. brevipes*	*Calonectris borealis* (Cb)	Terreros Is.-Almeria-NE coast Spain	H10
M114	*M. brevipes*	*Calonectris borealis* (Cb)	Desertas-Madeira	H36
M153	*M. brevipes*	*Calonectris borealis* (Cb)	Desertas-Madeira	H3
M154	*M. brevipes*	*Calonectris borealis* (Cb)	Desertas-Madeira	H38
M155	*M. brevipes*	*Calonectris borealis* (Cb)	Madalena do Mar-Madeira	H39
M156	*M. brevipes*	*Calonectris borealis* (Cb)	Madalena do Mar-Madeira	H40
M62	*M. brevipes*	*Calonectris borealis* (Cb)	Cova-Berlengas	H3
M63	*M. brevipes*	*Calonectris borealis* (Cb)	Cova-Berlengas	H3
M64	*M. brevipes*	*Calonectris borealis* (Cb)	Cova-Berlengas	H4
M65	*M. brevipes*	*Calonectris borealis* (Cb)	Cova-Berlengas	H27
M66	*M. brevipes*	*Calonectris borealis* (Cb)	Cova-Berlengas	H25
M57	*M. brevipes*	*Calonectris borealis* (Cb)	Poblet-Berlengas	H23
M58	*M. brevipes*	*Calonectris borealis* (Cb)	Poblet-Berlengas	H3
M59	*M. brevipes*	*Calonectris borealis* (Cb)	Poblet-Berlengas	H24
M60	*M. brevipes*	*Calonectris borealis* (Cb)	Poblet-Berlengas	H25
M61	*M. brevipes*	*Calonectris borealis* (Cb)	Poblet-Berlengas	H26
M76	*M. brevipes*	*Calonectris borealis* (Cb)	Pesqueiros-Corvo-Azores	H33
M78	*M. brevipes*	*Calonectris borealis* (Cb)	Castelo Branco-Faial-Azores	H34
M79	*M. brevipes*	*Calonectris borealis* (Cb)	Praia-Graciosa-Azores	H11
M159	*M. brevipes*	*Calonectris borealis* (Cb)	Praia-Graciosa-Azores	H3
M160	*M. brevipes*	*Calonectris borealis* (Cb)	Praia-Graciosa-Azores	H3
M161	*M. brevipes*	*Calonectris borealis* (Cb)	Praia-Graciosa-Azores	H41
M162	*M. brevipes*	*Calonectris borealis* (Cb)	Praia-Graciosa-Azores	H3
M82	*M. brevipes*	*Calonectris borealis* (Cb)	Vilafranca-Sao Miguel-Azores	H33
M157	*M. brevipes*	*Calonectris borealis* (Cb)	Vila-Santa Maria-Azores	H3
M158	*M. brevipes*	*Calonectris borealis* (Cb)	Vila-Santa Maria-Azores	H1
M84	*M. brevipes*	*Calonectris borealis* (Cb)	Veneguera-GCanaria-Canary Is.	H4
M85	*M. brevipes*	*Calonectris borealis* (Cb)	Veneguera-GCanaria-Canary Is.	H3
M86	*M. brevipes*	*Calonectris borealis* (Cb)	Veneguera-GCanaria-Canary Is.	H23
M87	*M. brevipes*	*Calonectris borealis* (Cb)	Veneguera-GCanaria-Canary Is.	H3
M88	*M. brevipes*	*Calonectris borealis* (Cb)	Veneguera-GCanaria-Canary Is.	H21
M32	*M. brevipes*	*Calonectris borealis* (Cb)	MClara-Lanzarote-Canary Is.	H3
M33	*M. brevipes*	*Calonectris borealis* (Cb)	MClara-Lanzarote-Canary Is.	H20
M34	*M. brevipes*	*Calonectris borealis* (Cb)	MClara-Lanzarote-Canary Is.	H21
M35	*M. brevipes*	*Calonectris borealis* (Cb)	MClara-Lanzarote-Canary Is.	H3
M36	*M. brevipes*	*Calonectris borealis* (Cb)	MClara-Lanzarote-Canary Is.	H22
M69	*M. brevipes*	*Calonectris borealis* (Cb)	Adeje-Tenerife-Canary Is.	H28
M70	*M. brevipes*	*Calonectris borealis* (Cb)	Adeje-Tenerife-Canary Is.	H29
M71	*M. brevipes*	*Calonectris borealis* (Cb)	Adeje-Tenerife-Canary Is.	H1
M72	*M. brevipes*	*Calonectris borealis* (Cb)	Adeje-Tenerife-Canary Is.	H30
M73	*M. brevipes*	*Calonectris borealis* (Cb)	Palm-Mar-Tenerife-Canary Is.	H31
M74	*M. brevipes*	*Calonectris borealis* (Cb)	Palm-Mar-Tenerife-Canary Is.	H21
M75	*M. brevipes*	*Calonectris borealis* (Cb)	Palm-Mar-Tenerife-Canary Is.	H32
M42	*M. brevipes*	*Calonectris edwardsii* (Ce)	Raso-Cape Verde	H4
M43	*M. brevipes*	*Calonectris edwardsii* (Ce)	Raso-Cape Verde	H42
M44	*M. brevipes*	*Calonectris edwardsii* (Ce)	Raso-Cape Verde	H3
M45	*M. brevipes*	*Calonectris edwardsii* (Ce)	Raso-Cape Verde	H4
M97	*M. brevipes*	*Calonectris edwardsii* (Ce)	Raso-Cape Verde	H44
M46	*M. brevipes*	*Calonectris edwardsii* (Ce)	Curral Velho-Boavista-Cape Verde	H3
M47	*M. brevipes*	*Calonectris edwardsii* (Ce)	Curral Velho-Boavista-Cape Verde	H21
M89	*M. brevipes*	*Calonectris edwardsii* (Ce)	Curral Velho-Boavista-Cape Verde	H43
M90	*M. brevipes*	*Calonectris edwardsii* (Ce)	Curral Velho-Boavista-Cape Verde	H3
M91	*M. brevipes*	*Calonectris edwardsii* (Ce)	Curral Velho-Boavista-Cape Verde	H5
B46	*B. puffini*	*Calonectris diomedea* (Cd)	Palomas Is.-Murcia-NE coast Spain	H1
B129	*B. puffini*	*Calonectris diomedea* (Cd)	Malvins-Ibiza-Balearic Is.	H1
B130	*B. puffini*	*Calonectris diomedea* (Cd)	Malvins-Ibiza-Balearic Is.	H1
B71	*B. puffini*	*Calonectris diomedea* (Cd)	S'Esparta-Ibiza-Balearic Is.	H4

Mite ID	Mite species	Host species	Locality	Haplotype
B127	*B. puffini*	*Calonectris diomedea* (Cd)	S'Esparta-Ibiza-Balearic Is.	H1
B128	*B. puffini*	*Calonectris diomedea* (Cd)	S'Esparta-Ibiza-Balearic Is.	H4
B70	*B. puffini*	*Calonectris diomedea* (Cd)	Ciutadella-Menorca-Balearic Is.	H1
B126	*B. puffini*	*Calonectris diomedea* (Cd)	Ciutadella-Menorca-Balearic Is.	H1
B69	*B. puffini*	*Calonectris diomedea* (Cd)	Porquerolles-Hyeres-France	H1
B67	*B. puffini*	*Calonectris diomedea* (Cd)	Grambusa-Crete-Greece	H1
B72	*B. puffini*	*Calonectris diomedea* (Cd)	Zembra-Tunis	H4
B131	*B. puffini*	*Calonectris diomedea* (Cd)	Zembra-Tunis	H1
B132	*B. puffini*	*Calonectris diomedea* (Cd)	Zembra-Tunis	H1
B133	*B. puffini*	*Calonectris diomedea* (Cd)	Zembra-Tunis	H4
B68	*B. puffini*	*Calonectris borealis* (Cb)	Terreros Is.-Almeria-NE coast Spain	H3
B74	*B. puffini*	*Calonectris borealis* (Cb)	Desertas-Madeira	H5
B139	*B. puffini*	*Calonectris borealis* (Cb)	Desertas-Madeira	H3
B55	*B. puffini*	*Calonectris borealis* (Cb)	Cova-Berlengas	H2
B77	*B. puffini*	*Calonectris borealis* (Cb)	Cova-Berlengas	H3
B76	*B. puffini*	*Calonectris borealis* (Cb)	Poblet-Berlengas	H6
B140	*B. puffini*	*Calonectris borealis* (Cb)	Poblet-Berlengas	H6
B147	*B. puffini*	*Calonectris borealis* (Cb)	Caldeira-Corvo-Azores	H3
B91	*B. puffini*	*Calonectris borealis* (Cb)	Pesqueiros-Corvo-Azores	H3
B92	*B. puffini*	*Calonectris borealis* (Cb)	Pesqueiros-Corvo-Azores	H10
B148	*B. puffini*	*Calonectris borealis* (Cb)	Pesqueiros-Corvo-Azores	H12
B149	*B. puffini*	*Calonectris borealis* (Cb)	Pesqueiros-Corvo-Azores	H13
B145	*B. puffini*	*Calonectris borealis* (Cb)	Baixo du Moiño-Flores-Azores	H5
B95	*B. puffini*	*Calonectris borealis* (Cb)	Faja Lopo Vaz-Flores-Azores	H2
B146	*B. puffini*	*Calonectris borealis* (Cb)	Faja Lopo Vaz-Flores-Azores	H3
B93	*B. puffini*	*Calonectris borealis* (Cb)	Castelo Branco-Faial-Azores	H3
B150	*B. puffini*	*Calonectris borealis* (Cb)	Castelo Branco-Faial-Azores	H5
B89	*B. puffini*	*Calonectris borealis* (Cb)	Praia-Graciosa-Azores	H3
B152	*B. puffini*	*Calonectris borealis* (Cb)	Praia-Graciosa-Azores	H3
B153	*B. puffini*	*Calonectris borealis* (Cb)	Praia-Graciosa-Azores	H15
B154	*B. puffini*	*Calonectris borealis* (Cb)	Praia-Graciosa-Azores	H3
B155	*B. puffini*	*Calonectris borealis* (Cb)	Praia-Graciosa-Azores	H3
B88	*B. puffini*	*Calonectris borealis* (Cb)	Vilafranca-Sao Miguel-Azores	H9
B151	*B. puffini*	*Calonectris borealis* (Cb)	Vilafranca-Sao Miguel-Azores	H14
B85	*B. puffini*	*Calonectris borealis* (Cb)	Vila-Santa Maria-Azores	H8
B141	*B. puffini*	*Calonectris borealis* (Cb)	Vila-Santa Maria-Azores	H3
B142	*B. puffini*	*Calonectris borealis* (Cb)	Vila-Santa Maria-Azores	H5
B143	*B. puffini*	*Calonectris borealis* (Cb)	Vila-Santa Maria-Azores	H8
B144	*B. puffini*	*Calonectris borealis* (Cb)	Vila-Santa Maria-Azores	H3
B79	*B. puffini*	*Calonectris borealis* (Cb)	Veneguera-GCanaria-Canary Is.	H3
B137	*B. puffini*	*Calonectris borealis* (Cb)	Veneguera-GCanaria-Canary Is.	H3
B138	*B. puffini*	*Calonectris borealis* (Cb)	Veneguera-GCanaria-Canary Is.	H2
B81	*B. puffini*	*Calonectris borealis* (Cb)	MClara-Lanzarote-Canary Is.	H7
B134	*B. puffini*	*Calonectris borealis* (Cb)	MClara-Lanzarote-Canary Is.	H3
B135	*B. puffini*	*Calonectris borealis* (Cb)	MClara-Lanzarote-Canary Is.	H1
B136	*B. puffini*	*Calonectris borealis* (Cb)	MClara-Lanzarote-Canary Is.	H11
B84	*B. puffini*	*Calonectris borealis* (Cb)	Palm-Mar-Tenerife-Canary Is.	H7
B47	*B. puffini*	*Calonectris edwardsii* (Ce)	Raso-Cape Verde	H16
B61	*B. puffini*	*Calonectris edwardsii* (Ce)	Raso-Cape Verde	H19
B62	*B. puffini*	*Calonectris edwardsii* (Ce)	Raso-Cape Verde	H19
B63	*B. puffini*	*Calonectris edwardsii* (Ce)	Raso-Cape Verde	H1
B156	*B. puffini*	*Calonectris edwardsii* (Ce)	Raso-Cape Verde	H18
B50	*B. puffini*	*Calonectris edwardsii* (Ce)	Curral Velho-Boavista-Cape Verde	H17
B53	*B. puffini*	*Calonectris edwardsii* (Ce)	Curral Velho-Boavista-Cape Verde	H17
B58	*B. puffini*	*Calonectris edwardsii* (Ce)	Curral Velho-Boavista-Cape Verde	H1
B59	*B. puffini*	*Calonectris edwardsii* (Ce)	Curral Velho-Boavista-Cape Verde	H17
B60	*B. puffini*	*Calonectris edwardsii* (Ce)	Curral Velho-Boavista-Cape Verde	H18
B198	*B. sp.1*	*Calonectris diomedea* (Cd)	Malvins-Ibiza-Balearic Is.	H2
B199	*B. sp.1*	*Calonectris diomedea* (Cd)	Malvins-Ibiza-Balearic Is.	H3
B200	*B. sp.1*	*Calonectris diomedea* (Cd)	Malvins-Ibiza-Balearic Is.	H2
B196	*B. sp.1*	*Calonectris diomedea* (Cd)	S'Esparta-Ibiza-Balearic Is.	H2
B202	*B. sp.1*	*Calonectris diomedea* (Cd)	Zembra-Tunis	H1

Mite ID	Mite species	Host species	Locality	Haplotype
B203	*B. sp.1*	*Calonectris diomedea* (Cd)	Zembra-Tunis	H2
B205	*B. sp.1*	*Calonectris borealis* (Cb)	Cova-Berlengas	H4
B206	*B. sp.1*	*Calonectris borealis* (Cb)	Poblet-Berlengas	H4
B208	*B. sp.1*	*Calonectris borealis* (Cb)	Castelo Branco-Faial-Azores	H5
B210	*B. sp.1*	*Calonectris borealis* (Cb)	Veneguera-GCanaria-Canary Is.	H2
B 193	*B. sp.1*	*Calonectris edwardsii* (Ce)	Raso-Cape Verde	H1
P11	*P. sp.1*	*Calonectris diomedea* (Cd)	Palomas Is.-Murcia-NE coast Spain	H8
P34	*P. sp.1*	*Calonectris diomedea* (Cd)	Palomas Is.-Murcia-NE coast Spain	H8
P65	*P. sp.1*	*Calonectris diomedea* (Cd)	Palomas Is.-Murcia-NE coast Spain	H8
P66	*P. sp.1*	*Calonectris diomedea* (Cd)	Palomas Is.-Murcia-NE coast Spain	H8
P67	*P. sp.1*	*Calonectris diomedea* (Cd)	Palomas Is.-Murcia-NE coast Spain	H8
P10	*P. sp.1*	*Calonectris diomedea* (Cd)	Malvins-Ibiza-Balearic Is.	H8
P9	*P. sp.1*	*Calonectris diomedea* (Cd)	S'Esparta-Ibiza-Balearic Is.	H8
P8	*P. sp.1*	*Calonectris diomedea* (Cd)	Grambusa-Crete-Greece	H8
P68	*P. sp.1*	*Calonectris diomedea* (Cd)	Zembra-Tunis	H8
P4	*P. sp.1*	*Calonectris borealis* (Cb)	Desertas-Madeira	H1
P5	*P. sp.1*	*Calonectris borealis* (Cb)	Desertas-Madeira	H8
P6	*P. sp.1*	*Calonectris borealis* (Cb)	Desertas-Madeira	H2
P7	*P. sp.1*	*Calonectris borealis* (Cb)	Desertas-Madeira	H3
P19	*P. sp.1*	*Calonectris borealis* (Cb)	Cova-Berlengas	H4
P20	*P. sp.1*	*Calonectris borealis* (Cb)	Cova-Berlengas	H1
P21	*P. sp.1*	*Calonectris borealis* (Cb)	Cova-Berlengas	H4
P17	*P. sp.1*	*Calonectris borealis* (Cb)	Poblet-Berlengas	H4
P18	*P. sp.1*	*Calonectris borealis* (Cb)	Poblet-Berlengas	H4
P24	*P. sp.1*	*Calonectris borealis* (Cb)	Caldeira-Corvo-Azores	H5
P45	*P. sp.1*	*Calonectris borealis* (Cb)	Pesqueiros-Corvo-Azores	H1
P47	*P. sp.1*	*Calonectris borealis* (Cb)	Castelo Branco-Faial-Azores	H9
P25	*P. sp.1*	*Calonectris borealis* (Cb)	Praia-Graciosa-Azores	H6
P76	*P. sp.1*	*Calonectris borealis* (Cb)	Praia-Graciosa-Azores	H3
P77	*P. sp.1*	*Calonectris borealis* (Cb)	Praia-Graciosa-Azores	H1
P78	*P. sp.1*	*Calonectris borealis* (Cb)	Praia-Graciosa-Azores	H12
P44	*P. sp.1*	*Calonectris borealis* (Cb)	Vila-Santa Maria-Azores	H7
P74	*P. sp.1*	*Calonectris borealis* (Cb)	Vila-Santa Maria-Azores	H1
P75	*P. sp.1*	*Calonectris borealis* (Cb)	Vila-Santa Maria-Azores	H11
P26	*P. sp.1*	*Calonectris borealis* (Cb)	Veneguera-GCanaria-Canary Is.	H8
P38	*P. sp.1*	*Calonectris borealis* (Cb)	Veneguera-GCanaria-Canary Is.	H8
P71	*P. sp.1*	*Calonectris borealis* (Cb)	Veneguera-GCanaria-Canary Is.	H8
P3	*P. sp.1*	*Calonectris borealis* (Cb)	MClara-Lanzarote-Canary Is.	H8
P41	*P. sp.1*	*Calonectris borealis* (Cb)	MClara-Lanzarote-Canary Is.	H10
P69	*P. sp.1*	*Calonectris borealis* (Cb)	MClara-Lanzarote-Canary Is.	H9
P70	*P. sp.1*	*Calonectris borealis* (Cb)	MClara-Lanzarote-Canary Is.	H9
P22	*P. sp.1*	*Calonectris borealis* (Cb)	Palm-Mar-Tenerife-Canary Is.	H9
P23	*P. sp.1*	*Calonectris borealis* (Cb)	Palm-Mar-Tenerife-Canary Is.	H9
P72	*P. sp.1*	*Calonectris borealis* (Cb)	Palm-Mar-Tenerife-Canary Is.	H8
P12	*P. sp.1*	*Calonectris edwardsii* (Ce)	Raso-Cape Verde	H13
P27	*P. sp.1*	*Calonectris edwardsii* (Ce)	Raso-Cape Verde	H17
P48	*P. sp.1*	*Calonectris edwardsii* (Ce)	Raso-Cape Verde	H20
P57	*P. sp.1*	*Calonectris edwardsii* (Ce)	Raso-Cape Verde	H14
P58	*P. sp.1*	*Calonectris edwardsii* (Ce)	Raso-Cape Verde	H14
P13	*P. sp.1*	*Calonectris edwardsii* (Ce)	Curral Velho-Boavista-Cape Verde	H14
P14	*P. sp.1*	*Calonectris edwardsii* (Ce)	Curral Velho-Boavista-Cape Verde	H8
P15	*P. sp.1*	*Calonectris edwardsii* (Ce)	Curral Velho-Boavista-Cape Verde	H15
P16	*P. sp.1*	*Calonectris edwardsii* (Ce)	Curral Velho-Boavista-Cape Verde	H16
P28	*P. sp.1*	*Calonectris edwardsii* (Ce)	Curral Velho-Boavista-Cape Verde	H18
P29	*P. sp.1*	*Calonectris edwardsii* (Ce)	Curral Velho-Boavista-Cape Verde	H14
P30	*P. sp.1*	*Calonectris edwardsii* (Ce)	Curral Velho-Boavista-Cape Verde	H19

Table S3. Pairwise genetic distances measured as Fst among eleven populations of *Zachvatkinia ovata*. Genetic distances based on the 12S gene are shown on the lower left matrix, whereas the genetic distances based on the 16S gene are shown on the upper right matrix.

	Creta	Balearic Is	Murcia	Hyeres	Almeria	Madeira	Berlengas	Canary Is	Azores Is	Zembra	Cape Verde
Creta		0.00095	0.00000	0.00000	0.00000	0.00000	0.00000	0.00085	0.00073	0.00000	0.00085
Balearic Is	0.00191		0.00095	0.00095	0.00095	0.00095	0.00095	0.00180	0.00168	0.00095	0.00180
Murcia	0.00274	0.00287		0.00000	0.00000	0.00000	0.00000	0.00085	0.00073	0.00000	0.00085
Hyeres	0.00219	0.00205	0.00274		0.00000	0.00000	0.00000	0.00085	0.00073	0.00000	0.00085
Almeria	0.00109	0.00123	0.00164	0.00109		0.00000	0.00000	0.00085	0.00073	0.00000	0.00085
Madeira	0.00306	0.00361	0.00493	0.00394	0.00328		0.00000	0.00085	0.00073	0.00000	0.00085
Berlengas	0.00344	0.00387	0.00493	0.00407	0.00328	0.00470		0.00085	0.00073	0.00000	0.00085
Canary Is	0.00194	0.00251	0.00347	0.00292	0.00182	0.00336	0.00386		0.00158	0.00085	0.00170
Azores Is	0.00271	0.00358	0.00493	0.00438	0.00328	0.00357	0.00434	0.00288		0.00073	0.00158
Zembra	0.00274	0.00287	0.00328	0.00274	0.00164	0.00493	0.00469	0.00347	0.00493		0.00085
Cape Verde	0.00243	0.00269	0.00347	0.00267	0.00182	0.00409	0.00433	0.00300	0.00400	0.00347	

Table S4. Pairwise genetic distances measured as Fst among eleven populations of *Microspalax brevipes*. Genetic distances based on the 12S gene are shown on the lower left matrix, whereas the genetic distances based on the 16S gene are shown on the upper right matrix.

	Canary Is	Creta	Balearic Is	Almeria	Murcia	Hyeres	Berlengas	Azores Is	Zembra	Madeira	Cape Verde
Canary Is		0.00200	0.00200	0.00216	0.00080	0.00080	0.00284	0.00148	0.00080	0.00216	0.00148
Creta	0.00290		0.00256	0.00272	0.00136	0.00136	0.00340	0.00204	0.00136	0.00272	0.00204
Balearic Is	0.00345	0.00257		0.00240	0.00120	0.00120	0.00317	0.00188	0.00120	0.00256	0.00188
Almeria	0.00202	0.00125	0.00184		0.00136	0.00136	0.00313	0.00204	0.00136	0.00272	0.00204
Murcia	0.00362	0.00291	0.00343	0.00208		0.00000	0.00204	0.00068	0.00000	0.00136	0.00068
Hyeres	0.00312	0.00249	0.00293	0.00208	0.00277		0.00204	0.00068	0.00000	0.00136	0.00068
Berlengas	0.00257	0.00187	0.00246	0.00062	0.00271	0.00270		0.00272	0.00204	0.00341	0.00272
Azores Is	0.00246	0.00162	0.00220	0.00062	0.00250	0.00228	0.00125		0.00068	0.00204	0.00136
Zembra	0.00390	0.00296	0.00353	0.00234	0.00390	0.00338	0.00296	0.00265		0.00136	0.00068
Madeira	0.00330	0.00287	0.00342	0.00187	0.00354	0.00312	0.00224	0.00237	0.00390		0.00204
Cape Verde	0.00266	0.00193	0.00248	0.00093	0.00260	0.00218	0.00156	0.00143	0.00296	0.00256	

Table S5. Pairwise genetic distances measured as Fst among eleven populations of *Brephosceles puffini*. Genetic distances based on the 12S gene are shown on the lower left matrix, whereas the genetic distances based on the 16S gene are shown on the upper right matrix.

	Murcia	Berlengas	Creta	Almeria	Hyeres	Balearic Is	Zembra	Madeira	Canary Is	Azores Is	Cape Verde
Murcia		0.02878	0.00000	0.02878	0.00000	0.00000	0.00000	0.02878	0.02519	0.02845	0.00141
Berlengas	0.02624		0.02878	0.00000	0.02878	0.02878	0.02878	0.00000	0.00360	0.00032	0.03028
Creta	0.00000	0.02624		0.02878	0.00000	0.00000	0.00000	0.02878	0.02519	0.02845	0.00141
Almeria	0.02624	0.00323	0.02624		0.02878	0.02878	0.02878	0.00000	0.00360	0.00032	0.03028
Hyeres	0.00000	0.02624	0.00000	0.02624		0.00000	0.00000	0.02878	0.02519	0.02845	0.00141
Balearic Is	0.00000	0.02624	0.00000	0.02624	0.00000		0.00000	0.02878	0.02519	0.02845	0.00141
Zembra	0.00000	0.02624	0.00000	0.02624	0.00000	0.00000		0.02878	0.02519	0.02845	0.00141
Madeira	0.02624	0.00323	0.02624	0.00000	0.02624	0.02624	0.02624		0.00360	0.00032	0.03028
Canary Is	0.02339	0.00651	0.02339	0.00530	0.02339	0.02339	0.02339	0.00530		0.00384	0.02667
Azores Is	0.02655	0.00352	0.02655	0.00059	0.02655	0.02655	0.02655	0.00059	0.00570		0.02994
Cape Verde	0.00096	0.02726	0.00096	0.02726	0.00096	0.00096	0.00096	0.02726	0.02439	0.02756	

Table S6. Pairwise genetic distances measured as Fst among six populations of *Brephosceles sp.1*. Genetic distances based on the 12S gene are shown on the lower left matrix, whereas the genetic distances based on the 16S gene are shown on the upper right matrix.

	Cape Verde	Balearic Is	Zembra	Berlengas	Azores Is	Canary Is
Cape Verde		0.00000	0.00000	0.08227	0.09040	0.00000
Balearic Is	0.00325		0.00000	0.08227	0.09040	0.00000
Zembra	0.00162	0.00162		0.08227	0.09040	0.00000
Berlengas	0.06484	0.06849	0.06667		0.00709	0.08227
Azores Is	0.06484	0.06849	0.06667	0.00000		0.09040
Canary Is	0.00325	0.00000	0.00162	0.06849	0.06849	

Table S7. Pairwise genetic distances measured as Fst among nine populations for feather mite species *Plicatalloptes sp.1*. Genetic distances based on the 12S gene are shown on the lower left matrix, whereas the genetic distances based on the 16S gene are shown on the upper right matrix.

	Canary Is	Madeira	Creta	Balearic Is	Murcia	Berlengas	Azores Is	Zembra	Cape Verde
Canary Is		0.12693	0.00000	0.00000	0.00000	0.16191	0.11941	0.00000	0.00788
Madeira	0.15313		0.12693	0.12693	0.12693	0.07194	0.06848	0.12693	0.12432
Creta	0.00188	0.15459		0.00000	0.00000	0.16191	0.11941	0.00000	0.00788
Balearic Is	0.00188	0.15459	0.00000		0.00000	0.16191	0.11941	0.00000	0.00788
Murcia	0.00188	0.15459	0.00000	0.00000		0.16191	0.11941	0.00000	0.00788
Berlengas	0.19956	0.06948	0.20211	0.20211	0.20211		0.07872	0.16191	0.15588
Azores Is	0.14526	0.08487	0.14745	0.14745	0.14745	0.07733		0.11941	0.11748
Zembra	0.00188	0.15459	0.00000	0.00000	0.00000	0.20211	0.14745		0.00788
Cape Verde	0.00844	0.15187	0.00945	0.00945	0.00945	0.19539	0.14379	0.00945	

CHAPTER 3

SPATIAL DISTRIBUTION AND TROPHIC ECOLOGY OF SEABIRD FEATHER MITES

3.1 NICHE PARTITIONING OF FEATHER MITES WITHIN A SEABIRD HOST, *CALONECTRIS BOREALIS*

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PARTICIÓN DEL NICHO DE LOS ÁCAROS DE LA PLUMA EN UNA AVE MARINA, *CALONECTRIS BOREALIS*

RESUMEN

De acuerdo con la teoría clásica del nicho, las especies pueden coexistir en entornos heterogéneos mediante la reducción de la competicia interespecífica a través de la partición del nicho, por ejemplo la partición trófica o espacial. Sin embargo, el papel de la competición en la partición del nicho sigue siendo controvertido. Aquí, hemos testado la partición espacial y trófica en ácaros de la pluma, un grupo diverso y abundante de artrópodos. Nos centramos en las dos especies de ácaros dominantes, *Microspalax brevipes* y *Zachvatkinia ovata*, que ocupan las plumas de vuelo de la pardela cenicienta, *Calonectris borealis*. Hemos realizado conteos de los ácaros a través y dentro de las primarias y plumas de la cola en pardelas que crían en una isla oceánica (Gran Canaria, Islas Canarias). Después, hemos investigado las relaciones tróficas entre las los especies de ácaros y el huésped utilizando análisis de isótopos estables de carbono y nitrógeno, tanto en los tejidos de los ácaros como en las posibles fuentes de alimento del huésped. La distribución de las dos especies de ácaros mostró una segregación espacial clara entre las plumas; *M. brevipes* mostró una alta preferencia para las primarias centrales, mientras que *Z. ovata* estaba restringida a las dos primarias más externas. Diferencias morfológicas entre *M. brevipes* y *Z. ovata* apoyan una base adaptativa para la segregación espacial de las dos especies de ácaros. No obstante, los dos ácaros se solapan en algunas primarias centrales y los modelos estadísticos mostraron que *Z. ovata* tiende a desplazar *M. brevipes*. Los análisis isotópicos indicaron valores isotópicos similares para las dos especies de ácaros y una fuerte correlación en las firmas de carbono entre los ácaros que habitan en el mismo individuo hospedador, lo que sugiere que la dieta de ambos se basa principalmente en recursos procedentes del huésped. Entre los cuatros tejidos candidatos examinados (sangre, restos de plumas, restos de piel y aceite de la glándula uropígeal, hemos concluido que la dieta de los ácaros más probable és la dominada por el aceite de la glándula uropígeal, mientras que la contribución del material exógeno a la dieta es menos marcada. Nuestros resultados indican que la competición para el espacio y los recursos juega un papel central en la estructuración de las comunidades de ácaros de la pluma. También ilustran que las infracomunidades simbióticas son excelentes sistemas modelo para estudiar la ecología trófica, y pueden mejorar nuestros conocimientos sobre los mecanismos de la diferenciación del nicho y la coexistencia de las especies.

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RESEARCH ARTICLE

Niche Partitioning of Feather Mites within a Seabird Host, *Calonectris borealis*

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Abstract

According to classic niche theory, species can coexist in heterogeneous environments by reducing interspecific competition via niche partitioning, e.g. trophic or spatial partitioning. However, support for the role of competition on niche partitioning remains controversial. Here, we tested for spatial and trophic partitioning in feather mites, a diverse and abundant group of arthropods. We focused on the two dominant mite species, *Microspalax brevipes* and *Zachvatkinia ovata*, inhabiting flight feathers of the Cory's shearwater, *Calonectris borealis*. We performed mite counts across and within primary and tail feathers on free-living shearwaters breeding on an oceanic island (Gran Canaria, Canary Islands). We then investigated trophic relationships between the two mite species and the host using stable isotope analyses of carbon and nitrogen on mite tissues and potential host food sources. The distribution of the two mite species showed clear spatial segregation among feathers; *M. brevipes* showed high preference for the central wing primary feathers, whereas *Z. ovata* was restricted to the two outermost primaries. Morphological differences between *M. brevipes* and *Z. ovata* support an adaptive basis for the spatial segregation of the two mite species. However, the two mites overlap in some central primaries and statistical modeling showed that *Z. ovata* tends to outcompete *M. brevipes*. Isotopic analyses indicated similar isotopic values for the two mite species and a strong correlation in carbon signatures between mites inhabiting the same individual host suggesting that diet is mainly based on shared host-associated resources. Among the four candidate tissues examined (blood, feather remains, skin remains and preen gland oil), we conclude that the diet is most likely dominated by preen gland oil, while the contribution of exogenous material to mite diets is less marked. Our results indicate that ongoing competition for space and resources plays a central role in structuring feather mite communities. They also illustrate that symbiotic infracommunities are excellent model systems to study trophic ecology, and can improve our understanding of mechanisms of niche differentiation and species coexistence.

Competing Interests: The authors have declared that no competing interests exist.

Introduction

A niche can be defined as the global environmental requirements of a species to complete its life cycle, and includes its impact on resource availability and on other organisms in the community [1]. According to classic niche theory, species can coexist in heterogeneous environments by reducing interspecific competition via niche partitioning [2,3]. Different types of niche partitioning can occur, such as spatial niche partitioning, when species share a food resource but use distinct subsets of the habitat, and trophic partitioning, when different species specialize on distinct food resources in sympatric habitats [4].

However, support for the role of competition on niche partitioning remains controversial. Observational studies quantifying static patterns among co-occurring species are difficult to interpret unequivocally [5,6]. A common problem is the lack of sufficient replicates that limits the detection and analysis of general patterns of community structure. In this regard, permanent obligate symbionts (commensals, mutualists or parasites) have been proposed as good models for understanding community structure and the dynamics of niche partitioning over small spatial scales. In these systems spatial and trophic resources are limited to the body of the host and each host represents a replica of a discrete habitat patch [7].

Intrinsic host factors along with extrinsic environmental factors can influence the distribution of obligate symbionts on or within a host, but structuring can also arise due to direct interaction among species [8]. Indeed, interspecific competition is considered to be a major process shaping symbiont infracommunities [7]. Spatial segregation has been examined for both endo- and ectosymbionts of fish, birds and mammals [9–12], but evidence from different studies is inconsistent, with some studies supporting a role for competition and others suggesting a tendency for co-occurring symbionts to aggregate in preferred areas of the host body [13].

Feather mites (Astigmata: Pterolichoidea, Analgoidea) are the most diverse obligate ectosymbionts living on birds [14] and have been reported from all avian orders with the exception of Rheiformes [15]. They do not have an off-host stage and are transferred by direct contact between mates, parents and offspring, and potentially other flock members if there is close contact (e.g., fighting or flock feeding). In contrast to skin-dwelling mites and feather lice, which are often transmitted horizontally among hosts by hippoboscid flies [16,17], there have been very few observations of such indirect transmission of feather-dwelling mites [18]. Previous studies have shown that these species often show marked differences in distribution among feathers, with some being restricted to certain feather types or regions within a feather [12,19–21]. Although the distribution of feather mites are at least partially related to specific habitat and trophic morphological specializations (e.g. body shape, setae, structure of the mouthpats) [14,22,23], the role of resource competition as a mechanism generating this diversity is largely unknown.

To date, a number of studies have investigated the spatial distribution of feather mites on individual hosts [12,19,21,24,25], but few have evaluated their trophic relationships and the nature of their ecological interactions with the host. Part of the difficulty in studying mite ecological relationships is due to their small size and the inability to maintain them off of the bodies of their normal hosts. Although some authors provide evidence that feather mites are parasites, causing damage to their hosts [26,27], most studies suggest that they are commensals living on the surface of host feathers [28,29]. Based on the morphological structure of the mouthparts and observations of the guts of slide-mounted mites, it has been suggested that feather mites feed principally on oil produced by the uropygial gland, and on debris trapped between the feather barbs such as fungal spores and pollen grains [30–32]. Skin remains and feather fragments have also been occasionally observed in mite guts but are common only in some species [14]. Indirect methods, such as stable isotope analyses (SIA), can be powerful

tools for studying trophic relationships of otherwise difficult to observe organisms [33]. This approach is based on the fact that isotopic signatures of different dietary sources are reflected in the tissues of consumers in a predictable manner [34]. Nitrogen ($^{15}N/^{14}N$) is typically used to infer the trophic position of consumers, and increases by approximately 2.5‰-5‰ with each trophic level [35], whereas carbon ($^{13}C/^{12}C$) is typically used to describe the diet sources, and shows only a limited enrichment between trophic levels (0–1‰) [36]. SIA has been successfully applied to study trophic interactions in different host-parasite systems including both endoparasites, such as intestinal nematodes and cestodes [37,38] and ectoparasites, such as lice, fleas and bat flies [39,40], but to the best of our knowledge has not been used to study mites.

Here, we examine the spatial organization and trophic structure of the two principal feather mite species inhabiting flight feathers of the Cory´s shearwater, *Calonectris borealis* (Cory) (Procellariiformes: Procellariidae). Our specific objectives were (1) to assess the occurrence of niche partitioning by examining relative within-host distribution and resource use of the two mite species, and (2) to test the extent of the spatial competition, that is, whether the distribution and abundance of one mite species limits the distribution and abundance of the other. If niche partitioning occurs, we expected that the two species would either (a) share the same food resource (i.e., share a common isotopic signature), but occupy distinct and non-overlapping regions of the host's body, (b) consume different foods (i.e. have different isotopic signatures) and occupy the same parts of the host or (c) segregate in both trophic resources and space use. These hypotheses are consistent with competition playing an important role in determining niche partitioning of these mites, but could also result from independent microhabitat adaptation. To explore the role of ongoing competition in determining mite distributions, we investigated changes in occupancy patterns among individual hosts. If one mite species actively excludes the other, we expected a shift in distribution and abundance when the competing species is present. If the distribution and abundance of one species does not affect that of the other but the two remain spatially segregated even in the absence of potential competitors, we considered spatial segregation to result from an independent adaptive process or from selective pressure from past competition (i.e. the ghost of competition past).

Materials and Methods

Study area and species

Our study focused on a population of Cory´s shearwater breeding in the location of Veneguera, Gran Canaria, Canary Islands (27°50'N, 15°47'W). The Cory´s shearwater breeds mainly in the northeast Atlantic Ocean, from the Canary to the Azores Archipelagos and hosts a wide array of ectosymbionts, such as lice, fleas, and ticks, along with at least six described species of feather mites: *Microspalax brevipes*, *Microspalax ardennae*, *Zachvatkinia ovata*, *Rhinozachvatkinia calonectris*, *Promegninia calonectris* and *Ingrassia calonectris* [41–46]. Fieldwork was carried out during the Cory's shearwater breeding season, from mid June to mid July 2011 and a total of 60 birds were captured and examined at night.

Feather mite counts

We performed mite counts directly on the birds in the field. In order to have sufficient and reliable data for each individual, we focused counts on the two most abundant feather mite species, *M. brevipes* (*Mb*) and *Z. ovata* (*Zo*), inhabiting flight feathers (primaries and rectrices) (Fig 1A and 1B). Other mite species were also observed on flight feathers, but they were occasionally found and were relatively difficult to distinguish at low magnification in the field, due to their poor pigmentation and their smaller body sizes compared to *Mb* and *Zo*. The two species are easily distinguishable from each other at low magnification. *Mb* male and female have heavily

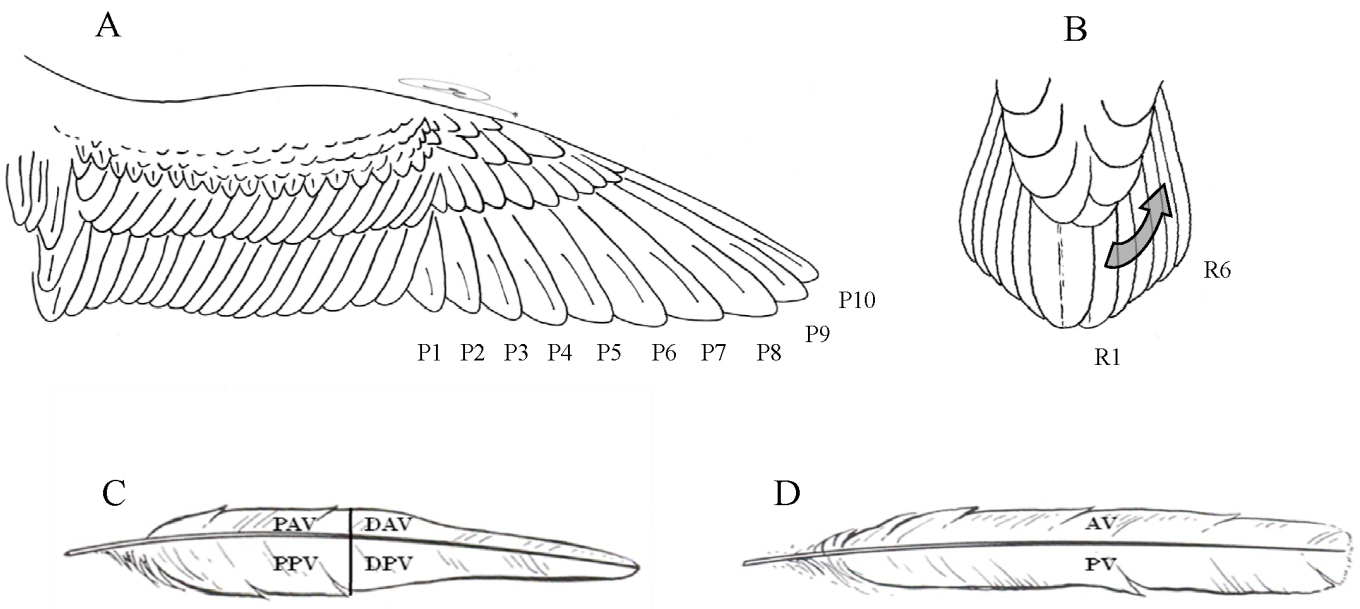

Fig 1. Primaries (A) and rectrices (B) of Cory´s shearwater (see [58]). Primaries were divided into four equal regions: PPV—proximal posterior vane, DPV—distal posterior vane, PAV—proximal anterior vane, DAV—distal anterior vane (C), while rectrices were divided into two regions: AV—anterior vane and PV—posterior vane (D).

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sclerotized ovoid bodies, short, broad forelegs and ventrally inserted hind legs and both sexes look similar to the unaided eye. *Zo* is 1.5 to 2 times longer than *Mb* and has long forelegs and laterally inserted hind legs. The posterior margin of *Zo* female body is rounded, whereas that of the male bears two terminal lobes. Adults of both species are darkly pigmented and so they stand out clearly against the light-coloured feathers, while juvenile mites are often too poorly pigmented to be reliably counted; we thus restricted the analysis to adults. For each bird, we counted the number of adult *Mb* and *Zo* present on the ten primary feathers (P1-P10) and on the six rectrices (tail flight feathers) (R1-R6) of the left side, using a 10X hand magnifier (S1 Table). Each primary feather was divided into four approximately equal regions (Fig 1C): proximal anterior vane (PAV), distal anterior vane (DAV), proximal posterior vane (PPV) and distal posterior vane (DPV), while rectrices were only divided into two regions, anterior (AV) and posterior (PV) vane, because of the relatively small number of feather mites found on these feathers (Fig 1D). In the case of P10, we observed in the field that the posterior region of the feather is unsuitable for mites due to structural features, and mites were therefore not counted in the DAV and PAV regions of this feather. To reduce handling time and associated stress on the bird, when more than 100 adult mites for one species were observed in a region, the count for this region was assigned to the category ">100".

To confirm the accuracy of the counting method used, we repeated counts on the same individual bird after one or two days, for a subset of nine birds. We then calculated the Intraclass Correlation Coefficient (ICC) [47] using a one-way random model for the total number of mites for each species and for the number of mites per feather. All counts of ">100 mites" were assigned an arbitrary value of 150.

Distribution of mites among and within feathers

Among flight feathers: To assess potential interactions between the two mite species on flight feathers, we first computed the total mite count per feather. For this analysis, the truncated

counts (those assigned to the ">100" category) were replaced by randomly selected values between 100 and 200, as counts only very rarely exceeded 200 mites per region. We then used generalized linear mixed models (GLMM) [48] to explain the count of a given feather mite species by three fixed-effect covariates: i) the log-transformed count of the other mite species (log2 (1+count)); ii) host sex and iii) the relative position of the feather in the wing, here defined as proximal: P1-P3, intermediate: P4-P7 and distal: P8-P10. The host individual was introduced as a random factor. The distribution of counts was assumed to be a zero-inflated negative binomial. Since this analysis depended on random values for the truncated counts, it was repeated 500 times, thus yielding 500 coefficient values and 500 P-values. In the results, we reported the average model values obtained for each mite species. The model estimations were performed using the R package glmmADMB [49]. The same analysis was applied to data from the rectrices, which were classified into only two relative positions, proximal (R1-R3) and distal feathers (R4-R6).

Among feather regions, within a primary feather: To analyze the interaction between the two mite species at the within-feather scale, we restricted our analysis to the presence/absence of each mite species within a feather region. For this purpose, we used a mixed binomial model, where the probability of presence of *Mb* in a given feather region was explained by the presence of *Zo* mites in that same region, the position of the region on the feather (PAV, DAV, PPV or DPV), plus a host random effect. In this analysis, we considered only primaries P6 to P9, where both species were potentially present. The result was reported as an odds-ratio, where a ratio smaller than 1 indicates a negative interaction between the two species.

Niche breadth and niche overlap

Niche breadth and overlap of the two mite species were measured at two different spatial scales using Levins' equations as described by Choe and Kim [19]. First, in order to examine interactions between co-occurring mite species along the entire wing, all primaries were treated as a data set and individual primaries were considered as states. Second, to describe the niche relationships between co-occurring mite species on different parts of the primary feather, the four feather regions were treated as a dataset and individual regions as states. An arbitrary value (150) was assigned for all ">100" counts. The values of niche breadth (B) and niche overlap (O) theoretically range from 0 to 1. However, the calculated value may exceed 1 when the broader-niched species has a larger carrying capacity [50]. Although there are no critical levels with which overlap values can be compared, it has been suggested that values higher than 0.6 should be considered as biologically significant [51].

Stable isotope analyses (SIA)

For SIA analyses, we sampled small fragments of feather barbs containing mites from 20 birds. The two mite species were sampled from the primaries where they were most abundant: P4, P5 or P6 for *Mb* and P9 or P10 for *Zo*. Mites from each individual feather were removed from the barbs, identified and separated by species into pools ranging from 30 to 226 individuals for *Mb* and from 18 to 164 individuals for *Zo*. The pools were then dried in an oven at 45°C for 6 hours, weighed and placed into ultra-clean tin capsules. Sample mass of each mite pool ranged from60 to 200 μg for *Mb* and from 60 to 230 μg for *Zo*, except for three samples for *Mb* and one sample for *Zo* with a low number of mites, resulting in a sample mass ranging from 32 to 58 μg. Barbs were washed in a 0.25 M sodium hydroxide solution, rinsed thoroughly in distilled water to remove any surface contamination, dried in an oven at 45°C to a constant mass and cut into small pieces manually. From the sampled birds, 0.5 ml of blood was also collected and preserved at -20°C. Host blood was lyophilized for 24 hours using a Telstar Cryodos-50 freeze-

dryer and then ground into powder manually. Samples ranging from 300 to 320 μg of blood powder or of feathers were weighed and placed into ultra-clean tin capsules. Fourteen samples of preen gland oil and 13 of wing skin were also analyzed. These samples were taken from dead frozen Cory´s shearwaters from the same island location that had been euthanized at the Recovery Wildlife Center Tafira (Gran Canaria) due to bone fractures. An incision was made in the uropygial gland and the contents were preserved in vials at -20°C. For skin samples, feathers were removed from a small area of the wing at the junction between the humerus and ulna and a sample of epidermis was removed with a scalpel and forceps. Subsequently, all uropygial and skin samples were treated as host blood. Lipids are usually extracted from lipid rich tissues before SIA since it has been shown that lipids are depleted in δ13C values [52]. However, we did not extract lipids from the preen gland oil because this tissue is basically only composed of lipids and it is thought that mites can feed on these secretions. Sample mass ranged from 285 to 335 μg for uropygial gland secretions and from 250 to 300 μg for wing skin. All samples were oxidized in a Flash EA1112 Elemental Analyzer and a pirolizator TC-EA coupled to a Delta C Finnigan MAT mass spectrometer through a Conflo III interface (ThermoFinnigan), where $\delta^{13}C$ and $\delta^{15}N$ signatures were determined (Isotopic ratio mass spectrometry, Serveis Científico-Tècnics of University of Barcelona, Spain). Isotope ratios were expressed conventionally as δ values in ppt (‰) according to the following equation:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$$

where X (‰) is ^{13}C and ^{15}N, and R are the corresponding ratios $^{13}C/^{12}C$ and $^{15}N/^{14}N$, related to the standard values: R_{standard} for ^{13}C is Vienna Pee Dee Belemnite (VPDB), for ^{15}N is atmospheric nitrogen (AIR) (S2 Table). International standards (IAEA CH_7 and IAEA CH_6 for C, IAEA N_1 and IAEA N_2 for N, USGS 34, USGS 40 and acetanilide for both C and N) were run every 12 samples to calibrate the system and compensate for any drift over time. Replicate assays of standard materials indicated measurement errors of ±0.1 and ±0.2‰ for carbon and nitrogen respectively, but these are likely underestimates of true measurement error for complex organics like feathers and mite tissues.

The statistical analyses for mite stable isotopes were performed using SPSS 15.0 for Windows (IBM SPSS Statistics). To test for differences in stable isotopic values among mite species and host tissues (blood and feathers), we applied a linear mixed model (LMM) using the restricted maximum likelihood (REML) estimation method. The type of tissue (*Mb*, *Zo*, host blood and feathers) was treated as a fixed factor and host identity as a random term. Bonferroni corrections on post-hoc comparisons were performed. Preen gland oil and wing skin were not included in the LMM analysis because these tissues were not isolated from the same living birds; however, the mean values for all host tissues and mites and their 95% confidence intervals were visually compared.

Ethics statements

This present work was carried out in a single location, Veneguera, Gran Canaria, Canary Islands and the permits to capture and examine live procellariiform birds were issued by Cabildo Insular de Gran Canaria (authorization n°1169/2011) and Gobierno de Canarias (authorization n° 0795/2011). No other locations were sampled for which specific permission was not required. Fieldwork involved handling a protected seabird species, the Cory's shearwater (*Calonectris borealis*), for which we obtained the corresponding permission. Birds were captured by night in their nests. We sampled small fragments of feather barbs containing mites from primaries P4, P5 or P6 and P9 or P10 and 0.5 ml of blood from the tarsal vein, using a 1 ml syringe, from 20 birds. All procedures were approved by local (Cabildo Insular de Gran

Canaria) and regional (Gobierno de Canarias) authorities and no approval was obtained from any animal ethics committee because authorities did not consider it necessary. All sampling procedures were specifically approved as part of obtaining the field permits. Samples of preen gland oil were taken from dead frozen Cory´s shearwaters obtained from the Recovery Wildlife Center Tafira (Gran Canaria). These birds had been euthanized due to bone fractures.

Results

Infestation and repeatability

All but one of the 60 captured birds harboured feather mites on the flight feathers from the left side of the body. From the 59 birds with mites, four were infested only with *Microspalax brevipes* (*Mb*), while the remaining 55 birds had both *Mb* and *Zachvatkinia ovata* (*Zo*). Usually, mites were located along the length of the rachis, at the base of the barbs, but in heavily laden host individuals, mites also occupied the ventral surfaces of the barbs distal to the rachis.

The repeatability analysis, based on the total number of mites, indicated that the two mite species counts were highly correlated (ICC = 0.983; $F_{[142,143]} = 113.32$; $P < 0.001$ for *Mb* and ICC = 0.956; $F_{[142,143]} = 44.6$; $P < 0.001$ for *Zo*). When considering counts per feather, there was still a significant correlation, but the relationship was weaker (ICC ranging from 0.877 to 1 out of 32 tests corresponding to each primary and tail feather for the two mite species, all $P < 0.001$ for *Mb* and from 0.683 to 1, $P < 0.05$ for *Zo*). Thus, this analysis confirms the validity of our approach to assess spatial distribution of feather mites.

Spatial distribution of feather mites

Among feathers: The two mite species showed differences in their distribution patterns among primary (P) feathers (Fig 2). *Mb* was mainly concentrated on the central primaries (P3-P7), whereas *Zo* showed its highest abundance on the outermost two primaries (P9-P10). However, the two species overlap on a number of distal primaries (from P6 to P9, Fig 2). If we consider the four birds that harboured only *Mb*, the distribution of this mite species was slightly displaced towards the tip of the wing, with the highest peaks reached on the P5-P7 feathers, but with almost no mites occupying the outermost primary feather (P10) (S1 Fig). Rectrices were occupied mainly by *Mb*, but in low numbers compared with primary feathers (S2 Fig). Only two specimens of *Zo* were found on the rectrices of two birds whose presence can be considered accidental.

The GLMM analysis indicated significant differences in the average proportion of mites among feathers. The model used to determine the average coefficient is a multiplicative one. Thus, there were 2.98 times more *Mb* on intermediate than on proximal primaries (average P-value < 0.001) and 1.61 times more *Mb* on distal than on proximal primaries (average P-value = 0.003). Counts of *Mb* were negatively associated with counts of *Zo* (average coef = 0.495; average $P < 0.001$) meaning an average drop of 50.5% in the counts of *Mb* with each doubling of *Zo* abundance. For *Zo*, only intermediate and distal primaries were considered in the analysis, as *Zo* was exceedingly rare on proximal primaries. In this case, differences were also significant *Zo* being 9.5 times more abundant on distal compared to intermediate primary feathers (average P-value < 0.001). As above, the relationship between the counts of *Zo* and *Mb* was negative (average coef = 0.555; average $P < 0.001$), indicating an average drop of 49.5% in the counts of *Zo* for each doubling of *Mb* abundance. On rectrices, the GLMM analysis showed no significant differences in mite numbers between the proximal and distal groups (coef = 0.947; P = 0.53). The effect of host sex was not significant for either primaries (average coef = 1.86; average P = 0.18 for *Mb* counts; average coef = 1.30; average P = 0.66 for *Zo* counts) or rectrices (*Mb* alone, coef = 1.16; P = 0.72).

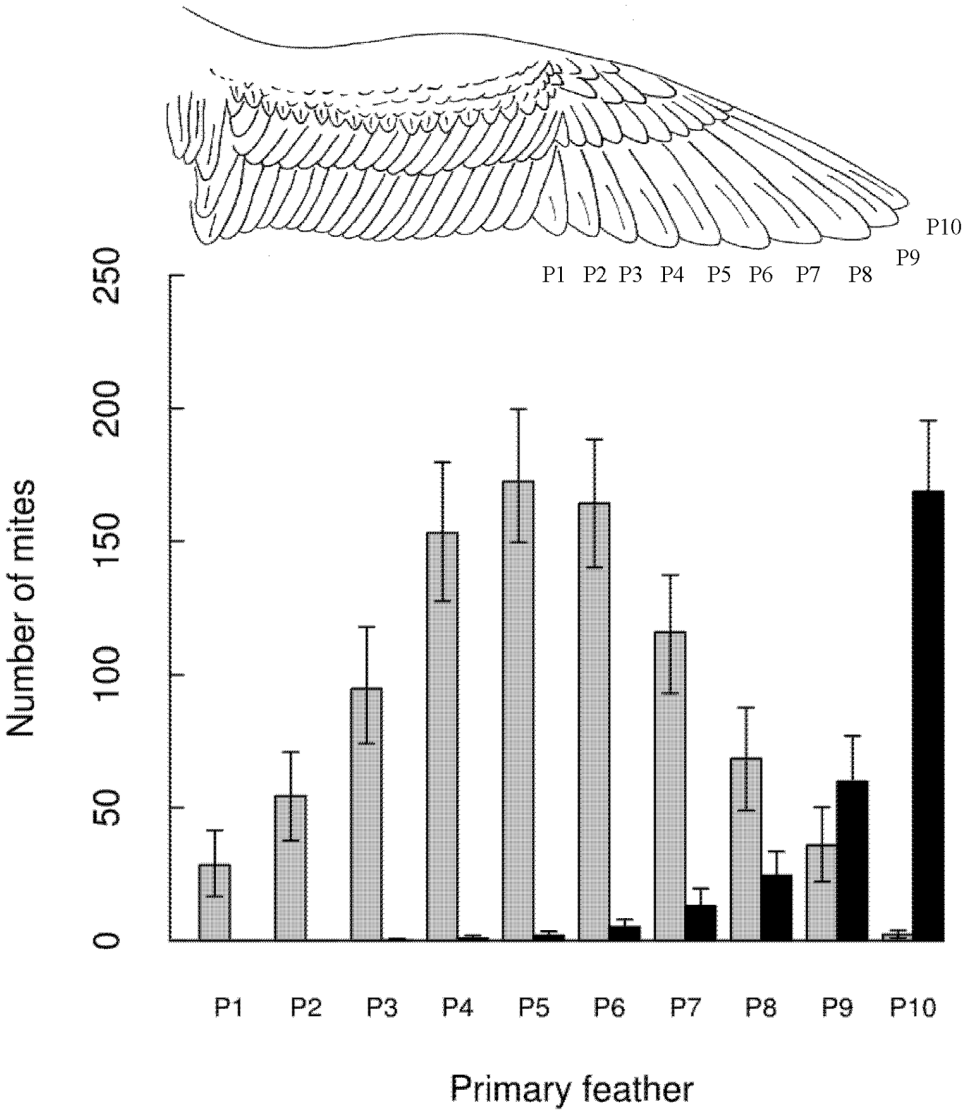

Fig 2. Distribution of *Mb* (gray) and *Zo* (black) in the ten primaries of Cory´s shearwater left wing. Feathers are ordered following their position in the wing from internal (P1) to external (P10) primary feathers. "Number of mites" represents the mean number of mites of each species per feather. The 95% confidence limits were computed by resampling using 500 bootstrapped values.

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Within feathers: Both mite species presented similar distributions among the four regions of the ten primaries, showing a clear preference for the posterior vane, in particular for the distal portion of the posterior vane (DPV), and avoiding the proximal anterior vane (PAV) region (Fig 3A). However, some spatial segregation arose where the two mite species co-occurred (P6-P9) (Fig 3B). In general, there was a tendency for a decreased abundance of the two species when both were present in the same region. By region, the decrease was more marked for *Zo* with respect to *Mb* in the proximal posterior vane region (PPV) and more marked for *Mb* with respect to *Zo* in both the distal (DAV) and the proximal anterior vane (PAV) regions. Overall, the odds-ratio for the presence of *Mb* according to the presence or absence of *Zo* was 0.41 ($P < 0.001$), indicating a reduction of the probability of *Mb* being present on a given feather region if *Zo* was also present on the same feather region.

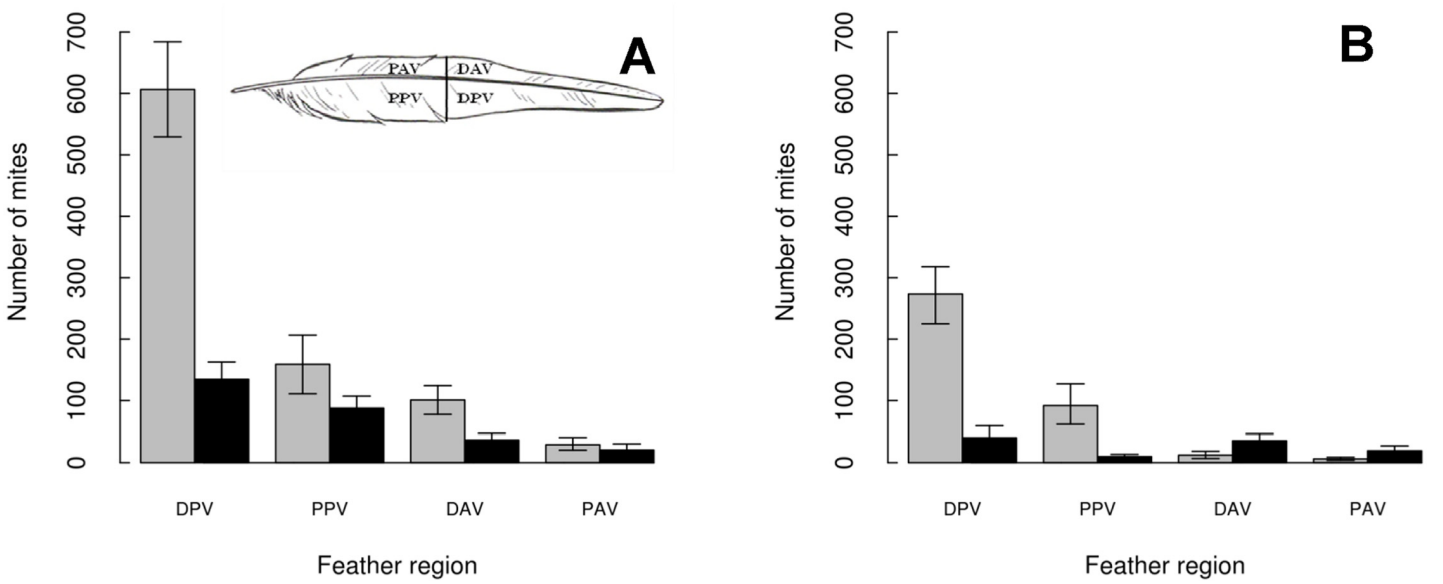

Fig 3. Mean number of mites and 95% confidence interval of *Mb* (grey) and *Zo* (black) across the four regions of all Cory´s shearwater primary feathers (A) and on P6-P9 feathers, where the two mite species co-occur (B). The "number of mites" represents the mean number of mites of each species per feather region. DPV = distal posterior vane; PPV = proximal posterior vane; DAV = distal anterior vane; PAV = proximal anterior vane.

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Niche breath and overlap

To test spatial niche differentiation between the two mite species, we first treated primary feathers as binary states. The niche breadth of *Mb* (B_{Mb} = 0.706) was found to be more than three times larger than that of *Zo* (B_{Zo} = 0.228). Overall, the niche spatial overlap was low between the two feather mite species, but with some asymmetry, so, the niches of *Mb* overlapped with *Zo* (O_{MbZo} = 0.208) to a greater extent than the reverse (O_{ZoMb} = 0.067). In contrast, when we reduced the spatial scale and considered the four feather regions within primaries as states, the niche breadth of *Zo* (B_{Zo} = 0.699) was found to be greater than that of *Mb* (B_{Mb} = 0.497). Within a feather, the niches of the two species overlapped significantly (O_{MbZo} = 0.804 and O_{ZoMb} = 1.131). When the same analyses were restricted to the range of primary feathers where the two species usually overlap, that is from P6 to P9, the within-feather niche breadth of *Zo* (B_{Zo} = 0.827) was also found to be greater than that of *Mb* (B_{Mb} = 0.436), and the two species also overlapped significantly (O_{MbZo} = 0.538 and O_{ZoMb} = 1.020), but there was a decrease in the overlap of *Mb* with *Zo* compared to the overlap when all primaries were considered (Fig 3A and 3B). These results suggest *Mb* specializes more on feather regions than on particular feathers, whereas *Zo* shows stronger affinities for particular feathers with a large use of feather regions.

Trophic relationships

Isotopic values for all tissues (mites, host blood, feathers, preen gland oil and wing skin) did not depart from normality for both ^{15}N and ^{13}C (Kolmogorov-Smirnov test, all $P > 0.05$), except host blood and feathers for ^{13}C ($P < 0.010$).

To investigate feeding preferences of mite ectosymbionts in relation to their hosts, we applied linear mixed model analyses (LMM) to compare the carbon and nitrogen stable isotope values of feather mites and host tissues. LMM showed that stable isotope values differed

Table 1. Mean and percentage of carbon and nitrogen stable isotope values for the two feather mite species and host tissues (feathers, blood, preen gland oil and wing skin), from Cory´s shearwaters breeding in Veneguera. Values report mean and standard error (n = number of analyzed samples).

	Mean C and N			Percentage of C and N	
	N	$\delta^{13}C$(‰)	$\delta^{15}N$(‰)	%C	%N
M. brevipes(Mb)	20	-17.165±0.094	14.044±0.176	49.160±1.889	10.399±0.440
Z. ovata (Zo)	20	-17.354±0.118	13.792±0.188	48.704±0.384	10.448±0.129
P4-P6	20	-14.136±0.126	13.062±0.125	47.475±0.101	14.878±0.052
P9-P10	19	-15.473±0.210	14.039±0.444	47.702±0.126	15.053±0.056
Blood	20	-16.994±0.137	12.022±0.078	47.203±0.437	13.997±0.133
Preen gland oil	14	-21.845±0.325	13.309±0.208	70.102±0.970	3.745±0.326
Wing skin	13	-16.571±0.395	14.262±0.239	50.455±0.802	13.995±0.421

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significantly among tissues (blood, feather and mite species) in both nitrogen ($F_{4, 75.37} = 17$, $P < 0.001$) and carbon ($F_{4, 75.35} = 119.674$, $P < 0.001$) values. Both mite species showed similar mean $\delta^{13}C$ and $\delta^{15}N$ values (Table 1, Fig 4) but no significant differences in nitrogen and carbon were found (D = 0.252, df = 75.195, P = 1.00 for nitrogen; D = 0.189, df = 75.177, P = 1.00 for carbon). Host blood showed the lowest mean value in nitrogen (12.022 ± 0.078), while *Mb* and feathers P9-P10 showed the highest (14.044 ± 0.176 and 14.039 ± 0.444, respectively) (Table 1, Fig 4). Furthermore, nitrogen comparisons among host blood and all other type tissues, including the two feather mite species and the host feathers, were all significant (*Mb*: D = −2.022, $P < 0.001$; *Zo*: D = −1.771, $P < 0.001$; feathers P4-P6: D = −1.040, P = 0.007; feathers P9-P10: D = −2.019, $P < 0.001$). Regarding carbon, the two feather mite species presented the lowest mean values (*Zo*: −17.354 ± 0.118; *Mb*: −17.165 ± 0.094), while feathers P4-P6 exhibited the highest mean value (−14.136 ± 0.126) (Table 1). We found significant differences between values of the two species of feather mites and their corresponding host feathers (*Mb*: D = −3.029, $P < 0.001$; *Zo*: D = −1.884, $P < 0.001$), but not between mites and the host blood (*Mb*: D = −0.171, P = 1.00; and *Zo*: D = −0.360, P = 0.477). Given that the preen gland oil and wing skin were isolated from dead birds, these two host tissues were not included in the linear mixed model analyses. However, preen gland oil presented the lowest mean $\delta^{13}C$ value of all tissue types (−21.845 ± 0.325), including the feather mites, whereas wing skin showed the highest $\delta^{15}N$ value (14.262 ± 0.239) (Table 1, Fig 4).

We also found a significant correlation in carbon isotopic values between each mite species and host blood (Pearson correlation coefficient, $r_{(18)} = 0{,}489$; P = 0.029 for *Mb* and $r_{(18)} = 0{,}618$; P = 0.004 for *Zo*, respectively) (Fig 5A) and between the two mite species inhabiting the same host ($r_{(18)} = 0{,}652$; P = 0.002) (Fig 5B) and in nitrogen isotopic values between *Zo* and P9-P10 feathers ($r_{(17)} = 0{,}746$; P = 0) (S3 Fig), but the latter value may have arisen from a type I error. These results suggest that feather mite diet is mainly based on shared host-associated resources.

Discussion

In the present study, we investigated the spatial distribution and trophic structure of two dominant and morphologically specialized feather mite species, *M. brevipes* and *Z. ovata*, inhabiting the flight feathers of Cory´s shearwaters; to determine whether these mites share the same habitats and food resources, i.e. niche partitioning, and whether inter-species competition for these resources is driving these patterns.

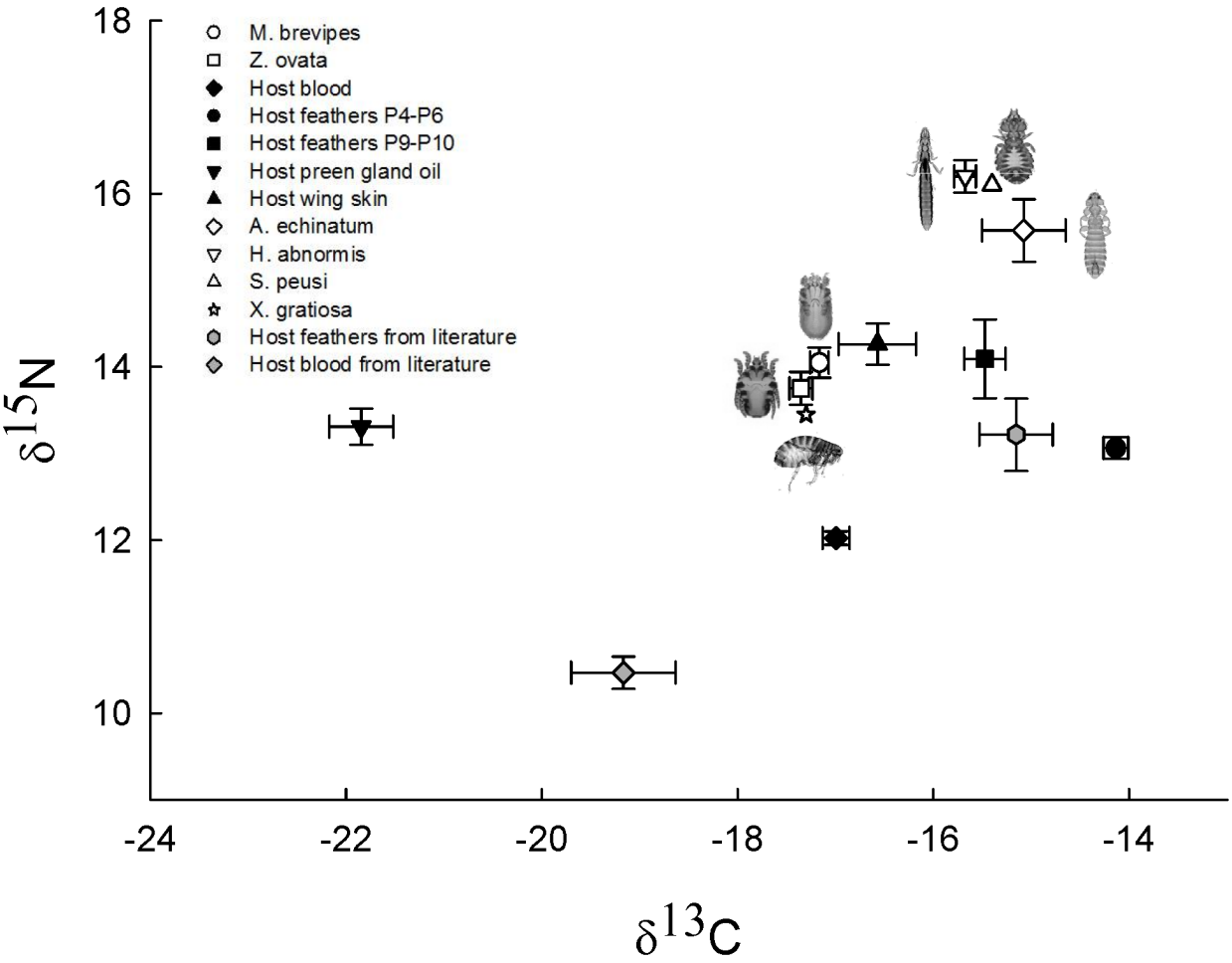

Fig 4. Mean $\delta^{13}C$ and $\delta^{15}N$ isotopic values of feather mites (*Mb* and *Zo*) and host tissues (blood, feathers, preen gland oil and wing skin) from Cory´s shearwater breeding in Veneguera. Preen gland oil and wing skin were isolated from dead birds belonging to the same species and same island location. *Mb* was sampled from P4-P6 feathers and *Zo* from P9-P10. Mean $\delta^{13}C$ and $\delta^{15}N$ isotopic values of other ectoparasite species (three louse species: Austromenopon echinatum, Halipeurus abnormis, Saemundssonia peusi and one species of flea: Xenopsylla gratiosa) and host tissues (blood and feathers) from Cory´s shearwater taken from Gómez-Díaz and González-Solís 2010 were also included. Error bars represent standard error. For X. gratiosa and S. peusi the error bars are not shown because of the small number of samples (n = 2 and n = 1, respectively). Isotopic values were not corrected for fractionation.

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Feather mite spatial distribution

Cory's shearwaters harbour at least nine feather mite species (L. M. Stefan personal observations), some inhabiting flight feathers, whereas others are restricted to contour feathers. The primary feathers of the Cory´s shearwater breeding in Veneguera, Canary Islands, are mainly inhabited by the two vane-dwelling mite species examined in this study.

The two studied species appear clearly segregated across the wing primary feathers of the host, with *Mb* mainly inhabiting the central primaries (P3-P7) and *Zo* mostly restricted to external primaries (P9-P10). In most of the published studies of within-host distribution of feather mites, the highest mite concentrations have been observed on central primary feathers, with low densities or absence on outer primaries and avoidance of first secondary feathers [12,19,21]. In the present study, the distribution of *Mb* followed this general pattern (concentration on central primaries), but for *Zo* the highest concentrations were found in the outermost two primaries (P9-P10). Our results regarding *Zo* are consistent to some extent with the

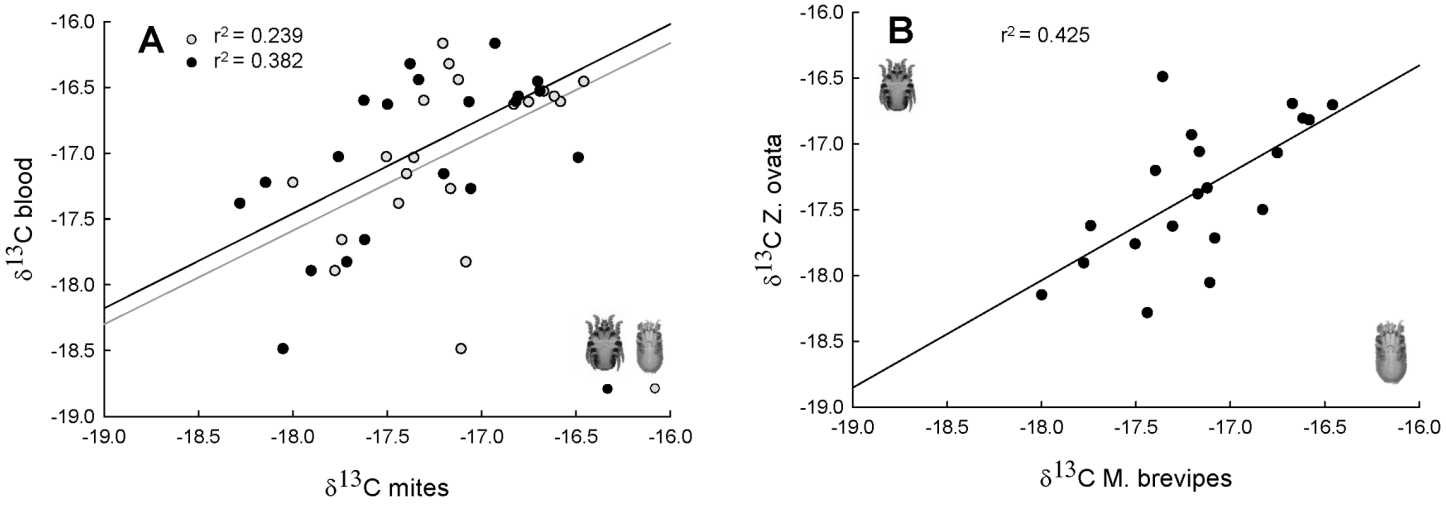

Fig 5. Correlations of carbon isotopic values between each mite species (*Mb* in grey circles and *Zo* in black circles) and host blood (A), and between *Mb* and *Zo* inhabititng the same individual host (B), for 20 Cory´s shearwaters sampled in Veneguera.

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distribution of *Zachvatkinia caspica* in the Caspian Tern primaries (*Hydroprogne caspia*) [53]. The plumage-space occupied by feather mites could be wider than estimated if the juvenile stages, whose distribution we could not assess by eye, occupy different regions of feathers or wings than do the adults. However, determining the niche occupied by juvenile stages would only be possible by destructive sampling (e.g. removing main primary feathers), which is not possible for a protected species such as *Calonectris borealis*. Contrary to the differences observed in spatial distribution among primary feathers, the two mite species studied here display similar habitat preferences at the within-feather scale. Both species seem to prefer the proximal and distal posterior vane (DPV and PPV regions) and to avoid the proximal anterior vane (PAV).

Several factors may be responsible for microhabitat selection in feather mites. As vane-dwelling feather mites normally inhabit the ventral surfaces of the barbs, barb size and spacing may be of primary importance [19,53]. Both species analyzed in this study have a flattened and heavily sclerotized body, but *Mb* individuals are smaller (adult length around 330 μm and width around 230 μm; measurements from present study) than *Zo* (adult male length around 670 μm and width around 420μm; adult female length around 420 μm and width around310μm; measurements from present study). These differences in body size could be due to species-specific habitat preferences. During fieldwork we observed that both species of mites usually lie along the rachis of the feather, and do not occupy the sides of the barbs (except in highly parasitized hosts), suggesting that the body length should match the interbarb width. But, the primary feathers most commonly occupied by the two mite species exhibited very similar interbarb widths (S4 Fig and S1 Text) and, therefore, interbarb space cannot explain observed differences in spatial segregation.

Another factor that may influence mite distributions could be air turbulence during flight. Due to the strong aerodynamic forces acting over the most external wing feathers, mites seem to avoid this wing region and prefer the median wing region, which may provide additional protection against wind turbulence and feather friction [19]. This is consistent with the distribution of the smaller *Mb* mainly on central primaries, but it does not explain however occupancy patterns of P9 and P10 by *Zo*, which seems associated with some specific morphological traits, in particular their leg structure. *Zo* possesses more separated and elongated forelegs and

more laterally inserted hind legs than *Mb*, possibly allowing them to withstand the strong air movement over the outer primaries. The mite distribution can also be influenced by the grooming behavior (preening and scratching) of birds and a number of studies had reported the role of bill and claw morphology for controlling parasites [54,55]. However, this could only be tested with manipulative experiments that alter the bird's ability to preen, experiments that are difficult to apply on seabirds.

The pattern of segregation observed between *Mb* and *Zo* could also be induced by past and/or current competition. Some indirect evidence has been reported on two mites inhabiting kittiwakes *Rissa* spp [19], and on three feather mite species inhabiting the flight feathers of common sandpiper *Actitis hypoleucos* [56]. In both cases, however, distribution data was partially obtained from unrelated host species. In addition, a recent study on two feather mite species inhabiting migratory and sedentary European blackcaps, *Sylvia atricapilla*, showed that mite distribution was primarily influenced by intrinsic, species-specific habitat preferences rather than interactions between the mite species; however, the authors found some evidence of interspecific competition when both mite species occurred on the same sedentary host individuals [25]. In the present study, the two mite species were generally segregated across the primary feathers and showed species-specific morphology, suggesting microhabitat adaptations from past competitive exclusion. However, there was also partial spatial overlap between the two species on P6-P9 feathers, which indicates potential for current habitat competition. Indeed, the distribution of *Mb* on the four birds harbouring only this mite species was slightly displaced towards the outermost primaries, usually occupied by *Zo*, in comparison with the distribution of *Mb* on birds sharing the two mite species (Fig 2 and S1 Fig). Likewise, under current competition, we would expect the abundance of one species to negatively affect the abundance of the competing species. Our results agree with this prediction when both species were present on the same feather, they showed lower overall numbers than when the same feather was occupied by a single species. Similarly, niche overlap among feather regions decreased when both species were present on the same feather. Moreover, the average coefficient of abundance based on individual counts, showed a negative relationship between the two species, that is, high counts of one species were associated with low counts of the other. In general, *Zo* appears as a stronger competitor than *Mb*, except for the PPV region where there was a stronger reduction of *Zo* abundance in the presence of Mb. Overall, these findings clearly support current competition as a factor shaping the distribution and abundance of feather mites within hosts.

Isotopic signatures of feather mites

Another way mites can diversify their niche to reduce competition is by consuming different food resources. To date, however, the feeding preferences and diet of feather mites remains largely unstudied. In our study, we used SIA analyses to investigate whether the two target species overlap in diet. Our study is the first to examine the trophic structure of feather mites using this method. Both feather mite species, *Mb* and *Zo*, exhibited similar carbon and nitrogen isotopic values. Likewise, the carbon signatures between the two species inhabiting the same individual host were highly correlated, suggesting similar dietary niches. This finding, together with the fact that the two mite species tend to inhabit different primary feathers, indicates that niche partitioning between the two species occurs through spatial rather than trophic segregation.

Here, we considered four possible food items for the mites: blood, skin or feather remains and preen gland oil. Interestingly, of the different host tissues compared, mite isotopic values matched most closely with host blood. That is, mites showed an enrichment of about 2‰ in nitrogen signatures compared to host blood, a value within the expected range of enrichments in nitrogen observed among consumers and their diets [57], and, of the two host tissues (blood

and feathers), only carbon isotopic values from blood matched those of the mites. Moreover, we found isotopic values of mites to be close to the values for fleas, known blood feeders, obtained in a previous study investigating the trophic structure of three louse and one flea species from *Calonectris* shearwaters using SIA [40] (see Fig 4). All together, these results imply that host blood is a major food resource for both mite species. However, several other lines of evidence argue against blood as a direct resource for feather mites. First, the chelicerae of both species have the usual chelate-dentate morphology as those of most feather mites [14] (S5 Fig), which is designed for scraping rather than piercing or sucking. These mites are, therefore, unable to puncture host tissues and are constrained to swallowing liquids or small solid materials attached to the feathers. Second, the examination of several slide-mounted specimens at high magnification showed no evidence of blood in their guts, but rather of clear oily material or small mineral-like fragments (S6 Fig). Finally, these mite species live along the feather rachis, where there is no blood to feed on, and there is no evidence that mites move to the skin of the host at any time.

Previous studies on mites suggested that the exogenous material that adhere to feather barbs (scurf, algae, fungi, bacteria, spores, or pollen grains) is one of the main resources for feather mite species [14,31]. However, this is in marked contrast with our isotopic results, which showed a significant correlation between carbon isotopic values of the mites and those from the blood of its individual host (Fig 5A). This correlation can only be explained if mites feed on some resources directly (e.g. blood, skin or preen gland oil) or indirectly (fleas and lice exuviae or excrements) derived from host tissues. Nevertheless, this does not completely discard the possibility that Cory's shearwater mites feed to some extent on exogenous material. However, measuring the isotopic ratios of the exogenous material caught in the plumage is virtually impossible to do and this limitation could have influenced our isotopic results.

Apart from exogenous material, skin scales and feather fragments have been found in the mite guts, but they were common only in one feather mite species from herons, *Ardeacarus ardeae* [14,30]. In this study both carbon and nitrogen values of the two species of mites were slightly depleted in relation to host skin and feathers (Fig 4), results which rule out these tissues as major food sources. However, it is important to mention that isotopic values of feather may not be as homogeneous as other tissues, because their isotopic values change according to the food consumed when each feather was grown [57,58]. Indeed, we found different isotopic values for P4-P6 compared to P9-P10, but values of the mite species occurring on each of these groups of feathers did not mirror these differences. So far, our results indicate that both mite species feed on some host tissue generated during breeding period (when both, blood and mites were sampled), but not directly on feathers themselves.

Finally, many authors suggest that preen gland oil (predominantly fatty acids and waxes) smeared onto the feathers to maintain feather condition and impermeability is an important food for feather mites [14,30,31]. Carbon values of mites were too enriched (4.49–4.68‰) in relation to preen gland oil, comparing with those previously reported for feather lice or fleas in relation to the tissues consumed on the same seabird host species [40]. However, the correlation in carbon isotopic values between mites and host blood may suggest carbon is taken from the preen gland oil, since its lipids contain mainly carbon and are deposited in uropygial gland through the blood, while nitrogen may be acquired from some exogenous material (i.e. bacteria, algae or fungi).

Conclusions

In this study, we examined the spatial and trophic segregation of feather mites co-occurring in a seabird host, as well as the role of interspecific competition in explaining these patterns. Our

results on spatial niche partitioning showed that the two mite species occupy clearly distinct regions in flight feathers: *Zo* occurs mainly in the outermost primaries and *Mb* in the intermediate primaries and this pattern results from a combination of microhabitat adaptations and ongoing competition. Regarding trophic segregation, our results on mite diet indicated that the two feather mite species show little trophic niche partitioning and likely share the same host food resources, probably preen gland oil, complemented with some exogenous food resources. These results support the prediction that spatial partitioning can only occur when feather mites share the same food requirements. We also show that although past microhabitat specialization may have led to specific morphological differences between the two feather mites allowing them to inhabit different feathers, current interference competition is still playing an important role in shaping the spatial community structure of feather mites. This study also opens new and exciting research perspectives on the trophic ecology of feather mites, calling into question the impact of these arthropods on their host. Our diet results are however preliminary and should be further confirmed and refined using next generation sequencing approaches and fatty acid analyses to identify specific food items in the mite gut. Finally, by combining spatial and trophic approaches in co-occurring seabird feather mites, our work illustrates how symbiotic infracommunities offer excellent models to obtain replicate communities and test niche partitioning hypotheses.

Supporting Information

S1 Fig. Distribution of *Microspalax brevipes* in the primary feathers of Cory′s shearwater left wing for four birds harbouring only this mite species (light gray) and for the 56 birds harbouring both mite species (dark gray). Feathers are ordered following their position in the wing from internal (P1) to external (P10) primary feathers.
(TIFF)

S2 Fig. Distribution of *Microspalax brevipes* in the six feathers of Cory′s shearwater left tail. Feathers are ordered following their position in the tail from internal (R1) to external (R6) feathers. "Number of mites" represents the mean number of mites of each species per feather. The 95% confidence limits were computed by resampling using 500 bootstraped values.
(TIFF)

S3 Fig. Correlations of nitrogen isotopic values between *Z. ovata* and P9-P10 feathers for 19 Cory′s shearwaters sampled in Veneguera. For one bird we did not sampled P9-P10 feathers.
(TIFF)

S4 Fig. Interbarb width across all ten primaries for each of the four feather regions. The boxplots correspond to the primary feathers, which are ordered following their position in the wing from internal (P1) to external (P10) feathers (from left to right). The interbarb width was measured on four dead birds. Error bars represent standard error. DPV = distal posterior vane; PPV = proximal posterior vane; DAV = distal anterior vane; PAV = proximal anterior vane. Note that mites were not counted in the DAV and PAV regions of the P10 due to structural features of this feather.
(TIFF)

S5 Fig. *Microspalax brevipes* (A) and *Zachvatkinia ovata* (B) chelicera.
(TIFF)

S6 Fig. Gut content of a *Zachvatkinia ovata* female from Cory´s shearwater showing a detritus bolus of small mineral fragments.
(TIFF)

S1 Table. *Microspalax brevipes* and *Zachvatkinia ovata* counts on the ten primaries (P1-P10) and six rectrices (R1-R6) for 60 birds.
(XLS)

S2 Table. Stable isotopic values obtained for the two feather mite species (*Microspalax brevipes* and *Zachvatkinia ovata)* and host tissues (feather, blood, preen gland oil and wing skin) analyzed in this study.
(XLS)

S1 Text. Interbarb width measurement.
(DOC)

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Author Contributions

Conceived and designed the experiments: JG-S EG-D. Performed the experiments: LMS EG-D. Analyzed the data: LMS EG-D EE. Contributed reagents/materials/analysis tools: JG-S. Wrote the paper: LMS EG-D HCP KDM JG-S.

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SUPPLEMENTARY INFORMATION

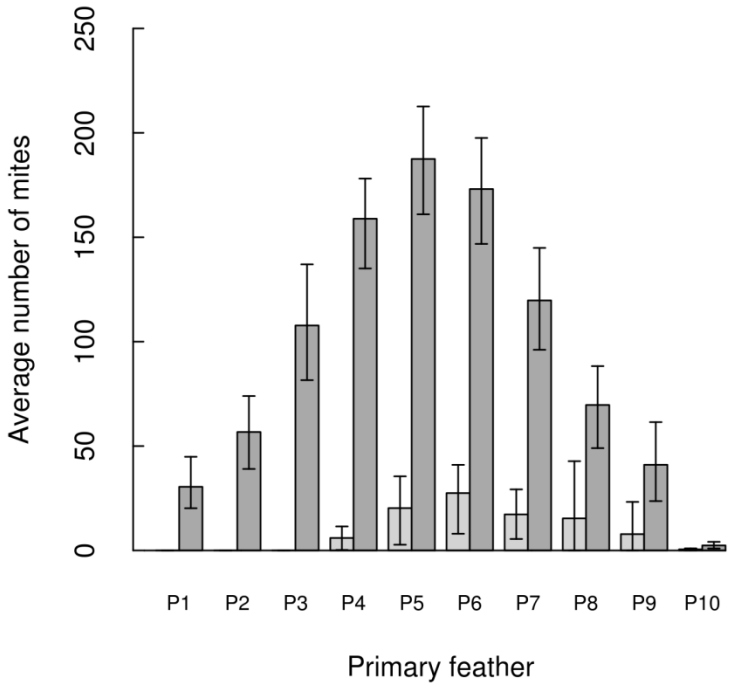

Figure S1. Distribution of *Microspalax brevipes* in the primary feathers of Cory´s shearwater left wing for four birds harbouring only this mite species (light gray) and for the 56 birds harbouring both mite species (dark gray). Feathers are ordered following their position in the wing from internal (P1) to external (P10) primary feathers.

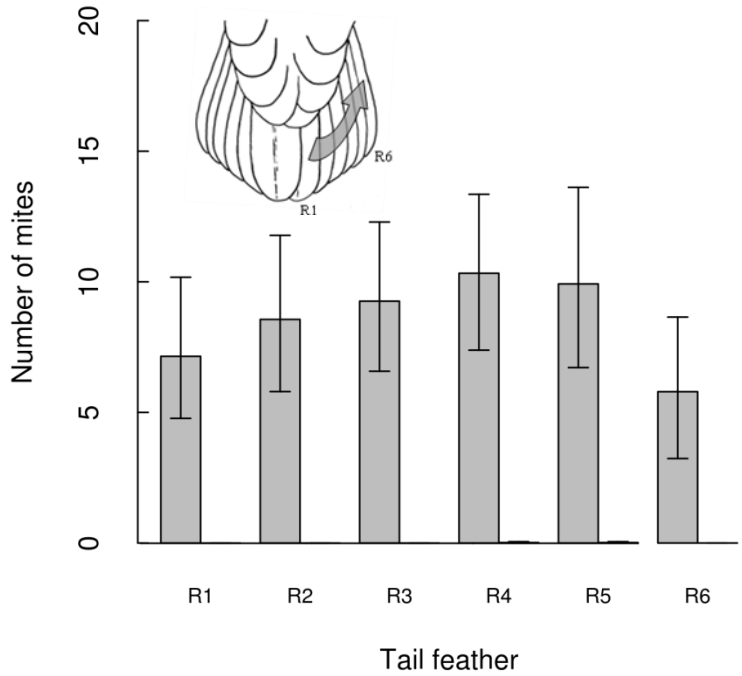

Figure S2. Distribution of *Microspalax brevipes* (gray) in the six feathers of Cory´s shearwater left tail. Feathers are ordered following their position in the tail from internal (R1) to external (R6) feathers. "Number of mites" represents the mean number of mites of each species per feather. The 95% confidence limits were computed by resampling using 500 bootstraped values.

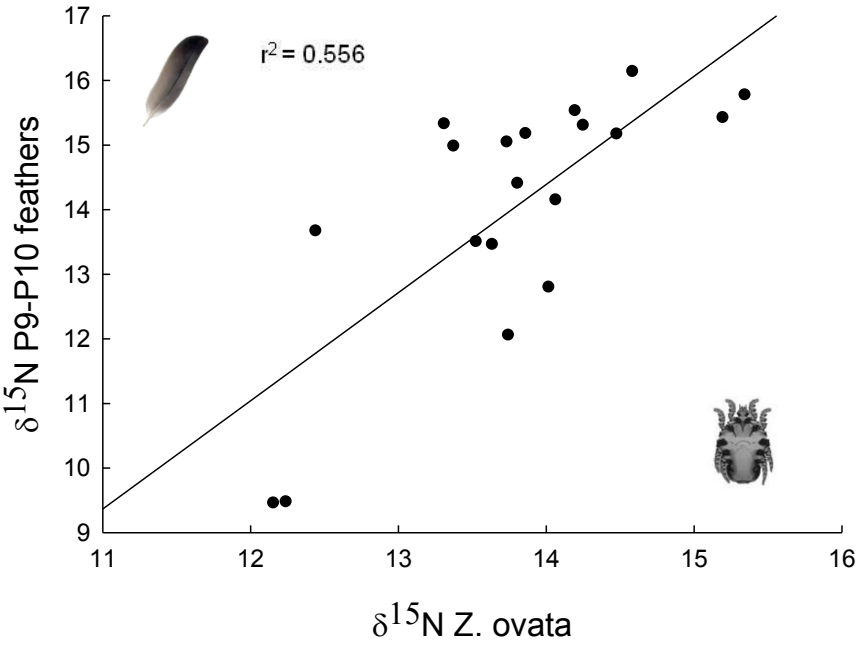

Figure S3. Correlations of nitrogen isotopic values between *Z. ovata* and P9-P10 feathers for 19 Cory´s shearwaters sampled in Veneguera. For one bird we did not sampled P9-P10 feathers.

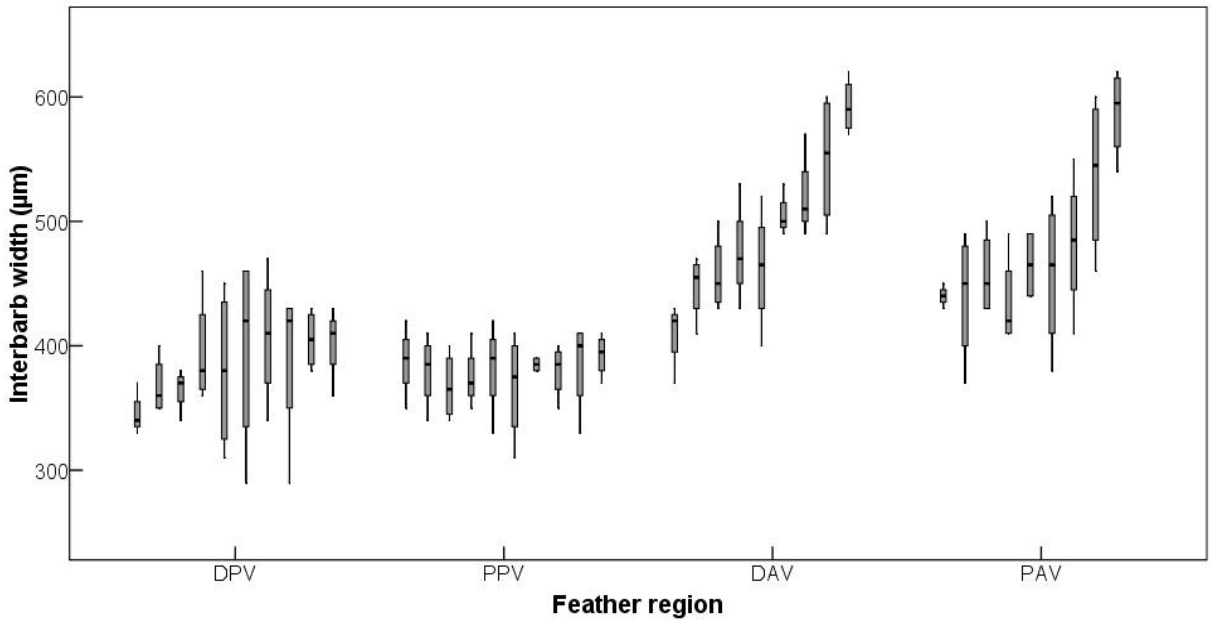

Figure S4. Interbarb width across all ten primaries for each of the four feather regions. The boxplots correspond to the primary feathers, which are ordered following their position in the wing from internal (P1) to external (P10) feathers (from left to right). The interbarb width was measured on four dead birds. Error bars represent standard error. DPV = distal posterior vane; PPV = proximal posterior vane; DAV = distal anterior vane; PAV = proximal anterior vane. Note that mites were not counted in the DAV and PAV regions of the P10 due to structural features of this feather.

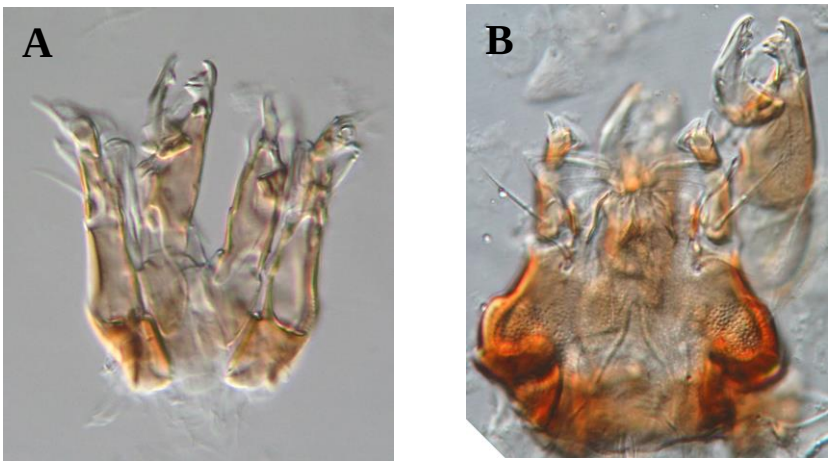

Figure S5. *Microspalax brevipes* (A) and *Zachvatkinia ovata* (B) chelicera.

Figure S6. Gut content of a *Zachvatkinia ovata* female from Cory´s shearwater showing a detritus bolus of small mineral fragments.

TEXT S1. INTERBARB WIDTH MEASUREMENT

During fieldwork we observed that both species of mites usually lie along the rachis of the feather, predicting that the length of their bodies should match the width of the interbarb space. Therefore, we measured the interbarb width from photographs of primaries (from dead birds belonging to the same species and from the same island location) to determine how much this varied among different primaries and along the length of a given primary feather, and to check whether this could be related to mite distribution. The interbarb width was measured in each of the four feather regions for all ten primaries in four birds using an Olympus SC30 camera for light microscopy adapted to an Olympus SZX10 stereo microscope. In each feather region, eight consecutive interbarb widths were measured and averaged.

The interbarb width measurements showed no significant differences among feather regions and among primary feathers (Supporting Information Fig. S4). DPV and PPV regions, which are preferred by both feather mite species, exhibited very similar interbarb widths. In PAV and DAV regions, interbarb widths appeared to be slightly higher on the outermost primaries, but also showed the lowest number of mites.

GENERAL DISCUSSION

GENERAL DISCUSSION

THE DIVERSITY OF FEATHER MITE COMMUNITIES

Feather mites are among the most diverse and common ectosymbionts living permanently on birds (Gaud and Atyeo 1996, Proctor and Owens 2000, Proctor 2003). Usually birds, including seabirds, harbour a great diversity of mites due to the topology of each feather that provides unique microhabitats, such that a single bird or even a single feather can have several mite species living in very well defined areas and interacting differently with their hosts (Gaud and Atyeo 1996, Proctor 2003). Despite their abundance and prevalence in birds (about 2 500 species described so far), little is known about the feather mite community of seabirds, especially Procellariiformes and Phaethontiformes.

The feather mite species previously identified from Procellariiformes and Phaethontiformes included six families (Alloptidae, Avenzoariidae, Dermationidae, Epidermoptidae, Xolalgidae and Freyanidae), with *Zachvatkinia*, *Microspalax* and *Brephosceles* being among the most frequent genera associated with these hosts (Peterson 1971, Mironov 1989a, Atyeo and Gaud 1991, Gaud and Atyeo 1996, Proctor 2003). In this thesis, I have examined feather mites from 12 procellariiform and phaethontiform species breeding in the NE Atlantic and Mediterranean area and found that this community is much more diverse than has been previously reported. The seabirds examined harboured a unique mite fauna composed of 10 genera and 38 species (eight genera and 33 species in 11 species of Procellariiformes; three genera and five species in one species of Phaenthontiformes). The acarofauna of Procellariiformes was distinct compared with the Phaethontiformes, *Ingrassia* being the only mite genus shared by the two seabird orders. Overall, 10 mite species belonged to the family Avenzoariidae (genera *Zachvatkinia*, *Rhinozachvatkinia* and *Promegninia*), 21 species to the family Alloptidae (genera *Microspalax*, *Brephosceles*, *Plicatalloptes*, *Laminalloptes* and *Onychalloptes*), and seven species to the family Xolalgidae (genera *Ingrassia* and *Opetiopoda)*. Indeed, *Zachvatkinia* and *Brephosceles* were among the most common feather mite genera, being found on all 11 procellariiform species, followed by *Microspalax* and *Ingrassia*, present in nine and 10 host species, respectively. Apart from the *Ingrassia aequinoctialis*, the only species of Phaethontiformes examined also hosted three feather mite species belonging to the genus *Laminalloptes* and one species belonging to the genus *Onychalloptes*. When considering the number of mite species per mite genus, *Brephosceles* was represented by 11 species, *Zachvatkinia* and *Ingrassia* by six species each, *Microspalax* by five species, *Laminalloptes* by three species, *Rhinozachvatkinia* and *Promegninia* by two species each and *Plicatalloptes*, *Onychalloptes* and *Opetiopoda* by one species each.

At the host genus level, *Hydrobates* hosted the highest number of mite species (10), followed by *Calonectris* with nine species, *Bulweria* with eight species, *Puffinus* with six species, *Phaethon* with five species and *Pterodroma* with only three mite species. The diversity is also high at the host species level. That is, I found that all seabirds hosted at least three feather mite species (e.g. Cape Verde petrel and Mediterranean shearwater), with Cory´s shearwaters, Cape Verde shearwaters and Bulwer´s petrels showing the richest mite community (nine and eight species, respectively). Furthermore, Manx shearwaters, Boyd´s shearwaters and European storm-petrels were inhabited by six feather mite species, Scopoli´s shearwaters, band-rumped storm-petrels and red-billed tropicbirds by five species and Macaronesian shearwaters by four species. Rarefaction curves on mite richness reached a plateau in all except four host species (Cape Verde shearwater, Mediterranean shearwater, Macaronesian shearwater and Cape Verde petrel), indicating that we detected all common mite species in most of the sampled hosts. Overall, seabird feather mites showed a clear specialization by host genus, with each seabird genus harbouring distinct feather mite species. Nevertheless, three mite species (*M. brevipes*, *B. puffini* and *Plicatalloptes sp.1*) were shared by *Calonectris* and *Puffinus* shearwaters. This finding could be explained by the close phylogenetic relationship between these two procellariid genera. Indeed, the separation of the two genera is relatively recent and remains contradictory (Gómez-Díaz et al. 2006, Nunn and Stanley 1998). Within each host genus, mite species co-occurred on different host species. For instance, five mite species (*Z. ovata*, *M. brevipes*, *B. puffini*, *B. sp.4* and *Plicatalloptes sp.1*) were shared by all *Calonectris* species, whereas three mite species (*I. calonectris*, *R.*

calonectris and *P. calonectris*) were found on Cory´s and Cape Verde shearwaters. In the case of *Puffinus* shearwaters, three mite species (*Z. sp.1*, *B. puffini* and *I. dubinini*) were found on all *Puffinus* hosts, one species (*M. brevipes*) was found on three *Puffinus* species, whereas two mite species (*P. sp.1* and *B. sp.5*) inhabited Manx shearwaters and Boyd´s shearwaters. Although, only one mite species of a given genus was typically found infesting each host genus, two different species of *Microspalax* co-occured in Cory´s shearwaters and the majority of procellariiform species harboured at least two *Brephosceles* species. This could be an indication that these mite genera evolve faster than their hosts, i.e. higher mutation rates, and/or that there have been some duplication events through their co-evolutionary history. These two types of scenarios have been previously described for lice (Page et al. 1997, Paterson et al. 2000, Johnson and Clayton 2003).

Through my studies I found a high proportion of new, undescribed species and several cases of cryptic diversity in seabird feather mites. Thus, among the 33 mite species found to inhabit Procellariiformes, 17 were new species, six of which were described in the context of this thesis (Stefan et al. 2013, 2014, Mironov et al. 2015) (Table 1). In recent years DNA barcoding has become the gold-standard for parasite species identification and the discovery of cryptic forms (Whiteman et al. 2006, Malenke et al. 2009, Locke et al. 2010, Doña et al. 2015). In this thesis, I provided DNA barcode data (600-bp fragment of the mitochondrial cytochrome *c* oxidase subunit I gene) for three mite species: *Rhinozachvatkinia calonectris*, *Promegninia calonectris* and *P. bulweriae* that can be used for their correct identification. Furthermore, based on data from two mitochondrial genes (12S and 16S), I revealed the presence of six cases of cryptic species. For example, *Zachvatkinia oceanodromae*, which is specific to the band-rumped storm-petrel, included a potentially cryptic species restricted to Ilheu de Cima islet. Morphology is in-line with the genetic patterns, but classical morphological features are not distinct enough to treat this new lineage as a distinct separate species solely based on traditional criteria (S. Mironov, personal observation). A similar case is reported for *L. simplex* inhabiting red-billed tropicbirds in Cape Verde. Four putative cryptic species from three morphospecies (*Brephosceles puffini*, *B. sp.1* and *Plicatalloptes sp.1)* were found on *Calonectris* shearwaters. Of these cryptic lineages, *B puffini* B and *P. sp.1* B were found to be widely distributed across colonies, whereas *B. sp.1* B was limited to two islands (Berlengas and Azores Is.) and *P. sp.1* C to Berlengas. From an evolutionary point of view, these observations could represent the initial stages of sympatric speciation, without the expression of specific morphological characters (McCoy et al. 2001, 2005). However, more specimens belonging to each of these potential cryptic species should be collected and redescribed using both detailed genetic and morphological methods (ex., geometric morphometrics, nuclear markers) in order to confirm that these new cryptic lineages represent distinct species and not simply strong intraspecific divergences.

Altogether, the high number of new and cryptic mite species I've found over the course of my research can be explained by the combination of a lack of detailed studies on seabird acarofauna and the specific biology of these hosts which spent most of their life at-sea and breed on isolated oceanic archipelagos. In this context, my thesis research fills an important gap in our knowledge, not only because it contributes to a better understanding of host-specificity in mites, i.e. seabird host-feather mite associations and community assemblages, but also because it has helped improve our overall understanding of the biodiversity and taxonomy of this group of arthropods.

COMMUNITY STRUCTURE IN FEATHER MITES AT DIFFERENT SPATIAL SCALES

In this thesis, I also examined the community structure of seabird feather mites using presence-absence data at different spatial scales, from a large geographic scale across all host species and sampled locations to among different seabird species within an archipelago and finally to within specific host genera and species. I found that the overall mite community was clearly structured by host genera, whereas the geographic structuring of feather mites within host genera or within a single host species was relatively weak and sometimes negligible.

Table 1. New feather mite species found on seabirds breeding in the NE Atlantic and Mediterranean area

New feather mite species	Host species	State of description
Fam. Avenzoariidae		
Zachvatkinia sp.1	*Puffinus puffinus, P. boydi, P. baroli, P. yelkouan*	undescribed
Zachvatkinia sp.2	*Bulweria bulwerii*	undescribed
Zachvatkinia sp.3	*Pterodroma feae*	undescribed
Rhinozachvatkinia calonectris	*Calonectris borealis, C. edwardsii*	Stefan et al. 2014
Rhinozachvatkinia sp.1	*Hydrobates pelagicus*	undescribed
Promegninia calonectris	*Calonectris borealis, C. edwardsii*	Mironov et al. 2015
Promegninia bulweriae	*Bulweria bulwerii*	Mironov et al. 2015
Fam. Alloptidae		
Brephosceles sp.1	*Bulweria bulwerii*	undescribed
Brephosceles sp.2	*Bulweria bulwerii*	undescribed
Brephosceles sp.3	*Bulweria bulwerii*	undescribed
Brephosceles sp.4	*Calonectris diomedea, C. borealis, C. edwardsii*	undescribed
Brephosceles sp.5	*Puffinus puffinus, P. boydi*	undescribed
Brephosceles sp.6	*Hydrobates pelagicus*	undescribed
Plicatalloptes sp.1	*Calonectris diomedea, C. borealis, C. edwardsii* *Puffinus puffinus, P. boydi*	undescribed
Fam. Xolalgidae		
Opetiopoda bulweriae	*Bulweria bulwerii*	Stefan et al. 2013
Ingrassia calonectris	*Calonectris borealis, C. edwardsii*	Stefan et al. 2013
Ingrassia micronota	*Bulweria bulwerii*	Stefan et al. 2013

The main seabird genera considered here (*Calonectris, Puffinus*, *Bulweria, Pterodroma* and *Hydrobates*) harboured clearly distinct feather mite infracommunities, although some overlap was observed among *Calonectris* and *Puffinus* samples. Some regional differences in feather mite communities were also observed (Western Mediterranean, Eastern Mediterranean, Northern NE Atlantic, Central NE Atlantic and Southern NE Atlantic), but these were not as evident as among host genera. The same pattern was also found at a smaller geographic scale (e.g. within Cape Verde Archipelago), where feather mite communities were clearly structured by host genus/species, even when species were breeding in sympatry. Structure was not observed among islands within an archipelago. These combined results suggest that feather mites tend to specialize on their host species. This presumably high degree of specialization could be inflated by the incomplete sampling of closely related host species. Indeed, some of the mite species detected in the present study were first records for the examined host species, but were previously found on other closely-related host species. One should therefore be careful about concluding on the degree of host specificity before all closely-related host species have been thoroughly sampled.

After the extensive survey in NE Atlantic and Mediterranean seabirds, the seabirds of the Cape Verde archipelago were found to harbour the richest diversity of feather mite species, with 27 out of 33 mite species. This archipelago may therefore represent an important biodiversity hotspot for avian feather mites. Although based on molecular data, similar results have also been reported for *Ornithodoros* seabird ticks (Gómez-Díaz et al. 2012). The high tick diversity found in Cape Verde archipelago was suggested to be the result of repeated colonization events via host movements followed by post-colonization adaptation to specific hosts. Indeed, as these islands lie approximately 700 km off the coast of Africa, they may represent an important stop-over spots for a diverse range of birds, resulting in the dissemination of associated parasites and pathogens.

Feather mite communities also appeared somewhat different among host species within a host genus (e.g. *Calonectris* and *Puffinus*), indicating some structure among closely related host species, possibly resulting from their parapatric distributions. For instance, due to the parapatric distribution of the three Calonectris species, the direct contact between their individuals is very limited, which may also limit mite transmission among these hosts, this leading to a more clear structuring of their mite communities. Interestingly, mite

community composition of Scopoli´s shearwaters was more similar to that of the Cape Verde shearwaters, despite the closer geographic proximity between the Cory´s and Cape Verde shearwaters. This may be a reflection of the higher relatedness between Scopoli´s and Cape Verde shearwaters, compared to the more ancestral Cory´s shearwater (Gómez-Díaz et al. 2006). Within a host species, no geographic structuring of feather mite infracommunities has been observed for Scopoli´s shearwaters in the Mediterranean Sea, whereas certain degree of segregation was found among localities for Cory´s shearwaters. The community structure observed in Cory´s shearwaters corresponds to a similarity by distance, as shown by the correlation between the matrice with the similarity index in mite communities and that with the geographic distances among sampled localities. Similar results have been reported for parasites of fish hosts, where adjacent localities displayed similar parasite communities than distant ones (Poulin and Morand 1999, Vidal-Martínez and Poulin 2003).

Finally, although not significant, there was a clear trend in larger seabird species to harbour a greater number of mite species. That is, on average *Calonectris* and *Puffinus* shearwaters, tended to host a greater number of species than the smaller seabirds, such as Bulwer´s petrels and European storm-petrels. Therefore, the number of mite species for a given bird may increase with the body mass of its species possibly because larger seabirds provide more micro-habitats for mite species not to compete among them.

UNDERSTANDING THE DIVERSIFICATION PROCESS IN SEABIRD FEATHER MITES

To investigate the factors and processes driving mite diversification and population structure, I applied a comparative and community approach to evaluate the relative importance of host and parasite factors. I first explored the genetic structure of feather mite species co-occurring on sympatric seabirds breeding in the Cape Verde archipelago to test the contribution of host specificity in driving the community structure and diversity in this group. Feather mites are considered highly host specific ectosymbionts and therefore, I expected to find strong host-dependent genetic structure for most feather mites. Host specificity is one of the most fundamental features of any parasite species because it reflects the breadth of a parasite's ecological niche and determines the likelihood that a parasite will successfully colonize new habitats or adapt to new hosts (Poulin and Mouillot 2003). The level of host specificity may simply be due to limited opportunities of parasites for dispersal and colonization of new hosts (Clayton et al. 1992, Johnson et al. 2002, Whiteman et al. 2004), but may also be determined by specific adaptations to particular hosts, such that parasites are incapable of surviving and reproducing on foreign hosts (Tompkins and Clayton 1999, Reed et al. 2000). For feather mites showing high host specificity, host adaptation may then, in turn, promote ectosymbiont specialization and diversification (Lajeunesse and Forbes 2002, Malenke et al. 2009).

In the Cape Verde archipelago several closely-related seabird species share the breeding habitat, such as the Cape Verde shearwater and Boyd´s shearwater which are both syntopic and sympatric (see detailed map of Cape Verde Archipelago in Chapter 2.1, Figure 1). This kind of configuration should provide some opportunities for mite exchange among host species. According to the host switching hypothesis, the three mite species that are shared among Cape Verde shearwater and Boyd´s shearwater could have jumped from one host species to another, whereas the remaining 29 unshared mite species should show specific adaptations to each host. Indeed, genetic analyses revealed variable patterns of genetic structure among feather mites. As expected, the great majority of feather mite species from Cape Verde Islands exhibited strong host-associated genetic structure, including two of the three shared species (*M. brevipes, B. puffini*). *Plicatalloptes sp.1* showed no significant genetic differentiation between host species, suggesting it may be a true generalist species compared to the other two species. These results highlight the importance of host species in shaping the genetic structure of feather mites. Host race formation, or specialization after a host shift, has been documented for several ectoparasites (i.e. lice and ticks) infesting sympatric avian hosts (Johnson et al. 2002, McCoy et al. 2001, 2003), and surely represent an important mechanism driving parasite diversification. However, why some mite genera specialize and not the others remains an open question. The differences observed in the degree of host specificity among mite species may reflect, at least partially, mite preferences for certain

microhabitats on the host body and/or different species-specific barriers to dispersal (see below for a further discussion).

I next examined the effect of geography by focusing analyses on three sister *Calonectris* hosts that share the same community of feather mites and are distributed across relatively large spatial scales. Since the three host species themselves are strongly structured spatially (Gómez-Díaz et al. 2006, 2009), I expected that the host traits leading to seabird divergence would also promote parasite isolation and differentiation. Interestingly, my results show that feather mites display contrasting patterns of genetic structure, with two mite species, *M. brevipes* and *Z. ovata*, exhibiting particularly low genetic diversity and high gene flow among hosts and localities, whereas the other species showed the opposite pattern. The wide-scale presence of *M. brevipes* and *Z. ovata* on the three hosts could suggest that these species evolve at lower rates than their hosts and that divergence by isolation may still be building up. However, in this case, we would have expected to see significant variation in haplotype frequencies among the host types. A more parsimonious explanation is that these mite species have failed to speciate in response to host divergence, and therefore, gene flow among parasite populations is currently higher than that of their hosts. In contrast to *M. brevipes* and *Z. ovata*, *Brephosceles* and *Plicatalloptes* feather mites showed high genetic diversity and significant structure among hosts/regions (e.g. only a single haplotype was shared among the three *Calonectris* species and three geographic regions, with cryptic lineages present on certain host species/geographic locations). These patterns could be due to the large scale isolation of these mite populations among regions; but this requires some explanation as the effect of isolation was not detectable for *M. brevipes* and *Z. ovata*. As the different geographic regions and the host species are confounded in our analysis, an alternative hypothesis is that patterns are linked to host-associated adaptation, which would fit well with our findings in the previous study where geographic distance was minimized to evaluate the role of the host species (see above). Within regions, where the host species was controlled for, no significant population structure among islands was found for any mite species, suggesting that gene flow at this spatial scale is high for all mite species. Gene flow at this spatial scale is most likely associated with social interactions during foraging and reproduction. However, gene flow at regional scale is harder to explain. .

The two molecular approaches I used for studying feather mite community structure (comparing mite communities among multiple sympatric hosts breeding in a restricted geographical area and among closely related host species from the same genus across a wide geographic range) indicated a role for both parasite and host factors in shaping the evolution and the population genetic structure of feather mites.

As highly specialized ectosymbionts, feather mites are adapted to inhabit well-defined host microhabitats (e.g. contour feathers, soft down feathers, skin surface, subcutaneous layers or feather quills) (Gaud and Atyeo 1996, Dabert and Mironov 1999, Proctor 2003). Feather mites are considered to be transmitted by direct physical contact between parents and offspring or between conspecifics during mating or other social interactions (e.g. fighting, flock feeding, grooming) (Dabert and Mironov 1999, Proctor 2003). The variation in the patterns of genetic structure and the degree of host specificity observed could be linked to the dispersal strategy of feather mites and to habitat preferences of different feather mite species (Dabert et al. 2015). In their study, Dabert et al. (2015) suggested that patterns of diversification and population structure in two feather mite species (*Zachvatkinia isolata* and *Alloptes stercorarii)* inhabiting the plumage of arctic and long-tailed skuas, were shaped by different rates of inter-host transmission conditioned by microhabitat use on the host. Our results support this hypothesis. While large vane-dwelling mites with dorso-ventrally flattened and heavily sclerotized bodies (e.g. *Z. ovata* and *M. brevipes*) are specialized to inhabit the ventral surfaces of flight feathers (Mironov 1989a, Stefan et al. 2015), other mite genera, such as *Brephosceles* and *Plicatalloptes*, include small and weakly sclerotized mites, which occupy more protected areas of the plumage (e.g. wing coverts and soft body feathers) (Peterson 1971, Bourgeois and Threlfall 1979, Dabert et al. 2015, L. Stefan personal observations). Therefore, mite exchange is more likely to occur for the more exposed vane-dwelling mites, such as *Zachvatkinia* and *Microspalax*, than for smaller feather mites living within more protected microhabitats, increasing dispersal potential and reducing the role of genetic drift in generating divergence. The higher dispersal potential of these mites is associated with a broader host range and should have

significant consequences for their population dynamics. Mite specific use of particular host habitats may explain patterns of gene flow at local scales, but some explanation for gene flow at regional scales is required. Indeed, procellariiform seabirds spend most of their life in the open ocean and breed on remote oceanic islands, features which should limit mite dispersal in time and space. However, studies have shown that different seabird populations can mix in specific and restricted foraging areas during the non-breeding period (González-Solís et al. 2007) and this may provide opportunities for ectosymbionts to switch among individual hosts, and ultimately among different host species. This hypothesis was suggested to explain the surprising homogeneity of populations of three louse species exploiting three *Calonectris* species (Gómez-Díaz et al. 2007). Mite dispersal between host populations could also be favored by juvenile birds prospecting other breeding colonies than their natal colony or adult birds changing their breeding locality (Boulinier et al. 2016). More detailed observations at sea during overwinter using modern tracking devices to identify the specific colonies that come into contact, combined with the use of highly polymorphic genetic markers for the mites to identify recent gene flow events, are now required to enable us to explore these hypotheses in more detail.

PROXIMATE FACTORS SHAPING MITE INFRACOMMUNITIES

According to classic niche theory, species can coexist in heterogeneous environments by reducing interspecific competition via niche partitioning (Schoener 1983). Different types of niche partitioning can occur, such as spatial niche partitioning, when species share a food resource but use different subsets of the habitat, and trophic partitioning, when different species specialize on distinct food resources in sympatric habitats (Amarasekare 2003). As more than one mite species inhabits the plumage of a bird species, mites can segregate among bird feathers, this niche partitioning being induced by either space or resource use. To answer this question, I investigated the spatial and trophic structure of two dominant and morphologically specialized feather mite species inhabiting the flight feathers of Cory´s shearwater *Calonectris borealis* to determine whether niche partitioning occurs among these mites (i.e. spatial or trophic partitioning) and whether interspecific competition for resources drives within host distributional patterns.

The distribution of *M. brevipes* and *Z. ovata* showed clear spatial segregation among flight feathers. *Microspalax brevipes* showed high preference for the central primaries (P3-P7) and tail feathers, whereas *Z. ovata* was restricted to the two outermost primaries (P9-P10). However, the two mite species overlapped on some central primaries (from P6 to P9), and statistical modeling showed that *Z. ovata* tended to outcompete *M. brevipes* when they co-occurred. Previous studies have examined the spatial distribution of vane-dwelling mites on individual hosts and at different levels (e.g. between feathers, within feathers) and some general patterns, such as low density or absence of mites on external wing feathers, mite concentration on central wing feathers and the avoidance of first secondary feathers, have been observed (Choe and Kim 1989, Jovani and Serrano 2004, Mestre et al. 2011, Fernández-González et al. 2015). The distribution of *M. brevipes* followed these general patterns, but not that of *Z. ovata*, which was consistent only to some extent with the distribution of *Zachvatkinia caspica* in the Caspian Tern primaries (*Hydroprogne caspia*) (Bridge 2003). While *Z. caspica* was found to inhabit the five outermost primaries with relatively few mites present on P10, *Z. ovata* showed the highest concentrations on the two external primaries (P9-P10). Contrary to the spatial distribution among feathers, the two mite species displayed similar habitat preferences at the within-feather scale. Both species showed a clear preference for the posterior vane, in particular for the distal portion of the posterior vane, and avoiding the proximal anterior vane. This contrasts with studies reporting spatial segregation of different mite species across longitudinal regions of individual feathers (Mestre et al. 2011, Fernández-González et al. 2015) and suggests that the relevant scale for examining mite competition is the between-feather scale.

The distribution of feather mites within and among feathers can be affected by several factors such as temperature, humidity, air turbulences or barb size (Bridge 2003, Wiles et al. 2000). As vane-dwelling feather mites normally inhabit the ventral surfaces of the barbs, barb size and spacing may be of primary importance. Both species analyzed here have a flattened and heavily sclerotized body and usually lie along the rachis of the feather, suggesting that the body length should match the interbarb width. *Microspalax brevipes* individuals are smaller than *Z. ovata*, differences that could be due to species-specific habitat preferences. However, the

primary feathers most commonly occupied by the two mite species exhibited very similar interbarb widths, indicating that interbarb space cannot explain observed differences in spatial segregation. Due to the strong aerodynamic forces in flight, air turbulence may have a significant impact. Mites may avoid the most external part and prefer the median wing region, which provides more protection against wind turbulence and feather friction (Choe and Kim 1989). This is consistent with the distribution of the smaller *M. brevipes* on central primaries, but it does not explain the occupancy pattern of *Z. ovata*. As *Z. ovata* possesses more separated and elongated forelegs and more laterally inserted hind legs than *M. brevipes*, these mites may be able to withstand the strong air movement over the outer primaries and thus better exploit this microhabitat on the host (Figure 1).

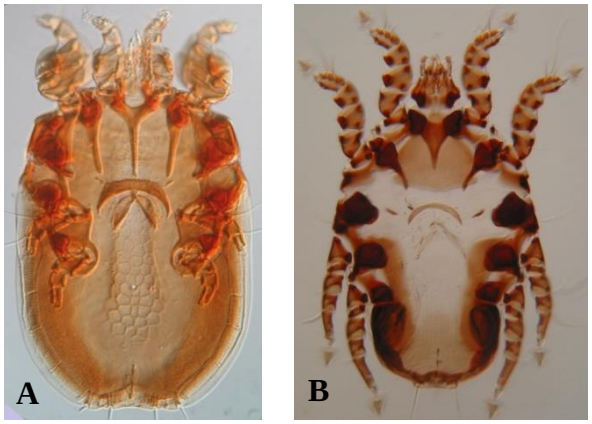

Figure 1. *Microspalax brevipes* (A) and *Zachvatkinia ovata* (B) inhabiting the flight feathers of *Calonectris borealis*.

I suggest that the pattern of segregation observed between *M. brevipes* and *Z. ovata* has been induced by either past and/or current competition as has been shown in a recent study of two feather-dwelling mite species, *Proctophyllodes sylviae* and *Trouessartia bifurcata*, inhabiting European blackcaps (Fernández-González et al. 2015). The segregation across the primary feathers and species-specific morphology, suggests that each species has adapted to exploit specific microhabitats, which may have resulted from past competitive exclusion. However, the partial spatial overlap observed between the two species on P6-P9 feathers also indicates the potential for current habitat competition. If competition for space is still occurring, we would expect the abundance of one species to negatively affect the abundance of the competing species. Our results agree with this prediction. When both species were present on the same feather, the average coefficient of abundance based on individual counts showed a negative relationship between the two species, e.g. high counts of one species were associated with low counts of the other. Similarly, niche overlap among feather regions decreased when both species were present on the same feather, suggesting the two mite species interfere with each other and segregate to different feather regions. In general, *Z. ovata* appeared to be a stronger competitor than *M. brevipes*, as in most feather areas, there was a stronger reduction of *M. brevipes* abundance in the presence of *Z. ovata*. On-going competition therefore still seems to be shaping the distribution and abundance of feather mites within hosts.

Another way mites can diversify their niche to reduce competition is by consuming different food resources. Studying feeding preferences and trophic relationships of feather mites is a difficult endeavor due to their small size and the inability to maintain them off of the bodies of their normal hosts. Previous studies have focused on the study of the morphological structure of the mouthparts and gut content and suggested that feather mites feed principally on oil produced by the uropygial gland, and on debris trapped between the feather barbs, such as fungal spores and pollen grains (Blanco et al. 2001, Galván et al. 2008) and sporadically skin remains and feather fragments (Proctor 2003). In this thesis, the trophic relationships between the two target mite species and the host have been investigated using a novel approach, the analysis of stable isotopes (SIA) (carbon and nitrogen) in mite tissues and from potential host food resources. The SIA revealed that all feather mite species exhibited similar carbon and nitrogen isotopic values and that isotopic signatures of mites inhabiting the same individual host were highly correlated, suggesting similar dietary niches.

I then went further with this analysis to examine four possible food items for the mites: host blood, skin, feather remains and preen gland oil. Interestingly, mites showed an enrichment of about 2‰ in nitrogen signatures compared to host blood and carbon isotopic values matched those of the blood. The value for nitrogen is within the expected range of enrichments in nitrogen observed among consumers and their diets (Ramos and González-Solís 2012). Isotopic values of mites are also close to the values for other known blood feeders, which were obtained in a previous study that used SIA to study the trophic ecology of various parasites, fleas and lice, of *Calonectris* shearwaters (Gómez-Díaz and González-Solís 2010). This suggested that host blood could be a major food resource for both mite species, either coming from mites feeding directly on this resource or indirectly via the exuviae or excrements of co-habiting fleas and lice. However, previous evidence argues against this host resource; chelate-dentate morphology of the chelicerae renders direct blooding feeding impossible and the absence of blood in the mite gut and along the feather rachis argue against an indirect source of host blood (Proctor 2003). The feathers themselves are an unlikely food source because of the mismatch in the SIA between feathers and mites. Many studies have suggested that preen gland oil represents an important diet resource for feather mites (Blanco et al. 2001, Proctor 2003). My results indicate that carbon values of mites are too enriched in relation to preen gland oil. However, the correlation in carbon isotopic values between mites and host blood may indicate that carbon is taken from the preen gland oil, since its lipids contain mainly carbon and are deposited in uropygial gland through the blood. The last possible source for food in feather mites is exogenous material adhering to feather barbs (Blanco et al. 2001, Proctor 2003). For now, this possibility cannot be discarded based on current evidence because measuring the isotopic ratios of the exogenous material caught in the plumage is virtually impossible to do.

The results of my study on trophic ecology therefore show that both competing mite species show similar resource use and within feather habitat preferences. However, they tend to inhabit different primary feathers, suggesting that niche partitioning between the two species mainly occurs through spatial rather than trophic segregation. Mite ecology likely plays an important role in structuring the community at host individual level, and may directly influence the evolutionary patterns observed at higher spatial scales. More detailed analyses of the microhabitat and resource use of other members of the mite community could help shed light on the importance of within-host competition in shaping community and population genetic structure.

CONCLUSIONS

CONCLUSIONS

1. A vast and largely unrecognized diversity of feather mites composed of 38 species, half of which represented new undescribed species, was found on seabirds breeding in the NE Atlantic Ocean and Mediterranean Sea. In addition to species described based on morphology, several putative cryptic species were found based on molecular analyses. These results indicate that true feather mite diversity is still largely underestimated due to a lack of detailed surveys, and that genetic, morphological and ecological data should be combined to better assess mite diversity.

2. The morphological and genetic studies of feather mite-seabird associations indicated clear host-associated structure of feather mites at both large (across all breeding colonies) and smaller geographical scale (within Cape Verde archipelago), with each seabird genus harbouring a relatively distinct mite community. However, a few mite species were more generalists and were shared by closely-related host genera. This differential degree of host specificity may reflect, at least partially, mite preferences for particular microhabitats on the host body (e.g. flight feathers vs. body feathers) along with more or less permissive barriers for dispersal. However, a complete sampling of all closely related host species should be performed before concluding on the degree of host specificity of the different seabird feather mite species.

3. Weak or non-existent geographic structure of seabird feather mite communities was detected within a host genus as well as among breeding locations within a single host species. These results suggest that mite dispersal regularly occurs between host populations and host species. This exchange could be favored by seabird mixing in breeding and wintering areas at sea or within interspecific colonies, by juvenile birds prospecting among breeding colonies or by adult birds that change their breeding locality. These findings support the hypothesis that host behaviour, here as limited inter- and intra-specific interactions, is of key importance for the exchange and dissemination of avian ectofauna.

4. Within host individuals, the distribution of two dominant vane-dwelling mite species inhabiting *Calonectris borealis* showed clear spatial segregation among flight feathers. While one species showed high preference for the central primaries the other one was restricted to the two outermost primaries. As isotopic analyses indicated similar values for the two mite species, their diet is similar and most likely based on preen gland oil, complemented with some exogenous food resources. These results suggest that spatial partitioning is limiting competition between these co-occuring mites and may lead to the evolution of microhabitat adaptations.

5. Altogether, this thesis provides a comprehensive characterization of seabird feather mite diversity, an outline of patterns of seabird-feather mite species/lineages associations and a significant contribution to our understanding of the ecological and evolutionary processes that have lead to these patterns. It demonstrates, in particular, the essential role of microhabitat adaptation for the evolution of ectosymbiont biodiversity, both due to its impact on reducing local resource competition and on conditioning dispersal probability at different spatial scales. Detailed examination of specific host and mite traits associated with host specificity, ecological studies to better understand interspecific host interactions and studies of co-phylogenies comparing patterns of mite-host diversification are now necessary to identify the relative roles of isolation and adaptation in generating mite diversity. Population genetic studies using highly variable nuclear markers (microsatellite or SNPs) would also be particularly informative to disentangle contemporary and historical patterns of the divergence and would help identify the associated processes.

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