UNIVERSIDADE ESTADUAL PAULISTA
“JÚLIO DE MESQUITA FILHO”
INSTITUTO DE BIOCIÊNCIAS

PROGRAMA DE PÓS-GRADUAÇÃO EM ZOOLOGIA

HORIZONTAL TRANSFER, GEOGRAPHIC DISTRIBUTION AND SPECIATION IN FEATHER MITES IN BRAZIL (ASTIGMATA)

TRANSFERÊNCIA HORIZONTAL, DISTRIBUIÇÃO GEOGRÁFICA E ESPECIAÇÃO EM ÁCAROS DE PENAS NO BRASIL (ASTIGMATA)

LUIZ GUSTAVO DE ALMEIDA PEDROSO

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Transferência horizontal, distribuição geográfica e especiação em ácaros de penas no Brasil (Astigmata)

Horizontal transfer, geographic distribution and speciation in feather mites in Brazil (Astigmata)

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RESUMO

A especificidade é um aspecto crucial que governa as interações entre simbiontes e hospedeiros. Geralmente a especificidade está ligada ao potencial de transmissão, à plasticidade adaptativa, e à disponibilidade de hospedeiros de simbiontes. Apesar da importância, a especificidade ainda é um assunto complexo em muitos sistemas simbionte-hospedeiro, especialmente quanto ao potencial de simbiontes emergirem em novos hospedeiros. Ácaros de penas (Astigmata: Analgoidea e Pterolichoidea) são exemplos de simbiontes altamente específicos. Por serem ectosimbiontes obrigatórios e de aparente baixa mobilidade, a transmissão em ácaros de penas ocorre de maneira íntima no contato entre hospedeiros. Ocorrendo primeiramente verticalmente, dos genitores para seus descendentes, durante o desenvolvido cuidado parental das aves. Acredita-se que a transmissão vertical seja um fator chave responsável pela alta especificidade observada em ácaros de penas, onde muitas espécies de ácaros são encontradas apenas em espécies intimamente relacionadas. Portanto, sistemas que alteram os padrões de transmissão de ácaros de penas oferecem uma oportunidade valiosa de investigação da relação entre transmissão, especificidade, e distribuição geográfica. Aqui entra o chupim (*Molothrus bonariensis*), uma ave nidoparasita generalista que depende de outras espécies de aves para encubar seus ovos e cuidar de seus ninhegos, o que impede a transferência vertical intraespecífica de ácaros de penas. Não é surpresa que esse sistema ainda não tenha sido estudado, já que o conhecimento sobre ácaros de penas ainda é incipiente na região neotropical. Portanto, aqui investigamos a fauna de ácaros de penas do chupim e de seus hospedeiros potenciais no Brasil. A presente tese se divide em duas partes principais: a primeira parte foca em inventariar ácaros de penas do chupim e busca entender como os ácaros encontrados se relacionam com a especificidade e a transmissão nesse sistema; a segunda parte foca na distribuição geográfica desses ácaros de penas no Brasil, também buscando correlacionar a especificidade. Por múltiplas linhas de evidência (abundância, prevalência, filogenia e cofilogenia) foi possível diferenciar ácaros específicos do chupim de ácaros adquiridos verticalmente de aves por ele parasitadas. Com base nessas diferenças foi possível estimar taxas de transmissão vertical e horizontal nesse sistema. Mesmo sem possuir transmissão vertical de ácaros de penas, o chupim apresentou uma fauna de ácaros específicos diversa, composta por cinco espécies em cinco gêneros. Essa especificidade é mantida por transferências horizontais intraespecíficas, estimadas a serem pelo menos três vezes maiores que do que as taxas de transmissão vertical. Extrapolando para outros sistemas, a transmissão vertical de ácaros de penas, ainda no ninho, é importante para uma primeira aquisição desses simbiontes, porém a transmissão horizontal é provavelmente a principal responsável pela difusão desses ácaros nas populações de seus hospedeiros. Quanto a padrões de distribuição, por análises de modulação geográfica foi possível identificar que a distribuição da fauna de ácaros não específicos no chupim segue padrões de preferências de uso de seus hospedeiros. Foi possível também corroborar a eficiência da transmissão horizontal em manter uniforme a distribuição de seus ácaros específicos. Por fim, são mostrados padrões de distribuição geográfica em ácaros de penas em diferentes populações de hospedeiros de ampla distribuição no Brasil, com potenciais espécies crípticas. Novas espécies de ácaros de penas também foram descritas. As descobertas e novidades aqui trazidas contribuem para um novo entendimento sobre a dispersão e organização de ácaros de penas em seus hospedeiros, comprovando um maior padrão de eficiência de transferências horizontais até então não estimado para o grupo. Os dados também indicam um papel fundamental da especificidade como fator limitante da distribuição geográfica e da colonização de novos hospedeiros por esses simbiontes.

Palavras-chave: Acariformes, Ave, Simbiose, Filogenia, Hospedeiro

ABSTRACT

The specificity is a crucial aspect ruling host-symbiont interactions. It is usually linked to the symbiont's transmission potential, adaptation plasticity, and availability of compatible hosts. Despite its importance, specificity is still a complex subject in many host-symbiont systems, especially regarding their potential to emerge into new hosts. Feather mites (Astigmata: Analgoidea and Pterolichoidea) are examples of such highly specific symbionts. Because of their obligatory association and apparent low mobility, their transmission occurs by intimate contact between avian hosts, usually through vertical transmission from parents to offspring. This vertical transmission is believed to be a key factor sustaining the high host specificity in feather mites, as many mite species are found solely on closely related hosts. Systems disrupting this transmission pattern offer valuable opportunities to investigate host specificity and other aspects of feather mite biology, such as geographic distribution. Here enters the shiny cowbird (*Molothrus bonariensis*), a brood parasitic bird that relies on other passerines to rear their chicks, preventing the usual vertical transmission of feather mites. It is no surprise that this system has never been studied as the knowledge of feather mites in the Neotropical region is still incipient. Therefore, here we investigate the feather mite fauna on the shiny cowbird and their most common hosts in Brazil. The present thesis is divided into two main subjects: a first part focused on recording the feather mite fauna from the shiny cowbird and understanding their relationship with aspects of host specificity and transmission; and a second part focused on the geographic distribution of feather mites in Brazil, also connecting it to host specificity properties. By multiple lines of evidence (abundance, prevalence, phylogenetic, and co-phylogenetic), it was possible to differentiate specific-to-cowbird mites from mites acquired from their foster parents and estimate rates of vertical and horizontal transmission in this system. Even lacking vertical intraspecific transmission, the shiny cowbird presented a diverse feather mite fauna composed of five species in five genera. This specific fauna is only transmitted horizontally, which occurs at a rate three times higher than vertical transmissions. Estimating for other systems, the vertical transmission of feather mites is important for a primary acquisition of these symbionts, while the horizontal transmission is likely the main responsible for the dispersal of these mites on host populations. Regarding their distribution, modularity analyzes identified patterns of distribution for the non-specific mites on shiny cowbirds explained by their preferences in host usage in different regions. It was also possible to corroborate the efficiency of horizontal transmissions in keeping their specific mite fauna evenly distributed in Brazil. Finally, patterns of the geographic distribution of feather mites on different host populations are shown in Brazil, with potential cryptic species. New feather mite species were also described. The novelties in the present work collaborate to understand the dispersion and organization of feather mites on their hosts, acknowledging a higher efficiency of horizontal transmissions than expected in these apparently low mobile symbionts. Our data also reinforce the importance of the host specificity as the limiting factor for the distribution and the colonization of new hosts by feather mites.

Keywords: Acariformes, Bird, Symbiosis, Phylogeny, Host

SUMMARY

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INTRODUCTION

GENERAL INTRODUCTION

Taxonomic concepts – what are feather mites?

Among the vastly diverse arthropod Subphylum Chelicerate, an expressive variety of the Arachnida Subclass Acari (mites) developed adaptations to fully or partially live in association with birds (Aves). These adaptations allowed mites to exploit nearly all possible habitats and microhabitats offered by these hosts, which in birds include their nesting sites, their external appendages (i.e., feathers), inside the quill of feathers, the superficial and subcutaneous layers of their skin, and reaching as deep as inside their respiratory tract and visceral tissues. This diversity of bird-associated mites sums more than 3,000 described species in at least 40 families (Knee et al. 2008), representing around 5.5% of all named mite diversity in the world, an astonishing number if we consider Acari as one of the most diverse metazoan groups with more than 54,000 named species (Beaulieu et al. 2019; Walter & Proctor 2013). Simultaneously, Acari is also one of the least known clades, with nearly 1 million species estimated in the group, which highlights the still long path to building a solid Acari knowledge.

Traditionally Acari is recognized as a monophyletic Subclass divided into two large Superorders – Parasitiformes and Acariformes. The Acari monophyly is, however, up to debate due to contrasting topologies in molecular phylogenetic studies, sometimes placing Acariformes more related to other Arachnida Orders such as Solifugae or Pseudoscorpiones than to Parasitiformes (Arribas et al. 2020; Dabert et al. 2010; Lozano-Fernandez et al. 2019; Pepato & Klimov 2015; Sharma et al. 2014). Debates aside, bird-associated Acari are found on both Superorders. Noteworthy bird-associated Parasitiformes include the Order Ixodida of soft (Argasidae) and hard ticks (Ixodidae), and the Order Mesostigmata, with the red mites (Dermanyssidae), the nasal mites (Rhinonyssidae), and the fowl mites (Macronyssidae), all of medical and veterinary importance (Bassini-Silva et al. 2019; Camargo-Mathias et al. 2020; Hilario-Pérez & Dowling 2020; Ogrzewalska & Pinter 2016). However, the vast majority of bird-associated mites are, however, in the Superorder Acariformes – also known as the "mite-like mites" (Walter & Proctor 2013). Acariformes further split into two major Orders, the Trombidiformes, which in association with birds includes the Suborder Prostigmata; and the Sarcoptiformes, represented on birds by the Suborder (or Hyporder) Astigmata (Krantz & Walter 2009; Mullen & OConnor 2019). The most common bird-associated Prostigmata are the quill mites of the family Syringophilidae, followed by the chiggers (Trombiculidae), and the harpirhynchine mites (Harpirhynchidae) – all true parasites that feed on their host’s fluids (e.g., blood, lymph) (Bochkov et al. 2015; Fain et al. 2002; Jacinavicius et al. 2018; Mullen & OConnor 2019; Skoracki et al. 2013). Astigmatan mites, on the other hand, are well-known as one of the most diverse mite groups to live in association with vertebrate hosts (Krantz & Walter 2009; OConnor 1982; Walter & Proctor 2013). On birds, Astigmata includes some of the most strikingly specialized mites, such as the quill wall mites (Laminosioptidae), the invasive visceral mites (deutonymphs of Hypoderatidae), and the nasal cavity mites (Tubinoptidae, Cytoditidae, Gastronyssidae, and Ereynetidae) (Beaulieu et al. 2019).

Remarkably, The most impressive diversity of mites on birds is the so-called “feather mites” from the Superfamilies Analgoidea and Pterolichoidea, with around 2,600 named species (Gaud & Atyeo 1996; Hernandes 2021). The former Superfamily Freyanoidea of feather mites, presented in a complete feather mite catalog to date done by Gaud and Atyeo (1996) – “Feather mites of the World”, is now considered nested inside Pterolichoidea by the majority of feather mite taxonomists following OConnor (1982) (Mironov 2003). The Analgoidea and Pterolichoidea, together with the mammal-specialized mites of the Superfamily Sarcoptoidea, form the monophyletic supercohort of symbiotic-mites Psoroptidia (Bochkov 2011; Klimov & Oconnor 2013; Mironov 2003). Therefore, the term “feather mites” referring to the Superfamilies Analgoidea and Pterolichoidea is phylogenetically artificial since molecular studies have placed Sarcoptoidea mites (mammals-only symbionts) inside the traditionally bird-only Analgoidea. In this regard, solely the around 15 families of avian mites in Analgoidea presented in Gaud and Atyeo (1996) are considered to be part of the “true feather mite” group along with Pterolichoidea (Gaud & Atyeo 1996; Klimov & Oconnor 2013). In addition, many experts also recognize the possibility of Analgoidea and Pterolichoidea to be a diphyletic group derived from different psoroptidian lineages, emphasizing the paraphyly in feather mites and the ecological restriction to the term “feather mite” (Mironov 2003). Moreover, it is noteworthy that by following Gaud and Atyeo (1996) classification, Analgoidea also includes the family Pyroglyphidae. Although this family include some species living in association with bird’s feathers, most pyroglyphids live on the nest of their hosts or are free-living mites, which include some medically-important taxa such as house-dust mites (i.e., *Dermoglyphus*) responsible for respiratory allergies in humans (e.g., asthma). This taxonomic relationship was later confirmed in a molecular study that nested the Pyroglyphidae lineage inside the Superfamily Analgoidea of almost exclusive obligate-symbiont mites, indicating the reversion or loss of this obligatory symbiotic lifestyle towards free-living species, a rare phenomenon (Klimov & Oconnor 2013).

Following the exposed above, the present doctoral thesis follows the feather mite concept presented in Gaud and Atyeo (1996), which includes all the ca. 33 families of obligatory-symbiotic psoroptidian mites associated with almost all modern bird orders. For suprafamilial ranks, this work partially follows the changes proposed by OConnor (1982) in respect of nesting the Superfamily Freyanoidea inside Pterolichoidea, but not regarding his decision to separate pyroglyphid-like mites into a new Pyroglyphoidea Superfamily (Mironov 2003).

Historical background

The knowledge of feather mites formally began in 1758 when the species *Acarus passerinus* was described from the Common chaffinch *Fringilla coelebs* L., 1758 (Fringillidae) by Carl Linnaeus, which today corresponds to the mite species *Analges passerinus* (Linnaeus, 1758) (Analgidae). This first step to building feather mite knowledge was named the "*primary feather mite investigation*" by Mironov (2003). Mironov (2003) also recognized and named other subsequent and important landmarks in the history of the feather mite knowledge, briefly described as follows (Mironov 2003). After Linnaeus, feather mites would receive attention again only at the end of the 19th century (from 1860 to 1920), with additional species descriptions, early taxonomic concepts for suprageneric ranks, and the concept of "feather mite" itself done by pioneers taxonomists and naturalists such as Robin, Trouessart, Neumann, Mégnin, and Oudemans, a period named as "*classical*" in feather mite studies (Mironov 2003). However, the feather mite studies bloomed around 1950 in a monography series dedicated to the group by Dubinin (1951, 1953, 1956). Dubinin settled feather mites as a monophyletic taxon in the Superfamily Analgoidea (as Analgesoidae) for the first time, building the background to feather mite systematics and ecology, a period named "*Renaissance*" in feather mite studies, lasting until 1970 (Gaud & Atyeo 1996; Mironov 2003). During the Renaissance, the most expressive and valuable contributions to feather mite systematics in the 20th century were developed, boosted by studies done by two prominent feather mite enthusiasts – Jean Gaud and Warren T. Atyeo. These authors studied feather mites from early 1950 until 1996. They described and established many new genera, families, and superfamilies of mites (e.g., Pterolichoidea and Freyanoidea) pushed by the crescent taxonomic descriptions (Gaud & Atyeo 1977). Concomitantly, another prominent acarologist, Alex Fain, also enormously expanded the knowledge of the field, exceptionally for skin mites of the families Dermationidae and Epidermoptidae (Fain 1965).

The advances in feather mite knowledge described above were restricted mainly to African and European taxa by that time. In the Renaissance timeframe, the first efforts to advance the feather mite knowledge in the Neotropical region were expressively made by Berla, in a series of works from 1950 to 1970 describing species from Brazil, and by Černy, describing species from Central America (e.g., Berla 1959; Černý 1974).

The "*Modern*" and last period in the construction of the feather mite knowledge defined by Mironov (2003) goes from the late 1970 and extends up to 2010. This period is marked not only by deeper investigations regarding the superfamilial ranks and new taxonomic concepts (e.g., OConnor 1982) but also by advances in underexplored fields such as feather mite ecology, systematics, and host-symbiont relationships (e.g. Dabert and Ehrnsberger 1999; Blanco et al. 2001). The Modern period can be extended up to the early years of 2010, to include the second wave of advances in feather mite systematics in underexplored regions of the world, exceptionally in the taxonomically rich tropical regions – including Brazil (e.g., Faccini et al. 1976; Valim and Hernandes 2008; Hernandes et al. 2010; Valim et al. 2011). This increased taxonomic effort overtime was responsible to named around 25% (ca. 2,600 species) of the total feather mite diversity estimated to the group globally, taking into account that each bird species (from around 10,000) can host multiple highly specific feather mite species due to microhabitat repartition, where even congeneric mites can be found living in synhospitality (i.e., mites sharing the same microhabitat without apparent competition) (Bochkov & Mironov 2008; Walter & Proctor 2013).

Herein I include a new phase to the feather mite knowledge timeline: the "*Contemporary*" period. This period is needed to embrace the astonishing advances achieved by using molecular data in feather mite studies, which started around early 2010 and extend to the present (Dabert et al. 2010; Knowles & Klimov 2011, but see Dabert et al. 2001). So far, the Contemporary period is giving new and important evidence corroborating earlier assumptions contrary to the general concept of feather mites as motionless symbionts, e.g., by recording multiple cases of historical host switch events in cophylogenetic assessments – also contesting the initial idea of high coevolutionary congruence between mites and birds. These studies also exposed our lack of knowledge regarding the parameters responsible for delimiting the generally high host specificity level in feather mites. It was also during the current time, especially pushed by a set of publications by Jorge Doña and his team, that other substantial advances in feather mite ecology, host interaction, and behavior have occurred (e.g., Doña et al. 2015, 2018b). The following sections briefly detail these expanded ecological ecological, biological, and phylogenetic aspects of feather mite natural history.

Host-symbiont specialization in feather mites

Pioneers in feather mite studies had already speculated about the prevalence of commensalism over parasitism regarding the impact of feather mites on their host's welfare. The first nominated feather mite genera, *Analges* Nitzsch, 1818, comes from the Greek word *analgēsía*, which means painless, which in turn is a combination of the prefix *an-* (without), and *algéō* (pain), and was likely attributed to this feather mite due to its apparent harmless effect on bird fitness. This innocuous property was later confirmed for the majority of feather mite species, especially those living on the stiff flight and tail feathers, i.e., far from their host's skin, as no correlation was found between the decrease in their host's fitness and the increase of mite abundance (Doña et al. 2018b). In fact, the opposite appears to be accurate, and better host conditions were recorded in high feather mite densities, suggesting a potential mutualistic relationship (Blanco et al. 2001; Dowling et al. 2001; Galván et al. 2012). Their feeding habit explains the commensalism-mutualism in feather mites: feather mites similarly use their chelicera as the movement of a "cloth wiping a sword," going barbule by barbule from the bottom up to capture tiny particles trapped in the uropygial secretions (i.e., preen oil) such as fungi, algae, bacteria, pollen, and other debris in which they feed upon (Doña et al. 2018b). By doing so, they likely prevent the development of potentially detrimental organisms to the bird's health (e.g., keratinophilic organisms) (Doña et al. 2018b). Recently, Labrador et al. (2021) indirectly estimated the cleaning potential of feathers by feather mites by roughly measuring the amount of organic material that each mite can eat from the feathers in a night of feeding. They found that feather mites can yearly clean an area of *ca.* 80,000 m^2 considering all European passerines, reinforcing their role as feather-cleaning agents. There is also the possibility of feather mites feeding on the preen oil that birds spread over their feathers to protect their integrity and give them a waterproof property (Moreno-Rueda 2017). If true, by removing this bioproduct from the feathers, two interpretations may be possible: 1) the mites could potentially help birds by preventing oil accumulation and the growth of pathogenic organisms; 2) the mites may put pressure on their hosts to replace the consumed preen oil, an energetically costly activity to birds (Moreno-Rueda 2017); however, the latter assumptions have never been tested.

Despite the non-detrimental impact of feather mites, especially those specialized to live on flight and tail feathers, some feather mites are undoubtedly parasites. This is the case for some mites living on the down and covert feathers and all mites living on the superficial layers of the skin and inside the quill of feathers (Dabert & Mironov 1999; Mironov 1987). The proper categorization of feather mites by their living microhabitat is fundamental, as it not only shapes the ecological interaction with their hosts, but apparently also affects their transmission, morphology, and evolutionary properties (Dabert et al. 2015). First attempts of mite categorization were done by Dubinin (1951) but properly described later by Mironov (1987) and Dabert and Mironov (1999). Brief descriptions of each category are given as follows.

Mites living on the ventral and dorsal sides of the flight and tail feathers are known as "vane-dwelling mites." Those mites are usually found motionless and organized in rows on the feather's vanes, i.e., the ventral space between the feather's barbs. Morphologically, vane mites usually present an elongated and dorsoventrally flattened body, short dorsal setae, and well sclerotized dorsal shields, which likely protect them from feather abrasion and water loss as they are more exposed to the external environment. The ambulacra, the disc-like "feet" of feather mites, is also more developed in vane mites and acts as a suction cup preventing the mite from being dislodged during their host's flight. The great majority of the feather mite diversity is composed of vane mites. Living on the more exposed flight feathers may be related to a higher rate of transmission between different host species (i.e., host switch) and may explain their higher diversity, as host switch events were found to be an important driver for feather mite speciation (Dabert et al. 2015; Doña et al. 2017b). Due to their exposed location, vane mites are most accessible and most abundant mites collected in feather mite surveys.

Contrarily to vane mites, which have adaptations against water loss and feather abrasion, mites living on the down feathers – also known as "down mites" – usually receive less selective pressure from the external environment. This feature reflects their morphology: down mites usually possess longer dorsal setae and less sclerotized bodies, exceptionally in females. The longer dorsal setae likely improve their navigation among the soft barbules, in which many representatives of down mites are found, grasped by modified spines and apophyses on their first pairs of legs. The parasitic influence of down mite is rare and seems to occur when the mite population on a bird increases abnormally, often in weak, immunosuppressed, and stressed domestic birds, or as a product of host switch, when a bird receives unspecific mites from other bird species (Hernandes et al. 2014). Down mites' effects on birds include itchy and dermatitis leading to mange (Faleiro et al. 2015). Examples of such effects include the mite *Allopsoroptoides galli* Mironov, 2013, a down feather mite of the family Psoroptoididae recorded to cause severe mange and dermatitis in laying-egg hens in Brazilian farms, responsible for dropping the egg production up to 30% (Mironov 2013; Soares et al. 2016; Tucci et al. 2014). Later on, it was found that this mite was transmitted to chickens from the Guira Cuckoo, *Guira guira* (Gmelin, 1788), a common cuculid in Brazil (Hernandes et al. 2014). This transmission represented a rare case of host switch and the first record of a mite from the family Psoroptoididae on a galliform bird (Mironov 2003). The lack of a previous host adaptation to this novel feather mite was likely responsible for the aggressive parasitic effect on domestic chickens. However, the stress in which the laying hens are submitted on commercial farms should also be taken into consideration, given that other down feather mites more adapted to chickens, especially from the genus *Megninia* (Analgidae), are also a problem in laying-egg hen systems (Faleiro et al. 2015; Horn et al. 2018; Tucci et al. 2005).

Similar to down mites, quill mites often possess longer corporal setae and weak sclerotized bodies since they spend most of their life in a stable habitat – inside the feather quills, only leaving during their larval and nymphal stages to disperse (Dabert & Mironov 1999). Quill mites often possess strong and hypertrophied chelicerae, which they likely use to rip off parts of the feather medulla, upon which they feed (Dabert & Mironov 1999). This feeding habit gives them the parasitic status, as quill mites may weaken the inner feather structure and facilitate its removal. Quill mites are usually rare and difficult to collect, as they require a careful examination of the feather quill.

Other categorically parasitic feather mites are the skin mites, found on the superficial layers of the skin, as its name implies. These mites usually have a smaller size than other feather mites, a flat and round idiosoma, and short legs. Due to affecting the superficial layers of the skin, these mites are often associated with dermatitis and mange in stressed and immune-depressed birds (Fain 1965). Similar to quill mites, skin mites are also among the most challenging feather mites to sample due to their direct attachment to their host skin, being mostly collected from dead hosts by the washing technique (Mironov & Galloway 2002a).

Overall, detecting detrimental effects of feather mites over their hosts is often tricky, even for categorical parasitic mites (i.e., quill and skin mites). Nevertheless, birds display a myriad of antiparasitic behaviors (e.g., grooming, anting, dustbathing, scratching) that are effective in controlling the population of other symbiotic arthropods, especially feather lice

(Phthiraptera: Ischnocera and Amblycera) (Clayton et al. 2015). A similar potential of symbiont control by birds can also be expected to work against feather mites, minimizing the possibility of harmful effects by controlling their load sizes. For example, Atyeo and Gaud (1979) mentioned they had observed white gulls brown in color due to an extremely high mite load in unhealthy hosts unable to beat their wings. However, unlike feather lice, no direct evidence was found about the bird’s ability to control feather mites. Likewise, birds are usually well adapted to their symbionts due to a near-linear coevolutionary history, which reduces the virulent effect of their symbionts. Conversely, more virulent effects are often associated with recent-colonized and not-adapted hosts (i.e., host switch), or triggered by disturbed environments or specific conditions, as noted in the few cases reported in the literature (Hernandes et al. 2014; Longdon et al. 2015).

Specificity and transmission

Due to their obligatory symbiotic properties, all feather mite species must be assigned to at least one host species upon its description and eventually add more host species as new records appear. The available data indicates that feather mites display high host specificity levels since many feather mite species are specifically recorded on a single host species or a set of phylogenetically close-related hosts (Doña et al. 2018a). The high host specificity in feather mites is likely connected to their primary mode of host transmission – vertically from parents to offspring during the bird parental care (Doña et al. 2017a; Mironov & Malyshev 2002). This transmission enhances the chance for an inherited line of mite acquisition, creating a historical host-symbiont association that promotes a parallel evolution between the groups, resulting in the observed intimate level of mite specificity and, to some extent, a phylogenetic congruence between feather mites and birds (Mironov et al. 2020). Conversely, multiple cases of host-symbiont phylogenetic dissimilarities have been recorded in feather mites, especially by advances in cophylogenetic studies (Doña et al. 2017b; Klimov et al. 2017; Matthews et al. 2018a). These studies confirmed previous assumptions of historical host switch events along with feather mite’s evolution and suggested that non-parental dispersions, i.e., horizontal transmissions, are likely as important as vertical transmissions for feather mite colonization.

Horizontal transmissions occur post the fledgling stage, when birds become independent from parental care and go into direct contact with unrelated hosts, e.g., during mating, territorial defense, grooming, and predation. Due to the outcome, horizontal transmissions can be classified into two categories: the ones between conspecific hosts, and the ones between different host species (i.e., interspecific). Evidence of conspecific horizontal transmission includes the absence of mites on nestlings of the Red-billed Choughs *Pyrrhocorax pyrrhocorax* Linnaeus, 1758 (Passeriformes: Corvidae) observed by Blanco et al. (1997); instead, the authors detected an increase in mite abundance along with the bird aging, suggesting a conspecific horizontal route of mite acquisition. Similar mite colonization occurs in Australian brushturkeys (Galliformes: Megapodidae) and some brood parasitic birds such as Cuckoos (Cuculiformes: Cuculidae), since these birds present a specific set of feather mite taxa even completely lacking any parental care behavior, therefore preventing conspecific vertical transmissions. These acquisitions of specific mites in birds lacking parental care are solely possible through horizontal contact between infected and non-infected conspecific birds (Atyeo & Gaud 1983a; Lindholm et al. 1998; Proctor & Jones 2004). Notoriously, these cases of strict conspecific horizontal transmissions have been able to maintain a highly specific fauna in those unconventional birds, confronting the traditional view of vertical transmission as the main route responsible for shaping host specificity.

Interspecific horizontal transmissions, on the other hand, appear to be rare and difficult to detect. Birds display a cornucopia of behaviors capable of promoting the interspecific transmission of feather mites, including altruistic interactions such as allopreening, mixed flocking, sharing nesting grounds, sharing dust and water baths, hybridization, adoption, using other bird species' feathers to build nests; as well as antagonistic such as predation, resources defense, and brood parasitism (Dabert et al. 2015; Johnson et al. 2002a; Ottenburghs 2019; Proctor & Jones 2004; Samplonius & Both 2014; Soler 2017). When the association is ephemeral, i.e., the atypical mite survives on a non-specific host just for a short time, the transmitted mite is recognized as a straggler (Doña et al. 2019b; Ròzsa 1993). In a recent study, Doña et al. (2019) recorded cases of straggler feather mites on 84 of 1,130 (7.4%) passerines in Spain, most of the shared mites on hosts with similar body sizes. Straggler mites were also occasionally recorded on birds of prey since some of these birds frequently carry passerine-related mites, although in low densities (Atyeo & Braasch 1966; Philips 2000). If a straggler mite successfully colonizes a new host, i.e., reproducing and dispersing on the new host population, the association becomes classified as a successful host switch event. Recent host switch events may explain the existence of the same mite species on phylogenetically distant hosts (i.e., polyxenous feather mites), such as the mite *Proctophyllodes polyxenus* Atyeo and Braasch, 1966, recorded on many host species from at least five passerine families (Atyeo & Braasch 1966). Although, some of those multi-host records may consist of complexes of cryptic mite species.

Successful host switch events are complex and still not fully comprehended in feather mites, neither regarding their transmission pathways nor the properties responsible for accommodating high specialized symbionts into new hosts. Host switch records include the case above of mite transmission from Guira-cuckoos to laying-egg hens in Brazil, resulting in a harmful effect on the new non-adapted host (Hernandes et al. 2014). Previous observations of possible host switch cases in feather mites were made by Gaud (1992), who acknowledged the possibility of the chicken mite *Megninia ginglymura* (Mégnin, 1877), also an economically important mite in the poultry industry, to be a product of host switch from its original host, the American wild turkey *Meleagris gallopavo* Linnaeus, 1758. In his work, Gaud (1992) also noted that domestic pigeons, *Columba livia* Gmelin, 1789, were recorded carrying mite species geographically related to the mite fauna found on native pigeons worldwide. Despite the lack of substantial evidence in his study, Gaud (1992) called attention to the more significant dispersal potential in feather mites than expected, given their apparent low mobility. As previously mentioned, historical host switch events were commonly recorded in bird-mite coevolutionary studies also acknowledging this event as an important driver for feather mite speciation (Doña et al. 2017b; Matthews et al. 2018a).

Unlike stragglers, in which the lack of prior adaptation partly explains the failure to colonize a new host, successful host switches likely depend on specific scenarios and conditions. Among these conditions are the frequency of interaction between the different host species (i.e., the exposition frequency), and the features responsible for shaping the selective pressure and the ecological fitting of alien mites into new hosts, such as the niche availability, the host immune response, and the host-symbiont physiological and morphological compatibility (Agosta et al. 2010; Wells & Clark 2019). However, the factors responsible for shaping the host specificity in feather mites are yet to be investigated.

The lack of knowledge regarding the host specificity in feather mites is partly explained by the challenges and difficulties of monitoring live feather mites on their hosts or keeping them alive *in vitro* (see Labrador et al. 2021). For example, their small size (*ca.* 200 to 500 micrometers) constrains some studies attempting to track or manipulate their movements and populations across hosts. For comparison, feather lice (Phthiraptera), also obligate ectosymbionts on birds, have almost tenfold the size (*ca.* 2 to 5 mm in length) of an average feather mite (Clayton et al. 2015). This difference certainly matters when it is necessary to manipulate and monitor feather mites in experiments across different hosts.

Contrary to feather mites, feather lice have been extensively tested for factors responsible to regulate their populations on hosts, including techniques that allow them to be tagged individually (Zohdy et al. 2012). Apparently, the regulation of lice populations is directly connected to their capacity to colonize new hosts, in a way that what regulates them also seems to regulate their specificity (Bush et al. 2019; Clayton et al. 2003, 2015; Tompkins & Clayton 1999). In the case of lice, the feather structure (correlated with host body size), the host coloration (correlated with the lice' ability to hide from host preening), and the host specialization (i.e., the bill shape), are decisive factors for an effective lice population control by birds, meaning that the host grooming pressure is decisive to remove any non-adapted lice (Bush et al. 2019; Bush & Clayton 2018; Clayton et al. 2003). In feather mites, the closest study experimentally testing the transmission and the factors responsible for mite control by birds was done by Tucci et al. (2014), dealing with the aforementioned case of mite transmission from the guira-cuckoo to laying-egg hens in Brazil (Hernandes et al. 2014; Mironov 2013). In this study, the authors experimentally tested the transmission of mites by placing previously infested chickens together with naïve chickens (i.e., free of mites) in the same controlled cages. They verified that those naïve chickens got infected after 7 days and presented the same symptoms (i.e., scaly dermatitis and mange) observed in naturally infected chickens after 15 days. More importantly, the authors observed that the host grooming ability, which is often impaired in laying-egg hens by practices such as beak trimming and confinement in small cages, appeared not to affect the mite population or prevent their harmful symptoms. This suggests that different from the observed in experiments with feather lice, the host grooming behavior has few effects on the feather mite populations and their specificity. There is also the possibility of feather mites being prone to food shortages making the food availability and the mite's potential to feed on different hosts a factor that may limit the interspecific colonization (Labrador et al. 2021).

The connection between transmission and specificity is strongly demonstrated in phoretic-transmitted feather mites. Some feather mite genera, such as the skin mites *Myialges* Trouessart, 1906 and *Promyialges* Fain, 1964, and the down mite genus *Strelkoviacarus* Dubinin, 1953, have been recorded in phoretic association with other bird-associated arthropods, such as hippoboscid flies (Diptera: Hippoboscidae) and feather lice (Philips & Fain 1991). Phoretic feather mites take advantage of the higher dispersion potential of these other bird symbionts and present lower levels of host specificity like them.

Alternatives to test specificity in feather mites

Despite the advances provided by molecular studies, some aspects of feather mite biology remain elusive, especially concerning the aforementioned host specificity. Given the data at hand, which unfolded host switch as an important event shaping the feather mite evolution and driving their diversification, it is surprising that complex host-symbiont systems promoting constant interaction between non-specific hosts, such as the brood parasitism, remain understudied. Brood parasitic birds do not build nests nor display parental care; instead, these birds lay their eggs on other bird species' nests which act as foster parents for the parasitic chick. This creates a scenario that disrupts the conventional conspecific vertical transmission of feather mites, allowing an effective way to investigate themes related to transmission, host switch, and specificity. Brood parasitism is displayed by around 1% of the bird species in the world (ca. 100 sp.), a behavior which evolved independently seven times in the bird lineage: thrice on cuckoos, represented by the old world tribes Cuculini and Phaenicophaeini, and the new world tribe Neomorphini; once in honeyguides (Piciformes: Indicatoridae); twice on passerines represented by the African whydahs and indigobirds (Passeriformes: Viduidae), and by the new world cowbirds *Molothrus* Swainson, 1832 (Passeriformes: Icteridae); and once in ducks, represented by a single species of duck in South America (Anatidae) (Lowther 2019; Soler 2017; Stevens 2013). The implications for the feather mite diversity in this three-level host-symbiont system (Vas et al. 2013), composed of the brood parasitic bird, the birds they parasitize, and their mites, are virtually unknown, despite their valuable and unique potential to collaborate fundamental understanding questions about the transmission and specificity in feather mites.

The first study concerning feather mites on brood parasitic birds was a review done by Atyeo and Gaud (1983). The authors acknowledged the potential of unspecific mite transmission by foster parents to brood parasitic chicks during parental care. The authors also listed the known mite fauna on each brood parasitic host group, comparing the mite records with their bird hosts and pointing to potential evidence for mite transmission and acquisition. The authors mentioned the record of the mite family Proctophyllodidae on brood parasitic honeyguides of the genus *Prodotiscus* Sundevall, 1850 (Piciformes: Indicatoridae), which brood parasitize passerines, as the most relevant example of potential mite acquisition during parental care from foster parents. Mites of the family Proctophyllodidae are commonly found on Passeriformes, whereas mites recorded on non-brood parasitic honeyguides are mostly the ones typically found on other birds of the order Piciformes, which evidences the potential mite acquisition and successful host switch from their passerine hosts to honeyguides. Concerning the other brood parasitic bird species, the few records allowed the authors to speculate on the colonization of phylogenetically compatible mites (i.e., not from foster parents) after the post-fledgling stage, especially in cuckoos, since no mites from their typical bird-hosts were recorded.

Another important contribution to the knowledge of feather mites on brood parasitic birds was done by Lindholm et al. (1998), which investigated the transmission of ectosymbionts from passerine foster parents to the diederik cuckoo *Chrysococcyx caprius* (Boddaert, 1783) (Cuculiformes: Cuculidae) in South Africa. In this study, Lindholm et al. (1998) recorded typical passerine mites on nestling cuckoos, an indicative of a vertical pathway of mite transmission during parental care. Notwithstanding, the finding of the mite *Pteronyssoides passeris* (Gaud, 1953) (Analgoidea: Pteronyssidae) on an individual adult cuckoo also indicated some level of mite persistence, as this was a common mite recorded on their passerine hosts. Finally, adult cuckoos also presented a predominant fauna of mites specific to cuckoos, indicating an expressive acquisition of cuckoo mites after leaving their foster parent's nest, likely by conspecific contact. This study provided the first evidences of transmission and persistence of foster parent mites in cuckoos, representing an important finding of host switch between phylogenetically distant related hosts: from Passeriformes to Cuculiformes. Since this study, no other brood parasitic system has been investigated regarding their feather mites. The diederick cuckoo is, therefore, the sole brood parasitic system truly investigated for feather mites and their vertical transmission.

The absence of records of mites acquired from foster parents on other vastly explored cuckoo species, such as the common cuckoo *Cuculus canorus* Linnaeus, 1758, is intriguing, and possibly indicates an incompatibility barrier of colonization still unknown in these symbionts. The knowledge of feather mites on brood parasitic birds phylogenetically closer to their hosts would certainly provide valuable answers and new perspectives on interspecific mite colonization. Whydahs and cowbirds are strong candidates in this category – both represent Passeriformes which parasitize other Passeriformes. They differ by their level of specialization: most whydahs show high levels of host specialization, in many cases parasitizing a single host species, especifically passerines of the family Estrildidae – a sister family to Viduidae (Sorenson et al. 2004); while cowbirds (*Molothrus* spp.) are among the most generalist species of brood parasitic birds, being the shiny cowbird, *Molothrus bonariensis* (Gmelin, 1789), the most generalist of them (Lowther 2019). In this perspective, the shiny cowbird may be one of the best organism models to investigate the potential for interspecific mite transmission and their settlement on new hosts, as this system is under constant pressure for the colonization by multiple non-specific feather mite species (from the multiple shiny cowbird host species). This adaptation plasticity pressure is a key feature to understand a symbiont's potential to emerge into new hosts (Araujo et al. 2015). Notwithstanding, the shiny cowbird network by itself provides an unmeasurable opportunity to investigate how feather mites adapt to complex systems.

Shiny cowbirds' eggs have been recorded in more than 270 bird species' nests, from which 97 have been recorded successfully rearing their chicks (Fiorini et al. 2019; Lowther 2019; Soler 2017). Natural from the South America Pampas, this species has been spreading its geographical range due to deforestation, being nowadays recorded in all South American countries, the West Indies, and certain North American regions (Cavalcanti 1988; Crespo-Pérez et al. 2016; Levy 2019; Marín 2000; Post et al. 1993; Sick 1997; Sykes Jr & Post 2001). From where it passes, the shiny cowbird is known to reduce its host population, decreasing their reproductive success (Astié & Reboreda 2006; Ortega et al. 2005; Sick 1997; Tuero et al. 2007). Its impact is exceptionally a concern to threatened species such as the yellow-shouldered blackbird *Agelaius xanthomus* (Sclater, 1862) (Passeriformes: Icteridae) in Puerto Rico, and the pale-headed bush-finch *Atlapetes pallidiceps* (Sharpe, 1900) (Aves: Passerellidae) in Ecuador (Azpiroz 2015; Cruz et al. 2005; Lowther 2019; Oppel et al. 2004; Smith et al. 2002). Regarding their symbionts, the shiny cowbird counts with few and sparse studies of feather lice, nasal mites, and helminths (Bernardon et al. 2016; Cicchino & Castro 1996; González-Acuña et al. 2006). For feather mites, there is two described species, the pterodectine *Amerodectes molothrus* (Mironov, 2008) and the proctophyllodine *Proctophyllodes molothrus* Pedroso and Hernandes, 2021, both from Brazil, and recent records of two other species of *Proctophyllodes* from Chile (Mena et al. 2020; Mironov et al. 2008). Therefore, deeper investigations of symbionts on shiny cowbirds, especially their feather mites, are needed for a proper inference of mite specificity and transmission.

Specificity and biogeography – a relationship?

When investigating the specificity of symbionts, another crucial feature must be considered – their geographic distribution (*i.e.*, their biogeography). This consideration is essential for obligate symbionts that complete their entire life cycle on a single host individual; such are feather mites. In these permanent attachment systems, symbionts' geographic distribution usually mirrors their host's distribution. This appears to be the case for most symbionts on geographically restricted hosts (e.g., endemic species); whereas in locally widespread or ubiquitous hosts (i.e., spread host populations), other factors such as climate variables, host ecology, dispersion potential, and natural barriers might be more relevant than the host to define their distribution (Wells & Clark 2019). Knowing the biogeography of symbionts is also an indirect way to give insights into their host's biogeography, phylogeny, ecology (Matthews et al. 2018a), and predict possible host-symbiont interactions preventing impacts on conservation (Alvarez et al. 2010).

In the systems described above, it is possible to estimate the distribution of symbionts in two ways: 1 – by recovering the symbiont composition along with a host species distribution, which gives insights into the dispersal ability and the environmental requirements of a symbiont based on the host sampling; and 2 – by assessing the distribution of a singular (or a set of) symbiont species, which may differ from the host distribution depending on the symbiont host specificity. The first measure requires a broad sampling of a specific host species along with its distribution, whereas the second requires sampling all potential hosts.

Regarding feather mites, examples of a broad sampling of mites on particular hosts include the first studies evaluating their biogeography, done by Gaud & Atyeo (1976). In this study, patchy distributions of mites were recognized on introduced and widespread hosts such as the Rock Pigeon *Columba livia* Gmelin, 1789, the House Sparrow *Passer domesticus* (Linnaeus, 1758), and Domestic Chickens *Gallus gallus domesticus* (Linnaeus, 1758) (Gaud & Atyeo 1976). These ubiquitous hosts have acquired distinct, yet congeneric, mite species according to their geographic location by interacting with local and phylogenetically similar hosts (Dabert 2004; Gaud 1992; Gaud & Atyeo 1976). In these situations, feather mite species from the set of their regular mite fauna may fail to disperse along with their hosts (i.e., founder effect), leaving available microhabitats for new species to colonize, an event known as "*missing the boat*" in cophylogenetic studies (MacLeod et al. 2010). The reverse is also possible, where the arrival of a new host may change the specificity of a locally adapted symbiont, ending in a successful host shift event that may expand the original symbiont's geographic distribution (Poulin et al. 2011; Wells & Clark 2019).

Unlike introduced hosts, mite composition on naturally widespread hosts is likely affected by past evolutionary and biogeographic events rather than by recent host-to-host interactions allowed by human expansion (Dabert 2004; Hernandes et al. 2014; Klimov et al. 2017). In these cases, different host populations may present different mite compositions evidenced by the presence, absence, or replacement of either precise morphologically established mite species, or “hidden” molecular structuration, often in the form of cryptic species (Doña et al. 2015). Barriers are usually responsible for these scenarios among host populations, preventing the mites from colonizing the totality of hosts, and creating vicariance events. An example of such a pattern is a report done by Dabert and Mironov (1999) regarding the feather mite genus *Scutulanyssus* (Pteronyssidae) on European populations of the Common House-Martin *Delichon urbicum* (Linnaeus, 1758) separated by the Ural mountains, where European and Asiatic populations of House-Martin presented distinct and morphologically well-defined species of *Scutulanysus*, indicating that the Ural mountains are a barrier for their hosts (Dabert & Mironov 1999). Other cases include different species of the mite genera *Falculifer* (Pterolichoidea: Falculiferidae) on different pigeon species around the world, where the species *F. rostratus* (Buchholz, 1869) is found in Eurasia, northern Africa, and South America, whereas *F. lacertosus* Gaud, 1976 occurs in central and southern Africa, India, and the far East (Dabert 2004; Dabert & Mironov 1999; Gaud & Atyeo 1976).

Further analysis of mite distribution on pigeons was done by Grossi and Proctor (2020) for domestic pigeons in Canada. In this study, the authors found that some of the feather mite species were patchily distributed according to humidity and temperature variables, e.g., regions with higher humidity presented a higher diversity of vane-dwelling mites compared to drier regions. Additionally, some of the mite species’ low load and low prevalence were also attributed to their inability to disperse among hosts (e.g., for down and skin dwellers feather mites), highlighting the ability to disperse as an important factor shaping their distribution. Melendéz et al. (2014) also detected irregular mite composition due to climate on passerines in Spain. Unlike Canadian pigeons, the mites in Spain presented higher infestation and prevalence in warmer and drier environments, being the temperature more relevant than precipitation for their distribution. The temperature also explained the decline in mite populations along the altitudinal elevation better than the variation in precipitation in Melendéz’s study. Effects of external temperature also influenced how feather mites were arranged on the feathers of blue tits *Cyanistes caeruleus* (Linnaeus, 1758) in the United Kingdom (Wiles et al. 2000); and is possibly one of the reasons behind the feather mite’s movements at night (Labrador et al. 2021).

The studies above indicate that the environmental conditions may affect feather mites’ biogeography, restricting their populations. Despite having a low impact when compared to biotic factors (i.e., host community), abiotic factors are also an important variable for shaping the feather mite richness globally, being the temperature more relevant than precipitation, i.e., warmer regions hold higher feather mite richness than temperate regions (Gusmão et al. 2020). The studies also show the importance of assessing symbiont's prevalence and abundance in host populations, as these metrics may give insights into the mite's potential to disperse. The prevalence and the mite load, on the other hand, might also vary according to a myriad of factors such as season of the year, reproductive status of the host, feather mite natural history, environmental condition, and host condition, turning the inference of the biogeography of feather mites a challenging task (Enout et al. 2012; Figureuerola 2000; Jovani & Serrano 2001; Marini et al. 1996; Matthews et al. 2018b; Thompson et al. 1997).

Despite the major macroevolutionary effect of host switch in feather mites (Doña et al. 2017b), the specificity and the host community (biotic factors) are undoubtedly essential features for feather mite disposition around the globe (Doña et al. 2018a; Gusmão et al. 2020). Examples include cophylogenetic studies, which intrinsically connect with biogeographic investigations, especially historical biogeography (Klimov et al. 2017; Matthews et al. 2018a; Štefka et al. 2011; Weckstein 2004). In feather mites, these studies differ by the taxonomic scale of the investigations, i.e., at micro- (intraspecific level) and macroevolutionary (between species, genus, and above) scales. Examples of the macroevolutionary scale include the historical biogeographic investigation of the mite genera *Proctophyllodes*, a genus presented globally on passeriform birds that shows clear patterns of geographic disposition (Klimov et al. 2017). Further macroevolutionary examples include cophylogenetic studies of the mite families Ptiloxenidae and Avenzoariidae, providing biogeographic insights into their present host-symbiont associations (Dabert et al. 2001; Dabert & Ehrnsberger 1998). On the microevolutionary side, the studies include investigating co-phylogeographic patterns of *Analges* populations on Galápagos mockingbirds (*Mimus* spp.), in the Galápagos archipelago (Štefka et al. 2011). In this study, the authors found strong accordance between bird and mite phylogenies with their distribution in the archipelago and, therefore, a high level of host co-speciation. Differently, in warblers (Parulidae) from North America, the distribution of *Amerodectes* and *Proctophyllodes* species was more related to their host ecology (i.e., nesting locations) than to host phylogeny or distribution (Matthews et al. 2018a).

Overall, data on the geographic distribution of feather mites are essential to understanding the requirements for their host specificity. However, the lack of substantial literature concerning feather mite biogeography, especially in the Neotropics, prevents any categorical inference regarding this subject.

Justification

The concept of this thesis comes from the need to understand aspects of the feather mite transmission modes and their connections with host specificity and geographic distribution. As exposed above, recent studies have shown peculiar aspects of feather mite biology, inferring a higher potential for horizontal transmissions and host shifts than previously thought. Feather mites have long seemed low mobile symbionts, with transmissions occurring mainly through a vertical route, from parents to offspring during parental care. This also partially justify their high levels of host specificity. Therefore, an association between specificity, transmission, and geographic distribution is expected. However, no substantial study has been devoted to detecting or understanding this association.

The shiny cowbird system fits this subject offering a unique way to explore the relationship among these properties in feather mites. Data regarding the effects of such a peculiar system, i.e., a generalist and widespread brood parasitic bird over the feather mite fauna, would certainly assist the interpretation of patterns in feather mite studies. If shiny cowbirds present both a set of specific symbionts independent of its passerine foster parent usage, and a set of miscellaneous mites recorded on passerine species which serve them as hosts, then it would be possible to accurately quantify the importance of vertical and horizontal transmissions of their feather mites. Based on these results, it would also be possible to give the first inferences regarding the host specificity in feather mites and how this specificity impacts this system. Results in this system could certainly be extended to feather mites in general and even to other ectosymbionts.

Notwithstanding, the expressive bird diversity in the Neotropics and the still long path to fill the knowledge gap regarding their feather mites also justify the present work. Especially for Brazil, a country where the last significant episode of host switch in feather mites was recorded, leading to economic losses in the poultry industry. Recognizing which factors are relevant and allowing these drastic specicificity changes are essential to identify and prevent potential new cases.

In this regard, the present thesis proposes to investigate the connection of host specificity, the transmission modes, and the geographic distribution of feather mites on widespread Brazilian passerines. Most of this investigation is based on the shiny cowbird system as a study model.

Thesis presentation

This thesis is presented in three parts, separated into a general introduction and two chapters. The first part introduces feather mite biology, giving the reader the main concepts and ideas regarding these astonishing symbionts. The following chapters are formatted as manuscripts. Chapter 1 investigates the feather mite fauna on the shiny cowbird. It gives a list of feather mite species recorded on shiny cowbirds from various sources, a classification of mite species based on their host specificity on shiny cowbirds corroborated with different lines of evidence (e.g., phylogenetic, cophylogenetic, dated phylogeny, indexes of occurrence), and the quantification of the importance of vertical vs. horizontal transmission in this system. This manuscript was submitted to the journal Molecular Ecology for publication.

Chapter 2 incorporates data from chapter one to analyze the connection between the host specificity, the horizontal transmission, and the geographic distribution in feather mites from shiny cowbirds. For this task, network analysis between geographic biomes and mite specificity classes was performed, and general patterns were discussed. Data on this analysis are yet to be submitted.

In the final Section, a list of published manuscripts with correlated data with the main chapters presented here is given. These include taxonomic descriptions of new mite species, and new data on aspects of host transmission, host specificity, and geographic distribution of feather mites.

OBJECTIVES

General Objectives

Investigate the feather mite fauna associated with the shiny cowbird *Molothrus bonariensis* (Icteridae) and its possible passerine hosts (i.e., common widespread passerines) to answer questions concerning the transmission, host specificity, and geographic distribution in feather mites.

Specific Objectives

- Inventory the feather mite fauna of the shiny cowbird (*Molothrus bonariensis*);
- Inventory the feather mite fauna of common and widespread passerines which serve as a host for shiny cowbirds;
- Characterize the mite fauna on shiny cowbirds based on patterns of their host specificity and transmission;
- Estimate rates of vertical and horizontal transmission of feather mites found on the shiny cowbird;
- Identify based on molecular and phylogenetic data patterns of molecular partition among different feather mite populations;
- Identify the feather mite species and describe new taxa;
- Analyze the relationship of feather mites from the shiny cowbird with mites from their potential foster parents phyllogenetically;
- Use dated phylogenetic analysis to give timed based evidence for coevolutionary events;
- Perform cophylogentic analysis to identify possible ancient host switch events in feather mites found on shiny cowbirds;
- Look for a relationship between the mite fauna found on shiny cowbirds with its host usage and biome preferences.

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CHAPTER 1 – HOST SPECIFICITY AND TRANSMISSION

Relative contribution of vertical versus horizontal transmission in host colonization: A case study of feather mites from the brood parasitic cowbird (*Molothrus bonariensis*)

ABSTRACT

In host-symbiont systems, host switches (via horizontal transfers) are widespread and can lead to host-symbiont phylogenetic incongruence. In contrast, vertical transfers (from parents to offspring) often result in high host specificity and nearly congruent host-symbiont phylogenies. The relative importance of vertical and horizontal transmission is, therefore, key to understanding host specificity and co-phylogenetic patterns of symbionts. In bird-feather mite systems, vertical transmission of mites is considered dominant, while horizontal transmission is thought to be minimal. However, incongruent avian and feather mite phylogenies are common. Here we investigated a host species (the shiny cowbird, *Molothrus bonariensis*) where the rates of horizontal and vertical transmission can be accurately estimated because this species is an obligate brood parasite. We discovered that mites dispersing via horizontal transmission are nearly three times more likely to colonize new hosts than mites dispersing via vertical transmission. Cowbird-to-cowbird horizontal transmission usually occurs via adult social contacts, maintaining cowbird-specific mite species (5 species, overall abundance 74.8%). Yet, cowbirds can receive non-specific mites vertically from foster parents (24 species, overall abundance 25.2%). This system highlights the unexpectedly high rate of horizontal transmission of feather mites on a microevolutionary scale. Ancestral host switches in *Molothrus* mites corroborate these results. Remarkably, vertical transmission was not required to maintain high host specificity. That is, horizontal transmission solely accounted for the maintenance of cowbird-specific symbionts. These data suggest that horizontal transmission may be a major factor shaping coevolutionary patterns in host-symbiont systems, because it can generate both congruent and incongruent co-phylogenetic patterns and maintain both single-host and multi-host symbionts.

Keywords: symbiont transmission, feather mites, cowbirds, specificity, host transfer, host switch

INTRODUCTION

With the advance of co-phylogenetic techniques, many host-symbiont systems have been assessed for the patterns of codiversification between hosts and symbionts (Clayton & Johnson, 2003; Dabert, 2004; Dabert et al., 2021; Doña et al., 2018; Doña et al., 2017a; 2018; Engelbrecht et al., 2016; Klimov et al., 2017, 2007; Light & Hafner, 2007; Matthews et al., 2018; Štefka et al., 2011; Sweet et al., 2018; Weckstein, 2004). Most studies have suggested that strict co-speciation between host and their symbionts is rare even for highly host specific symbionts (Araujo et al., 2015; Clayton et al., 2004; De Vienne et al., 2013; Doña et al., 2017a; Fecchio et al., 2018; Klimov et al., 2017; Matthews et al., 2018; Page, 2003;

Weckstein, 2004). Generally, disagreement between host and symbiont phylogenetic branching patterns is caused by several evolutionary events, such as duplication (speciation of a symbiont within a single host species), sorting (extinction and missing the boat), failure to speciate, and host switching (or host shift), with the latter typically being the most common event (Araujo et al., 2015; Banks & Paterson, 2005; Clayton et al., 2015; Doña & Johnson, 2020; Fecchio et al., 2018). Host switching is also a biologically intriguing event, especially when it involves host-specific symbionts associated with a single or closely related host species. Most host switches occur via interspecific horizontal transfers (Figure 1: q_{h1}), generating incongruence in host and symbiont phylogenies, and on a microevolutionary scale maintaining multi-host symbionts (i.e. low host specificity) (Banks & Paterson, 2005; Doña et al., 2019a). In contrast, conspecific vertical transmission (i.e. from parents to offspring) (Figure 1: q_v) is expected to produce congruent host and symbiont phylogenies (strict co-speciation) and maintain single-host symbionts (i.e. high host specificity). Yet, despite perceived dominance of vertical transmission, some host-symbiont systems may display incongruent co-phylogenetic patterns.

A major and well-studied host-symbiont system is that of feather mites (Acariformes: Analgoidea and Pterolichoidea) and birds, where mites have high levels of dependence and specificity with their avian hosts (Dabert, 2004; Doña et al., 2018; Gaud & Atyeo, 1996; Proctor, 2003). These symbiotic mites live in four principal microhabitats on hosts (flight feathers, downy feathers, cavities of quills, and the skin surface), allowing a number of mite species to co-exist on a single host individual due to niche partitioning (Bochkov & Mironov, 2008; Dabert & Mironov, 1999; Hernandes & Mironov, 2015; Hernandes & OConnor, 2017; Perez & Atyeo, 1984; Valim et al., 2011). For example, the “average” New World oscine passerine bird usually has a set of six host-specific mite species commonly represented by the genera *Amerodectes*, *Proctophyllodes*, *Trouessartia* (on flight feathers), *Analges*, *Mesalgoides*, and *Xolalgoides* (on downy feathers). These symbiotic organisms spend their entire life cycle on the host and not only lack a specialized dispersal stage but also seem to lack any other adaptations for long-range dispersal (OConnor 1994). Therefore, the most important dispersal mode of feather mites across host individuals is via parental care, i.e. vertical conspecific transmission from host parents to offspring (Figure 1: case 1: q_v) (Brooke 2010; Clayton et al. 2015; Doña et al. 2017b; Johnson et al. 2011; Mironov & Malyshev 2002). Consequently, the diversification of these symbionts is expected to be driven largely by co-divergence. However, multiple co-phylogenetic studies have shown that host switches are relatively common in feather mites, mostly among ecologically similar hosts (Dabert et al. 2021; Doña et al., 2018; Doña et al., 2017a; Ehrnsberger et al., 2001; Klimov et al., 2017; Matthews et al., 2018), suggesting that such events are one of the main drivers of feather mite diversification (Doña et al., 2017a; Klimov et al., 2017). On the microevolutionary scale, interspecific horizontal transmission (Figure 1: q_{h1}) had also been detected, but its contribution relative to other transmissions (q_v and q_h) is unknown and these data were not analyzed in a macroevolutionary context (Doña et al., 2019b; Gaud, 1992; Hernandes et al., 2014; Mironov, 2013). Therefore, given the discordance of current biologically informed expectations (vertical transmission should be common hence host and parasite phylogenies should be congruent vs observations of widespread phylogenetic incongruence), it is important to understand the relative contribution of different types of horizontal and vertical transmission in shaping feather mite diversity (Figure 1). This may help to assess the factors influencing general co-evolutionary patterns on both macroevolutionary and microevolutionary scales. However, the relative magnitude of these two modes of transmission is difficult to study (i.e. q_v vs q_h), since feather mites are challenging to manipulate experimentally.

The brood parasitic shiny cowbird, *Molothrus bonariensis* (Passeriformes: Icteridae), provides an excellent experimental model to investigate transmission pathways in feather mites. Like all obligate brood parasites, this bird neither builds nests nor displays parental care, effectively preventing conspecific vertical transmission (i.e. from biological parents to chicks) of host-specific mites ($q_v=0$). Therefore, host-specific mites can be transferred only horizontally (Figure 1: case 2: q_h), by contact between conspecific hosts (i.e. other shiny cowbirds), while non-host specific mites (i.e. from the cowbird's foster parents) would be transferred mostly vertically (Figure 1: case 2: q_{v1}). It is worth noting that in this system, foster parent-to-chicks transmission (q_{v1}) is equivalent to biological parent-to-chicks transmission (q_v). Horizontal vs vertical types of mite transmission are not easily disentangled in most birds with parental care (Figure 1: case 1: q_v vs q_h), but in the cowbird system, they can be assessed by quantifying host-specific (acquired by horizontal transmission, q_h) and non-host specific mite species (acquired mostly by vertical transmission, q_{v1}) since q_{h1} is low (Figure 1: case 4, see justification below). The cowbird system, therefore, offers a unique natural experiment to evaluate the rates of horizontal versus vertical transmission of feather mites.

Here we study the *M. bonariensis* feather mite system to investigate the degree of mite host specificity and origin (i.e., mites specific to *Molothrus bonariensis*, its foster parents, or multi-host generalists) using various lines of evidence: mite species richness, prevalence, geographic distribution, genetic distances, dated phylogenetics, and comparison with a related bird species (*Molothrus ater*). We also use co-phylogenetic reconciliation analyses to quantify the number of co-evolutionary events that occurred on the macroevolutionary scale in this system. Using these data, we then evaluate the horizontal versus vertical mite transmission rates and discuss the implications of our results to explain the observed macroevolutionary and microevolutionary patterns in this host-symbiont system. Our general null hypothesis is that if conspecific transmission (rates q_v and q_h) is greater than interspecific transmission (rates q_{v1} and q_{h1}) then both host specificity and cophylogenetic congruence should be high (Figure 1).

MATERIALS AND METHODS

Taxon Sampling

To investigate patterns of host switching of feather mites in the *M. bonariensis* system, we conducted a large-scale survey of *M. bonariensis* and its most common foster parent bird species (for example, *Turdus* spp., *Zonotrichia capensis*, *Sicalis* spp., *Pitangus sulphuratus*, *Thraupis* spp.; see Supplementary File 1 for a complete list) in different regions in Brazil. We sampled mites from live birds, dead birds, and bird skins from 6 museums (Clayton & Walther, 1997; Gaud & Atyeo, 1996). Fieldwork To investigate patterns of host switching of feather mites in the *M. bonariensis* system, we conducted a large-scale survey of *M. bonariensis* and its most common foster parent bird species (for example, *Turdus* spp., *Zonotrichia capensis*, *Sicalis* spp., *Pitangus sulphuratus*, *Thraupis* spp.; see Supplementary File 1 for a complete list) in different regions in Brazil. We sampled mites from live birds, dead birds, and bird skins from 6 museums (Clayton & Walther, 1997; Gaud & Atyeo, 1996). Fieldwork was carried out in September–November of 2017 and 2018 in 10 Brazilian states. Bird captures have also been done throughout these years in partnership with the bird banding ornithological group of the São Paulo State University (UNESP) in Rio Claro. In the field, birds were captured using mist nets and had their feather mites collected by removing infested feathers (usually one primary and tertiary flight feather, plus random body feathers when no downy-mites were spotted) (permit MMA 57944-3), preserving them in plastic vials filled with 96% ethanol and refrigerated (when possible), or stored in individual plastic bags for subsequent processing in the lab (yielding either live or dead mites; dead dried mites were

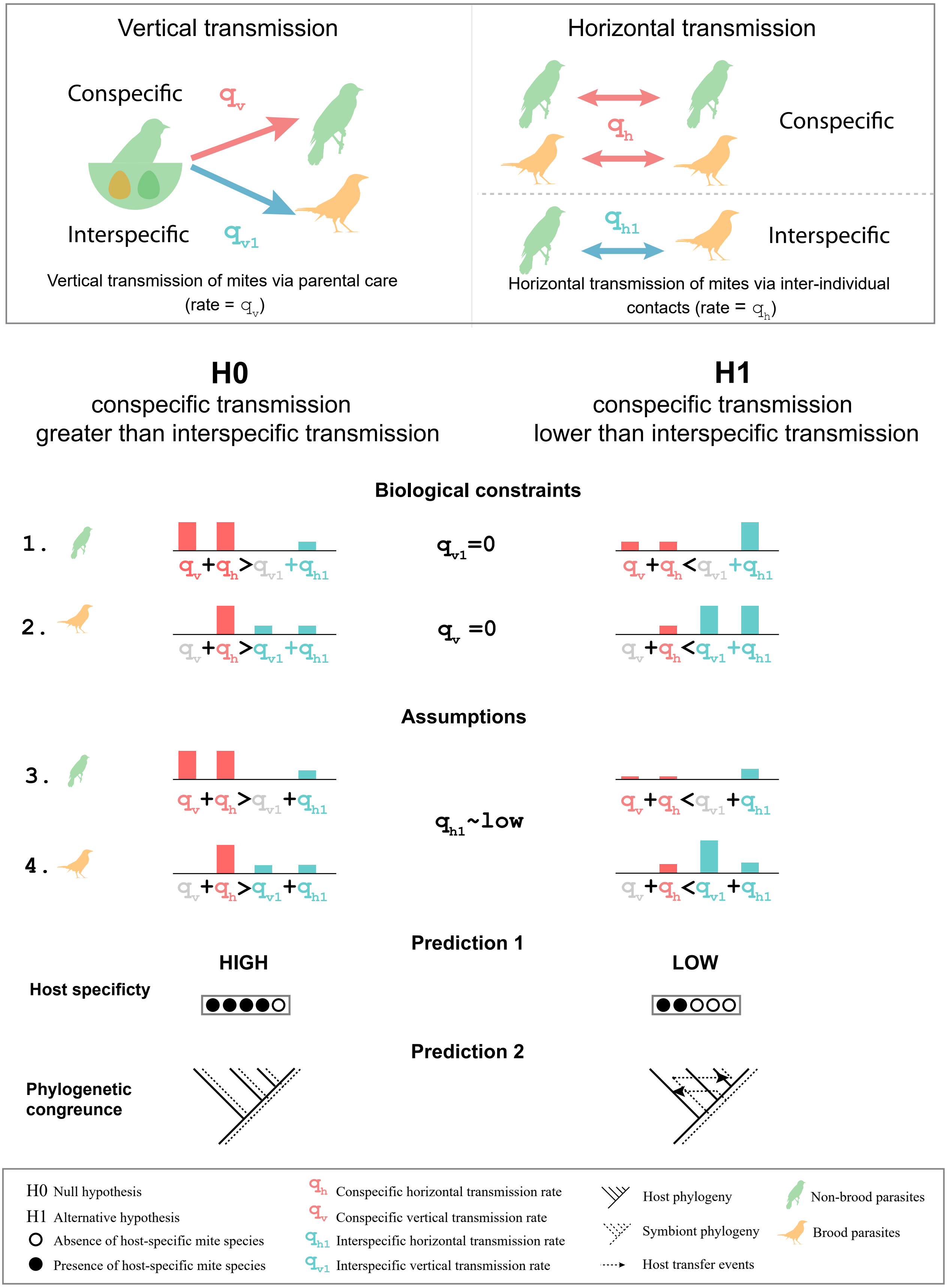

Figure 1. Vertical vs horizontal, conspecific vs interspecific transmissions in different bird systems (brood parasites and non-brood parasites), with schematic representation of two major hypotheses on how different symbiont transmission types may affect mite host specificity and co-phylogenetic congruence.

still suitable for DNA extraction). In the lab, all field samples were visually inspected to identify different morphospecies under a dissecting microscope; each morphospecies was then individually selected for DNA isolation and stored at -20 °C in 96% ethanol. At least one representative of each mite morphospecies of the two common proctophyllodid subfamilies (Proctophyllodinae, Pterodectinae) and one family (Trouessartiidae) was chosen per bird species and per region for DNA sequencing (Supplementary File 1). A total of 118 mite specimens from 29 passerine species (22 genera, 10 families) were sequenced; in addition, 153 GenBank sequences of 153 mite species from 127 bird species (90 genera, 36 families) were included as well (Supplementary File 1). Most mites collected in the field belonged to the genera commonly inhabiting New World passerines: *Amerodectes*, *Proctophyllodes*, *Metapterodectes*, *Tyrannidectes*, *Nycteridocaulus*, *Trouessartia*, *Analges*, *Mesalgoides*, and *Xolalgoides* (Gaud & Atyeo, 1996; Valim et al., 2011).

Museum Samples

Feather mites usually remain on dead hosts and, therefore, could be sampled from dry bird skins in museums (Gaud & Atyeo, 1996; Hernandes, 2020; Mironov & Proctor, 2008). However, museum bird skins could be a source of cross contamination between multiple bird species when they are processed by ornithologists in bulk (i.e. no individual bird separation), creating opportunities for mites to be transferred across adjacent bird specimens (Choudhury et al., 2002; Gaud, 1992; Gaud & Atyeo, 1996). To account for possible museum cross-contamination, each mite species was ranked from 0 to 2 based on its estimated abundance (Supplementary File 2: Column “Confidence Score”). Score 2 represents true mite-bird associations with high confidence (mites recovered from washing, from live birds in the field, or from museum skins with at least 3 males and 3 females of a given mite species found on a single host). Score 1 represents potentially true associations which failed the 3 male / 3 female criterion. Score 1 is a realistic measure of mite associations because birds captured in the wild often have small mite infrapopulation sizes (e.g., only 2 specimens per bird can often be observed). Finally, score 0 represents likely contaminations (e.g., atypical, non-passerine mite species) or undersampled hosts.

Mites were sampled from six museums: Museu da Fundação Zoobotânica de Porto Alegre (MCN, Porto Alegre, Rio Grande do Sul); Museu de Ciências e Tecnologia da PUC (MCT, Porto Alegre, Rio Grande do Sul); Museu de História Natural Capão da Imbuia (MHNCI, Curitiba, Paraná); Museu de Zoologia da Universidade de São Paulo (MZUSP, São

Paulo, São Paulo), Museu Paraense Emílio Goeldi (MPEG, Belém, Pará), and University of Michigan Museum of Zoology (UMMZ, Ann Arbor, Michigan) (mite collection only) (Supplementary File 2). Museum bird skins were sampled for mites by the feather-ruffling technique – bird's flight and body feathers were gently ruffled using a knitting needle over a clean, white paper; this material (debris, feather follicles, mites, etc.) was transferred to microtubes and then screened for mites in the lab under a dissecting microscope. Mites retrieved from museum skins were cleared in 30% lactic acid at 50°C for 48h before mounting on microscopic slides in Hoyer's medium; mites collected by washing and from live birds were left for 24h in lactic acid before mounting (Krantz & Walter, 2009). Mite exoskeletons retrieved from the non-destructive DNA extraction (see below) were placed in 30% lactic acid and briefly heated to remove internal air bubbles before mounting on slides. Mites were identified using the following references (Atyeo & Braasch, 1966; Gaud & Atyeo, 1996; Mironov, 2012; Pedroso & Hernandes 2021; Santana, 1976; Valim & Hernandes, 2010). Sequential numbers (e.g. sp.1, sp.2) were assigned to undescribed species, which are common in the New World (Barreto et al., 2012; Pedroso & Hernandes, 2016; Valim et al., 2011). Slide-mounted mites were deposited at the Department of Ecology and Zoology of the Universidade Federal de Santa Catarina (ECZ–UFSC).

Host specificity categories

We classified the feather mite fauna found on the shiny cowbird in three distinct groups based the following biologically informed criteria: expectation that the average neotropical passerine should harbor a set of six species belonging to six different genera, species richness, prevalence, phylogenetic relationships and genetic distances as compared to mites from foster parents or a related brood parasitic species, *Molothrus ater*.

(i) *Molothrus-specific* mite species – this diversity should be centered around six species, each in a separate genus (as observed in common, non-brood parasitic oscine passerine species having the general set of host-specific species: *Proctophyllodes*, *Amerodectes*, *Trouessartia*, *Mesalgoides*, *Xolalgoides*, and *Analges*); these mites should potentially have high prevalence and abundance; and in molecular trees they should be distantly related to mites known from foster parent passerines, and be closely related to mites from phylogenetically related hosts (e.g., *Molothrus ater*).

(ii) *Molothrus-alien* (foster parent mites) – these mites should have a higher species richness, without the presence of the typical general set of 6-species-in-6-genera (see above); have lower prevalence; in phylogenetic trees they should be closely related (i.e. have zero length or shallow branches) to mites specific to a particular foster parent passerine species.

(iii) *Multi-host* mites – this group is expected to include families and genera other than the ones found in the two previous categories, with low prevalence, and be closely related to (i.e. have zero or shallow branches) mites from multiple species of passerines. This group also includes mites having higher dispersal capabilities as they are hyperparasitic or phoretic on bird parasitic insects, some of which can fly (e.g., hippoboscid flies).

Our central expectation is: if there is a set of 6-species-in-6-genera (as in typical neotropical passerines) and these 6 species are most prevalent and have close phylogenetic similarities with mites from *Molothrus ater*, then this group of mite species are *Molothrus*-specific, while other species should be either *Molothrus-alien* or *Multi-host* (see above). We expect that prevalence of *Molothrus-specific* vs *Molothrus-alien* and *Multi-host* should be statistically significant. Otherwise, all mites are either *Molothrus-alien* or *Multi-host* (prevalence pattern is nearly flat because the mites mostly come from multiple species of foster parents).

DNA Amplification and Sequencing

DNA was isolated from individual mites using the QIAmp DNA Micro Kit (Qiagen) following the manufacturer's protocol with the following modifications: (i) each mite was pierced using a sterile pin under a dissecting microscope in a drop of ATL buffer and then transferred to a sterile microtube containing 180 µL ATL buffer and 20 µL of proteinase K, (ii) to avoid the mite being stuck to the tube wall, this solution was not pulse-vortexed, but (iii) was directly transferred to a shaking incubator (56° C, 24 h, lowest shaking speed), (iv) tubes were not pulse-vortexed after adding AL buffer but gently inverted several times to mix the reagents, (v) the DNA bound to the silica membrane was eluted in 25 µL of AE buffer and incubated for 5 min before the last centrifugation step. A similar approach was described in Klimov and OConnor (2008) and Matthews et al. (2018). After DNA isolation, mites' exoskeletons were mounted on microscopic slides and deposited (as morphological vouchers) at the Department of Ecology and Zoology of the Universidade Federal de Santa Catarina

(ECZ—UFSC). Specimens labeled with BMOC codes used in this study are deposited in the University of Michigan Museum of Zoology (UMMZ).

For DNA amplification, we first amplified the mitochondrial cytochrome c oxidase subunit I (CO1) gene (1026 nt) to identify unique haplotypes. The CO1 gene is a useful marker in the majority of feather mite species delimitation analyses, but it may not work to reconstruct phylogenies above the genus level (Doña et al. 2015, 2019b; Matthews et al. 2018a). Thus, to reconstruct deeper mite divergences we considered 5 candidate loci (EF1-α, SRP54, HSP70, 28S and 18S) used in a recent phylogenetic inference of the feather mite family Proctophyllodidae (Klimov et al. 2017), and selected the nuclear heat shock protein cognate 5 Hsc70-5 (HSP70) gene (1674 nt) based on its highest Internode Certainty index (IC) value in RaxML 8.2.10 (Salichos et al. 2014; Stamatakis 2014), and amplified this gene for all mites having unique CO1 haplotypes. Both genes were amplified using a nested PCR, which is appropriate for low concentration DNA templates. Our PCR mix (20 µL total volume) had 2.0 µL of 10x PCR buffer, 1.4 µL of 50 mM $MgSO_4$, 1.4 µL of dNTPs (10mM), 0.8 µL of each 10 µM primer, 0.08 µL of Platinum® *Taq* Polymerase (Invitrogen), and from 0.44 to 3.5 µL of DNA template, depending on DNA quality and concentration as assessed by a semiquantitative PCR using universally conserved eukaryotic primers for the 28S domain D9-10 rDNA: 28SV (GTAGCCAAATGCCTCGTCA) and 28SX (CACAATGATAGGAAGAGCC) (Klimov and OConnor 2008). Amplification of CO1 and HSP70 genes was done following previous published protocols for psoroptidian mites (Bochkov et al., 2014; Klimov et al., 2017; Klimov & Oconnor, 2013; Klimov & OConnor, 2008; Knowles & Klimov, 2011; Matthews et al., 2018). Amplicons from nested reactions were visualized on a 1.5% agarose gel and purified using Agencourt® AMPure® magnetic beads. Molecular work was done at the Molecular Lab of the Research Museums Center of the University of Michigan and sequenced at the University of Michigan Sequencing Core.

Chromatograms were assembled and edited in GeneStudio 2.2.0.0 (Genestudio, Suwanee, GA, USA). Contigs were aligned in Mesquite v. 3.6 (Maddison and Maddison, 2018) using previous feather mite sequences as a reference (Klimov et al. 2017). A small number of sequences were truncated due to sequencing inconsistencies. To place our sequences on a phylogenetic tree, we also used a large scale dataset with 144 terminals and six genes (18S, 28S, EF1-α, SRP54, HSP70 and CO1 (8546 bp total) for the feather mite families Proctophyllodidae and Trouessartiidae generated in a previous study (Klimov et al., 2017); 9 additional proctophyllodid terminals (CO1 only) (Hernandes et al., 2018; Matthews et al., 2018) were also included (Supplementary File 2). *Gabucinia* (Pterolichoidea:

Gabuciniidae) was used as a distant outgroup following previous works (Klimov et al. 2017; Matthews et al. 2018). Our final aligned matrix had 271 terminals, of which 118 were newly sequenced (Supplementary File 1: GenBank accession numbers, CO1: MW814590–MW814707; HSP70: MW829221–MW829276).

Phylogenetic Inference

We inferred a Maximum Likelihood (ML) phylogeny in IQ-Tree 1.6.10 (Nguyen et al., 2015) under a codon model for the protein-coding genes. Branch support values were estimated by Ultrafast bootstrap with 1000 replicates for the consensus tree (Minh et al., 2013) (Figure 2). The best model for each gene partition was estimated in IQ-Tree prior to analyses using the ModelFinder algorithm and corrected Akaike Information Criterion (AICc) (Kalyaanamoorthy et al., 2017): 18S + 28S (GTR+F+I+G4), EF1-α (KOSI07+F3X4+G4), SRP54 (MGK+F1X4+G4), HSP70 (MG+F3X4+G4) and CO1 (MG+F3X4+G4). All these analyses were run using a single command: *iqtree -s data.phy -st CODON5 -alrt 1000 -bb 1000 -nt 7 -p model*. The consensus tree was visualized and edited in FigureTree 1.4.4 (Rambaut, 2018). The tree was rooted using the outgroup genus *Gabucinia* (Pterolichoidea) after the analysis.

Species Delimitation

Given that morphological identification can be challenging as cryptic species may exist, here we used the CO1 locus for DNA-based species delimitation (Doña et al., 2015; Hebert et al., 2003; Santana et al., 2019); see Klimov et al. (2019) for limitations of CO1-only species delimitations. We used Automatic Barcode Gap Discovery (ABGD), which groups putative species based on a gap between inter- and intraspecific genetic distances (Puillandre et al., 2012). To evaluate whether putative species form monophyletic lineages, we also inferred a CO1 phylogeny in RaxML 8.2.10 using the GTR+G+I model and 100 bootstrap replicates (Stamatakis, 2014). In our study, we calculated K2P distances in the R package ‘ape’ v.5.3 (Paradis & Schliep, 2019).

Divergence Time Estimation

We also performed a Bayesian divergence time estimation in BEAST v2.6.1 (Bouckaert et al., 2014) using a Relaxed Clock Log Normal and the Birth and Death prior model, expecting multiple extinctions in feather mites (Klimov et al., 2017). Partition schemes and substitution models were found in PartitionFinder v 2.1.1 (GTR+I+G for all partitions, except for the CO1 position 3: GTR+G). Time calibration points follow those of a previous study (Klimov et al., 2017), which estimated divergence times only for the family Proctophyllodidae. Therefore, we limited our estimations to this family. We performed two time divergence analyses, one using fossil-mite divergence times based on previous estimates (Klimov et al., 2017), and for comparison, one using bird host diversification events as estimated in Barker et al. (2004). Both analyses used the same three nodes for calibration points as in Klimov et al. (2017) – the split of the Proctophyllodinae subfamily into the *Proctophyllodes* lineage and the *Nycteridocaulus* lineage, which corresponds to the oscine/suboscine avian split estimated at 45.1 Mya by fossil-mite data (sigma σ=3.0) and to 76.5 Mya by host divergence data (σ=3.0); the second calibration point refers to the diversification of the *thraupis* + *quadratus Proctophyllodes* groups, estimated as 25.3 Mya by fossil-mite data (σ=4.0), which corresponds to the 21 Mya (σ=2.85) dispersal to the New World of the bird superfamily Emberizoidea (also known as Nine-Primaried Oscines); and the third calibration point refers to the *Amerodectes* generic clade, estimated to be around 44.3 Mya (σ=3.5) by the fossil-mite data, which also corresponds to the Emberizoidea arrival in the New World (21 Mya, σ=2.85). Because different divergence times for Passeriformes have also been reported in the later works (Barker et al., 2015; Claramunt & Cracraft, 2015; Oliveros et al., 2019; Prum et al., 2015; Selvatti et al., 2015), we did another divergence time estimation analyses using data from Oliveros et al. (2019), which estimated an earlier divergence time for the oscine/subsoscine split (around 44 Mya) and to the New World Emberizoidea clade (around 17.5 Mya). The mean and sigma for this calibration were set to 44 and 5.0 for oscine/suboscine split; and to 17.5 and 3.0 for the New World Emberizoidea, respectively.

Six independent BEAST runs were performed with a sampling frequency of 5000 and 50 million generations in the CIPRES science gateway (Miller et al., 2010). Each run was inspected for convergence in Tracer v1.7.1 (Rambaut & Drummond, 2009); burn-in was 15-50%. LogCombiner v2.6.2 was used to combine MCMC stationary samples from the six independent runs using a single 50% burn-in threshold, and TreeAnnotator v2.6.1 was used to summarize the 12,504 postburnin trees into a maximum credibility tree with node heights calculated as median heights. The maximum credibility tree was visualized and edited in FigureTree 1.4.4 (Rambaut, 2018). None of the runs using the Barker et al. (2004) time calibration recovered either a good effective sample size (>200) or convergence and were therefore discarded, whereas all other runs presented ESSs above 200 and good convergence.

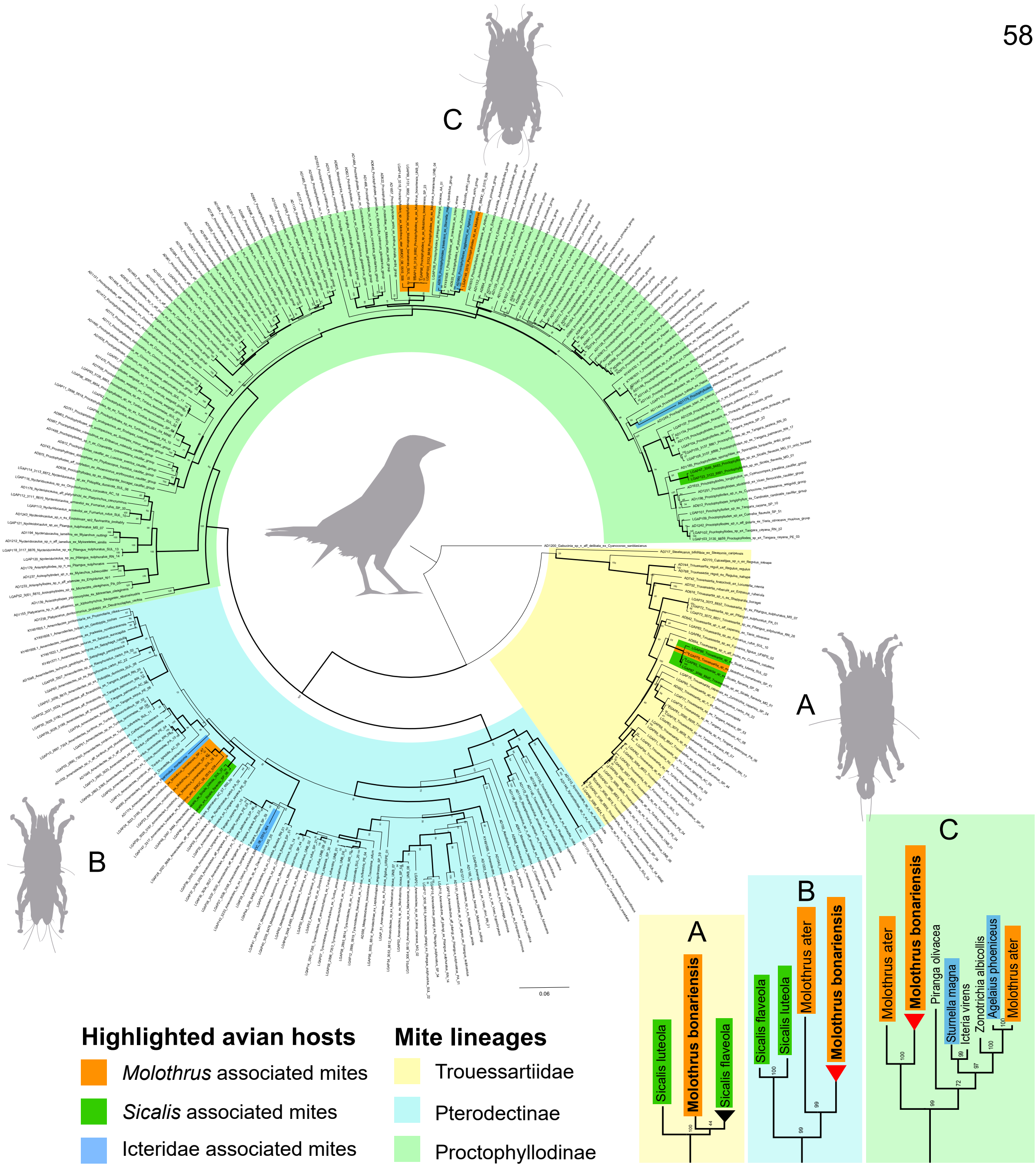

Figure 2. Maximum Likelihood phylogeny of feather mites based on 6 genes (5 nuclear, 1 mitochondrial). Nodal support higher than 75% for 1000 replicates (estimated by ultrafast bootstrap) is shown by thicker lines. The major mite lineages, Trouessartiidae, Proctophyllodinae and Pterodectinae are highlighted. Mites from cowbirds (*Molothrus bonariensis* and *M. ater*), finches (*Sicalis flaveola* and *S. luteola*), and Icteridae are highlighted. Portions of this phylogeny, exemplifying important host shifts to *Molothrus* are given on insets (A-C); these cases are further considered in detail on Fig. 4 and Table 2.

Table 1. Prevalence, abundance, and host specificity of feather mites from the shiny cowbird. Species are grouped by host specificity categories.

Mite (n=29)	**Host Specificity**	**Prevalence by host individual (%)**	**Prevalence by mite record (%)**	**Host-parasite records (n=365)**	**Mite Abundance (n=1241)**	**Mite Abundance (%)**
Amerodectes molothrus	Molothrus-Specific	59.59	23.84	87	350	28.20
Mesalgoides sp. 1	Molothrus-Specific	30.14	12.05	44	122	9.83
Proctophyllodes molothrus	Molothrus-Specific	58.90	23.56	86	344	27.72
Trouessartia sp. 6	Molothrus-Specific	13.01	5.21	19	49	3.95
Xolalgoides sp. 1	Molothrus-Specific	25.34	10.14	37	115	9.27
subtotal			**74.79**	**273**	**980**	**78.97**
Amerodectes bilineatus	Molothrus-Alien	0.68	0.27	1	5	0.40
Analges sp. 1	Molothrus-Alien	1.37	0.55	2	33	2.66
Analges sp. 5	Molothrus-Alien	0.68	0.27	1	7	0.56
Analges sp. 6	Molothrus-Alien	1.37	0.55	2	11	0.89
Analges ticotico	Molothrus-Alien	0.68	0.27	1	6	0.48
Mesalgoides sp. 2	Molothrus-Alien	7.53	3.01	11	14	1.13
Mesalgoides sp. 3	Molothrus-Alien	2.74	1.10	4	7	0.56
Platyacarus sp.	Molothrus-Alien	1.37	0.55	2	12	0.97
Proctophyllodes aff. atyeoi	Molothrus-Alien	2.74	1.10	4	16	1.29
Proctophyllodes cf. thraupis	Molothrus-Alien	2.74	1.10	4	12	0.97
Proctophyllodes sp. 16	Molothrus-Alien	1.37	0.55	2	7	0.56
Proctophyllodes sp. 4	Molothrus-Alien	2.74	1.10	4	8	0.64
Proctophyllodes sp. 5	Molothrus-Alien	4.11	1.64	6	13	1.05
Proctophyllodes carmenmirandae	Molothrus-Alien	3.42	1.37	5	9	0.73
Trouessartia aff. megaplax	Molothrus-Alien	1.37	0.55	2	13	1.05
Trouessartia capensis	Molothrus-Alien	6.85	2.74	10	18	1.45
Trouessartia sp. 7	Molothrus-Alien	2.05	0.82	3	10	0.81
Trouessartia cf. sicaliae	Molothrus-Alien	0.68	0.27	1	2	0.16
Xolalgoides sp. 2	Molothrus-Alien	2.74	1.10	4	11	0.89
subtotal			**18.90**	**69**	**214**	**17.24**
Dermationidae	Multi-Host Parasite	4.11	1.64	6	10	0.81
Dermoglyphus cf. passerinus	Multi-Host Parasite	5.48	2.19	8	16	1.29
Microlichus cf. americanus	Multi-Host Parasite	2.74	1.10	4	4	0.32
Metamicrolichus cf. phasianus	Multi-Host Parasite	1.37	0.55	2	7	0.56
Strelkoviacarus brasiliensis	Multi-Host Parasite	2.05	0.82	3	10	0.81
subtotal			**6.30**	**23**	**47**	**3.79**
Total	29	146	365	365	1241	175.18

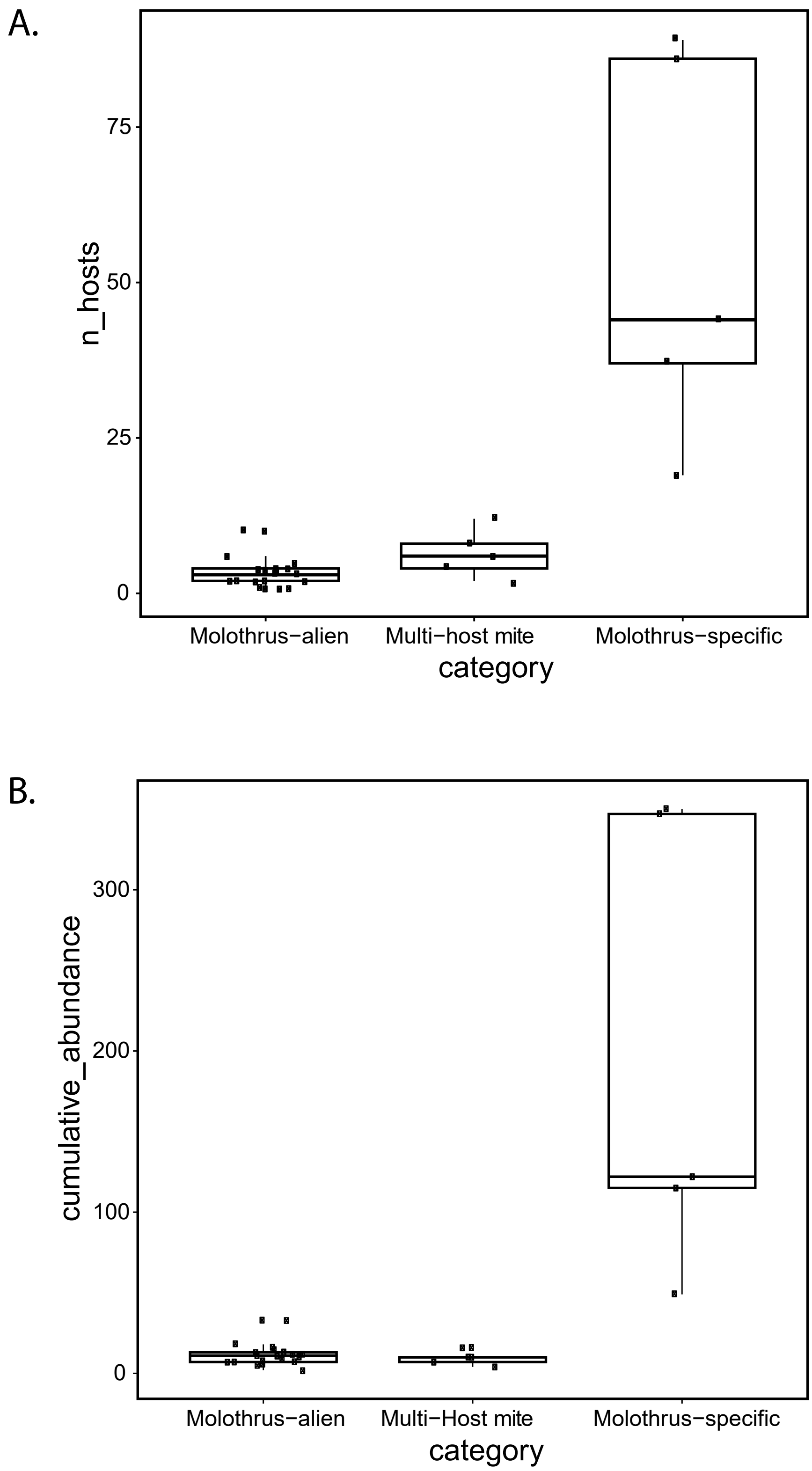

Figure 3. Boxplots of the three mite groups ranked by the number of their host records (host specimen count per mite species) (A) and cumulative abundance of mites (B). In both graphs the *Molothrus-specific* mite group is statistically different from other groups, *Molothrus-alien* and *Multi-Host* mite ($p < 0.05$, Wilcoxon paired-rank test). Abundances for *Molothrus-specific* category were underestimated due to the large number of specimens per bird individual, particularly for *Amerodectes molothrus* and *Proctophyllodes molothrus*.

Similarly, Klimov et al. (2017) reported difficulties in achieving convergence in 8 of 18 BEAST runs using a similar dataset.

We compared our divergence time estimates with the following known hosts' time divergence estimates: *Molothrus* (originated 7.4, diversified 4.3 Mya); *Molothrus ater/bonariensis* split 1.0-2.2 Mya; *Sicalis* (originated 9.1 Mya, diversified 7.2 Mya), *Sicalis flaveola/luteola* split 4.8-5.6 Mya (Jetz et al., 2012). Other published estimates of the *Molothrus ater/bonariensis* split range from 0.8-1.2 to 2.8-3.8 Mya (Barker et al., 2015; Gómez & Lois-Milevicich, 2020; Remsen et al., 2016; Rothstein et al., 1999).

Cophylogenetic analyses

To quantify the number of different co-evolutionary events in the *Molothrus* system, we performed parsimony-based reconciliation cophylogenetic analyses in eMPRess (Santichaivekin et al., 2021). Default event cost values were used as the software automatically selects the average best fitting reconciliations. Symbiont trees were inferred in IQ-Tree 1.6.10 as above (see the 'Phylogenetic Inference' section). Bird phylogenies were obtained from BirdTree (Jetz et al., 2012). TreeAnnotator v2.6.1 was used to summarize the 1,000 host trees into a maximum credibility tree with node heights calculated as median heights. We found phylogenetic information for all bird species except *Polioptila dumicola* (Vieillot, 1817). For these analyses, mites' operational taxonomic units (OTU) were recognized and named accordingly to avoid conflict with the putative mite morpho-species.

RESULTS

Mite species richness

A total of 146 shiny cowbirds specimens were inspected for feather mites, 22 captured in the wild, 10 from washes, and 114 from museums. Of these, 7 bird individuals lacked any mites, and 139 individuals had mites (confidence scores 0-2, see Materials and Methods: Host specificity categories). Of the group of birds harboring mites, there were 365 mite records having confidence scores 1-2, representing 29 mite morphospecies (12 genera, 8 families), including 12 named species (Supplementary File 2). The most speciose genera were *Proctophyllodes* with 7 species, followed by *Trouessartia* with 5 species (Table 1).

Table 2. Feather mite transmission on *Molothrus bonariensis*. For host individuals, counts and percentages are given. For mites, values are counts (percentages) of unique host-symbiont record counts (=cases). Data are summarized from 365 mite records sampled from 139 bird individuals (7 additional host individuals that lacked any mites were excluded). Host counts may overlap since a host individual may harbor mites from different host-specificity categories.

Transmission	**Host individuals**	***Molothrus-specific*** (5 species)	***Molothrus-alien*** (19 species)	***Multi-host*** (5 species)
1. Horizontal only (birds hosting Molothrus-specific mites only)	73 (52.5%)	147 (40.3%)	0	0
2. Horizontal + Vertical + Multi-host (birds hosting both specific and alien mites)	57 (41.0%)	126 (34.5%)	59 (16.2%)	21 (5.7%)
3. Vertical only (birds hosting alien mites only)	7 (5.0%)	0	10 (2.7%)	0
4. Uncertain only (hosting multi-host only)	2 (1.4%)	0	0	2 (0.5%)
Horizontal transmission total (1+2)	130	**273 (74.8%)**	-	-
Vertical transmission total (2+3)	64	-	**69 (18.9%)**	-
Transmission events, total (1+2+3+4)	139 (100%)	273 (74.8%)	69 (18.9%)	**23 (6.3%)**

A relationship between host specificity vs prevalence and abundance

Based on prevalence, shiny cowbird mites were classified into three categories of host specificity: *Molothrus-specific*, *Multi-host* mites, and *Molothrus-alien* (Table 1; Figure 3; Supplementary File 2). *Molothrus-specific* mites (5 species) were consistently found on multiple host specimens with moderate to high prevalence (>13%, Table 1): *Proctophyllodes molothrus*; *Amerodectes molothrus*; *Xolalgoides* sp.1; *Mesalgoides* sp.1 and *Trouessartia* sp.6. All five genera in this set of taxa are present in the subset of the 6 core genera that are expected on a common oscine passerine in the New World (see Material and Methods: Host specificity categories). The only exception was a species of the genus *Analges* having low prevalence (< 1.5%), and therefore was not considered a *Molothrus-specific* mite here (Table 1). *Molothrus-alien* mites (19 species, Table 1) are species recorded on few cowbird individuals (prevalence < 7.5%). Lastly, *Multi-host* mites (5 species, Table 1) are similar to the *Molothrus-alien* category as these mites were also present at low prevalence (< 5%). We classified these mites as *Multi-host* based mostly on the literature data: they are naturally rare, live on the host skin (e.g. *Microlichus*, *Metamicrolichus*, *Strelkoviacarus*) and inside quills (*Dermoglyphus*). The aforementioned skin-inhabiting mites have an ability to be horizontally transferred across interspecific and intraspecific hosts via phoresy on louse flies (Diptera:

Hippoboscidae) (Fain, 1965; Fain & Grootaert, 1996; Mironov et al., 2005), which may explain the fact they are found across several host species. The differences in prevalence of *Molothrus-specific* vs *Molothrus-alien* or *Multi-host* mites were statistically significant (Wilcoxon paired-rank test $p = 0.0007$ and 0.0079, respectively), but not between *Molothrus-alien* and *Multi-host* mites ($p = 0.0509$) (Figure 3). Cumulative mite abundances (the total number of all mite specimens in each category) were also statistically different in *Molothrus-specific* vs *Molothrus-alien* or *Multi-host* mites categories ($p = 0.0008$ and 0.011, respectively), but not in *Molothrus-alien* vs *Multi-host* mites ($p = 0.568$) (Figure 3). This indicates that abundant mite species are also more likely to be *Molothrus-specific*, while less abundant mite species are likely to originate from foster parents (*Molothrus-alien*) or be a generalist, multi-host species, reinforcing the categorization. While under an alternative expectation (all mites originate from multiple foster parent species), the abundance pattern is expected to be nearly flat, reflecting the pattern of usage of different species of foster parents by *Molothrus*. The *Molothrus-specific* category also showed a uniform distribution of mite species across geographic biomes in comparison with *Molothrus-alien* and *Multi-host* mites ($p < 0.5$) (Supplementary File 3), suggesting a relationship between geographic distribution and specificity. In particular, *Molothrus-alien* mites are restricted to certain areas whereas *Molothrus-specific* mites are widespread along the host distribution.

The co-occurrence of *Molothrus-specific* and *Molothrus-alien* or *Multi-host mites*, important to analyze competitive exclusion scenarios as well the magnitude of interspecific horizontal transmission (Figure 1: case 4: q_{h1}), was also evidenced by our quantitative data: (i) in 52.5% of cases only specific mites were found on a single host individual; while (ii) *Molothrus-specific* mites were more prevalent (34.5% vs 16.2%) when both specific and foster parent mites were found together (see Table 2, line 2, *Molothrus-specific* and *Molothrus-alien* columns); and (iii) only in 2.7% of cases were mites only originating from the foster parent were found (Table 2).

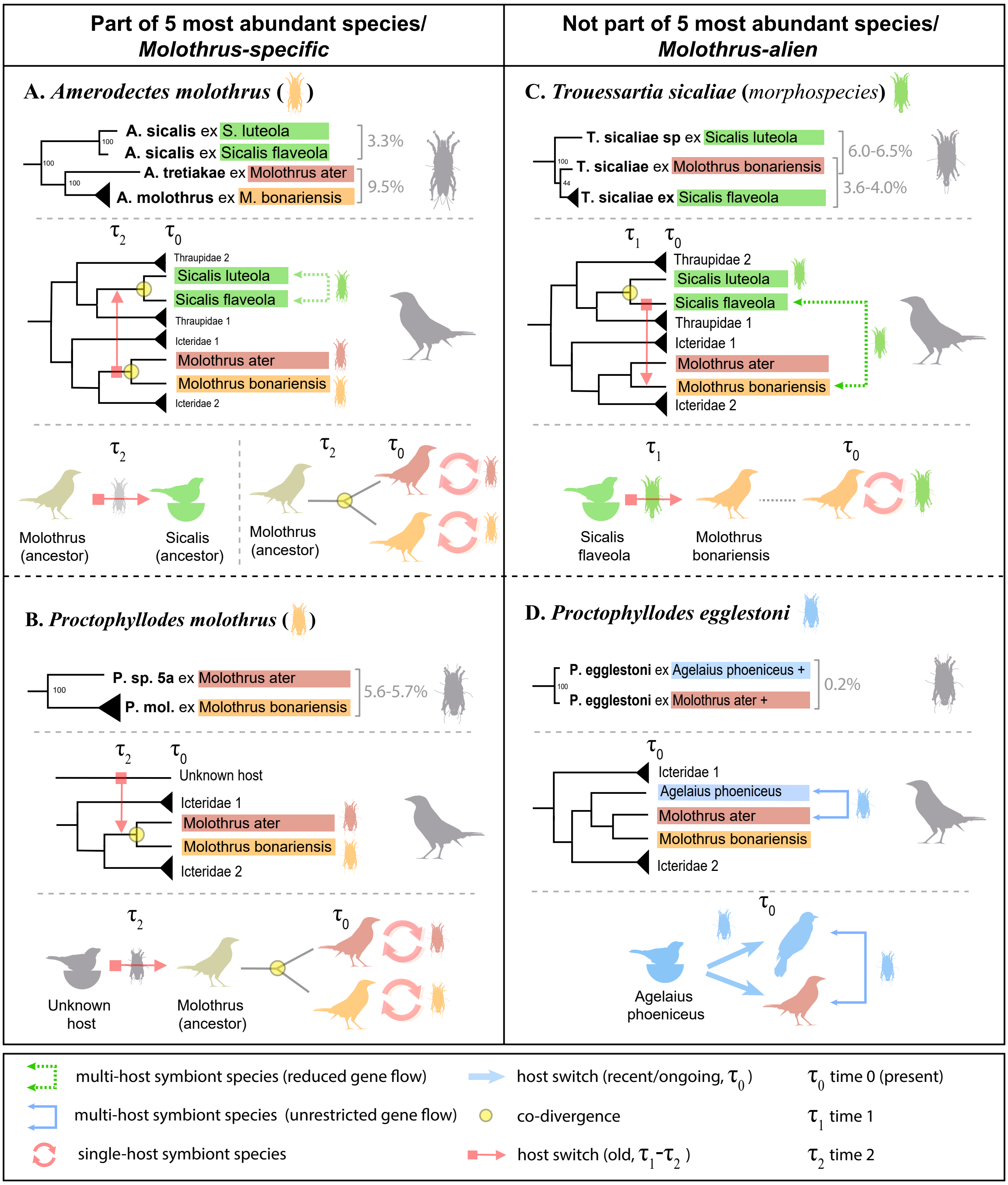

Figure 4. A–D Schematic representation of molecular phylogenetic and cophylogenetic subtrees of *Molothrus*-related mites (see Fig. 2; and Supplementary Files 5, 6, 7, 8, and 9 for complete phylogenies). Nodal support is given for each branch (ultrafast bootstrap, 1000 replicates). Barcode CO1 K2P genetic distances are given in percentage. Cophylogenetic event representations after eMPRess analyses.

Table 3. Vertical and horizontal transfers of select *Molothrus-specific* mites and their temporal context. Transmissions were estimated based on the mite prevalence per host individual.

	A. *Trouessartia sicaliae* complex	**B**. *Proctophyllodes egglestoni*	**C**. *Amerodectes molothrus* complex	**D**. *Proctophyllodes* sp1. complex
Host switch time (Mya)† host/fossil	Not estimated	0-1.0/0-1.8	7.9/15.5	1.9-5.0/3.7-9.6
Host switch from	Foster parent (*Sicalis flaveola*)	Foster parent/social contact (*Agelaius phoeniceus*)	ancestral *Molothrus*	Unknown
Host switch to	*Molothrus bonariensis*	*Molothrus ater*	foster parent (ancestral *Sicalis*)	ancestral *Molothrus*
Mite speciation on ancestral *Molothrus*	No	No	Yes	Yes
Mite genetic partitioning on *Molothrus* species	Yes	No	Yes	Yes
M↔ M horizontal transmission	Yes§	Yes	Yes	Yes
M↔M horizontal transmission estimate (M. bon.)	0.68%	N/A	59.59%	58.9%
FP→M horizontal transmission	No‡	Yes	No	No
FP→M vertical transmission	Yes§	Yes	No	No
FP→M vertical transmission estimate (M. bon.)	0	N/A	0	0

FP=foster parents; M=*Molothrus*; M. bon.= *Molothrus bonariensis* † =host/fossil time calibration estimates, ‡ =Yes (under incomplete sampling assumption), § =No (under incomplete sampling assumption)

Species distance in Molothrus-specific mites

Despite our modest sampling, we detected three mite species associated with *M. ater*. Two of them were very similar – yet not the same – to mite species associated with *M. bonariensis*: *Proctophyllodes* sp. 5a related to *Proctophyllodes molothrus* ex *M. bonariensis* (CO1 K2P = 5.5%); and *Amerodectes tretiakae* Mironov & Galloway (2021) related to *Amerodectes molothrus* ex *M. bonariensis* (CO1 K2P = 9.5%). A barcode gap analysis (ABGD) grouped these two genetically distinct *Proctophyllodes* lineages either as a single or separate species depending on the barcoding gap proxy (X) prior value (from 0.001 to 0.04). The two *Amerodectes* lineages had a very well-defined barcoding gap and all species delimitation analyses unambiguously placed these lineages as two separate species (Figure 4A, B). The similarity is also phylogenetic, which indicates a historical association of these mites with *Molothrus* hosts, therefore, resulting from codivergence events. The third mite species associated with *M. ater, Proctophyllodes egglestoni* is a multi-host species (Atyeo & Braasch, 1966), forming very shallow CO1 genetic distances (K2P = 0.2%) with mites from an icterid, *Agelaius phoeniceus*, a common foster parent of *M. ater* (Figure 4D). The implication of this finding is that *Proctophyllodes egglestoni* associated with *M. ater* and its foster parents displays properties that make it impossible to estimate the relative importance of vertical and horizontal transfer rates for this species, since this mite species can probably employ both modes of transfer (as evidenced by the absence of a genetic structure in mites from *M. ater* and its foster parents). However, in mites associated with *Molothrus bonariensis*, such a host-related genetic structure is present, i.e. K2P CO1 distances range from 3.6 to 9.5% in *Trouessartia*, *Amerodectes*, and *Proctophyllodes* (Figure 4). This indicates that successful vertical transmission from foster parents to *Molothrus* does not occur in mites assigned to the *Molothrus-specific* category. This important property allowed us to accurately quantify the rate of vertical transmission in *M. bonariensis*.

Cophylogenetic and temporal context for host shifts

The corollary of the hypothesis assuming a greater rate of horizontal versus vertical symbiont transmission is the presence of host switching on both macroevolutionary and microevolutionary scales in feather mites (Figure 1, 4). We used phylogenetics, co-evolutionary and molecular clock analysis (Figure 2, 4; Supplementary Files 5, 6, 7, 8, 9) to infer phylogenetic relationships of mites from brood parasitic cowbirds and their foster parents, and then used these data to identify either ongoing (with gene flow) or historical host switching (no gene flow). Our time estimates provide temporal context for mite-bird colonization events (Table 3). Below we give several topology- and divergence time-informed co-evolutionary scenarios in the cowbird system, focusing on host switches (Figure 3A-D).

A. *Trouessartia sicaliae* complex: Likely host switch to *M. bonariensis* from foster parents followed by on-host divergence. One DNA sequence of *Trouessartia* from *M. bonariensis* was recovered as nested among the *Trouessartia sicaliae* morphospecies associated with thraupids *Sicalis* spp. (Figure 4C), which are known foster parents of *M. bonariensis*. However, the *Trouessartia* lineage from *M. bonariensis* had substantial CO1 genetic distance (3.6%), indicating that this *Sicalis* to *Molothrus* switch occurred sometime in the past, resulting in a fully or partially genetically distinct lineage formed on *M. bonariensis*. Ongoing gene flow via conspecific horizontal transmission occurring at low rate cannot be excluded in this system and may be confirmed in the future using a denser sampling.

B. *Proctophyllodes egglestoni*: Ongoing mite transmission from foster parents and possibly by social contact (Figure 4D). Mites from *Molothrus ater* clustered with those of the red-winged blackbird, *Agelaius phoeniceus*, and their CO1 genetic distances were nearly identical (0.2%). The high sequence identity is indicative of an ongoing mite transmission from foster parent to *Molothrus* or via social contacts in mixed flocks. This is a multi-host mite, mostly associated with icterids (Atyeo and Braasch, 1966).

C. *Amerodectes molothrus* complex: A putative host switch onto ancestral *Molothrus*, followed by host switch of *Amerodectes* mites from ancestral *Molothrus* to their foster parents (ancestral *Sicalis*) which resulted in their co-divergence on *Molothrus* and possibly in *Sicalis* (Figure 4A). This unexpected scenario is evidenced in all retrieved cophylogenetic reconciliations and by the topology rendering both *Sicalis* and *Molothrus* mites as monophyletic sister groups. Our time estimates for this host switch (7.9 Mya, host-based calibration) makes this switch temporally possible, while the 15.5 Mya estimate (fossil mite calibration) is not plausible given that it occurred before the origin of both *Molothrus* and *Sicalis* (Supplementary Files 5, 6). Our divergence time estimates of mites from *Molothrus ater* and *M. bonariensis* (4.4/3.7 Mya, host/fossil calibration) predate the divergence time estimates of their hosts (i.e. around 1 Mya), however, they are close to the extreme value (3.8 Mya) from the literature (Barker et al., 2015; Remsen et al., 2016; Gómez & Lois-Milevicich, 2020). In contrast, *Amerodectes* mites associated with *Sicalis flaveola*/*luteola* originated after their hosts split into species (0.6/1.2 Mya vs 4.8-5.6 Mya) (Supplementary Files 5, 6). Taken together, our cophylogenetic evidence and time estimates suggest that in the *Amerodectes* *molothrus* complex, a host switch occurred from the ancestral *Molothrus* to ancestral *Sicalis*, contrarily to expectations of host switch from foster parents to brood parasitic birds. Ongoing mite transfer is apparently not possible, given the large genetic distances (12.4–19.6%) between mites from *Molothrus* and its foster parents.

D. *Proctophyllodes molothrus* complex: A putative host switch onto ancestral *Molothrus*, followed by co-divergence on *Molothrus* (Supplementary File 8). Given the data at hand and current knowledge of *Proctophyllodes* diversity and distribution in the New World, the source host cannot be identified. Since the sister group of the *Proctophyllodes molothrus* complex is a lineage associated with various icterid hosts (*Sturnella magna* and *Agelaius phoeniceus*), the ancestral host could be an unsampled icterid (Figure 2). Our time estimates for this host switch (1.9-5.0 Mya host-based calibration or 3.7-9.6 Mya fossil mite calibration) are both plausible, given that they are completely (former) or partially (latter) within the timing of origin of *Molothrus*. Ongoing mite gene flow can be ruled out given the large genetic distances (10.5–18.7%) between these mites from *Molothrus* and its foster parents. However, it also cannot be completely ruled out that mites of the *Proctophyllodes molothrus* complex represent the native feather mites of the genus *Molothrus*, inherited from the ancestor in the family Icteridae in the process of its divergence.

In conclusion, there was a total of 2 codivergences and 2 host switches for *Molothrus*-specific mites and 2 codivergences and 3 host switches for all mites, counting only macroevolutionary events and only those occurred in our system of interest, *Molothrus* (Figure 4). These data indicate that there was no substantial predominance of either of these co-evolutionary events although host switches were slightly more common.

Estimation of horizontal vs vertical mite transfer rate based on host specificity

The 29 mite species found on *Molothrus bonariensis* were classified into three groups based on their host specificity: *Molothrus-specific* (5 species), *Molothrus-alien* (19 species, foster parent specific mites), and *multi-host* mites (5 species, host generalists, may naturally occur on a broad range of hosts, including *Molothrus* and its foster parents) (Table 1, Supplementary File 2). Among these categories, all cases (unique host records) were distributed as follows: 74.8%, 18.9%, and 6.3%, respectively (Table 2). Assuming that each mite species on each host individual resulted from a single colonization event and everything else being equal, these Figures should reflect relative transmission rates in each host specificity-category. For example, in the two first categories, *Molothrus-specific* mites are 3.9

times (74.8/18.9) more likely to colonize new host individuals than *Molothrus-alien* mite species (Table 2). Since *Molothrus-specific* mites can only disperse between shiny cowbird individuals via horizontal transmission and *Molothrus-alien* mites predominantly disperse via vertical transmission from foster parents, one can conclude that horizontal transmission is at least 3.9 times more frequent than vertical transmission in this system. However, in the third group (*multi-host*), mites can disperse either vertically (foster parents to *Molothrus*) or horizontally (by host contacts or via phoresy on hippoboscid flies). Assuming that multi-host mites disperse either only vertically or horizontally, we estimate the overall ratio between horizontal and vertical transmission in the *Molothrus* system is within the interval of 3.0-4.3 (74.8/25.2-81.1/18.9) (Table 2), where the lower value (3.0) is a conservative estimate of horizontal vs vertical transmission rate.

Foster parent identification based on Molothrus-alien mites

T There were a total of 52 *Molothrus-alien* records (Supplementary File 4). Based on morphology and molecular evidence, 42 records and 8 mite species could be confirmed to originate from known shiny cowbird foster parents (Batisteli et al., 2019; Cavalcanti, 1988; Fraga, 1978; King, 1973; Lowther, 2019; Sick, 1997): *Trouessartia sicaliae* from *Sicalis* spp. (Figure 4C); *Proctophyllodes* cf. *thraupis*, *Trouessartia* aff. *megaplax* and *Amerodectes bilineatus* from the sayaca tanager, *Thraupis sayaca*; and *Trouessartia capensis*, *Analges ticotico, Strelkoviacarus brasiliensis*, and *Proctophyllodes carmenmirandae* from the rufous-collared sparrow, *Zonotrichia capensis*. Unfortunately, the remaining records could not be assigned to any known foster parent bird species due to insufficient knowledge of feather mite diversity in the Neotropic region (Pedroso & Hernandes, 2016; Valim et al., 2011).

DISCUSSION

To investigate the relative rates of different transmissions of a symbiont, we extensively surveyed a generalist brood parasitic passerine, the shiny cowbird (*Molothrus bonariensis*) for its feather mites. This cowbird system offers a unique natural experiment to evaluate the relative rate of horizontal versus vertical mite transmission in a bird-feather mite system (Fig 1: case 4). For this task, accurate identification of *Molothrus-specific* mite species (horizontal transmission q_h only) and mites originating from foster parents (vertical transmission q_{v1} only) was needed. Our data strongly indicate that *Molothrus-specific* mites could be confidently identified because they had several distinct properties: constrained species richness (centered around 5 species in 5 genera as expected in the "average" neotropical paserine), high host specificity, high prevalence (>13%), high cumulative abundance (>49 mite individuals), and the absence of gene flow with mites from foster parents. In contrast, mites originating with the foster parents (*Molothrus-alien*) had a higher species richness (19 species, 7 genera), lower prevalence (<5%), and evidence of gene flow among mites from cowbirds and their foster parents. Based on the known biology of the shiny cowbird, horizontal transmission of *Molothrus-specific* mites are only possible via social contact between cowbird individuals (Figure 1: q_h), which can occur during the formation of foraging and roosting flocks after fledging, during courtship and copulation, and during other conspecific interactions (Linz et al., 2017; Louder et al., 2015; Ortega et al., 2005; Sick, 1997; Soler, 2017). Furthermore, *Molothrus-specific* mites do not occur on any other bird species (including cowbird foster parents) as confirmed by morphological and molecular data. There is thus no evidence that these mites are transmitted vertically via parental care (Figure 2, Table 2). In other words, cowbird foster parents do not serve as vectors of *Molothrus-specific* mites in our system. Furthermore, interspecific horizontal transmission (Fig 1: case 4: q_{h1}) should be minimal here as *alien*-only mites were found only in 2.7% of birds (Table 2); and even this small figure can be fully or partially attributed to vertical transmission. Thus, based on the above data, horizontal and vertical mite transmission (q_{v1} and q_h) could be confidently identified based on the level of host specificity of each mite species, and quantified based on mite occurrence per host individual in most cases. However, a small group of *multi-host* mite species (6.3% of all cases) could disperse both horizontally and vertically (Table 1). Given this uncertainty, we conservatively estimated that in the cowbird system, horizontal transmission (q_h) was at least 3.0 times more frequent than vertical transmission (q_{v1}); i.e. 74.8% (*Molothrus*-specific) vs 25.2% (foster parent mites and *multi-host* mites) (Table 2). Overall, mites were present on 95.2% of host individuals, while only 4.8% of bird individuals did not have mites (Table 2).

In the cowbird system, all mites of the specific host specificity group were transmitted horizontally (via social contacts), which likely occurred gradually with host age as the birds experienced an increasing rate of social contact, which is similar to what is observed with megapode (Galliformes: Megapodiidae) feather mites (Proctor & Jones, 2004). This sequential acquisition of feather mites, acquiring alien mites first followed by *Molothrus*-specific mites, evidenced by the co-occurrence of *Molothrus*-specific and alien mites, creates the possibility of a competitive exclusion scenario, where specific mites replace or cohabit with the foster parent mites (Table 2; Supplementary File 2). On a microevolutionary scale, these horizontal transmissions maintained host specificity and also provided the continuity of mites' generations. The result is complete or partial replacement of mites on cowbirds originating from foster parents. On a macroevolutionary scale, our co-evolutionary scenarios also revealed a dramatic pattern of host switching. As an example, the two most common and abundant mite species, *Amerodectes molothrus* and *Proctophyllodes molothrus*, either originated as the result of host switching of their ancestral mite species from an unrelated host (*P. molothrus*) or actively switching from *Molothrus* ancestors to new hosts (*Sicalis*) (Figure 4A, B). Subsequently, the colonizing mite lineages have become genetically isolated and specific to their new hosts. These colonizing mites apparently replaced the original core mites belonging to the same two genera via competitive exclusion.

The literature also suggests the presence of conspecific horizontal transmission of symbionts in other brood parasitic birds, albeit with no quantitative data. Two other brood-parasitic lineages, European cuckoos (*Cuculus canoris*) and indigobirds (*Vidua*), acquire their symbionts (mites or lice) predominantly via horizontal transmission from conspecifics (Atyeo & Gaud, 1983; Balakrishnan & Sorenson, 2007; Brooke & Nakamura, 1998; Hromada et al., 2016; Vas et al., 2013). Horizontal transmission has been also observed as the main transmission route even in non-brood parasitic systems, such as in feather mites from the red-billed choughs (Corvidae) (Blanco et al., 1997), and in feather lice from bee-eaters (Darolova et al., 2001). A mixture of horizontal and vertical transmission, as exemplified by the presence of specific and foster parent symbiotic arthropods, has been recorded in cowbirds and other systems, but again without quantitative data (Atyeo & Gaud, 1983; Hahn et al., 2000; Hilario-Pérez & Dowling, 2018; Lindholm et al., 1998; Mena et al., 2020). A recent study of non-brood parasitic birds also indicated that horizontal transfers in feather mites may be more frequent than previously thought (Doña et al., 2019b). Thus, our data on the high rate of horizontal transmission in the brood-parasitic shiny cowbird system potentially represent a more general pattern that needs to be accounted for in non-brood parasitic bird systems as well.

In host-symbiont systems, the general expectation is that parent-offspring vertical transmission results in both phylogenetic congruence and high host specificity on the macroevolutionary scale (Clayton et al., 2015; Dick et al., 2009; Mironov et al. 2020; Page, 2003). However, in the feather mite-bird symbiotic system, low co-phylogenetic congruence and relatively high host specificity have been detected in the same systems (Dabert et al. 2021; Doña et al., 2018; Doña et al., 2017a; Klimov et al., 2017; Matthews et al., 2018). If we assume that most feather mites disperse vertically (Figure 1: case 3) (Dabert & Mironov, 1999; Doña et al., 2017b; Mironov & Malyshev, 2002), only the high host specificity can be explained; the low co-phylogenetic congruence cannot be explained in terms of larger contribution of vertical vs horizontal transmission. Our work tries to reconcile these opposing observations by (i) estimation of relative rates of ongoing horizontal and vertical transmission (microevolutionary scale) and (ii) quantifying codivergence vs non-codivergence co-evolutionary events (macroevolutionary scale). Horizontal conspecific transmission (q_h) was estimated to be at least 3 times more frequent than vertical transmission (q_{v1}), with 2 codivergence events vs 2 host switches in *Molorthrus*-specific mites (Figure 4). The high host specificity observed in the *Molothrus*-specific mites can be therefore explained solely by horizontal conspecific transmission (q_h), and no vertical transmission is required to maintain host specificity. On the macroevolutionary scale, in brood parasitic birds having q_h larger than q_{v1}, a codivergence scenario is expected (Figure 1: case 4), but was not observed in reality as the number of codivergence vs non-codivergence events was the same. We therefore can conclude that on the microevolutionary scale both vertical and horizontal transmissions (q_v, q_h) can affect host specificity of feather mite, while these transmissions may not substantially influence their co-evolutionary scenarios on the macroevolutionary scale. For example, host switches (followed by establishment on the host) may depend on multiple factors, such as competitive abilities of a particular mite species, but not solely on the rate of interspecific transmission (Bush & Clayton, 2006; Clayton et al., 2015).

In summary, our work highlights that in the shiny cowbird-feather mite system, the symbiont horizontal transmission via host social contacts are an important mode of mite dispersal onto new host individuals, and alone (without parent-offspring vertical transmission) can maintain highly abundant, dominant, and host-specific species of obligate mite symbionts on their hosts. Our data provide further evidence challenging the traditional view of the importance of vertical transmission as the sole force generating host specificity and phylogenetic congruence in feather mite systems (Wells and Clark, 2019; Doña et al., 2018). Horizontal transmission alone may generate both congruent and incongruent co-phylogenetic patterns, as shown by the co-divergences of *Molothrus*' mites, and also maintain both single-host and multi-host symbionts.

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Supplementary File 1. Genbank accession numbers, host, and collection information.

EC (LGAP)	Host Code	Host Family	Host Species	Mite Species	COX1	HSP70	SRP54	EF1a	28S	18S
1	SP-04	Turdidae	T. leucomelas	Amerodectes turdinus	MW814651	MW829254	-	-	-	-
2	SUL-04	Turdidae	T. amaurochalinus	Trouessartia incisa	MW814590	-	-	-	-	-
3	SUL-11	Turdidae	T. rufiventris	Amerodectes turdinus	MW814652	-	-	-	-	-
5	PA-10	Turdidae	T. leucomelas	Amerodectes turdinus	MW814653	MW829255	-	-	-	-
6	RN-08	Turdidae	T. leucomelas	Amerodectes turdinus	MW814654	-	-	-	-	-
7	UNB-06	Turdidae	T. amaurochalinus	Tyrannidectes amaurochalinus	MW814655	MW829256	-	-	-	-
8	SUL-20	Turdidae	T. leucomelas	Tyrannidectes? -	MW814656	-	-	-	-	-
9	MS-10	Turdidae	T. leucomelas	Tyrannidectes amaurochalinus	MW814657	-	-	-	-	-
10	SP-02	Turdidae	T. amaurochalinus	Amerodectes turdinus	MW814658	-	-	-	-	-
11	SUL-04	Turdidae	T. amaurochalinus	Proctophyllodes sp. ?	MW814621	-	-	-	-	-
12	PE-04	Turdidae	T. rufiventris	Tyrannidectes fissuratus	MW814659	-	-	-	-	-
13	PE-04	Turdidae	T. rufiventris	Amerodectes turdinus	MW814660	-	-	-	-	-
14	UNB-01	Turdidae	T. rufiventris	Tyrannidectes amaurochalinus	MW814661	-	-	-	-	-
15	AC-09	Turdidae	T. ignobilis	Amerodectes turdinus	MW814662	MW829257	-	-	-	-
16	SP-34	Tyrannidae	P. sulphuratus	Amerodectes pitangi	MW814663	MW829258	-	-	-	-
17	SUL-22	Tyrannidae	P. sulphuratus	Amerodectes pitangi	MW814664	-	-	-	-	-
18	PA-01	Tyrannidae	P. sulphuratus	Amerodectes sp. 1	MW814665	MW829259	-	-	-	-
19	RN-14	Tyrannidae	P. sulphuratus	Amerodectes pitangi	MW814666	MW829260	-	-	-	-
21	MG-02	Tyrannidae	X. cinereus	Amerodectes sp. 1?	MW814667	MW829261	-	-	-	-
22	SP-30	Passerellidae	Z. capensis	Amerodectes sp. 1	MW814668	MW829262	-	-	-	-
23	SP-42	Icteridae	M. bonariensis	Amerodectes molothrus	MW814669	MW829263	-	-	-	-
24	SP-47	Icteridae	M. bonariensis	Amerodectes molothrus	MW814670	-	-	-	-	-
26	SUL-18	Icteridae	M. bonariensis	Amerodectes molothrus	MW814671	-	-	-	-	-
27	SP-53	Thraupidae	T. sayaca	Amerodectes tangarae	MW814672	-	-	-	-	-
28	AC-07	Thraupidae	T. palmarum	Amerodectes storkani	MW814673	-	-	-	-	-
29	AC-07	Thraupidae	T. palmarum	Amerodectes thraupicola	MW814674	-	-	-	-	-
30	RN-17	Thraupidae	T. palmarum	Amerodectes thraupicola	MW814675	-	-	-	-	-
32	RN-20	Thraupidae	T. sayaca	Amerodectes thraupicola	MW814676	-	-	-	-	-
33	PE-06	Thraupidae	T. sayaca	Amerodectes bilineatus	MW814677	MW829264	-	-	-	-
34	PE-06	Thraupidae	T. sayaca	Amerodectes thraupicola	MW814678	MW829265	-	-	-	-
35	SP-48	Thraupidae	T. palmarum	Amerodectes tangarae	MW814679	-	-	-	-	-
36	SP-10	Thraupidae	T. cayana	Amerodectes tangarae	MW814680	-	-	-	-	-
37	PE-03	Thraupidae	T. cayana	Amerodectes tangarae	MW814681	MW829266	-	-	-	-
38	RN-22	Thraupidae	T. cayana	Amerodectes tangarae	MW814682	-	-	-	-	-
39	MS-05	Thraupidae	D. cayana	Amerodectes sp.	MW814683	MW829267	-	-	-	-
40	SP-44	Mimidae	M. saturninus	Metapterodectes saturninus	MW814684	-	-	-	-	-
41	SUL-14	Mimidae	M. saturninus	Metapterodectes saturninus	MW814685	-	-	-	-	-

42	UNB-02	Mimidae	M. saturninus	Metapterodectes saturninus?	MW814686	MW829268	-	-	-	-
43	SP-51	Thraupidae	C. flaveola	Amerodectes sp.	MW814687	MW829269	-	-	-	-
44	RN-01	Thraupidae	C. flaveola	Amerodectes sp. 2	MW814688	-	-	-	-	-
45	RN-21	Vireonidae	V. chivi	Amerodectes vireonis	MW814689	MW829270	-	-	-	-
46	SP-06	Thraupidae	S. flaveola	Amerodectes sicalis	MW814690	MW829271	-	-	-	-
47	MG-01	Thraupidae	S. flaveola	Proctophyllodes sp. nov.	MW814647	-	-	-	-	-
48	SUL-07	Thraupidae	S. luteola	Amerodectes sicalis?	MW814691	-	-	-	-	-
49	SP-27	Furnariidae	F. rufus	Metapterodectes furnarius?	MW814692	-	-	-	-	-
50	UNB-09	Furnariidae	F. rufus	Metapterodectes furnarius?	MW814693	MW829272	-	-	-	-
51	UFRPE-01	Furnariidae	F. Figureulus	Tyrannidectes sp.	MW814694	MW829273	-	-	-	-
52	PA-05	Rhynchocyclidae	M. oleagineus	Anisophyllodes aff. pipromorphae	MW814695	-	-	-	-	-
53	SP-54	Tyrannidae	M. rixosa	Tyrannidectes sp. nov.	MW814696	MW829274	-	-	-	-
54	UNB-07	Tyrannidae	M. rixosa	Tyrannidectes sp. nov.	MW814697	-	-	-	-	-
55	UNB-08	Tyrannidae	M. rixosa	Tyrannidectes sp. nov.	MW814698	-	-	-	-	-
56	SP-39	Furnariidae	L. angutirostris	Pterodectinae -	MW814699	-	-	-	-	-
57	SUL-06	Polioptilidae	P. dumicula	Amerodectes? sp. nov.	MW814700	-	-	-	-	-
58	PA-02	Thraupidae	R. carbo	Amerodectes aff. tiaris	MW814703	-	-	-	-	-
59	PA-02	Thraupidae	R. carbo	Amerodectes aff. storkani	MW814701	MW829275	-	-	-	-
60	AC-22	Thraupidae	R. carbo	Amerodectes cf. dumetellae ou tiaris	MW814702	MW829276	-	-	-	-
61	SP-04	Turdidae	T. leucomelas	Trouessartia serrana/incisa/megaplax	MW814591	-	-	-	-	-
62	SUL-20	Turdidae	T. leucomelas	Trouessartia serrana/incisa/megaplax	MW814592	MW829221	-	-	-	-
63	PA-09	Turdidae	T. leucomelas	Trouessartia serrana/megaplax	MW814593	MW829222	-	-	-	-
64	RN-15	Turdidae	T. leucomelas	Trouessartia serrana?	MW814594	MW829223	-	-	-	-
65	SP-05	Turdidae	T. amaurochalinus	Trouessartia aff. Incisa	MW814595	-	-	-	-	-
66	SUL-04	Turdidae	T. amaurochalinus	Trouessartia serrana/incisa/megaplax	MW814596	-	-	-	-	-
67	UNB-06	Turdidae	T. amaurochalinus	Trouessartia incisa?	MW814597	-	-	-	-	-
68	PE-04	Turdidae	T. rufiventris	Trouessartia serrana?	MW814598	-	-	-	-	-
69	PE-04	Turdidae	T. rufiventris	Trouessartia sp. Nov.?	MW814599	-	-	-	-	-
70	UNB-01	Turdidae	T. rufiventris	Trouessartia incisa?	MW814600	-	-	-	-	-
71	AC-09	Turdidae	T. ignobilis	Trouessartia serrana?	MW814601	MW829224	-	-	-	-
72	PA-01	Tyrannidae	P. sulphuratus	Trouessartia sp. Nov. aff. Chaquensis	MW814602	MW829225	-	-	-	-
73	RN-26	Tyrannidae	P. sulphuratus	Trouessartia sp. Nov. aff. Chaquensis	MW814603	-	-	-	-	-
74	MS-07	Tyrannidae	P. sulphuratus	Trouessartia sp. Nov. aff. Chaquensis	MW814604	-	-	-	-	-
75	SP-24	Passerellidae	Z. capensis	Trouessartia capensis	MW814605	MW829226	-	-	-	-
76	SP-41	Icteridae	M. bonariensis	Trouessartia sp.	MW814606	MW829227	-	-	-	-
77	SP-53	Thraupidae	T. sayaca	Trouessartia sp. 1	MW814607	MW829228	-	-	-	-
78	PE-07	Thraupidae	T. sayaca	Trouessartia sp. 2	MW814608	MW829229	-	-	-	-
79	AC-08	Thraupidae	T. palmarum	Trouessartia sp. 3?	MW814609	MW829230	-	-	-	-
80	RN-17	Thraupidae	T. palmarum	Trouessartia sp. 2	MW814610	-	-	-	-	-
81	PA-06	Thraupidae	T. episcopus	Trouessartia sp. 4?	MW814611	-	-	-	-	-
82	SUL-10	Furnariidae	F. rufus	Trouessartia incisa?	MW814612	MW829231	-	-	-	-

83	SUL-10	Furnariidae	F. rufus	Trouessartia sp. Nov	MW814613	MW829232	-	-	-	-
84	UFRPE-02	Furnariidae	F. Figureulus	Trouessartia sp. Nov	MW814614	MW829233	-	-	-	-
85	SP-06	Thraupidae	S. flaveola	Trouessartia sicaliae	MW814615	MW829234	-	-	-	-
86	SUL-02	Thraupidae	S. luteola	Trouessartia cf. sicaliae	MW814616	MW829235	-	-	-	-
87	MG-01	Thraupidae	S. flaveola	Trouessartia sicaliae	MW814617	-	-	-	-	-
88	SP-44	Mimidae	M. saturninus	Trouessartia aff. Incisa	MW814618	MW829236	-	-	-	-
89	AC-22	Thraupidae	R. carbo	Trouessartia sp.	MW814619	-	-	-	-	-
90	PA-02	Thraupidae	R. carbo	Trouessartia sp.	MW814620	MW829237	-	-	-	-
92	SP-04	Turdidae	T. leucomelas	Proctophyllodes sp.	MW814634	MW829245	-	-	-	-
93	SUL-20	Turdidae	T. leucomelas	Proctophyllodes sp.	MW814635	-	-	-	-	-
94	PA-10	Turdidae	T. leucomelas	Proctophyllodes sp.	MW814622	MW829238	-	-	-	-
95	SP-05	Turdidae	T. amaurochalinus	Proctophyllodes sp.	MW814625	MW829240	-	-	-	-
96	SUL-21	Turdidae	T. amaurochalinus	Proctophyllodes sp.	MW814626	-	-	-	-	-
97	SUL-11	Turdidae	T. rufiventris	Proctophyllodes sp.	MW814627	MW829241	-	-	-	-
98	SP-23	Icteridae	M. bonariensis	Proctophyllodes sp.	MW814623	MW829239	-	-	-	-
99	SUL-15	Icteridae	M. bonariensis	Proctophyllodes sp.	MW814624	-	-	-	-	-
100	UNB-04	Icteridae	M. bonariensis	Proctophyllodes sp.	MW814628	-	-	-	-	-
101	SP-10	Thraupidae	T. cayana	Proctophyllodes sp.	MW814629	MW829242	-	-	-	-
102	RN-22	Thraupidae	T. cayana	Proctophyllodes sp.	MW814630	MW829243	-	-	-	-
103	PE-03	Thraupidae	T. cayana	Proctophyllodes sp.	MW814631	-	-	-	-	-
104	SP-22	Thraupidae	T. sayaca	Proctophyllodes sp.	MW814632	MW829244	-	-	-	-
105	RN-20	Thraupidae	T. sayaca	Proctophyllodes sp.	MW814633	-	-	-	-	-
107	AC-07	Thraupidae	T. palmarum	Proctophyllodes sp.	MW814636	MW829246	-	-	-	-
108	RN-17	Thraupidae	T. palmarum	Proctophyllodes sp.	MW814637	-	-	-	-	-
109	SP-51	Thraupidae	C. flaveola	Proctophyllodes sp.	MW814638	MW829247	-	-	-	-
110	RN-06	Thraupidae	C. flaveola	Proctophyllodes sp.	MW814639	MW829248	-	-	-	-
112	SP-33	Furnariidae	F. rufus	Nycteridocaulus sp.	MW814640	-	-	-	-	-
113	SUL-10	Furnariidae	F. rufus	Nycteridocaulus sp.	MW814641	MW829249	-	-	-	-
114	SUL-06	Polioptilidae	P. dumicula	Nycteridocaulus sp.	MW814642	-	-	-	-	-
116	AC-18	Rhynchocyclidae	O. coronatus	Nycteridocaulus sp.	MW814643	MW829250	-	-	-	-
118	SUL-13	Tyrannidae	P. sulphuratus	Nycteridocaulus sp.	MW814644	-	-	-	-	-
120	RN-14	Tyrannidae	P. sulphuratus	Nycteridocaulus sp.	MW814645	MW829251	-	-	-	-
121	MS-07	Tyrannidae	P. sulphuratus	Nycteridocaulus sp.	MW814646	MW829252	-	-	-	-
123	MG-01	Thraupidae	S. flaveola	Proctophyllodes sp.	MW814648	-	-	-	-	-
125	UNB-05	Icteridae	M. bonariensis	Proctophyllodes sp.	MW814649	-	-	-	-	-
128	AA-01	Thraupidae	P. olivacea	Proctophyllodes pirangae	MW814650	MW829253	-	-	-	-
142	BMOC 08-0515-484	Icteridae	I. pustulatus	Amerodectes sp.	MW814707	-	-	-	-	-
147	BMOC 08-0515-508	Icteridae	M. ater	Amerodectes tretiakae	MW814704	-	-	-	-	-
148	BMOC 08-0515-508	Icteridae	M. ater	Proctophyllodes sp.	MW814705	-	-	-	-	-
149	BMOC 08-0515-508	Icteridae	M. ater	Proctophyllodes sp.	MW814706	-	-	-	-	-
-	KY491636.1	Parulidae	I. virens	Proctophyllodes trisetosus	KY491636.1	-	-	-	-	-

-	KY491632.1	Parulidae	V. chrysoptera	Proctophyllodes quadratus	KY491632.1	-	-	-	-	-
-	KY491631.1	Parulidae	L. peregrina	Proctophyllodes quadratus	KY491631.1	-	-	-	-	-
-	KY491577.1	Parulidae	S. ruticilla	Amerodectes ischyros	KY491577.1	-	-	-	-	-
-	KY491622.1	Parulidae	S. aurocapilla	Amerodectes seiurus	KY491622.1	-	-	-	-	-
-	KY491608.1	Parulidae	G. trichas	Amerodectes hribari	KY491608.1	-	-	-	-	-
-	KY491605.1	Parulidae	P. citrea	Amerodectes protonotaria	KY491605.1	-	-	-	-	-
-	KY491606.1	Parulidae	P. noveboracensis	Amerodectes jonesborensis	KY491606.1	-	-	-	-	-
-	KY491595.1	Parulidae	S. dominica	Amerodectes charitomenos	KY491595.1	-	-	-	-	-
-	AD1200	Corvidae	C. sanblasianus	Gabucinia sp. n. aff. delibata	KU203072	JQ001387	JQ001072	JQ000771	JQ000467	JQ000159
-	AD717	Steatornithidae	S. caripensis	Steatacarus bifiditibia	KU203090	JQ001492	JQ001177	JQ000872	JQ000572	JQ000264
-	AD770	Regulidae	R. satrapa	Calcealges sp. n.	KU203091	JQ001493	JQ001178	JQ000873	JQ000573	JQ000265
-	AD752	Muscicapidae	E. rubecula	Trouessartia rubecula	KU203092	JQ001494	JQ001179	JQ000874	JQ000574	JQ000266
-	AD952	Parulidae	S. aurocapilla	Trouessartia sp. n.	KU203093	JQ001495	JQ001180	JQ000875	JQ000575	JQ000267
-	AD742	Locustellidae	L. naevia	Trouessartia kratochvili	KU203094	JQ001496	JQ001181	JQ000876	JQ000576	JQ000268
-	AD744	Regulidae	R. R.	Trouessartia reguli	KU203095	JQ001497	JQ001182	JQ000877	JQ000577	JQ000269
-	AD768	Regulidae	R. satrapa	Trouessartia reguli	KU203096	JQ001498	JQ001183	JQ000878	JQ000578	JQ000270
-	AD694	Turdidae	C. ustulatus	Trouessartia sp. n. aff. incisa	KU203097	JQ001499	JQ001184	JQ000879	JQ000579	JQ000271
-	AD642	Thraupidae	T. olivaceus	Trouessartia sp. n. aff. capensis	KU203098	JQ001500	JQ001185	EU152786	JQ000580	JQ000272
-	AD616	Muscicapidae	S. bocagei	Trouessartia sp. n.	KU203099	JQ001501	JQ001186	JQ000880	JQ000581	JQ000273
-	AD1131	Zosteropidae	Z. erythropleurus	Proctophyllodes aff. ceratophyllus	KU203109	KU202833	KU202982	KU202758	KU202908	KU203248
-	AD1468	Aegithalidae	A. caudatus	Proctophyllodes valchukae	KU203110	KU202834	KU202983	KU202759	KU202909	KU203249
-	AD1472	Acrocephalidae	A. scirpaceus	Proctophyllodes vassilevi	KU203111	KU202835	KU202984	KU202760	KU202910	KU203250
-	AD812	Muscicapidae	L. svecica	Proctophyllodes caulifer	KU203112	KU202836	KU202985	KU202761	KU202911	KU203251
-	AD1469	Muscicapidae	C. cyanomelana	Proctophyllodes sp. n.	KU203113	KU202837	KU202986	KU202762	KU202912	KU203252
-	AD997	Muscicapidae	E. rubecula	Proctophyllodes rubeculinus	KU203114	KU202838	KU202987	KU202763	KU202913	KU203253
-	AD875	Muscicapidae	P. erythronotus	Proctophyllodes aff. cotyledon	KU203115	KU202839	KU202988	KU202764	KU202914	KU203254
-	AD743	Phylloscopidae	P. trochilus	Proctophyllodes doleophyes	KU203116	JQ001513	JQ001198	JQ000892	JQ000593	JQ000285
-	AD638	Muscicapidae	S. bocagei	Proctophyllodes sp.	KU203117	JQ001514	JQ001199	EU152793	JQ000594	JQ000286
-	AD963	Scolopacidae	S. minor	Proctophyllodes aff. scolopacinus	KU203118	KU202840	KU202989	KU202765	KU202915	KU203255
-	AD751	Scolopacidae	S. rusticola	Proctophyllodes scolopacinus	KU203119	JQ001515	JQ001200	JQ000893	JQ000595	JQ000287
-	AD1459	Turdidae	T. merula	Proctophyllodes weigoldi	KU203120	KU202841	KU202990	KU202766	KU202916	KU203256
-	AD1470	Turdidae	T. merula	Proctophyllodes weigoldi	KU203121	KU202842	KU202991	KU202767	KU202917	KU203257
-	AD1638	Sittidae	S. europaea	Proctophyllodes vitzthumi	KU203122	KU202843	KU202992	KU202768	KU202918	KU203258
-	AD712	Corvidae	C. corone	Proctophyllodes detruncatus	KU203123	JQ001516	JQ001201	JQ000894	JQ000596	JQ000288
-	AD715	Corvidae	C. monedula	Proctophyllodes detruncatus	KU203124	JQ001517	JQ001202	JQ000895	JQ000597	JQ000289
-	AD1460	Corvidae	C. macrorhynchos	Proctophyllodes detruncatus	KU203125	KU202844	KU202993	KU202769	KU202919	KU203259
-	AD822	Motacillidae	M. alba	Proctophyllodes motacillae	KU203126	KU202845	KU202994	KU202770	KU202920	KU203260
-	AD1630	Motacillidae	A. spinoletta	Proctophyllodes schwerinensis	KU203127	KU202846	KU202995	KU202771	KU202921	KU203261
-	AD1464	Fringillidae	C. coccothraustes	Proctophyllodes fuchsi	KU203128	KU202847	KU202996	KU202772	KU202922	KU203262
-	AD823	Corvidae	G. glandarius	Proctophyllodes glandarinus	KU203129	KU202848	KU202997	KU202773	KU202923	KU203263
-	AD1466	Fringillidae	L. curvirostra	Proctophyllodes loxiae	KU203130	KU202849	KU202998	KU202774	KU202924	KU203264

-	AD645	Bombycillidae	B. cedrorum	Proctophyllodes ampelidis	KU203131	HM165125	JQ001203	HM165095	HM165065	HM165035
-	AD1047	Parulidae	S. caerulescens	Proctophyllodes sp. aff. breviquadratus	KU203132	KU202850	KU202999	KU202775	KU202925	KU203265
-	AD1140	Parulidae	S. magnolia	Proctophyllodes dendroicae	KU203133	KU202851	KU203000	KU202776	KU202926	KU203266
-	AD1147	Parulidae	C. pusilla	Proctophyllodes aff. dendroicae	KU203134	KU202852	KU203001	KU202777	KU202927	KU203267
-	AD1148	Parulidae	O. peregrina	Proctophyllodes quadratus	KU203135	KU202853	KU203002	KU202778	KU202928	KU203268
-	AD1154	Thraupidae	T. abbas	Proctophyllodes thraupis	KU203136	KU202854	KU203003	KU202779	KU202929	KU203269
-	AD1178	Thraupidae	T. episcopus cana	Proctophyllodes thraupis	KU203137	KU202855	KU203004	KU202780	KU202930	KU203270
-	AD1239	Fringillidae	E. hirundinacea	Proctophyllodes euphoniae	KU203138	KU202856	KU203005	KU202781	KU202931	KU203271
-	AD1144	Cardinalidae	H. rubica	Proctophyllodes habiae	KU203139	KU202857	KU203006	KU202782	KU202932	KU203272
-	AD1175	Icteridae	P. montezuma	Proctophyllodes attenuatus	KU203140	KU202858	KU203007	KU202783	KU202933	KU203273
-	AD1185	Thraupidae	S. torqueola	Proctophyllodes sporophilae	KU203141	KU202859	KU203008	KU202784	KU202934	KU203274
-	AD1633	Cardinalidae	C. parellina	Proctophyllodes longiphyllus	KU203142	KU202860	KU203009	KU202785	KU202935	KU203275
-	AD1242	Thraupidae	T. olivaceus	Proctophyllodes sp. n. aff. gularis	KU203143	KU202861	KU203010	KU202786	KU202936	KU203276
-	AD1251	Vireonidae	V. flavoviridis	Proctophyllodes stoddardi	KU203144	KU202862	KU203011	KU202787	KU202937	KU203277
-	AD1249	Icteridae	I. pustulatus	Proctophyllodes icteri	KU203145	KU202863	KU203012	KU202788	KU202938	KU203278
-	AD1198	Corvidae	C. sanblasianus	Proctophyllodes sp. n.	KU203146	KU202864	KU203013	KU202789	KU202939	KU203279
-	AD912	Cardinalidae	C. cardinalis	Proctophyllodes longiphyllus	KU203147	KU202865	KU203014	KU202790	KU202940	KU203280
-	AD975	Icteridae	S. magna	Proctophyllodes trisetosus	KU203148	KU202866	KU203015	KU202791	KU202941	KU203281
-	AD925	Emberizidae	Z. albicollis	Proctophyllodes aff. polyxenus	KU203149	HM165126	KU203016	HM165096	HM165066	HM165036
-	AD965	Icteridae	A. phoeniceus	Proctophyllodes egglestoni	KU203150	HM165127	KU203017	HM165097	HM165067	HM165037
-	AD1657	Motacillidae	A. trivialis	Proctophyllodes anthi	KU203151	KU202867	KU203018	KU202792	KU202942	KU203282
-	AD1658	Motacillidae	A. campestris	Proctophyllodes markovetsi	KU203152	KU202868	KU203019	KU202793	KU202943	KU203283
-	AD745	Prunellidae	P. modularis	Joubertophyllodes modularis	KU203153	HM165128	JQ001204	HM165098	HM165068	HM165038
-	AD1129	Emberizidae	E. spodocephala	Joubertophyllodes modularis	KU203154	KU202869	KU203020	HM165099	HM165069	HM165039
-	AD854	Emberizidae	E. schoeniclus	Joubertophyllodes proximus	KU203155	HM165130	JQ001205	HM165100	HM165070	HM165040
-	AD1132	Emberizidae	E. aureola	Joubertophyllodes ampullaceus	KU203156	HM165131	JQ001206	HM165101	HM165071	HM165041
-	AD1027	Prunellidae	P. atrogularis	Proctophyllodes megaphyllus	KU203157	HM165132	KU203021	KU202794	HM165072	HM165042
-	AD923	Cardinalidae	P. ludovicianus	Proctophyllodes pheuctici	KU203158	KU202870	KU203022	KU202795	KU202944	KU203284
-	AD1130	Paradoxornithidae	S. webbiana	Proctophyllodes sp. n.	KU203159	KU202871	KU203023	HM165103	HM165073	HM165043
-	AD846	Acrocephalidae	A. schoenobaenus	Proctophyllodes clavatus	KU203160	HM165134	KU203024	HM165104	HM165074	HM165044
-	AD847	Sylviidae	S. curruca	Proctophyllodes clavatus	KU203161	HM165135	KU203025	HM165105	HM165075	HM165045
-	AD734	Sylviidae	S. borin	Proctophyllodes clavatus	KU203162	HM165136	JQ001207	HM165106	HM165076	HM165046
-	AD995	Sylviidae	S. atricapilla	Proctophyllodes sylviae	KU203163	HM165138	KU203026	KU202796	HM165078	HM165048
-	AD1007	Cettiidae	C. cetti	Proctophyllodes cetti	KU203164	HM165137	KU203027	HM165107	HM165077	HM165047
-	AD924	Fringillidae	H. mexicanus	Proctophyllodes sp. n. vegetans	KU203165	HM165139	KU203028	HM165109	HM165079	HM165049
-	AD1636	Fringillidae	U. sibiricus	Proctophyllodes sp. n.	KU203166	KU202872	KU203029	KU202797	KU202945	KU203285
-	AD738	Fringillidae	S. spinus	Proctophyllodes spini	KU203167	HM165140	JQ001208	HM165110	HM165080	HM165050
-	AD772	Fringillidae	S. tristis	Proctophyllodes spini	KU203168	HM165141	KU203030	HM165111	HM165081	HM165051
-	AD1054	Fringillidae	S. pinus	Proctophyllodes spini	KU203169	HM165143	KU203031	HM165113	HM165083	HM165053
-	AD625	Sittidae	S. canadensis	Proctophyllodes canadensis	KU203170	HM165144	JQ001209	HM165114	HM165084	HM165054
-	AD859	Passeridae	P. hispaniolensis	Proctophyllodes aff. troncatus	KU203171	HM165145	KU203032	HM165115	HM165085	HM165055

-	AD970	Passeridae	P. domesticus	Proctophyllodes troncatus	KU203172	HM165146	KU203033	HM165116	HM165086	HM165056
-	AD866	Fringillidae	C. chloris	Proctophyllodes pinnatus	KU203173	HM165147	KU203034	HM165117	HM165087	HM165057
-	AD873	Fringillidae	C. cannabina	Proctophyllodes pinnatus	KU203174	HM165148	KU203035	HM165118	HM165088	HM165058
-	AD1128	Fringillidae	C. sinica	Proctophyllodes pinnatus	KU203175	HM165149	KU203036	HM165119	HM165089	HM165059
-	AD815	Emberizidae	E. leucocephalos	Proctophyllodes ciae	KU203176	HM165150	KU203037	HM165120	HM165090	HM165060
-	AD996	Emberizidae	E. citrinella	Proctophyllodes ciae	KU203177	HM165151	KU203038	HM165121	HM165091	HM165061
-	AD998	Fringillidae	L. curvirostra	Proctophyllodes neopinnatus	KU203178	HM165152	KU203039	HM165122	KU202946	HM165062
-	AD1261	Laniidae	L. excubitor	Proctophyllodes ludovicianus	KU203179	HM165153	KU203040	HM165123	HM165093	HM165063
-	AD1002	Emberizidae	E. schoeniclus	Proctophyllodes schoenicli	KU203180	HM165154	KU203041	HM165124	HM165094	HM165064
-	AD821	Locustellidae	L. naevia	Proctophyllodes locustellae	KU203181	KU202873	KU203042	KU202798	KU202947	KU203286
-	AD1659	Laniidae	L. collurio	Proctophyllodes leptocaulus	KU203182	KU202874	KU203043	KU202799	KU202948	KU203287
-	AD1201	Troglodytidae	T. sinaloa	Proctophyllodes troglodytes	KU203183	KU202875	KU203044	KU202800	KU202949	KU203288
-	AD961	Turdidae	T. migratorius	Proctophyllodes aff. musicus	KU203184	KU202876	KU203045	KU202801	KU202950	KU203289
-	AD584	Turdidae	T. migratorius	Proctophyllodes aff. musicus	KU203185	KU202877	KU203046	KU202802	KU202951	KU203290
-	AD1001	Turdidae	T. philomelos	Proctophyllodes musicus	KU203186	KU202878	KU203047	KU202803	KU202952	KU203291
-	AD1655	Muscicapidae	S. rubetra	Proctophyllodes hipposideros	KU203187	KU202879	KU203048	KU202804	KU202953	KU203292
-	AD1026	Turdidae	T. viscivorus	Proctophyllodes tenericaulus	KU203188	KU202880	KU203049	KU202805	KU202954	KU203293
-	AD830	Corvidae	P. infaustus	Proctophyllodes sp. n. aff. picae	KU203189	KU202881	KU203050	KU202806	KU202955	KU203294
-	AD1463	Corvidae	C. cyanus	Proctophyllodes sp. n. aff. picae	KU203190	KU202882	KU203051	KU202807	KU202956	KU203295
-	AD786	Tyrannidae	E. minimus	Proctophyllodes empidonicis	KU203191	KU202883	KU203052	KU202808	KU202957	KU203296
-	AD1000	Muscicapidae	M. striata	Proctophyllodes acanthicaulus	KU203192	KU202884	KU203053	KU202809	KU202958	KU203297
-	AD696	Turdidae	C. ustulatus	Proctophyllodes hylocichlae	KU203193	KU202885	KU203054	KU202810	KU202959	KU203298
-	AD681	Mimidae	D. carolinensis	Proctophyllodes apanaskevichi	KU203194	JQ001518	JQ001210	JQ000896	JQ000598	JQ000290
-	AD566	Mimidae	T. rufum	Proctophyllodes gallowayi	KU203195	KU202886	KU203055	KU202811	KU202960	KU203299
-	AD1036	Paridae	P. carolinensis	Proctophyllodes sp. n. aff. ateri	KU203196	KU202887	KU203056	KU202812	KU202961	KU203300
-	AD824	Paridae	P. ater	Proctophyllodes ateri	KU203197	KU202888	KU203057	KU202813	KU202962	JQ000292
-	AD1134	Paridae	P. minor	Proctophyllodes stylifer	KU203198	KU202889	KU203058	KU202814	KU202963	KU203301
-	AD737	Paridae	P. palustris	Proctophyllodes stylifer	KU203199	JQ001519	JQ001211	JQ000897	JQ000599	JQ000291
-	AD1465	Troglodytidae	T. troglodytes	Proctophyllodes microstylifer	KU203200	KU202890	KU203059	KU202815	KU202964	KU203302
-	AD769	Regulidae	R. satrapa	Proctophyllodes reguli	KU203201	JQ001520	JQ001212	JQ000898	JQ000600	JQ000292
-	AD736	Muscicapidae	P. phoenicurus	Proctophyllodes mesocaulus	KU203202	JQ001521	JQ001213	JQ000899	JQ000601	JQ000293
-	AD1654	Muscicapidae	P. phoenicurus	Proctophyllodes mesocaulus	KU203203	KU202891	KU203060	KU202816	KU202965	KU203303
-	AD1635	Fringillidae	P. pyrrhula griseiventris	Proctophyllodes simillimus	KU203204	KU202892	KU203061	KU202817	KU202966	KU203304
-	AD741	Fringillidae	F. coelebs	Monojoubertia microphylla	KU203205	JQ001522	JQ001214	JQ000900	JQ000602	JQ000294
-	AD825	Fringillidae	F. montiF.	Monojoubertia hemiphylla	KU203206	JQ001523	JQ001215	JQ000901	JQ000603	JQ000295
-	AD1238	Furnariidae	D. certhia	Platyacarus dontocoronius probably	KU203207	JQ001524	JQ001216	JQ000902	JQ000604	JQ000296
-	AD1155	Furnariidae	X. flavigaster eburneirostris	Platyacarus sp. n. aff. sittasomi	KU203208	JQ001525	JQ001217	JQ000903	JQ000605	JQ000297
-	AD1237	Tyrannidae	M. tuberculifer	Anisophyllodes sp. n.	KU203209	JQ001526	JQ001218	JQ000904	JQ000606	JQ000298
-	AD1194	Tyrannidae	M. nuttingi	Nycteridocaulus lamellus	KU203210	JQ001527	JQ001219	JQ000905	JQ000607	JQ000299
-	AD1212	Tyrannidae	M. similis	Nycteridocaulus sp. n. aff. lamellus	KU203211	JQ001528	JQ001220	JQ000906	JQ000608	JQ000300
-	AD1243	Tyrannidae	E. sp2 flaviventris probably	Nycteridocaulus sp. n.	KU203212	JQ001529	JQ001221	JQ000907	JQ000609	JQ000301

-	AD1176	Tyrannidae	P. cancrominus	Nycteridocaulus sp. n.	KU203213	JQ001530	JQ001222	JQ000908	JQ000610	JQ000302
-	AD1233	Tyrannidae	E. sp. 1	Anisophyllodes sp. n. aff. elaeniae	KU203214	JQ001531	JQ001223	JQ000909	JQ000611	JQ000303
-	AD1179	Tyrannidae	P. sulphuratus	Anisophyllodes sp. n.	KU203215	JQ001532	JQ001224	JQ000910	JQ000612	JQ000304
-	AD1139	Tyrannidae	M. oleagineus	Anisophyllodes pipromorphae	KU203216	JQ001543	JQ001235	JQ000921	JQ000623	JQ000315
-	AD617	Muscicapidae	C. natalensis	Montesauria leioplax	KU203217	JQ001533	JQ001225	JQ000911	JQ000613	JQ000305
-	AD755	Alaudidae	L. arborea	Alaudicola bureschi	KU203218	JQ001534	JQ001226	JQ000912	JQ000614	JQ000306
-	AD760	Hirundinidae	H. rustica	Pterodectes rutilus	KU203219	KU202893	KU203062	KU202818	KU202967	KU203305
-	AD1046	Parulidae	S. pensylvanica	Amerodectes sp. n. aff. geothlypis	KU203220	JQ001535	KU203063	JQ000913	JQ000615	JQ000307
-	AD1174	Icteridae	P. montezuma	Amerodectes gracilis	KU203221	JQ001536	JQ001228	JQ000914	JQ000616	JQ000308
-	AD680	Mimidae	D. carolinensis	Amerodectes dumetellae	KU203222	JQ001537	JQ001229	JQ000915	JQ000617	JQ000309
-	AD1203	Vireonidae	V. hypochryseus	Amerodectes sp. n.	KU203223	KU202894	KU203064	KU202819	KU202968	KU203306
-	AD1040	Tyrannidae	E. minimus	Amerodectes sp. n. aff. caribaeus	KU203224	KU202895	KU203065	KU202820	KU202969	KU203307
-	AD1211	Tyrannidae	M. similis	Amerodectes sp. n.	KU203225	KU202896	KU203066	KU202821	KU202970	KU203308
-	AD1181	Tyrannidae	P. sulphuratus	Amerodectes sp. n. aff. atyeoi	KU203226	KU202897	KU203067	KU202822	KU202971	KU203309
-	AD1195	Tyrannidae	M. nuttingi	Tyrannidectes berlai	KU203227	JQ001538	JQ001230	JQ000916	JQ000618	JQ000310
-	AD1032	Turdidae	C. fuscescens	Amerodectes sp. n. aff. turdinus	KU203228	KU202898	KU203068	KU202823	KU202972	KU203310
-	AD1049	Turdidae	H. mustelina	Amerodectes sp. n. aff. plumbeus	KU203229	KU202899	KU203069	KU202824	KU202973	KU203311
-	AD648	Pellorneidae	I. fulvescens	Montesauria sp. n. macronous-group	KU203230	JQ001539	JQ001231	JQ000917	JQ000619	JQ000311
-	AD556	Mimidae	T. rufum	Metapterodectes toxostomae	KU203231	JQ001540	JQ001232	JQ000918	JQ000620	JQ000312
-	AD1213	Trochilidae	A. rutila	Xynonodectes sp. n.	KU203232	JQ001541	JQ001233	JQ000919	JQ000621	JQ000313
-	AD1146	Trochilidae	A. candida	Xynonodectes sp. n.	KU203233	JQ001542	JQ001234	JQ000920	JQ000622	JQ000314
-	AD1138	Trochilidae	A. rutila	Trochilodectes buconvexus	KU203234	JQ001544	JQ001236	JQ000922	JQ000624	JQ000316
-	AD1236	Trochilidae	P. superciliosus	Trochilodectes bicuspidus	KU203235	JQ001545	JQ001237	JQ000923	JQ000625	JQ000317
-	AD1145	Trochilidae	A. candida	Toxerodectes sp. n.	KU203236	JQ001546	JQ001238	JQ000924	JQ000626	JQ000318
-	AD1149	Trochilidae	P. superciliosus	Allodectes wetmori	KU203237	JQ001547	JQ001239	JQ000925	JQ000627	JQ000319
-	AD1170	Trochilidae	C. excellens	Allodectes paulicaulus	KU203238	JQ001548	JQ001240	JQ000926	JQ000628	JQ000320
-	AD1150	Trochilidae	P. superciliosus	Rhamphocaulus vachoni	KU203239	JQ001549	JQ001241	JQ000927	JQ000629	JQ000321
-	AD1158	Trochilidae	A. prevostii	Rhamphocaulus sp. n. aff. sinuatus	KU203240	KU202900	KU203070	KU202825	KU202974	KU203312
-	AD1172	Trochilidae	C. excellens	Rhamphocaulus sinuatus	KU203241	KU202901	KU203071	KU202826	KU202975	KU203313

Supplementary File 2. Mite collection and data information of the selected mites with confidence score 1 and 2. N = number of mites; M = male; F = female; Atlant. For. = Atlantic Forest; C.S. = Confidence Score; Coll. Method = Collecting Method.

Host Code	Mite Family	Mite Genus	Mite Species	N	M	F	City	State	Biome	Coll. Date	Latitude	Longitude	C.S.	Category	Coll. Method
W/O ID 01	Proctophyllodidae	*Proctophyllodes*	*molothrus*	14	9	5	Campinas	SP	Atlant. For.	-	-22.90	-47.05	2	Molothrus-specific	Wash
W/O ID 01	Proctophyllodidae	*Amerodectes*	*molothrus*	14	9	5	Campinas	SP	Atlant. For.	-	-22.9	-47.05	2	Molothrus-specific	Wash
W/O ID 01	Psoroptoididae	*Mesalgoides*	*sp. 1*	4	3	1	Campinas	SP	Atlant. For.	-	-22.9	-47.05	2	Molothrus-specific	Wash
(4) N. 42	Proctophyllodidae	*Proctophyllodes*	*sp. 4*	2	1	1	Pelotas	RS	Pampa	30.mar.2006	-31.76	-52.33	2	Molothrus-alien	Wash
(4) N. 42	Proctophyllodidae	*Amerodectes*	*molothrus*	2	1	1	Pelotas	RS	Pampa	30.mar.2006	-31.76	-52.33	2	Molothrus-specific	Wash
SP-47 [F64117]	Proctophyllodidae	*Proctophyllodes*	cf. *thraupis*	1	0	1	Rio Claro	SP	Atlant. For.	13.dec.2018	-22.41	-47.56	2	Molothrus-alien	Field
SP-47 [F64117]	Proctophyllodidae	*Amerodectes*	*molothrus*	14	7	7	Rio Claro	SP	Atlant. For.	13.dec.2018	-22.41	-47.56	2	Molothrus-specific	Field
SP-47 [F64117]	Psoroptoididae	*Mesalgoides*	*sp. 1*	2	0	2	Rio Claro	SP	Atlant. For.	13.dec.2018	-22.41	-47.56	2	Molothrus-specific	Field
SUL-19	Proctophyllodidae	*Proctophyllodes*	*molothrus*	10	5	5	Londrina	PR	Atlant. For.	05.oct.2017	-23.31	-51.16	2	Molothrus-specific	Field
3 - N.43	Analgidae	*Analges*	*sp. 1*	10	1het 1homo	6	-	RS	Pampa	20.mar.2006	-31.76	-52.33	2	Molothrus-alien	Wash
MHNCI 359	Proctophyllodidae	*Amerodectes*	*molothrus*	2	1	1	S. Pedro do Paraná	PR	Atlant. For.	sept.1945	-22.82	-53.22	1	Molothrus-specific	Museum
MHNCI 359	Psoroptoididae	*Mesalgoides*	*sp. 1*	1	0	1	S. Pedro do Paraná	PR	Atlant. For.	sept.1945	-22.82	-53.22	1	Molothrus-specific	Museum
MHNCI 359	Proctophyllodidae	*Proctophyllodes*	*molothrus*	3	2	1	S. Pedro do Paraná	PR	Atlant. For.	sept.1945	-22.82	-53.22	1	Molothrus-specific	Museum
BMOC 88-1230-130	Trouessartiidae	*Trouessartia*	sp. 6	5	3	2	PARAGUAY	EX	Chaco	26.sep.1988	-20.20	-58.16	2	Molothrus-specific	Wash
BMOC 88-1230-130	Trouessartiidae	*Trouessartia*	*capensis*	1	1	0	PARAGUAY	EX	Chaco	26.sep.1988	-20.20	-58.16	2	Molothrus-alien	Wash
BMOC 88-1230-130	Psoroptoididae	*Mesalgoides*	*sp. 1*	8	3	5	PARAGUAY	EX	Chaco	26.sep.1988	-20.20	-58.16	2	Molothrus-specific	Wash
BMOC 88-1230-130	Xolalgidae	*Xolalgoides*	*sp. 1*	11	4	1	PARAGUAY	EX	Chaco	26.sep.1988	-20.20	-58.16	2	Molothrus-specific	Wash
BMOC 88-1230-130	Proctophyllodidae	*Amerodectes*	*molothrus*	1	0	1	PARAGUAY	EX	Chaco	26.sep.1988	-20.20	-58.16	2	Molothrus-specific	Wash
BMOC 88-1230-254	Proctophyllodidae	*Proctophyllodes*	*molothrus*	12	9	3	PARAGUAY	EX	Chaco	16.oct.1988	-25.29	-57.65	2	Molothrus-specific	Wash
Col. Yoshika 1	Proctophyllodidae	*Amerodectes*	*molothrus*	1	0	1	Rio Claro	SP	Atlant. For.	05.dec.2000	-22.41	-47.56	1	Molothrus-specific	Museum
Col. Yoshika 1	Trouessartiidae	*Trouessartia*	capensis	1	1	0	Rio Claro	SP	Atlant. For.	05.dec.2000	-22.41	-47.56	1	Molothrus-alien	Museum
Col. Yoshika 2	Proctophyllodidae	*Amerodectes*	*molothrus*	1	1	0	Rio Claro	SP	Atlant. For.	07.sep.1988	-22.41	-47.56	1	Molothrus-specific	Museum
Col. Yoshika 2	Psoroptoididae	*Mesalgoides*	*sp. 1*	2	2	0	Rio Claro	SP	Atlant. For.	07.sep.1988	-22.41	-47.56	1	Molothrus-specific	Museum
FM 58299	Proctophyllodidae	*Proctophyllodes*	sp. 5	1	0	1	Concepción	EX	Chaco	31.jan.1919	-27.34	-65.58	1	Molothrus-alien	Museum
FM 58299	Proctophyllodidae	*Proctophyllodes*	*molothrus*	1	1	3	Concepción	EX	Chaco	31.jan.1919	-27.34	-65.58	1	Molothrus-specific	Museum
FM 58442	Proctophyllodidae	*Proctophyllodes*	*sp. 5*	5	3	2	Concepción	EX	Chaco	31.jan.1919	-22.41	-47.56	2	Molothrus-alien	Museum
SP-46 [G133449]	Proctophyllodidae	*Proctophyllodes*	*molothrus*	2	0	2	Rio Claro	SP	Atlant. For.	13.dec.2018	-22.41	-47.56	2	Molothrus-specific	Field
SP-46 [G133449]	Proctophyllodidae	*Amerodectes*	*molothrus*	3	0	3	Rio Claro	SP	Atlant. For.	13.dec.2018	-22.00	-47.89	2	Molothrus-specific	Field
Mb São Carlos	Proctophyllodidae	*Proctophyllodes*	cf. *thraupis*	5	3	2	São Carlos	SP	Cerrado	15.jan.2018	-22.00	-47.89	2	Molothrus-alien	Wash
Mb São Carlos	Proctophyllodidae	*Amerodectes*	*molothrus*	6	3	3	São Carlos	SP	Cerrado	15.jan.2018	-22.00	-47.89	2	Molothrus-specific	Wash
Mb São Carlos	Analgidae	*Analges*	*sp. 6*	4	1homo	3	São Carlos	SP	Cerrado	15.jan.2018	-22.00	-47.89	2	Molothrus-alien	Wash
Mb São Carlos	Xolalgidae	*Xolalgoides*	*sp. 1*	1	1	0	São Carlos	SP	Cerrado	15.jan.2018	-22.00	-47.89	2	Molothrus-specific	Wash
Mb São Carlos	Trouessartiidae	*Trouessartia*	aff. *megaplax*	7	5	2	São Carlos	SP	Cerrado	15.jan.2018	-32.41	-52.82	2	Molothrus-alien	Wash
MB-1	Proctophyllodidae	*Amerodectes*	*molothrus*	32	16	16	Rio Grande	RS	Pampa	19.feb.2014	-32.41	-52.82	2	Molothrus-specific	Wash
MB-1	Proctophyllodidae	*Proctophyllodes*	*sp. 4*	4	3	1	Rio Grande	RS	Pampa	19.feb.2014	-32.41	-52.82	2	Molothrus-alien	Wash
MB-1	Xolalgidae	*Xolalgoides*	*sp. 1*	4	1	3	Rio Grande	RS	Pampa	19.feb.2014	-32.41	-52.82	2	Molothrus-specific	Wash
MB-1	Psoroptoididae	*Mesalgoides*	*sp. 1*	11	7	4	Rio Grande	RS	Pampa	19.feb.2014	-32.41	-52.82	2	Molothrus-specific	Wash
MB-4 (N.21)	Proctophyllodidae	*Proctophyllodes*	*sp. 4*	1	1	0	Rio Grande	RS	Pampa	2014	-32.41	-52.82	2	Molothrus-alien	Wash

MB-4 (N.21)	Proctophyllodidae	*Amerodectes*	*molothrus*	3	1	2	Rio Grande	RS	Pampa	2014	-32.41	-52.82	2	Molothrus-specific	Wash
MB-4 (N.21)	Xolalgidae	*Xolalgoides*	*sp. 1*	13	4	9	Rio Grande	RS	Pampa	2014	-32.41	-52.82	2	Molothrus-specific	Wash
MB-4 (N.21)	Psoroptoididae	*Mesalgoides*	*sp. 1*	6	2	4	Rio Grande	RS	Pampa	2014	-32.41	-52.82	2	Molothrus-specific	Wash
MCN 1520	Proctophyllodidae	*Proctophyllodes*	*sp. 5*	1	1	0	Rio Grande	RS	Pampa	29.sep.2000	-32.41	-52.82	1	Molothrus-alien	Museum
MCN 1520	Proctophyllodidae	*Amerodectes*	*molothrus*	3	2	1	Rio Grande	RS	Pampa	29.sep.2000	-32.41	-52.82	1	Molothrus-specific	Museum
MCN 1520	Xolalgidae	*Xolalgoides*	*sp. 2*	1	0	1	Rio Grande	RS	Pampa	29.sep.2000	-32.41	-52.82	1	Molothrus-alien	Museum
MCN 1607	Proctophyllodidae	*Proctophyllodes*	*molothrus*	1	1	0	Caçapava do Sul	RS	Pampa	28.jan.1975	-30.8	-53.66	1	Molothrus-specific	Museum
MCN 1607	Proctophyllodidae	*Proctophyllodes*	*sp. 5*	2	1	1	Caçapava do Sul	RS	Pampa	28.jan.1975	-30.8	-53.66	1	Molothrus-alien	Museum
MCN 1607	Psoroptoididae	*Mesalgoides*	*sp. 1*	2	1	1	Caçapava do Sul	RS	Pampa	28.jan.1975	-30.8	-53.66	1	Molothrus-specific	Museum
MCN 1607	Trouessartiidae	*Trouessartia*	*capensis*	1	1	0	Caçapava do Sul	RS	Pampa	28.jan.1975	-30.8	-53.66	1	Molothrus-alien	Museum
MCN 1608	Analgidae	*Strelkoviacarus*	*brasiliensis*	4	2	1	Dom Pedrito	RS	Pampa	21.mar.1972	-30.98	-54.67	1	Multi-host Parasite	Museum
MCN 1608	Trouessartiidae	*Trouessartia*	*capensis*	4	0	2	Dom Pedrito	RS	Pampa	21.mar.1972	-30.98	-54.67	1	Molothrus-alien	Museum
MCN 1609	Proctophyllodidae	*Proctophyllodes*	aff. *atyeoi*	2	1	1	Vacaria	RS	Atlant. For.	24.april.1974	-28.51	-50.93	1	Molothrus-alien	Museum
MCN 1609	Proctophyllodidae	*Amerodectes*	*molothrus*	1	1	0	Vacaria	RS	Atlant. For.	24.apr.1974	-28.51	-50.93	1	Molothrus-specific	Museum
MCN 1609	Xolalgidae	*Xolalgoides*	*sp. 1*	2	1	1	Vacaria	RS	Atlant. For.	24.apr.1974	-28.51	-50.93	1	Molothrus-specific	Museum
MCN 1610	Proctophyllodidae	*Proctophyllodes*	*sp. 5*	1	1	0	Bom Jesus	RS	Atlant. For.	01.nov.1970	-28.66	-50.41	1	Molothrus-alien	Museum
MCN 1610	Proctophyllodidae	*Proctophyllodes*	*molothrus*	2	1	1	Bom Jesus	RS	Atlant. For.	01.nov.1970	-28.66	-50.41	1	Molothrus-specific	Museum
MCN 1610	Proctophyllodidae	*Amerodectes*	*molothrus*	1	0	1	Bom Jesus	RS	Atlant. For.	01.nov.1970	-28.66	-50.41	1	Molothrus-specific	Museum
MCN 1610	Xolalgidae	*Xolalgoides*	*sp. 1*	1	0	1	Bom Jesus	RS	Atlant. For.	01.nov.1970	-28.66	-50.41	1	Molothrus-specific	Museum
MCN 1610	Psoroptoididae	*Mesalgoides*	*sp. 2*	1	1	0	Bom Jesus	RS	Atlant. For.	01.nov.1970	-28.66	-50.41	1	Molothrus-alien	Museum
MCN 1611	Proctophyllodidae	*Proctophyllodes*	*molothrus*	1	1	0	Uruguaiana	RS	Pampa	11.oct.1971	-29.75	-57.08	1	Molothrus-specific	Museum
MCN 1611	Proctophyllodidae	*Amerodectes*	*molothrus*	3	1	2	Uruguaiana	RS	Pampa	11.oct.1971	-29.75	-57.08	1	Molothrus-specific	Museum
MCN 1611	Analgidae	*Strelkoviacarus*	*brasiliensis*	1	1	0	Uruguaiana	RS	Pampa	11.oct.1971	-29.75	-57.08	1	Multi-host Parasite	Museum
MCN 1611	Psoroptoididae	*Mesalgoides*	*sp. 1*	2	1	1	Uruguaiana	RS	Pampa	11.oct.1971	-29.75	-57.08	1	Molothrus-specific	Museum
MCN 187	Proctophyllodidae	*Proctophyllodes*	*molothrus*	1	0	1	São Gabriel	RS	Pampa	03.jan.1999	-30.33	-54.32	1	Molothrus-specific	Museum
MCN 187	Psoroptoididae	*Mesalgoides*	*sp. 2*	2	0	2	São Gabriel	RS	Pampa	03.jan.1999	-30.33	-54.32	1	Molothrus-alien	Museum
MCN 187	Trouessartiidae	*Trouessartia*	*capensis*	3	1	2	São Gabriel	RS	Pampa	03.jan.1999	-30.33	-54.32	1	Molothrus-alien	Museum
MCN 2003	Proctophyllodidae	*Proctophyllodes*	*molothrus*	7	4	3	Bom Jesus	RS	Atlant. For.	July.1980	-28.66	-50.41	2	Molothrus-specific	Museum
MCN 2003	Proctophyllodidae	*Amerodectes*	*molothrus*	7	3	4	Bom Jesus	RS	Atlant. For.	july.1980	-28.66	-50.41	2	Molothrus-specific	Museum
MCN 2003	Psoroptoididae	*Mesalgoides*	*sp. 1*	3	1	2	Bom Jesus	RS	Atlant. For.	july.1980	-28.66	-50.41	1	Molothrus-specific	Museum
MCN 2004	Proctophyllodidae	*Proctophyllodes*	*molothrus*	1	0	1	Porto Alegre	RS	Pampa	02.june.1961	-30.05	-51.17	1	Molothrus-specific	Museum
MCN 2004	Proctophyllodidae	*Amerodectes*	*molothrus*	10	3	7	Porto Alegre	RS	Pampa	02.jun.1961	-30.05	-51.17	2	Molothrus-specific	Museum
MCN 2004	Xolalgidae	*Xolalgoides*	*sp. 1*	1	1	0	Porto Alegre	RS	Pampa	02.jun.1961	-30.05	-51.17	1	Molothrus-specific	Museum
MCN 2005	Proctophyllodidae	*Proctophyllodes*	*molothrus*	1	1	0	Canoas	RS	Pampa	24.aug.1957	-29.91	-51.16	1	Molothrus-specific	Museum
MCN 2005	Proctophyllodidae	*Proctophyllodes*	*sp. 4*	1	0	1	Canoas	RS	Pampa	24.aug.1957	-29.91	-51.16	1	Molothrus-alien	Museum
MCN 2007	Proctophyllodidae	*Amerodectes*	*molothrus*	2	1	1	Bom Jesus	RS	Atlant. For.	15.jan.1958	-28.66	-50.41	1	Molothrus-specific	Museum
MCN 2007	Psoroptoididae	*Mesalgoides*	*sp. 3*	1	1	0	Bom Jesus	RS	Atlant. For.	15.jan.1958	-28.66	-50.41	1	Molothrus-alien	Museum
MCN 2007	Trouessartiidae	*Trouessartia*	*capensis*	1	1	0	Bom Jesus	RS	Atlant. For.	15.jan.1958	-28.66	-50.41	1	Molothrus-alien	Museum
MCN 2043	Proctophyllodidae	*Proctophyllodes*	*molothrus*	2	1	1	Viamão	SC	Pampa	10.dec.1959	-28.8	-49.72	1	Molothrus-specific	Museum
MCN 2043	Proctophyllodidae	*Amerodectes*	*molothrus*	1	0	1	Viamão	RS	Pampa	10.dec.1959	-30.08	-51.02	1	Molothrus-specific	Museum
MCN 2043	Xolalgidae	*Xolalgoides*	*sp. 1*	3	1	2	Viamão	RS	Pampa	10.dec.1959	-30.08	-51.02	1	Molothrus-specific	Museum
MCN 2043	Psoroptoididae	*Mesalgoides*	*sp. 1*	1	1	0	Viamão	RS	Pampa	10.dec.1959	-30.08	-51.02	1	Molothrus-specific	Museum
MCN 2044	Proctophyllodidae	*Proctophyllodes*	*molothrus*	3	1	2	Camaquã	RS	Pampa	17.oct.1959	-30.85	-51.81	1	Molothrus-specific	Museum
MCN 2044	Psoroptoididae	*Mesalgoides*	*sp. 1*	1	0	1	Camaquã	RS	Pampa	17.oct.1959	-30.85	-51.81	1	Molothrus-specific	Museum

MCN 2044	Trouessartiidae	*Trouessartia*	*capensis*	1	0	1	Camaquã	RS	Pampa	17.oct.1959	-30.85	-51.81	1	Molothrus-alien	Museum
MCN 2850	Proctophyllodidae	*Proctophyllodes*	*molothrus*	1	0	1	Guaíba	RS	Pampa	07.sep.2009	-30.1	-51.31	1	Molothrus-specific	Museum
MCN 2926	Psoroptoididae	*Mesalgoides*	*sp. 2*	2	1	1	Bagé	RS	Atlant. For.	13.oct.1987	-31.31	-54.1	1	Molothrus-alien	Museum
MCN 3038	Proctophyllodidae	*Proctophyllodes*	*carmenmirandae*	3	1	2	Porto Alegre	RS	Pampa	20.oct.2010	-30.05	-51.17	1	Molothrus-alien	Museum
MCN 3038	Proctophyllodidae	*Proctophyllodes*	*molothrus*	3	2	1	Porto Alegre	RS	Pampa	20.oct.2010	-30.05	-51.17	1	Molothrus-specific	Museum
MCN 3038	Proctophyllodidae	*Amerodectes*	*molothrus*	3	2	1	Porto Alegre	RS	Pampa	20.oct.2010	-30.05	-51.17	1	Molothrus-specific	Museum
MCN 3256	Proctophyllodidae	*Proctophyllodes*	*molothrus*	1	1	0	Palmares do Sul	RS	Pampa	16.jun.2011	-30.45	-50.46	1	Molothrus-specific	Museum
MCN 3256	Proctophyllodidae	*Amerodectes*	*molothrus*	1	0	1	Palmares do Sul	RS	Pampa	16.jun.2011	-30.45	-50.46	1	Molothrus-specific	Museum
MCN 3341	Proctophyllodidae	*Amerodectes*	*molothrus*	1	0	1	São Gabriel	RS	Pampa	05.jun.2009	-30.33	-54.32	1	Molothrus-specific	Museum
MCN 3341	Xolalgidae	*Xolalgoides*	*sp. 1*	2	1	1	São Gabriel	RS	Pampa	05.jun.2009	-30.33	-54.32	1	Molothrus-specific	Museum
MCN 3341	Psoroptoididae	*Mesalgoides*	*sp. 1*	1	1	0	São Gabriel	RS	Pampa	05.jun.2009	-30.33	-54.32	1	Molothrus-specific	Museum
MCN 3341	Psoroptoididae	*Mesalgoides*	*sp. 2*	1	0	1	São Gabriel	RS	Pampa	05.jun.2009	-30.33	-54.32	1	Molothrus-alien	Museum
MCN 4604	Psoroptoididae	*Mesalgoides*	*sp. 1*	1	0	1	Sta. Vit. do Palmar	RS	Pampa	16.oct.2013	-33.51	-53.36	1	Molothrus-specific	Museum
MCN 579	Proctophyllodidae	*Proctophyllodes*	*molothrus*	1	0	1	Viamão	RS	Pampa	29.sep.1980	-30.08	-51.02	1	Molothrus-specific	Museum
MCN 579	Proctophyllodidae	*Amerodectes*	*molothrus*	4	2	2	Viamão	RS	Pampa	29.sep.1980	-30.08	-51.02	2	Molothrus-specific	Museum
MCN 579	Psoroptoididae	*Mesalgoides*	*sp. 1*	1	1	0	Viamão	RS	Pampa	29.sep.1980	-30.08	-51.02	1	Molothrus-specific	Museum
MCP 157	Proctophyllodidae	*Proctophyllodes*	*sp. 5*	3	1	2	Porto Alegre	RS	Pampa	30.sep.1998	-30.05	-51.17	1	Molothrus-alien	Museum
MCP 157	Proctophyllodidae	*Proctophyllodes*	*molothrus*	2	1	1	Porto Alegre	RS	Pampa	30.sep.1998	-30.05	-51.17	1	Molothrus-specific	Museum
MCP 157	Proctophyllodidae	*Amerodectes*	*molothrus*	1	0	1	Porto Alegre	RS	Pampa	30.sep.1998	-30.05	-51.17	1	Molothrus-specific	Museum
MCP 157	Xolalgidae	*Xolalgoides*	*sp. 2*	6	3	3	Porto Alegre	RS	Pampa	30.sep.1998	-30.05	-51.17	2	Molothrus-alien	Museum
MCP 157	Psoroptoididae	*Mesalgoides*	*sp. 1*	1	1	0	Porto Alegre	RS	Pampa	30.sep.1998	-30.05	-51.17	1	Molothrus-specific	Museum
MCP 157	Dermationidae	Dermationidae		1	0	1	Porto Alegre	RS	Pampa	30.sep.1998	-30.05	-51.17	1	Multi-host Parasite	Museum
MCP 161	Proctophyllodidae	*Proctophyllodes*	*molothrus*	2	1	1	Porto Alegre	RS	Pampa	19.sep.1998	-30.05	-51.17	1	Molothrus-specific	Museum
MCP 161	Proctophyllodidae	*Amerodectes*	*molothrus*	1	0	1	Porto Alegre	RS	Pampa	29.sep.1998	-30.05	-51.17	1	Molothrus-specific	Museum
MCP 2926	Proctophyllodidae	*Proctophyllodes*	*carmenmirandae*	1	1	0	Bagé	RS	Pampa	13.oct.1987	-31.31	-54.1	1	Molothrus-alien	Museum
MCP 2926	Proctophyllodidae	*Proctophyllodes*	*molothrus*	2	1	1	Bagé	RS	Pampa	13.oct.1987	-31.31	-54.1	1	Molothrus-specific	Museum
MCP 938	Proctophyllodidae	*Proctophyllodes*	*carmenmirandae*	2	1	1	Rio grande	RS	Pampa	09.jan.2001	-32.41	-52.82	1	Molothrus-alien	Museum
MCP 938	Analgidae	*Analges*	*sp. 5*	7	2het 2hom	3	Rio Grande	RS	Pampa	09.jan.2001	-32.41	-52.82	2	Molothrus-alien	Museum
MCP 938	Trouessartiidae	*Trouessartia*	*capensis*	4	2	2	Rio Grande	RS	Pampa	09.jan.2001	-32.41	-52.82	1	Molothrus-alien	Museum
MHNCI 1679	Proctophyllodidae	*Amerodectes*	*molothrus*	8	4	4	Palmas	PR	Atlant. For.	august.1954	-26.48	-51.99	2	Molothrus-specific	Museum
MHNCI 1836	Proctophyllodidae	*Proctophyllodes*	*molothrus*	1	0	1	Serra dos Dourados	PR	Atlant. For.	oct.1955	-23.76	-53.32	1	Molothrus-specific	Museum
MHNCI 1870	Proctophyllodidae	*Proctophyllodes*	*molothrus*	6	3	3	Curitiba	PR	Atlant. For.	04.oct.1995	-25.42	-49.27	2	Molothrus-specific	Museum
MHNCI 1873	Proctophyllodidae	*Proctophyllodes*	*molothrus*	4	2	2	Curitiba	PR	Atlant. For.	04.oct.1995	-25.42	-49.27	1	Molothrus-specific	Museum
MHNCI 1873	Proctophyllodidae	*Amerodectes*	*molothrus*	2	1	1	Curitiba	PR	Atlant. For.	04.oct.1995	-25.42	-49.27	1	Molothrus-specific	Museum
MHNCI 1876	Proctophyllodidae	*Proctophyllodes*	*molothrus*	2	1	1	Curitiba	PR	Atlant. For.	04.oct.1995	-25.42	-49.27	1	Molothrus-specific	Museum
MHNCI 2635	Proctophyllodidae	*Proctophyllodes*	*molothrus*	5	3	2	São Mateus do Sul	PR	Atlant. For.	dec.1985	-25.87	-50.38	2	Molothrus-specific	Museum
MHNCI 2635	Psoroptoididae	*Mesalgoides*	*sp. 2*	1	1	0	São Mateus do Sul	PR	Atlant. For.	dec.1985	-25.87	-50.38	1	Molothrus-alien	Museum
MHNCI 358	Proctophyllodidae	*Proctophyllodes*	*molothrus*	2	1	1	Curitiba	PR	Atlant. For.	August.1945	-25.42	-49.27	1	Molothrus-specific	Museum
MHNCI 358	Proctophyllodidae	*Amerodectes*	*molothrus*	2	1	1	Curitiba	PR	Atlant. For.	august.1945	-25.42	-49.27	1	Molothrus-specific	Museum
MHNCI 358	Psoroptoididae	*Mesalgoides*	*sp. 1*	1	0	1	Curitiba	PR	Atlant. For.	August.1945	-25.42	-49.27	1	Molothrus-specific	Museum
MHNCI 3847	Proctophyllodidae	*Proctophyllodes*	*molothrus*	4	3	1	Pinhão	PR	Atlant. For.	25.sep.1991	-25.69	-51.66	1	Molothrus-specific	Museum
MHNCI 3847	Psoroptoididae	*Mesalgoides*	*sp. 1*	2	0	2	Pinhão	PR	Atlant. For.	25.sep.1991	-25.69	-51.66	1	Molothrus-specific	Museum
MHNCI 3865	Proctophyllodidae	*Amerodectes*	*molothrus*	1	0	1	Pinhão	PR	Atlant. For.	28.sep.1991	-25.69	-51.66	1	Molothrus-specific	Museum
MHNCI 3865	Psoroptoididae	*Mesalgoides*	*sp. 2*	1	1	0	Pinhão	PR	Atlant. For.	28.sep.1991	-25.69	-51.66	1	Molothrus-alien	Museum

MHNCI 5969	Xolalgidae	*Xolalgoides*	*sp. 2*	3	1	2	Pontal do Sul	PR	Atlant. For.	20.aug.2005	-25.57	-48.35	1	Molothrus-alien	Museum
MHNCI 641	Proctophyllodidae	*Amerodectes*	*molothrus*	1	0	1	Curitiba	PR	Atlant. For.	04.oct.1995	-25.42	-49.27	1	Molothrus-specific	Museum
MHNCI 762	Psoroptoididae	*Mesalgoides*	*sp. 1*	1	1	0	Antonina	PR	Atlant. For.	oct.1947	-24.57	-51.33	1	Molothrus-specific	Museum
MHNCI 79	Xolalgidae	*Xolalgoides*	*sp. 1*	1	0	1	Telemaco Borba	PR	Pampa	30.sep.1939	-24.32	-50.61	1	Molothrus-specific	Museum
MPEG 52288	Proctophyllodidae	*Amerodectes*	*molothrus*	2	2	0	Belém	PA	Amazonia	24.jan.1995	-14.42	-48.40	2	Molothrus-specific	Museum
MPEG 18762	Proctophyllodidae	*Amerodectes*	*molothrus*	6	3	3	Bragança	PA	Amazonia	feb.1961	-1.06	-46.77	2	Molothrus-specific	Museum
MPEG 18762	Xolalgidae	*Xolalgoides*	*sp. 1*	3	2	1	Bragança	PA	Amazonia	feb.1961	-1.06	-46.77	1	Molothrus-specific	Museum
MPEG 18762	Trouessartiidae	*Trouessartia*	*sp. 6*	4	3	1	Bragança	PA	Amazonia	feb.1961	-1.06	-46.77	1	Molothrus-specific	Museum
MPEG 20701	Proctophyllodidae	*Proctophyllodes*	aff. *atyeoi*	3	2	1	Araguatins	TO	Cerrado	17.oct.1963	-5.65	-48.11	1	Molothrus-alien	Museum
MPEG 20701	Proctophyllodidae	*Proctophyllodes*	*molothrus*	3	0	3	Araguatins	TO	Cerrado	17.oct.1963	-5.65	-48.11	1	Molothrus-specific	Museum
MPEG 20701	Proctophyllodidae	*Amerodectes*	*molothrus*	5	2	3	Araguatins	TO	Cerrado	17.oct.1963	-5.65	-48.11	2	Molothrus-specific	Museum
MPEG 20701	Xolalgidae	*Xolalgoides*	*sp. 1*	1	1	0	Araguatins	TO	Cerrado	17.oct.1963	-5.65	-48.11	1	Molothrus-specific	Museum
MPEG 21667	Proctophyllodidae	*Proctophyllodes*	*carmenmirandae*	1	1	0	Boa Vista	RR	Amazonia	16.mar.1963	2.51	-60.89	1	Molothrus-alien	Museum
MPEG 21667	Proctophyllodidae	*Proctophyllodes*	*molothrus*	6	4	2	Boa Vista	RR	Amazonia	16.mar.1963	2.51	-60.89	2	Molothrus-specific	Museum
MPEG 21667	Proctophyllodidae	*Amerodectes*	*molothrus*	4	2	2	Boa Vista	RR	Amazonia	16.mar.1963	2.51	-60.89	2	Molothrus-specific	Museum
MPEG 21667	Xolalgidae	*Xolalgoides*	*sp. 1*	4	3	1	Boa Vista	RR	Amazonia	16.mar.1963	2.51	-60.89	2	Molothrus-specific	Museum
MPEG 21667	Trouessartiidae	*Trouessartia*	*sp. 6*	2	1	1	Boa Vista	RR	Amazonia	16.mar.1963	2.51	-60.89	1	Molothrus-specific	Museum
MPEG 21672	Proctophyllodidae	*Amerodectes*	*molothrus*	4	2	2	Boa Vista	RR	Amazonia	12.mar.1963	2.51	-60.89	2	Molothrus-specific	Museum
MPEG 21672	Xolalgidae	*Xolalgoides*	*sp. 1*	3	0	3	Boa Vista	RR	Amazonia	12.mar.1963	2.51	-60.89	1	Molothrus-specific	Museum
MPEG 21672	Trouessartiidae	*Trouessartia*	*sp. 6*	1	0	1	Boa Vista	RR	Amazonia	12.mar.1963	2.51	-60.89	1	Molothrus-specific	Museum
MPEG 21877	Proctophyllodidae	*Proctophyllodes*	*molothrus*	1	0	1	Goiânia	GO	Cerrado	05.jan.1964	-16.66	-49.25	2	Molothrus-specific	Museum
MPEG 21877	Psoroptoididae	*Mesalgoides*	*sp. 2*	1	0	1	Goiânia	GO	Cerrado	05.jan.1964	-16.66	-49.25	1	Molothrus-alien	Museum
MPEG 23289	Proctophyllodidae	*Proctophyllodes*	*molothrus*	5	3	3	Macapá	AP	Amazonia	26.jun.1952	0.038	-51.07	2	Molothrus-specific	Museum
MPEG 23292	Proctophyllodidae	*Amerodectes*	*molothrus*	4	2	2	Bragança	PA	Amazonia	25.oct.1956	-1.16	-46.63	2	Molothrus-specific	Museum
MPEG 23292	Xolalgidae	*Xolalgoides*	*sp. 1*	2	1	1	Bragança	PA	Amazonia	25.oct.1956	-1.16	-46.63	1	Molothrus-specific	Museum
MPEG 23293	Proctophyllodidae	*Amerodectes*	*molothrus*	6	3	3	Foz Rio Curuá	PA	Amazonia	25.dec.1936	-3.80	-52.66	2	Molothrus-specific	Museum
MPEG 23300	Proctophyllodidae	*Proctophyllodes*	*molothrus*	1	0	1	Macapá	AP	Amazonia	23.jun.1952	0.038	-51.07	1	Molothrus-specific	Museum
MPEG 23300	Proctophyllodidae	*Amerodectes*	*molothrus*	6	3	3	Macapá	AP	Amazonia	23.jun.1952	0.038	-51.07	2	Molothrus-specific	Museum
MPEG 23300	Psoroptoididae	*Mesalgoides*	*sp. 1*	1	0	1	Macapá	AP	Amazonia	23.jun.1952	0.038	-51.07	1	Molothrus-specific	Museum
MPEG 23311	Proctophyllodidae	*Amerodectes*	*molothrus*	2	2	0	Oiapoque	AP	Amazonia	17.apr.1952	3.21	-51.23	1	Molothrus-specific	Museum
MPEG 23311	Xolalgidae	*Xolalgoides*	*sp. 1*	2	0	2	Oiapoque	AP	Amazonia	17.apr.1952	3.21	-51.23	1	Molothrus-specific	Museum
MPEG 23311	Psoroptoididae	*Mesalgoides*	*sp. 1*	1	0	1	Oiapoque	AP	Amazonia	17.apr.1952	3.21	-51.23	1	Molothrus-specific	Museum
MPEG 23311	Trouessartiidae	*Trouessartia*	*sp. 6*	1	1	0	Oiapoque	AP	Amazonia	17.apr.1952	3.21	-51.23	1	Molothrus-specific	Museum
MPEG 25859	Proctophyllodidae	*Proctophyllodes*	*molothrus*	4	1	3	Cachoeira do Arari	PA	Amazonia	05.feb.1966	-1.01	-48.96	1	Molothrus-specific	Museum
MPEG 25859	Proctophyllodidae	*Amerodectes*	*molothrus*	4	2	2	Cachoeira do Arari	PA	Amazonia	05.feb.1966	-1.01	-48.96	2	Molothrus-specific	Museum
MPEG 25859	Dermoglyphidae	*Dermoglyphus*	*cf. passerinus*	1	1	0	Cachoeira do Arari	PA	Amazonia	05.feb.1966	-1.01	-48.96	1	Multi-host Parasite	Museum
MPEG 25862	Proctophyllodidae	*Proctophyllodes*	*molothrus*	3	2	1	Cachoeira do Arari	PA	Amazonia	05.feb.1966	-1.01	-48.96	1	Molothrus-specific	Museum
MPEG 25862	Proctophyllodidae	*Amerodectes*	*molothrus*	1	0	1	Cachoeira do Arari	PA	Amazonia	05.feb.1966	-1.01	-48.96	1	Molothrus-specific	Museum
MPEG 25862	Psoroptoididae	*Mesalgoides*	*sp. 1*	1	0	1	Cachoeira do Arari	PA	Amazonia	05.feb.1966	-1.01	-48.96	1	Molothrus-specific	Museum
MPEG 41369	Proctophyllodidae	*Proctophyllodes*	*molothrus*	3	2	1	Itacarambi	MG	Cerrado	19.oct.1987	-15.09	-44.10	1	Molothrus-specific	Museum
MPEG 47180	Proctophyllodidae	*Proctophyllodes*	*molothrus*	8	4	4	P. de Monte Alto	BA	Caatinga	12.sep.1991	-14.26	-43.16	2	Molothrus-specific	Museum
MPEG 47180	Proctophyllodidae	*Amerodectes*	*molothrus*	6	3	3	P. de Monte Alto	BA	Caatinga	12.sep.1991	-14.26	-43.16	2	Molothrus-specific	Museum
MPEG 47180	Epidermoptidae	*Microlichus*	*cf. americanus*	1	0	1	P. de Monte Alto	BA	Caatinga	12.sep.1991	-14.26	-43.16	1	Multi-host Parasite	Museum
MPEG 47181	Proctophyllodidae	*Proctophyllodes*	*molothrus*	5	2	3	P. de Monte Alto	BA	Caatinga	12.sep.1991	-14.26	-43.16	2	Molothrus-specific	Museum

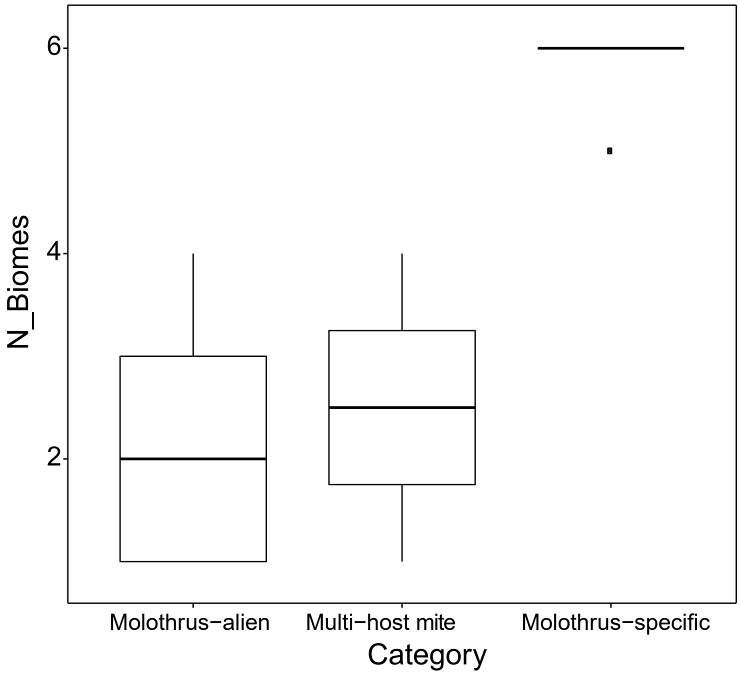
MPEG 47181	Proctophyllodidae	*Amerodectes*	*molothrus*	1	1	0	P. de Monte Alto	BA	Caatinga	12.sep.1991	-14.26	-43.16	1	Molothrus-specific	Museum
MPEG 47181	Psoroptoididae	Mesalgoides	*sp. 1*	2	0	2	P. de Monte Alto	BA	Caatinga	12.sep.1991	-14.26	-43.16	1	Molothrus-specific	Museum
MPEG 47181	Dermationidae	Dermationidae		1	1	0	P. de Monte Alto	BA	Caatinga	12.sep.1991	-14.26	-43.16	1	Multi-host Parasite	Museum
MPEG 47596	Dermoglyphidae	*Dermoglyphus*	*cf. passerinus*	2	0	2	Ilha Caviana	PA	Amazonia	09.feb.1992	-0.16	-49.98	1	Multi-host Parasite	Museum
MPEG 52288	Proctophyllodidae	*Proctophyllodes*	aff. *atyeoi*	4	2	2	Belém	PA	Amazonia	24.jan.1995	-14.421	-48.446	2	Molothrus-alien	Museum
MPEG 52288	Psoroptoididae	*Mesalgoides*	*sp. 1*	2	0	2	Belém	PA	Amazonia	24.jan.1995	-14.42	-48.45	1	Molothrus-specific	Museum
MPEG 52288	Dermoglyphidae	*Dermoglyphus*	*cf. passerinus*	6	0	6	Belém	PA	Amazonia	24.jan.1995	-14.42	-48.45	2	Multi-host Parasite	Museum
MPEG 52288	Trouessartiidae	*Trouessartia*	*sp. 6*	1	0	1	Belém	PA	Amazonia	24.jan.1995	-14.42	-48.45	1	Molothrus-specific	Museum
MPEG 56794	Proctophyllodidae	*Proctophyllodes*	*molothrus*	3	0	3	Juriti	PA	Amazonia	17.sep.2002	-2.15	-56.09	1	Molothrus-specific	Museum
MPEG 56794	Xolalgidae	*Xolalgoides*	*sp. 1*	7	4	3	Juriti	PA	Amazonia	17.sep.2002	-2.15	-56.09	2	Molothrus-specific	Museum
MPEG 56794	Psoroptoididae	*Mesalgoides*	*sp. 1*	4	1	3	Juriti	PA	Amazonia	17.sep.2002	-2.15	-56.09	1	Molothrus-specific	Museum
MPEG 56794	Trouessartiidae	*Trouessartia*	*sp. 6*	3	2	1	Juriti	PA	Amazonia	17.sep.2002	-2.15	-56.09	2	Molothrus-specific	Museum
MPEG 61380	Proctophyllodidae	*Amerodectes*	*molothrus*	4	1	3	Rio Branco	AC	Amazonia	09.nov.2006	-9.99	-67.81	1	Molothrus-specific	Museum
MPEG 61380	Trouessartiidae	*Trouessartia*	*sp. 6*	1	1	0	Rio Branco	AC	Amazonia	09.nov.2006	-9.99	-67.81	1	Molothrus-specific	Museum
MPEG 63849	Proctophyllodidae	*Proctophyllodes*	aff. *atyeoi*	7	4	3	Feijó	AC	Amazonia	20.nov.2007	-8.16	-70.35	2	Molothrus-alien	Museum
MPEG 63849	Proctophyllodidae	*Amerodectes*	*molothrus*	6	3	3	Feijó	AC	Amazonia	20.nov.2007	-8.16	-70.35	2	Molothrus-specific	Museum
MPEG 63849	Psoroptoididae	*Mesalgoides*	*sp. 1*	1	0	1	Feijó	AC	Amazonia	20.nov.2007	-8.16	-70.35	1	Molothrus-specific	Museum
MPEG 63849	Dermoglyphidae	*Dermoglyphus*	*cf. passerinus*	3	1	1	Feijó	AC	Amazonia	20.nov.2007	-8.16	-70.35	1	Multi-host Parasite	Museum
MPEG 63849	Trouessartiidae	*Trouessartia*	*sp. 6*	6	3	3	Feijó	AC	Amazonia	20.nov.2007	-8.16	-70.35	2	Molothrus-specific	Museum
MPEG 65662	Proctophyllodidae	*Platyacarus*	*sp.*	5	4	1	Itaituba	PA	Amazonia	29.jul.2008	-4.28	-55.98	1	Molothrus-alien	Museum
MPEG 65662	Psoroptoididae	Mesalgoides	*sp. 1*	4	0	4	Itaituba	PA	Amazonia	29.jul.2008	-4.28	-55.98	1	Molothrus-specific	Museum
MPEG 71961	Proctophyllodidae	*Proctophyllodes*	*molothrus*	6	3	3	Blumenau	SC	Atlant. For.	22.dec.2010	-26.86	-49.06	2	Molothrus-specific	Museum
MPEG 71961	Proctophyllodidae	*Amerodectes*	*molothrus*	6	3	3	Blumenau	SC	Atlant. For.	22.dec.2010	-26.86	-49.06	2	Molothrus-specific	Museum
MPEG 71961	Xolalgidae	*Xolalgoides*	*sp. 1*	3	1	2	Blumenau	SC	Atlant. For.	22.dec.2010	-26.86	-49.06	1	Molothrus-specific	Museum
MPEG 71961	Psoroptoididae	*Mesalgoides*	*sp. 1*	3	1	2	Blumenau	SC	Atlant. For.	22.dec.2010	-26.86	-49.06	1	Molothrus-specific	Museum
MPEG 78128	Proctophyllodidae	*Proctophyllodes*	*molothrus*	6	3	3	Araguaína	TO	Cerrado	09.nov.2013	-7.19	-48.21	2	Molothrus-specific	Museum
MPEG 78128	Proctophyllodidae	*Platyacarus*	*sp.*	7	6	1	Araguaína	TO	Cerrado	09.nov.2013	-7.19	-48.21	2	Molothrus-alien	Museum
MPEG 78128	Proctophyllodidae	*Amerodectes*	*molothrus*	5	2	3	Araguaína	TO	Cerrado	09.nov.2013	-7.19	-48.21	2	Molothrus-specific	Museum
MPEG 78128	Xolalgidae	*Xolalgoides*	*sp. 1*	5	2	3	Araguaína	TO	Cerrado	09.nov.2013	-7.19	-48.21	2	Molothrus-specific	Museum
MPEG 78128	Dermationidae	Dermationidae		1	0	1	Araguaína	TO	Cerrado	09.nov.2013	-7.19	-48.21	1	Multi-host Parasite	Museum
MZUSP 10756	Proctophyllodidae	*Amerodectes*	*molothrus*	3	2	1	Pres. Epitácio	SP	Atlant. For.	17.jun.1926	-21.76	-52.1	1	Molothrus-specific	Museum
MZUSP 10756	Epidermoptidae	*Microlichus*	*cf. americanus*	1	0	1	Pres. Epitácio	SP	Atlant. For.	17.jun.1926	-21.76	-52.1	1	Multi-host Parasite	Museum
MZUSP 11655	Proctophyllodidae	*Amerodectes*	*molothrus*	4	3	1	S. Miguel Arcanjo	SP	Atlant. For.	05.sep.1929	-23.87	-47.99	1	Molothrus-specific	Museum
MZUSP 11655	Xolalgidae	*Xolalgoides*	*sp. 1*	1	1	0	S. Miguel Arcanjo	SP	Atlant. For.	05.sep.1929	-23.87	-47.99	1	Molothrus-specific	Museum
MZUSP 11655	Psoroptoididae	*Mesalgoides*	*sp. 1*	2	0	2	S. Miguel Arcanjo	SP	Atlant. For.	05.sep.1929	-23.87	-47.99	1	Molothrus-specific	Museum
MZUSP 1194	Proctophyllodidae	*Proctophyllodes*	*molothrus*	2	2	0	São Paulo	SP	Atlant. For.	26.sep.1900	-23.59	-46.58	1	Molothrus-specific	Museum
MZUSP 1194	Proctophyllodidae	*Amerodectes*	*molothrus*	1	0	1	São Paulo	SP	Atlant. For.	26.sep.1900	-23.59	-46.58	1	Molothrus-specific	Museum
MZUSP 1194	Dermoglyphidae	*Dermoglyphus*	*cf. passerinus*	1	0	1	São Paulo	SP	Atlant. For.	26.sep.1900	-23.59	-46.58	1	Multi-host Parasite	Museum
MZUSP 14275	Proctophyllodidae	*Amerodectes*	*molothrus*	3	1	2	Curupeba	BA	Atlant. For.	06.feb.1933	-12.61	-38.66	1	Molothrus-specific	Museum
MZUSP 14275	Psoroptoididae	*Mesalgoides*	*sp. 3*	2	1	1	Curupeba	BA	Atlant. For.	06.feb.1933	-12.61	-38.66	1	Molothrus-alien	Museum
MZUSP 14275	Trouessartiidae	*Trouessartia*	*sp. 6*	1	0	1	Curupeba	BA	Atlant. For.	06.feb.1933	-12.61	-38.66	1	Molothrus-specific	Museum
MZUSP 15136	Proctophyllodidae	*Proctophyllodes*	*molothrus*	2	1	1	Jaraguá	GO	Cerrado	05.sep.1934	-15.75	-49.33	1	Molothrus-specific	Museum
MZUSP 15136	Proctophyllodidae	*Amerodectes*	*molothrus*	3	2	1	Jaraguá	GO	Cerrado	05.sep.1934	-15.75	-49.33	1	Molothrus-specific	Museum
MZUSP 15136	Psoroptoididae	*Mesalgoides*	*sp. 2*	1	0	1	Jaraguá	GO	Cerrado	05.sep.1934	-15.75	-49.33	1	Molothrus-alien	Museum

MZUSP 16014	Xolalgidae	*Xolalgoides*	*sp. 1*	1	0	1	Maria da Fé	MG	Atlant. For.	25. dec. 1935	-22.3	-45.37	1	Molothrus-specific	Museum
MZUSP 16014	Psoroptoididae	*Mesalgoides*	*sp. 1*	7	3	4	Maria da Fé	MG	Atlant. For.	25.dec.1935	-22.3	-45.37	2	Molothrus-specific	Museum
MZUSP 17132	Proctophyllodidae	*Proctophyllodes*	*molothrus*	4	2	2	Cuiabá	MT	Cerrado	21.sep.1937	-15.59	-56.09	2	Molothrus-specific	Museum
MZUSP 17132	Psoroptoididae	*Mesalgoides*	*sp. 3*	1	1	0	Cuiabá	MT	Cerrado	21.sep.1937	-15.59	-56.09	1	Molothrus-alien	Museum
MZUSP 17132	Psoroptoididae	*Mesalgoides*	*sp. 1*	2	1	1	Cuiabá	MT	Cerrado	21.sep.1937	-15.59	-56.09	1	Molothrus-specific	Museum
MZUSP 24673	Proctophyllodidae	*Proctophyllodes*	*molothrus*	1	0	1	Ibiraçu	ES	Atlant. For.	19.aug.1940	-19.83	-40.37	1	Molothrus-specific	Museum
MZUSP 24673	Xolalgidae	*Xolalgoides*	*sp. 1*	2	2	0	Ibiraçu	ES	Atlant. For.	19.aug.1940	-19.83	-40.37	1	Molothrus-specific	Museum
MZUSP 26576	Proctophyllodidae	*Proctophyllodes*	*molothrus*	4	2	2	Emburá	SP	Atlant. For.	20.dec.1940	-23.91	-46.67	2	Molothrus-specific	Museum
MZUSP 26576	Dermationidae	Dermationidae		4	0	4	Emburá	SP	Atlant. For.	20.dec.1940	-23.91	-46.67	2	Multi-host Parasite	Museum
MZUSP 27252	Proctophyllodidae	*Amerodectes*	*molothrus*	4	2	2	Rio Muriaé	RJ	Atlant. For.	02.sep.1941	-21.71	-41.36	2	Molothrus-specific	Museum
MZUSP 27252	Psoroptoididae	*Mesalgoides*	*sp. 1*	3	2	1	Rio Muriaé	RJ	Atlant. For.	02.sep.1941	-21.71	-41.36	1	Molothrus-specific	Museum
MZUSP 27252	Psoroptoididae	*Mesalgoides*	*sp. 2*	1	0	1	Rio Muriaé	RJ	Atlant. For.	02.sep.1941	-21.71	-41.36	1	Molothrus-alien	Museum
MZUSP 27252	Trouessartiidae	*Trouessartia*	*capensis*	1	0	1	Rio Muriaé	RJ	Atlant. For.	02.sep.1941	-21.71	-41.36	1	Molothrus-alien	Museum
MZUSP 28637	Proctophyllodidae	*Amerodectes*	*molothrus*	5	3	2	Guarapari	ES	Atlant. For.	15.oct.1942	-20.65	-40.51	2	Molothrus-specific	Museum
MZUSP 28637	Xolalgidae	*Xolalgoides*	*sp. 1*	2	1	1	Guarapari	ES	Atlant. For.	15.oct.1942	-20.65	-40.51	1	Molothrus-specific	Museum
MZUSP 28879	Proctophyllodidae	*Proctophyllodes*	*molothrus*	6	3	3	Amparo	SP	Atlant. For.	30.jan.1943	-22.7	-46.75	2	Molothrus-specific	Museum
MZUSP 28879	Proctophyllodidae	*Amerodectes*	*molothrus*	6	3	3	Amparo	SP	Atlant. For.	30.jan.1943	-22.7	-46.75	2	Molothrus-specific	Museum
MZUSP 29122	Proctophyllodidae	*Proctophyllodes*	*molothrus*	6	3	3	Cajurú	SP	Atlant. For.	11.may.1943	-21.26	-47.3	2	Molothrus-specific	Museum
MZUSP 29122	Proctophyllodidae	*Amerodectes*	*molothrus*	1	1	0	Cajurú	SP	Atlant. For.	11.may.1943	-21.26	-47.3	1	Molothrus-specific	Museum
MZUSP 29239	Proctophyllodidae	*Proctophyllodes*	*molothrus*	5	3	2	Serra da Bocaína	RJ	Atlant. For.	31.aug.1941	-22.04	-44.66	2	Molothrus-specific	Museum
MZUSP 29239	Proctophyllodidae	*Amerodectes*	*molothrus*	2	1	1	Serra da Bocaína	RJ	Atlant. For.	31.aug.1941	-22.04	-44.66	1	Molothrus-specific	Museum
MZUSP 29239	Xolalgidae	*Xolalgoides*	*sp. 1*	1	1	0	Serra da Bocaína	RJ	Atlant. For.	31.aug.1941	-22.04	-44.66	1	Molothrus-specific	Museum
MZUSP 29239	Psoroptoididae	*Mesalgoides*	*sp. 1*	5	2	3	Serra da Bocaína	RJ	Atlant. For.	31.aug.1941	-22.04	-44.66	2	Molothrus-specific	Museum
MZUSP 29239	Epidermoptidae	*Metamicrolichus*	*cf. phasianus*	1	1	0	Serra da Bocaína	RJ	Atlant. For.	31.aug.1941	-22.04	-44.66	1	Multi-host Parasite	Museum
MZUSP 30894	Proctophyllodidae	*Proctophyllodes*	*molothrus*	1	0	1	Cuiabá	MT	Cerrado	23.may.1944	-15.59	-56.09	1	Molothrus-specific	Museum
MZUSP 30894	Xolalgidae	*Xolalgoides*	*sp. 2*	1	1	0	Cuiabá	MT	Cerrado	23.may.1944	-15.59	-56.09	1	Molothrus-alien	Museum
MZUSP 30894	Psoroptoididae	*Mesalgoides*	*sp. 1*	5	1	4	Cuiabá	MT	Cerrado	23.may.1944	-15.59	-56.09	1	Molothrus-specific	Museum
MZUSP 3126	Proctophyllodidae	*Proctophyllodes*	*molothrus*	1	1	0	Ilhabela	SP	Atlant. For.	08.oct.1896	-23.81	-45.37	1	Molothrus-specific	Museum
MZUSP 3126	Proctophyllodidae	*Proctophyllodes*	cf. *thraupis*	1	0	1	Ilhabela	SP	Atlant. For.	08.oct.1896	-23.81	-45.37	1	Molothrus-alien	Museum
MZUSP 3126	Proctophyllodidae	*Amerodectes*	*bilineatus*	5	4	1	Ilhabela	SP	Atlant. For.	08.oct.1896	-23.81	-45.37	1	Molothrus-alien	Museum
MZUSP 3126	Proctophyllodidae	*Amerodectes*	*molothrus*	6	3	3	Ilhabela	SP	Atlant. For.	08.oct.1896	-23.81	-45.37	2	Molothrus-specific	Museum
MZUSP 3126	Psoroptoididae	*Mesalgoides*	*sp. 1*	3	1	2	Ilhabela	SP	Atlant. For.	08.oct.1896	-23.81	-45.37	1	Molothrus-specific	Museum
MZUSP 3126	Psoroptoididae	*Mesalgoides*	*sp. 2*	1	1	0	Ilhabela	SP	Atlant. For.	08.oct.1896	-23.81	-45.37	1	Molothrus-alien	Museum
MZUSP 31927	Proctophyllodidae	*Proctophyllodes*	*molothrus*	4	2	2	R. Paranapanema	SP	Atlant. For.	17.nov.1946	-22.66	-53.08	2	Molothrus-specific	Museum
MZUSP 31927	Proctophyllodidae	*Amerodectes*	*molothrus*	4	2	2	P. Paranapanema	SP	Atlant. For.	17.nov.1946	-21.95	-51.41	2	Molothrus-specific	Museum
MZUSP 31927	Psoroptoididae	*Mesalgoides*	*sp. 1*	5	1	4	R. Paranapanema	SP	Atlant. For.	17.nov.1946	-22.66	-53.08	1	Molothrus-specific	Museum
MZUSP 31927	Dermationidae	Dermationidae		2	0	2	R. Paranapanema	SP	Atlant. For.	17.nov.1946	-22.66	-53.08	1	Multi-host Parasite	Museum
MZUSP 31927	Trouessartiidae	*Trouessartia*	*sp. 6*	2	0	2	R. Paranapanema	SP	Atlant. For.	17.nov.1946	-22.66	-53.08	1	Molothrus-specific	Museum
MZUSP 35314	Proctophyllodidae	*Amerodectes*	*molothrus*	4	2	2	São Domingos	MT	Amazonia	21.sep.1949	-15.29	-59.06	2	Molothrus-specific	Museum
MZUSP 35314	Xolalgidae	*Xolalgoides*	*sp. 1*	1	0	1	São Domingos	MT	Amazonia	21.sep.1949	-15.29	-59.06	1	Molothrus-specific	Museum
MZUSP 35314	Psoroptoididae	*Mesalgoides*	*sp. 1*	1	0	1	São Domingos	MT	Amazonia	21.sep.1949	-15.29	-59.06	1	Molothrus-specific	Museum
MZUSP 35314	Trouessartiidae	*Trouessartia*	*sp. 6*	1	1	0	São Domingos	MT	Amazonia	21.sep.1949	-15.29	-59.06	1	Molothrus-specific	Museum
MZUSP 37692	Proctophyllodidae	*Proctophyllodes*	*molothrus*	6	3	3	Quebrangulo	AL	Atlant. For.	10.nov.1951	-9.31	-36.47	2	Molothrus-specific	Museum

MZUSP 37692	Proctophyllodidae	*Amerodectes*	*molothrus*	4	2	2	Quebrangulo	AL	Atlant. For.	10.nov.1951	-9.31	-36.47	2	Molothrus-specific	Museum
MZUSP 37692	Xolalgidae	*Xolalgoides*	*sp. 1*	1	0	1	Quebrangulo	AL	Atlant. For.	10.nov.1951	-9.31	-36.47	1	Molothrus-specific	Museum
MZUSP 37692	Psoroptoididae	*Mesalgoides*	*sp. 1*	5	3	2	Quebrangulo	AL	Atlant. For.	10.nov.1951	-9.31	-36.47	2	Molothrus-specific	Museum
MZUSP 39270	Proctophyllodidae	*Proctophyllodes*	*molothrus*	4	3	1	Usina Sinimbú	AL	Atlant. For.	22.feb.1957	-9.88	-36.15	2	Molothrus-specific	Museum
MZUSP 39270	Proctophyllodidae	*Amerodectes*	*molothrus*	4	2	2	Usina Sinimbú	AL	Atlant. For.	22.feb.1957	-9.88	-36.15	2	Molothrus-specific	Museum
MZUSP 39270	Psoroptoididae	*Mesalgoides*	*sp. 1*	4	2	2	Usina Sinimbú	AL	Atlant. For.	22.feb.1957	-9.88	-36.15	2	Molothrus-specific	Museum
MZUSP 39270	Trouessartiidae	*Trouessartia*	*sp. 6*	3	3	3	Usina Sinimbú	AL	Atlant. For.	22.feb.1957	-9.88	-36.15	2	Molothrus-specific	Museum
MZUSP 40479	Proctophyllodidae	*Proctophyllodes*	*molothrus*	5	3	2	Coremas	PB	Caatinga	19.jun.1957	-7.00	-37.93	2	Molothrus-specific	Museum
MZUSP 40479	Proctophyllodidae	*Amerodectes*	*molothrus*	4	2	2	Coremas	PB	Caatinga	19.jun.1957	-7.00	-37.93	2	Molothrus-specific	Museum
MZUSP 40480	Proctophyllodidae	*Amerodectes*	*molothrus*	1	1	0	Coremas	PB	Caatinga	13.jun.1957	-7.00	-37.93	1	Molothrus-specific	Museum
MZUSP 48919	Proctophyllodidae	*Proctophyllodes*	*molothrus*	4	3	1	São Paulo	SP	Atlant. For.	18.sep.1962	-23.58	-46.61	1	Molothrus-specific	Museum
MZUSP 48919	Proctophyllodidae	*Amerodectes*	*molothrus*	1	1	0	São Paulo	SP	Atlant. For.	18.sep.1962	-23.58	-46.61	1	Molothrus-specific	Museum
MZUSP 48919	Epidermoptidae	*Microlichus*	*cf. americanus*	1	0	1	São Paulo	SP	Atlant. For.	18.sep.1962	-23.58	-46.61	1	Multi-host Parasite	Museum
MZUSP 4923	Proctophyllodidae	*Proctophyllodes*	*molothrus*	6	3	3	Itapira	SP	Atlant. For.	sept.1904	-22.25	-47.82	2	Molothrus-specific	Museum
MZUSP 4923	Proctophyllodidae	*Amerodectes*	*molothrus*	6	3	3	Itapira	SP	Atlant. For.	sept.1904	-22.43	-46.82	2	Molothrus-specific	Museum
MZUSP 4925	Proctophyllodidae	*Proctophyllodes*	*molothrus*	2	1	1	Itirapina	SP	Cerrado	sept.1904	-22.25	-47.82	1	Molothrus-specific	Museum
MZUSP 4925	Xolalgidae	*Xolalgoides*	*sp. 1*	4	3	1	Itirapina	SP	Cerrado	sept.1904	-22.25	-47.82	1	Molothrus-specific	Museum
MZUSP 5302	Proctophyllodidae	*Proctophyllodes*	*molothrus*	4	3	1	Mariana	MG	Atlant. For.	1905	-20.37	-43.41	1	Molothrus-specific	Museum
MZUSP 5302	Proctophyllodidae	*Amerodectes*	*molothrus*	4	2	2	Mariana	MG	Atlant. For.	1905	-20.37	-43.41	2	Molothrus-specific	Museum
MZUSP 5302	Xolalgidae	*Xolalgoides*	*sp. 1*	1	1	0	Mariana	MG	Atlant. For.	1905	-20.37	-43.41	1	Molothrus-specific	Museum
MZUSP 5302	Trouessartiidae	*Trouessartia*	*sp. 6*	1	1	0	Mariana	MG	Atlant. For.	1905	-20.37	-43.41	1	Molothrus-specific	Museum
MZUSP 53031	Proctophyllodidae	*Proctophyllodes*	*molothrus*	3	2	1	Araguatins	TO	Cerrado	24.sep.1963	-5.65	-48.11	1	Molothrus-specific	Museum
MZUSP 53031	Proctophyllodidae	*Amerodectes*	*molothrus*	5	2	3	Araguatins	TO	Cerrado	24.sep.1963	-5.65	-48.11	2	Molothrus-specific	Museum
MZUSP 53031	Xolalgidae	*Xolalgoides*	*sp. 1*	6	3	3	Araguatins	TO	Cerrado	24.sep.1963	-5.65	-48.11	2	Molothrus-specific	Museum
MZUSP 53031	Psoroptoididae	*Mesalgoides*	*sp. 1*	3	1	2	Araguatins	TO	Cerrado	24.sep.1963	-5.65	-48.11	2	Molothrus-specific	Museum
MZUSP 53031	Dermoglyphidae	*Dermoglyphus*	*cf. passerinus*	1	0	1	Araguatins	TO	Cerrado	24.sep.1963	-5.65	-48.11	1	Multi-host Parasite	Museum
MZUSP 53031	Trouessartiidae	*Trouessartia*	*sp. 6*	6	3	3	Araguatins	TO	Cerrado	24.sep.1963	-5.65	-48.11	2	Molothrus-specific	Museum
MZUSP 53032	Proctophyllodidae	*Proctophyllodes*	*molothrus*	6	3	3	Araguatins	TO	Cerrado	06.oct.1963	-5.65	-48.11	2	Molothrus-specific	Museum
MZUSP 53032	Proctophyllodidae	*Amerodectes*	*molothrus*	4	3	1	Araguatins	TO	Cerrado	06.oct.1963	-5.65	-48.11	1	Molothrus-specific	Museum
MZUSP 53032	Xolalgidae	*Xolalgoides*	*sp. 1*	3	0	3	Araguatins	TO	Cerrado	06.oct.1963	-5.65	-48.11	1	Molothrus-specific	Museum
MZUSP 53032	Trouessartiidae	*Trouessartia*	*sp. 6*	2	1	1	Araguatins	TO	Cerrado	06.oct.1963	-5.65	-48.11	1	Molothrus-specific	Museum
MZUSP 53032	Trouessartiidae	*Trouessartia*	*capensis*	1	1	0	Araguatins	TO	Cerrado	06.oct.1963	-5.65	-48.11	1	Molothrus-alien	Museum
MZUSP 53034	Proctophyllodidae	*Proctophyllodes*	*molothrus*	1	0	1	Goiânia	GO	Cerrado	05.sep.1963	-16.66	-49.25	1	Molothrus-specific	Museum
MZUSP 53964	Proctophyllodidae	*Proctophyllodes*	*molothrus*	6	4	2	Avaré	SP	Atlant. For.	09.nov.1963	-23.08	-48.91	2	Molothrus-specific	Museum
MZUSP 63530	Proctophyllodidae	*Amerodectes*	*molothrus*	3	1	2	Agrestina	PE	Caatinga	12.jun.1971	-8.45	-35.93	2	Molothrus-specific	Museum
MZUSP 63530	Psoroptoididae	*Mesalgoides*	*sp. 3*	3	1	2	Agrestina	PE	Caatinga	12.jun.1971	-8.45	-35.93	1	Molothrus-alien	Museum
MZUSP 63530	Trouessartiidae	*Trouessartia*	*sp. 7*	4	3	1	Agrestina	PE	Caatinga	12.jun.1971	-8.45	-35.93	1	Molothrus-alien	Museum
MZUSP 63530	Trouessartiidae	*Trouessartia*	*sp. 6*	2	1	1	Agrestina	PE	Caatinga	12.jun.1971	-8.45	-35.93	1	Molothrus-specific	Museum
MZUSP 69174	Proctophyllodidae	*Proctophyllodes*	*molothrus6*	1	0	1	Rio Branco	AC	Amazonia	30.may.1968	-9.99	-67.81	1	Molothrus-alien	Museum
MZUSP 69174	Proctophyllodidae	*Amerodectes*	*molothrus*	4	2	2	Rio Branco	AC	Amazonia	30.may.1968	-9.99	-67.81	2	Molothrus-specific	Museum
MZUSP 69174	Xolalgidae	*Xolalgoides*	*sp. 1*	2	2	0	Rio Branco	AC	Amazonia	30.may.1968	-9.99	-67.81	1	Molothrus-specific	Museum
MZUSP 69174	Trouessartiidae	*Trouessartia*	*sp. 6*	1	1	0	Rio Branco	AC	Amazonia	30.may.1968	-9.99	-67.81	1	Molothrus-specific	Museum
MZUSP 69174	Trouessartiidae	*Trouessartia*	*sp. 7*	3	1	2	Rio Branco	AC	Amazonia	30.may.1968	-9.99	-67.81	1	Molothrus-alien	Museum
MZUSP 69175	Proctophyllodidae	*Amerodectes*	*molothrus*	4	3	1	Rio Branco	AC	Amazonia	30.may.1968	-9.99	-67.81	1	Molothrus-specific	Museum

MZUSP 69175	Dermoglyphidae	*Dermoglyphus*	*cf. passerinus*	1	0	1	Rio Branco	AC	Amazonia	30.may.1968	-9.99	-67.81	1	Multi-host Parasite	Museum
MZUSP 7171	Proctophyllodidae	*Amerodectes*	*molothrus*	4	2	2	Humb. de Campos	MA	Cerrado	27.apr.1907	-2.59	-43.46	2	Molothrus-specific	Museum
MZUSP 7171	Xolalgidae	*Xolalgoides*	*sp. 1*	4	2	2	Humb. de Campos	MA	Cerrado	27.apr.1907	-2.59	-43.46	2	Molothrus-specific	Museum
MZUSP 74542	Proctophyllodidae	*Proctophyllodes*	*molothrus*	4	2	2	Três Lagoas	MS	Cerrado	21.oct.1964	-20.75	-51.67	2	Molothrus-specific	Museum
MZUSP 74542	Proctophyllodidae	*Amerodectes*	*molothrus*	2	1	1	Três Lagoas	MS	Cerrado	21.oct.1964	-20.75	-51.67	1	Molothrus-specific	Museum
MZUSP 74542	Psoroptoididae	*Mesalgoides*	*sp. 2*	2	1	1	Três Lagoas	MS	Cerrado	21.oct.1964	-20.75	-51.67	1	Molothrus-alien	Museum
MZUSP 74543	Proctophyllodidae	*Proctophyllodes*	*molothrus*	5	3	2	Três Lagoas	MS	Cerrado	21.oct.1964	-20.75	-51.67	2	Molothrus-specific	Museum
MZUSP 77611	Proctophyllodidae	*Proctophyllodes*	*molothrus6*	6	3	3	Tailândia	PA	Amazonia	january 2004	-2.94	-48.95	2	Molothrus-alien	Museum
MZUSP 77611	Proctophyllodidae	*Proctophyllodes*	*molothrus*	6	3	3	Tailândia	PA	Amazonia	january 2004	-2.94	-48.95	2	Molothrus-specific	Museum
MZUSP 77611	Proctophyllodidae	*Amerodectes*	*molothrus*	3	2	1	Tailândia	PA	Amazonia	january.2004	-2.94	-48.95	1	Molothrus-specific	Museum
MZUSP 77611	Xolalgidae	*Xolalgoides*	*sp. 1*	2	0	2	Tailândia	PA	Amazonia	january.2004	-2.94	-48.95	1	Molothrus-specific	Museum
MZUSP 77611	Dermoglyphidae	*Dermoglyphus*	*cf. passerinus*	1	0	1	Tailândia	PA	Amazonia	January.2004	-2.94	-48.95	1	Multi-host Parasite	Museum
MZUSP 77907	Proctophyllodidae	*Proctophyllodes*	*molothrus*	5	3	2	Caracol	PI	Caatinga	16.jan.2002	-9.27	-43.33	2	Molothrus-specific	Museum
MZUSP 77907	Analgidae	*Analges*	*ticotico*	6	3het 1hom	2	Caracol	PI	Caatinga	16.jan.2002	-9.27	-43.33	2	Molothrus-alien	Museum
MZUSP 77907	Xolalgidae	*Xolalgoides*	*sp. 1*	1	0	1	Caracol	PI	Caatinga	16.jan.2002	-9.27	-43.33	1	Molothrus-specific	Museum
MZUSP 77907	Dermationidae	Dermationidae		1	0	1	Caracol	PI	Caatinga	16.jan.2002	-9.27	-43.33	1	Multi-host Parasite	Museum
MZUSP 77907	Trouessartiidae	*Trouessartia*	*sp. 7*	3	1	2	Caracol	PI	Caatinga	16.jan.2002	-9.27	-43.33	1	Molothrus-alien	Museum
MZUSP 78517	Proctophyllodidae	*Proctophyllodes*	*molothrus*	1	1	0	Fordlândia	PA	Amazonia	04.oct.1970	-3.6	-55.33	1	Molothrus-specific	Museum
MZUSP 78517	Proctophyllodidae	*Amerodectes*	*molothrus*	5	3	2	Fordlândia	PA	Amazonia	04.oct.1970	-3.6	-55.33	2	Molothrus-specific	Museum
MZUSP 78517	Xolalgidae	*Xolalgoides*	*sp. 1*	3	3	0	Fordlândia	PA	Amazonia	04.oct.1970	-3.6	-55.33	1	Molothrus-specific	Museum
MZUSP 78517	Epidermoptidae	*Microlichus*	*cf. americanus*	1	0	1	Fordlândia	PA	Amazonia	04.oct.1970	-3.6	-55.33	1	Multi-host Parasite	Museum
MZUSP 78517	Trouessartiidae	*Trouessartia*	*sp. 6*	6	3	3	Fordlândia	PA	Amazonia	04.oct.1970	-3.6	-55.33	2	Molothrus-specific	Museum
MZUSP 8503	Proctophyllodidae	*Proctophyllodes*	*carmenmirandae*	2	1	1	São Paulo	SP	Atlant. For.	oct.1913	-23.58	-46.61	1	Molothrus-alien	Museum
MZUSP 8511	Proctophyllodidae	*Proctophyllodes*	*molothrus*	5	3	2	Barra	BA	Cerrado	sept.1913	-11.08	-43.14	2	Molothrus-specific	Museum
MZUSP 8511	Proctophyllodidae	*Amerodectes*	*molothrus*	1	1	0	Barra	BA	Cerrado	sept.1913	-11.08	-43.14	1	Molothrus-specific	Museum
MZUSP 9883	Proctophyllodidae	*Proctophyllodes*	*molothrus*	6	3	3	São Paulo	SP	Atlant. For.	05.dec.1916	-23.59	-46.58	2	Molothrus-specific	Museum
MZUSP 9883	Psoroptoididae	*Mesalgoides*	*sp. 1*	1	0	1	São Paulo	SP	Atlant. For.	05.dec.1916	-23.59	-46.58	1	Molothrus-specific	Museum
MZUSP 9883	Epidermoptidae	*Metamicrolichus*	*cf. phasianus*	6	2	3	São Paulo	SP	Atlant. For.	05.dec.1916	-23.59	-46.58	2	Multi-host Parasite	Museum
N.44	Analgidae	*Analges*	*sp. 1*	23	4hom 4het	13	-	RS	Pampa	14.mar.2006	-31.76	-52.33	2	Molothrus-alien	Wash
SUD (sem id)	Proctophyllodidae	*Proctophyllodes*	cf. *thraupis*	5	3	2	Campinas	SP	Atlant. For.	-	-22.9	-47.05	2	Molothrus-alien	Wash
SUD (sem id)	Analgidae	*Analges*	*sp. 6*	7	3het 3hom	2	Campinas	SP	Atlant. For.	-	-22.9	-47.05	2	Molothrus-alien	Wash
SUD (sem id)	Analgidae	*Strelkoviacarus*	*brasiliensis*	5	1	4	Campinas	SP	Atlant. For.	-	-22.9	-47.05	2	Multi-host Parasite	Wash
SUD (sem id)	Xolalgidae	*Xolalgoides*	*sp. 1*	5	3	2	Campinas	SP	Atlant. For.	-	-22.9	-47.05	2	Molothrus-specific	Wash
SUD (sem id)	Trouessartiidae	*Trouessartia*	aff. *megaplax*	6	3	3	Campinas	SP	Atlant. For.	-	-22.9	-47.05	2	Molothrus-alien	Wash
SUL-01	Proctophyllodidae	*Amerodectes*	*molothrus*	1	1	0	Rio Grande	RS	Pampa	12.sep.2017	-32.41	-52.82	2	Molothrus-specific	Field
SUL-15	Proctophyllodidae	*Proctophyllodes*	*molothrus*	8	3	5	Londrina	PR	Atlant. For.	05.oct.2017	-23.32	-51.19	2	Molothrus-specific	Field
SUL-16	Proctophyllodidae	*Proctophyllodes*	*molothrus*	8	4	4	Londrina	PR	Atlant. For.	04.oct.2017	-23.32	-51.19	2	Molothrus-specific	Field
SUL-16	Proctophyllodidae	*Amerodectes*	*molothrus*	6	3	3	Londrina	PR	Atlant. For.	04.oct.2017	-23.32	-51.19	2	Molothrus-specific	Field
SUL-16	Psoroptoididae	*Mesalgoides*	*sp. 1*	4	2	2	Londrina	PR	Atlant. For.	04.oct.2017	-23.32	-51.19	2	Molothrus-specific	Field
SUL-17	Proctophyllodidae	*Proctophyllodes*	*molothrus*	2	0	2	Londrina	PR	Atlant. For.	04.oct.2017	-23.32	-51.19	2	Molothrus-specific	Field
SUL-18	Proctophyllodidae	*Proctophyllodes*	*molothrus*	4	2	2	Londrina	PR	Atlant. For.	04.oct.2017	-23.32	-51.19	2	Molothrus-specific	Field
SUL-18	Proctophyllodidae	*Amerodectes*	*molothrus*	6	3	3	Londrina	PR	Atlant. For.	04.oct.2017	-23.32	-51.19	2	Molothrus-specific	Field
SP-23 [G133416]	Proctophyllodidae	*Proctophyllodes*	*molothrus*	4	3	1	Rio Claro	SP	Atlant. For.	31.aug.2017	-22.41	-47.56	2	Molothrus-specific	Field
SP-25 [F64540]	Proctophyllodidae	*Amerodectes*	*molothrus*	2	1	1	Rio Claro	SP	Atlant. For.	31.aug.2017	-22.41	-47.56	2	Molothrus-specific	Field

SP-26 [G133415]	Proctophyllodidae	*Proctophyllodes*	*molothrus*	6	3	3	Rio Claro	SP	Atlant. For.	31.aug.2017	-22.41	-47.56	2	Molothrus-specific	Field
SP-26 [G133415]	Proctophyllodidae	*Amerodectes*	*molothrus*	6	3	3	Rio Claro	SP	Atlant. For.	31.aug.2017	-22.41	-47.56	2	Molothrus-specific	Field
SP-28 [G133425]	Proctophyllodidae	*Amerodectes*	*molothrus*	1	0	1	Rio Claro	SP	Atlant. For.	31.aug.2017	-22.41	-47.56	2	Molothrus-specific	Field
SP-29 [G133421]	Proctophyllodidae	*Proctophyllodes*	*molothrus*	2	0	2	Rio Claro	SP	Atlant. For.	31.aug.2017	-22.41	-47.56	2	Molothrus-specific	Field
SP-29 [G133421]	Proctophyllodidae	*Amerodectes*	*molothrus*	2	0	2	Rio Claro	SP	Atlant. For.	31.aug.2017	-22.41	-47.56	2	Molothrus-specific	Field
SP-32 [G133434]	Proctophyllodidae	*Proctophyllodes*	*molothrus*	5	3	2	Rio Claro	SP	Atlant. For.	02.feb.2018	-22.41	-47.56	2	Molothrus-specific	Field
SP-36	Proctophyllodidae	*Proctophyllodes*	*molothrus*	10	5	5	Rio Claro	SP	Atlant. For.	26.sep.2018	-22.41	-47.56	2	Molothrus-specific	Field
SP-36	Psoroptoididae	*Mesalgoides*	*sp. 1*	1	0	1	Rio Claro	SP	Atlant. For.	26.sep.2018	-22.41	-47.56	2	Molothrus-specific	Field
SP-36	Xolalgidae	*Xolalgoides*	*sp. 1*	6	3	3	Rio Claro	SP	Atlant. For.	26.sep.2018	-22.41	-47.56	2	Molothrus-specific	Field
SP-40 [G133442]	Proctophyllodidae	*Proctophyllodes*	*molothrus*	6	3	3	Rio Claro	SP	Atlant. For.	04.oct.2018	-22.41	-47.56	2	Molothrus-specific	Field
SP-41 [G133439]	Trouessartiidae	*Trouessartia*	cf. *sicaliae*	2	2	0	Rio Claro	SP	Atlant. For.	04.oct.2018	-22.41	-47.56	2	Molothrus-alien	Field
SP-41 [G133439]	Psoroptoididae	*Mesalgoides*	*sp. 1*	1	1	0	Rio Claro	SP	Atlant. For.	04.oct.2018	-22.41	-47.56	2	Molothrus-specific	Field
SP-41 [G133439]	Proctophyllodidae	*Proctophyllodes*	*molothrus*	4	2	2	Rio Claro	SP	Atlant. For.	04.oct.2018	-22.41	-47.56	2	Molothrus-specific	Field
SP-42 [G133441]	Proctophyllodidae	*Amerodectes*	*molothrus*	6	3	3	Rio Claro	SP	Atlant. For.	04.oct.2018	-22.41	-47.56	2	Molothrus-specific	Field
SP-42 [G133441]	Proctophyllodidae	*Proctophyllodes*	*molothrus*	6	3	3	Rio Claro	SP	Atlant. For.	04.oct.2018	-22.41	-47.56	2	Molothrus-specific	Field
SP-45 [G133450]	Proctophyllodidae	*Proctophyllodes*	*molothrus*	1	0	1	Rio Claro	SP	Atlant. For.	13.dec.2018	-22.41	-47.56	2	Molothrus-specific	Field
SP-45 [G133450]	Proctophyllodidae	*Amerodectes*	*molothrus*	10	5	5	Rio Claro	SP	Atlant. For.	13.dec.2018	-22.41	-47.56	2	Molothrus-specific	Field
UNB-04	Proctophyllodidae	*Proctophyllodes*	*molothrus*	6	3	3	Brasília	DF	Cerrado	06.nov.2018	-15.76	-47.86	2	Molothrus-specific	Field
UNB-04	Proctophyllodidae	*Amerodectes*	*molothrus*	6	3	3	Brasília	DF	Cerrado	06.nov.2018	-15.76	-47.86	2	Molothrus-specific	Field
UNB-05	Proctophyllodidae	*Proctophyllodes*	*molothrus*	6	3	3	Brasília	DF	Cerrado	07.nov.2018	-15.76	-47.86	2	Molothrus-specific	Field

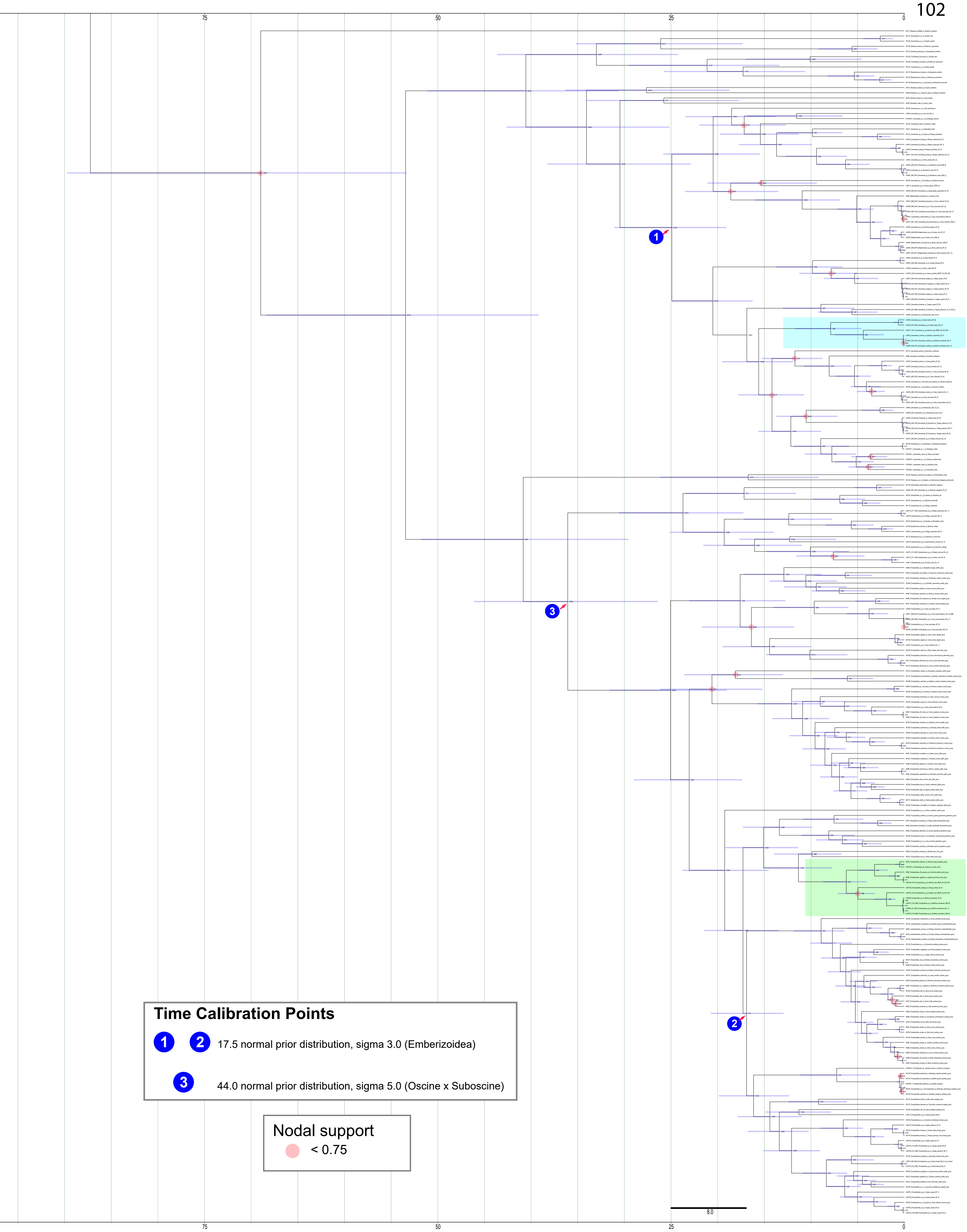


Supplementary File 3. Boxplot showing the difference between the three host-specificity categories based on their number of recorded biomes. The *Molothrus-specific* mite group was statistically different from other groups, *Molothrus-alien* and *Multi-Host* mite ($p < 0.05$, Wilcoxon paired-rank test).

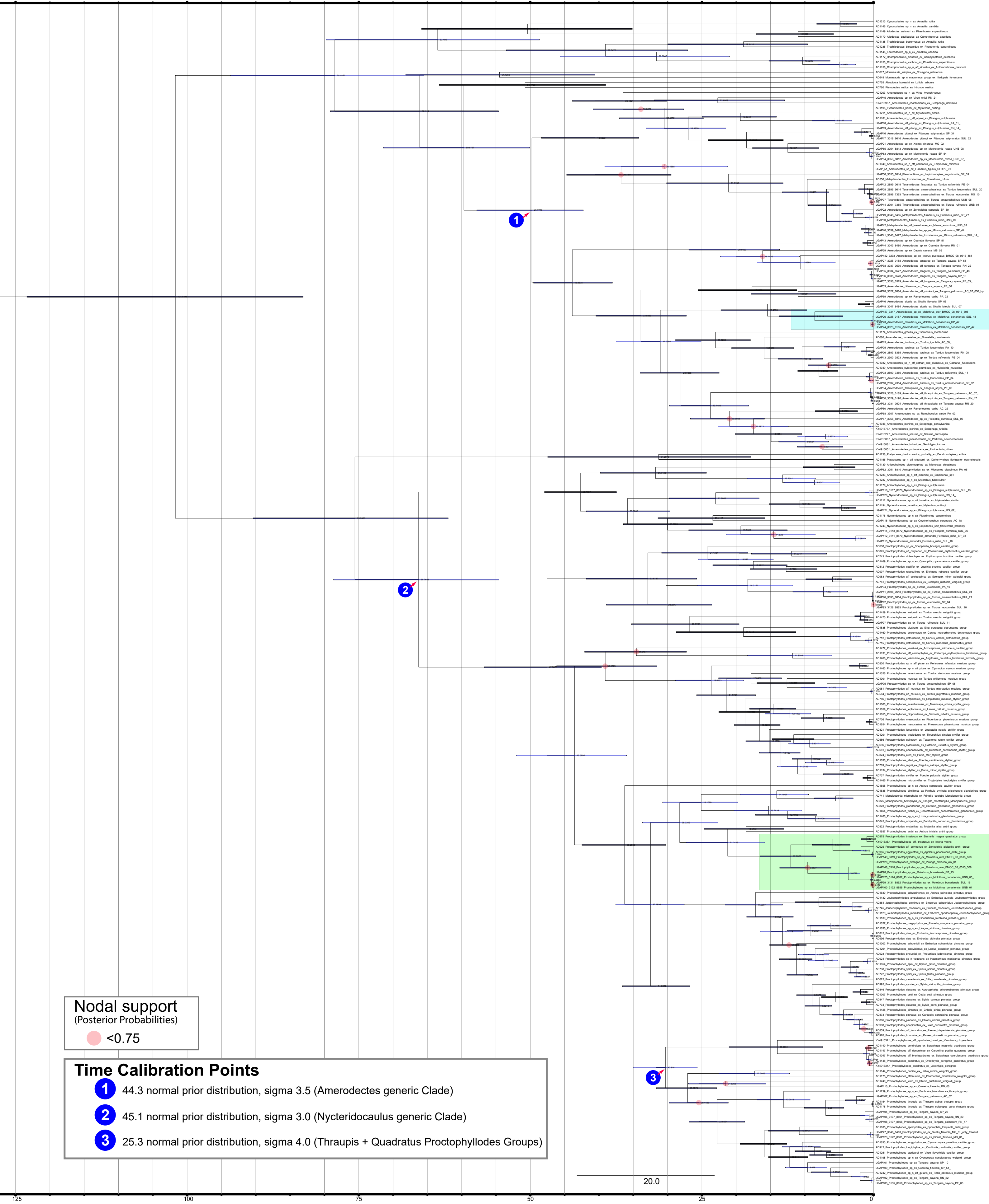
Supplementary File 4. Collection data and likely data for foster parents (*Molothrus-alien*) and *Strelkoviacarus brasiliensis* (*Multi-host*) categories.

Bird Code	Feather Mites ID	Possible host	Presence of cowbird specific mites	Congener	Putative Cowbird Host ID	Bird count
(4) N. 42	Proctophyllodes sp. 4	probably same species of P. sp. 2 from Mena et al. 2020	yes	no	1	1
SP-47 [F64117]	Proctophyllodes cf. thraupis	Tangara host	no	no	1	1
3 - N.43	Analges sp. 1	?	no	no		1
88-1230-130	Trouessartia capensis	Zonotrichia capensis	yes	yes	1	1
Col. Yoshika 1	Trouessartia capensis	Zonotrichia capensis	yes	no	1	1
FM 58299	Proctophyllodes sp. 5	probably Icteridae - same species of P. sp. 1 from Mena et al. 2020	yes	yes	1	1
FM 58442	Proctophyllodes sp. 5	probably Icteridae - same species of P. sp. 1 from Mena et al. 2020	no	no	1	1
Mb São Carlos	Proctophyllodes cf. thraupis	Tangara host	yes	no	1	1
	Analges sp. 6	Tangara host		no		
	Trouessartia aff. megaplax	Tangara host		no		
MB-1	Proctophyllodes sp. 4	probably same species of P. sp. 2 from Mena et al. 2020	yes	no	1	1
MB-4 (N.21)	Proctophyllodes sp. 4	probably same species of P. sp. 2 from Mena et al. 2020	yes	no	1	1
MCN 1520	Proctophyllodes sp. 5	probably Icteridae - same species of P. sp. 1 from Mena et al. 2020	yes	no	1	1
	Xolalgoides sp. 2	?		no		
MCN 1607	Proctophyllodes sp. 5	probably same species of P. sp. 1 from Mena	yes	yes	1	1
	Trouessartia capensis	Zonotrichia capensis		no		
MCN 1608	Strelkoviacarus brasiliensis	Zonotrichia capensis	no	no	1	1
	Trouessartia capensis	Zonotrichia capensis		no		
MCN 1609	Proctophyllodes aff. atyeoi	Probably Icteridae	yes	no	1	1
MCN 1610	Proctophyllodes sp. 5	probably Icteridae same species of P. sp. 1 from Mena et al. 2020	yes	yes	1	1
	Mesalgoides sp. 2	Zonotrichia capensis		no		
MCN 1611	Strelkoviacarus brasiliensis	Zonotrichia capensis	yes	no	1	1
MCN 187	Mesalgoides sp. 2	Zonotrichia capensis	yes	no	1	1
	Trouessartia capensis	Zonotrichia capensis		no		
MCN 2005	Proctophyllodes sp. 4	probably same species of P. sp. 2 from Mena et al. 2020	yes	yes	1	1
MCN 2007	Mesalgoides sp. 3	?	yes	no	1	1
	Trouessartia capensis	Zonotrichia capensis		no		
MCN 2044	Trouessartia capensis	Zonotrichia capensis	yes	no	1	1
MCN 2926	Mesalgoides sp. 2	Zonotrichia capensis	no	no	1	1
MCN 3038	Proctophyllodes sp. 7	Zonotrichia capensis	yes	yes	1	1
MCN 3341	Mesalgoides sp. 2	Zonotrichia capensis	yes	yes	1	1
MCP 157	Proctophyllodes sp. 5	probably Icteridae - same species of P. sp. 1 from Mena et al. 2020	yes	yes	1	1
	Xolalgoides sp. 2	?		no		
MCP 2926	Proctophyllodes sp. 7	Zonotrichia capensis	yes	yes	1	1
MCP 938	Proctophyllodes sp. 7	Zonotrichia capensis	no	no	1	1
	Trouessartia capensis	Zonotrichia capensis		no		
	Analges sp. 5	Zonotrichia capensis		no		
MHNCI 2635	Mesalgoides sp. 2	Zonotrichia capensis	yes	no	1	1
MHNCI 3865	Mesalgoides sp. 2	Zonotrichia capensis	yes	no	1	1
MHNCI 5969	Xolalgoides sp. 2	?	no	no		1
MPEG 20701	Proctophyllodes aff. atyeoi	Probably an Icteridae	yes	yes	1	1
MPEG 21667	Proctophyllodes sp. 7	Zonotrichia capensis	yes	no	1	1
MPEG 21877	Mesalgoides sp. 2	Zonotrichia capensis	yes	no	1	1
MPEG 52288	Proctophyllodes aff. atyeoi	Probably Icteridae	yes	no	1	1

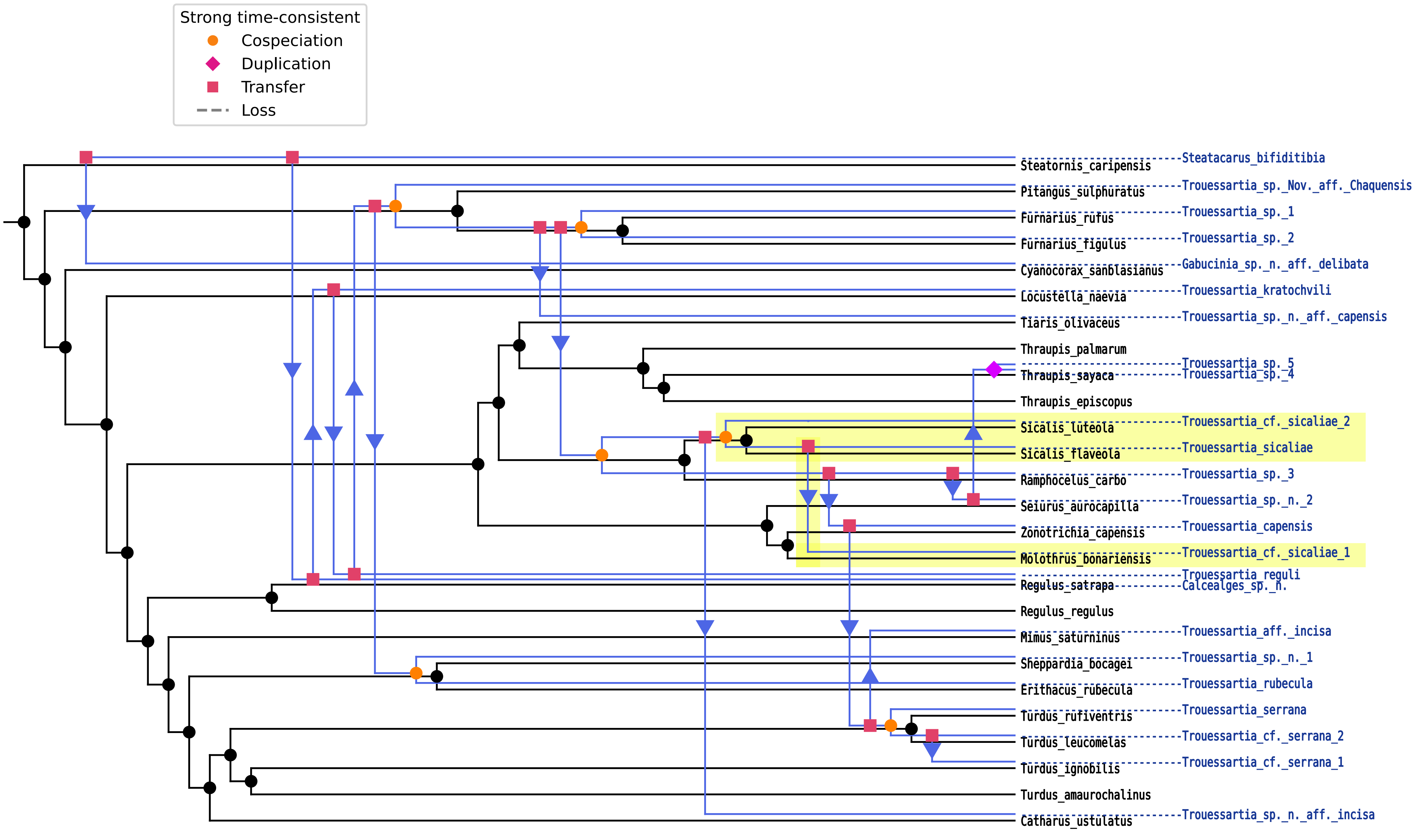
MPEG 63849	Proctophyllodes aff. atyeoi	Probably Icteridae	yes	no	1	1
	Mesalgoides sp. 2	Zonotrichia capensis		yes		
MPEG 65662	Platyacarus sp.	?	yes	no		1
MPEG 78128	Platyacarus sp.	?	yes	no		1
MZUSP 14275	Mesalgoides sp. 3	?	yes	no		1
MZUSP 15136	Mesalgoides sp. 2	Zonotrichia capensis	yes	no	1	1
MZUSP 17132	Mesalgoides sp. 3	?	yes	yes		1
MZUSP 27252	Mesalgoides sp. 2	Zonotrichia capensis	yes	yes	1	1
	Trouessartia capensis	Zonotrichia capensis		no		
MZUSP 30894	Xolalgoides sp. 2	?	yes	no		1
MZUSP 3126	Proctophyllodes cf. thraupis	Tangara host	yes	yes	1	1
	Amerodectes bilineatus	Tangara host		no		
	Mesalgoides sp. 2	Zonotrichia capensis		no		
MZUSP 53032	Trouessartia capensis	Zonotrichia capensis	yes	yes	1	1
MZUSP 63530	Mesalgoides sp. 3	?	yes	yes	1	1
	Trouessartia sp. 7	?		no		
MZUSP 69174	Proctophyllodes sp. 16	?	yes	yes		1
	Trouessartia sp. 7	?		no		
MZUSP 74542	Mesalgoides sp. 2	Zonotrichia capensis	yes	no	1	1
MZUSP 77611	Proctophyllodes sp. 16	?	yes	yes		1
MZUSP 77907	Analges ticotico	Zonotrichia capensis	yes	no	1	1
	Trouessartia sp. 7	?		no		
MZUSP 8503	Proctophyllodes sp. 7	Zonotrichia capensis	no	no	1	1
N.44	Analges sp. 1	?	no	no		1
SUD (sem id)	Proctophyllodes cf. thraupis	Tangara host	yes	no	1	1
	Analges sp. 6	Tangara host		no		
	Strelkoviacarus brasiliensis	Zonotrichia capensis		no		
	Trouessartia aff. megaplax	Tangara host		no		
SP-41 [G133439]	Trouessartia sicaliae	Sicalis spp.	yes	no	1	1
					42	52



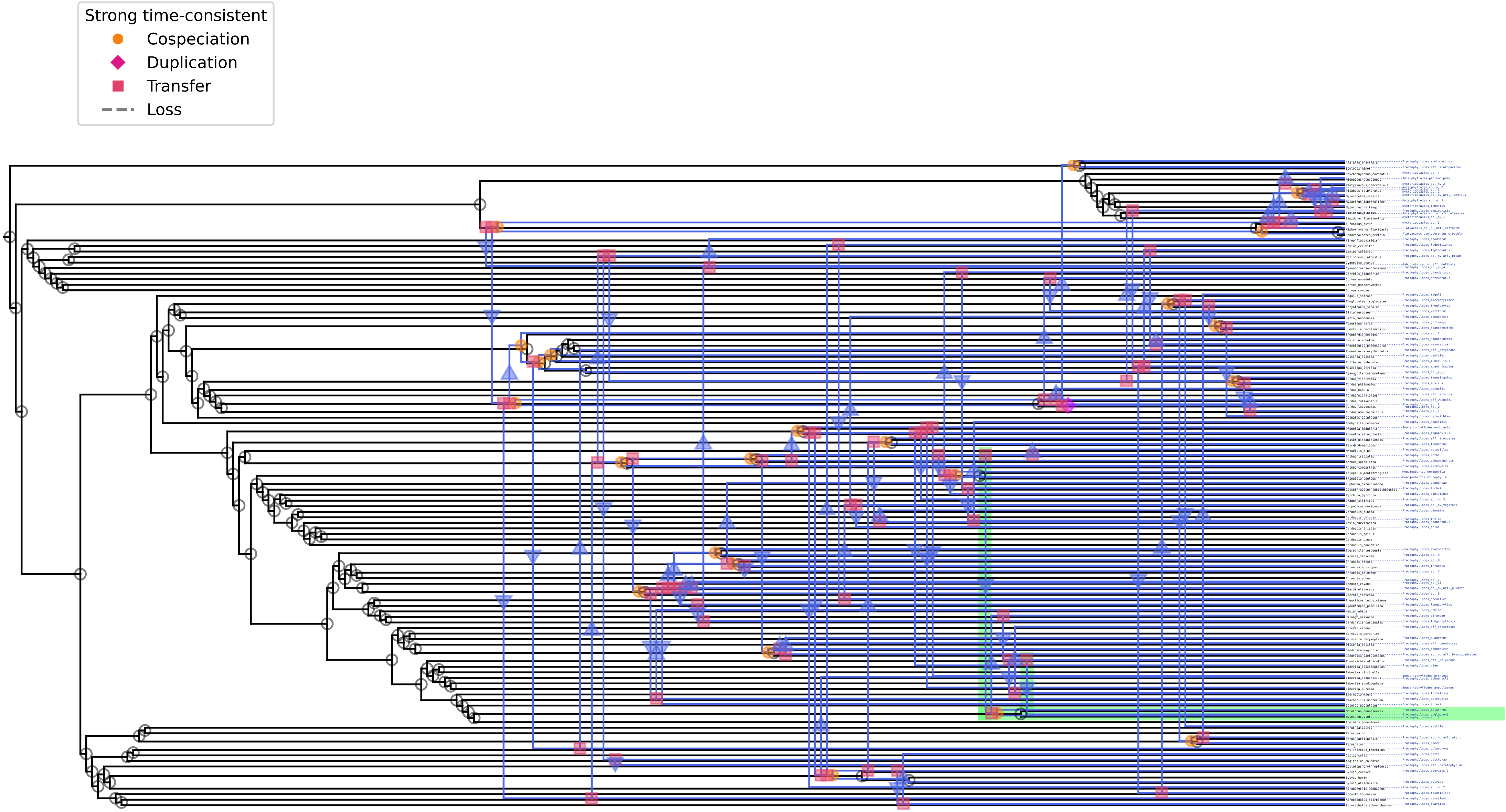
Supplementary File 5. Divergence time estimates for the mite family Proctophyllodidae shown on a maximum credibility tree inferred in BEAST v2.6.1. For node calibration (points 1, 2 and 3), host phylobiogeographic information Oliveros et al. (2019) was used. Median time estimates and their 95% highest posterior densities (bars) are given for each branch. Clades of interest are highlighted.



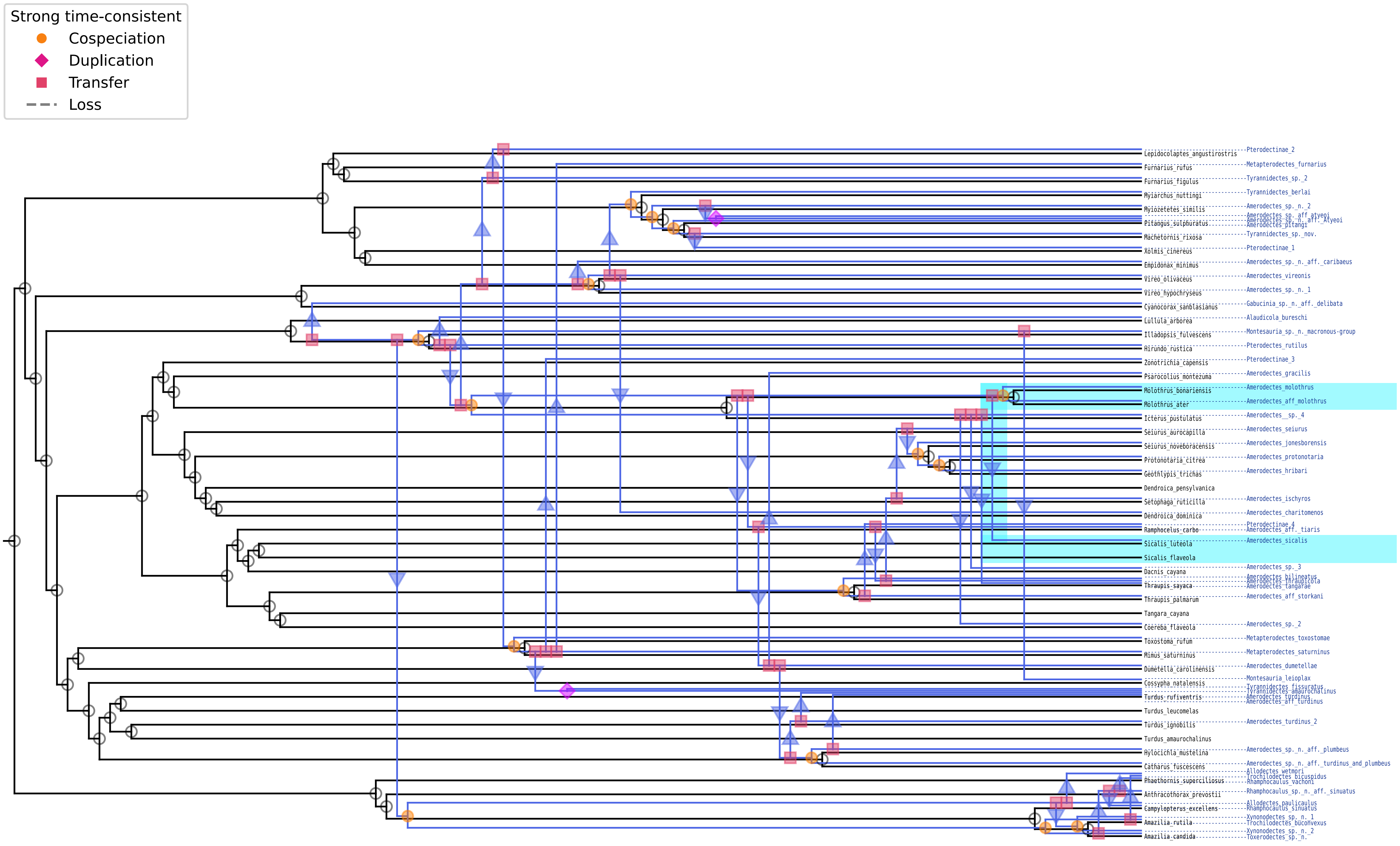
Supplementary File 6. Divergence time estimates for the mite family Proctophyllodidae shown on a maximum credibility tree inferred BEAST v2.6.1. For node calibration (points 1, 2 and 3), secondary calibration points inferred mite using mite fossil information previously (Klimov et al. 2017) (Points 1, 2 and 3). Median time estimates and their 95% highest posterior densities (bars) are given for each branch. Clades of interest are highlighted: light blue = Amerodectes; light green = Proctophyllodes.



Supplementary File 7. Maximum parsimony cophylogenetic reconciliation estimated for the mite family Trouessartiidae. Cophylogenetic events infered for *Molothrus* and *Molothrus*-related mites are highlighted. A better representation for the highlighted events in given in Fig. 2.



Supplementary File 8. Maximum parsimony cophylogenetic reconciliation estimated for the mite subfamily Proctophyllodinae. Cophylogenetic events infered for *Molothrus* and *Molothrus*-related mites are highlighted. A better representation for the highlighted events in given in Fig. 2.



Supplementary File 9. Maximum parsimony cophylogenetic reconciliation estimated for the mite subfamily Proctophyllodinae. Cophylogenetic events infered for *Molothrus* and *Molothrus*-related mites are highlighted. A better representation for the highlighted events in given in Fig. 2.

CHAPTER 2 – HOST SPECIFICITY AND GEOGRAPHIC DISTRIBUTION

CHAPTER 2

Host specificity and transmission on the geographic distribution of symbionts – a case of study with feather mites (Astigmata) from the shiny cowbird *Molothrus bonariensis* (Aves: Icteridae)

ABSTRACT

The host specificity and the transmission method are important features defining the geographic distribution and the evolutionary properties in host-symbiont systems. Symbionts with high levels of host specificity and intimate transmission properties are prone to present congruent distributions with their hosts. Feather mites fit in this category, as they are obligate symbionts of birds with high levels of host specificity and mainly transmitted vertically from parents to offspring during parental care. Therefore, systems disrupting the usual transmission route of feather mites offer unique ways to investigate the effects of different levels of host specificity and transmissions over the geographic distribution of these symbionts. Brood parasitic birds represent such peculiar systems. These hosts not only lack intraspecific vertical transmission but also challenge the host specificity by receiving mites from foster parents. By investigating the feather mites from the brood parasite shiny cowbird (*Molothrus bonariensis*) in Brazil, it was possible to recognize mites specific-to-cowbirds transmitted horizontally by conspecific contact (*Molothrus-specific*) from mites received vertically from foster parents (*Molothrus-alien*). We found a strong connection between host specificity and geographic distribution, where *Molothrus-specific* mites presented an overall even geographic distribution along with their hosts. *Molothrus-alien* was patchy distributed, likely reflecting the shiny cowbird's host usage. The specificity was responsible for the stability of a specific mite fauna along with the shiny cowbird distribution even under a constant pressure for the colonization of different mite species from foster parents. The transmission method was also important, indicating that horizontal transmissions were able to maintain evenly distributed and high specific symbionts independent from vertical transmissions. Yet, we detected a geographic structuration of feather mites on shiny cowbirds based on absence and presence of mite species related to cowbird subspecies in Brazil and between Brazilian and Chilean cowbird populations. Further studies, especially including molecular data, may reveal hidden geographic patterns among some of these widespread cowbird-specific mite species.

Keywords: biogeography, ectosymbionts, Acariformes, obligate symbionts, dispersion

INTRODUCTION

The transmission potential of obligate symbionts likely has a direct impact on their specificity degree with their hosts, i.e., symbionts with superior transmission properties have higher chances to colonize more host species (e.g., multi-host symbionts, generalist or polixenous), while symbionts with limited transmission are often associated to a single or close related host species (e.g., oligo- or monoxenous) (Harbison & Clayton 2011; Martinů et al. 2015). Other features such as the host behavior (i.e., gregarious or solitary), the host pressure (the host defenses against symbionts), and the host biogeography (the pool of potential hosts a host species interact with), aligned with the symbiont ecological fitting (the phenotypic potential of a symbiont to colonize new hosts and survive environmental adversities), also plays an important role outlining the specificity of symbionts (Agosta et al. 2010; Araujo et al. 2015; Balakrishnan & Sorenson 2007; Bush & Clayton 2006; Dick & Patterson 2007; Fecchio et al. 2019; Wells & Clark 2019). The host specificity, in turn, may reflect on the geographic distribution of symbionts, and the higher the specificity and the transmission potential, the more uniform the host-symbiont distributions tend to be (Clayton et al. 2015; Page 2003). This creates a triad connecting the level of host specificity, the geographic distribution, and the transmission potential of symbionts. Aspects of this connection, however, have been seldom explored in arthropod symbionts with limited dispersion and high host specificity (Štefka et al. 2009).

Obligate ectosymbionts of birds, such as feather mites (Acariformes: Analgoidea and Pterolichoidea) and feather lice (Phthiraptera: Amblycera and Ischnocera), are remarkable examples of symbionts displaying high levels of host specificity due to their complete ontogeny on their hosts (Clayton et al. 2015; Doña et al. 2018). However, feather mites stand out because of their restricted dispersion, dominated by vertical transmissions during the sophisticated parental care of birds (Doña et al. 2017; Mironov & Malyshev 2002). Additionally, differently from feather lice, only a few feather mite groups (e.g., skin mites) were recorded using hippoboscid flies as phoretic vehicles for transmission (Bartlow et al. 2016; Fain 1965; Jovani et al. 2001). This inherited and intimate mite acquisition in feather mites is likely one of the main reasons responsible for their high levels of host specificity, in which most mite species are found on single host species or on a set of phylogenetically similar hosts (Doña et al. 2018). Despite the high host specificity and limited transmission, multiple cases of historical host switches have been recorded in cophylogenetic studies with feather mites, suggesting a higher potential for horizontal transmission than expected due their low mobility (Blanco et al. 1997; Blanco & Frías 2001; Doña et al. 2017; Gaud 1992; Klimov et al. 2017; Matthews et al. 2018). Therefore, feather mites of birds represent exceptional host-symbiont models for the investigation of aspects and patterns related to host specificity and transmission in symbionts (Dabert 2004; Doña et al. 2018; Gaud & Atyeo 1996).

On top of that, there are bird behaviors, such as the brood parasitism, that prevent the usual conspecific vertical transmission of feather mites. Brood parasitic birds lack any contact with their conspecific parents during their nesting stage of development, and instead, a different bird species act as foster parent rearing the imposter chick as one of its own (Lowther 2019; Soler 2017; Stevens 2013). This behavior not only prevents the vertical transmission, a phenomenon also seen in bush turkeys (Proctor & Jones 2004), but also enhances the host switch pressure over brood parasitic birds to acquire symbionts from their interspecific foster parents. Additionally, differences among bird’s brood parasitic systems may also impact this “triplet system”, formed by the brood parasitic bird, the birds they parasitize, and their ectosymbionts (Vas et al. 2013). For example, indigobirds (Viduidae) present high levels of host specialization and mostly parasitize a single species of passerine from the family Estrildidae (phyllogenetically sister to Viduidae), which limits the array of symbionts it can acquire from foster parents; while cuckoos (Cuculidae) present opposite features, and parasitize phylogenetically distant hosts in comparison to other brood parasites (Cuculiformes vs. Passeriformes), which restrict the possibility of symbiont transference. However, in both cases the available data suggest minimal transmission and persistence of non-specific mites on these brood parasites (Balakrishnan & Sorenson 2006; Lindholm et al. 1998; Vas et al. 2013). On the other hand, the shiny cowbird *Molothrus bonariensis* (Gmelin, 1789) (Passeriformes: Icteridae), is one of the most generalist brood parasitic birds, being recorded successfully parasitizing at least 97 passerine species (Fiorini et al. 2019; Lowther 2019; Soler 2017). This condition is likely the main reason for its wide distribution – native from the South America Pampas, the shiny cowbird is expanding its distribution throughout the South American, the West Indies and several North American regions, mostly due to deforestation (Cavalcanti 1988; Crespo-Pérez et al. 2016; Levy 2019; Marín 2000; Post et al. 1993; Sick 1997; Sykes Jr & Post 2001). Therefore, the generalist but yet phyllogenetically similar host choice of shiny cowbirds (Passeriformes vs. Passeriformes), along with its wide geographic range, offers a unique system to test the relationship between the host specificity and the geographic distribution in host-symbiont systems.

Preliminary data of feather mites on shiny cowbirds indicate some level of geographic partition of mites between Chilean and Brazilian populations (Mena et al. 2020; Pedroso & Hernandes 2021). Therefore, here we analyze the feather mite fauna on the shiny cowbird in Brazil in order to investigate how the host specificity and the transmission method correlate with the geographic distribution in these highly specific symbionts. Based on the complexity of this system, we expect to find a pattern of different mites species on shiny cowbirds based on their host usage in different geographic regions.

MATERIAL AND METHODS

Sampling

To investigate the biogeographic distribution of feather mites on shiny cowbirds we conducted a large-scale survey of *M. bonariensis* covering the widest geographic range possible in Brazil. We sampled feather mites from live birds, by washing dead birds, and from museum bird skins (Clayton & Walther 1997; Gaud & Atyeo 1996).

Field sampling

During field expeditions, the shiny cowbirds were captured using mist nets and had their feather mites collected by plucking the infested feathers (permit MMA 57944-3). Due to the dark coloration of the shiny cowbird's feathers, the field assessment of the infested feathers was not always precise, and often random feathers were also collected. After a careful examination of each feather in the lab, those randomly plucked feathers that apparently had no mites, had a few specimens of feather mites from the genus *Proctophyllodes*, located very close to the feather rachis. The collected mites and feathers in the field were preserved in plastic vials filled with 96% ethanol and refrigerated (when possible), or stored in individual plastic bags for subsequent processing in the lab. In the lab, all field samples were carefully inspected for different mite morphospecies under a dissecting microscope. The selected mites were mounted in microscopic slides for morphological identification (see below).

Museum sampling

The majority of feather mites collected on shiny cowbirds were sampled from six museums: Museu da Fundação Zoobotânica de Porto Alegre (MCN, Porto Alegre, Rio Grande do Sul); Museu de Ciências e Tecnologia da PUC (MCT, Porto Alegre, Rio Grande do Sul); Museu de História Natural Capão da Imbuia (MHNCI, Curitiba, Paraná); Museu de Zoologia da Universidade de São Paulo (MZUSP, São Paulo, São Paulo), Museu Paraense Emílio Goeldi (MPEG, Belém, Pará), and University of Michigan Museum of Zoology (UMMZ, Ann Arbor, Michigan) (mite collection only). Taxidermized bird skins have been sampled for mites by the feather-ruffling technique over a clean, white paper; this material (debris, feather follicles, mites, etc) was transferred to microtubes and then screened for mites in the lab.

Because feather mites are small-sized symbionts (200 to 500 micrometers) and highly adapted to their microhabitat on their hosts, they usually remain on the dead body of their hosts, dying firmly attached to them. This turns possible to collect mite samples from dry bird skins in museum collections. Museum bird skins represent an important source for feather mite information from different time and space scales or from difficult to sample hosts (Gaud & Atyeo 1996; Hernandes 2020; Mironov & Proctor 2008). However, collecting feather mites from museum collections create the possibility of cross contamination from other birds, a problem in feather mite assessments as every mite species must be associated to a host species (Choudhury et al. 2002; Gaud & Atyeo 1996). Therefore, a study analyzing feather mites from museum skins must consider this contamination (Gaud 1992; Gaud & Atyeo 1996). To account and avoid contamination in the present study we followed a conservative criterion where mites have been separated in 3 categories (0, 1 and 2) according to their source and recovered infrapopulation size (all individuals of a mite species recorded on a single bird). Score 2 records represent strong signal for a true mite-bird association. This score included mites recovered from the washing technique, from live birds in the field, and from museum samples where at least 3 males and 3 females of a given mite species was recorded from a host specimen. Score 1 records represented a likely true association, these mites have been identified as the same species of the mites recorded multiple times in the score 2, or recorded multiple times from different host specimens, and from different museum collections, but failed to reach the score 2 requirements (e.g. less than 3 males and 3 females on a host). The score 1 criterion is an important measure of mite association because live birds captured with mist nets were often recorded with a low mite infrapopulation size (e.g. 2 specimens of a mite species on a host). Therefore, including only score 2 records would underrepresent the mite fauna from museum skin samples. Lastly, score 0 records represented clear contaminations (e.g. atypical mite associations with passerines), or mites with insufficient records to be considered. Score 0 records, although common, were readily identified and excluded from the subsequent analysis (Supplementary File 2).

Bird-wash sampling

Roadkill specimens of shiny cowbird were donated to our lab and washed to collect their feather mites. We used water and detergent to wash the birds. The residual water was then filtered using common filter papers. The feather mites were collected manually from the filter paper under a dissecting microscope. A similar procedure is described in Mironov & Galloway (2002).

Microscopic slide preparation

Mites retrieved from museum skins were cleared in 30% lactic acid at 50°C for 48h before mounting on microscopic slides in Hoyer's medium; mites collected by washing and from live birds in the field were left for 24h in lactic acid before mounting (Krantz & Walter 2009). Mite were identified using the following and additional relevant references (Atyeo and Braasch 1966; Santana 1976; Gaud and Atyeo 1996; Valim and Hernandes 2010; Mironov 2012). Consecutive numbers were assigned for undescribed mite species, which are very common in the New World (Barreto et al. 2012; Pedroso & Hernandes 2016; Valim et al. 2011). Slide-mounted mites were deposited at the Department of Ecology and Zoology of the Universidade Federal de Santa Catarina (ECZ–UFSC).

Host specificity categorization

The idea behind our hypothesis of relationship between specificity and geographic distribution in feather mites from the shiny cowbird requires the recognition of different classes of host specificity among the sampled mites. This characterization was previously done in the study Pedroso et al. "*Relative importance of vertical versus horizontal transmission in host colonization: A case study of feather mites from the brood parasitic cowbird (Molothrus bonariensis)*". Were we properly categorized the feather mite fauna found on the shiny cowbird in three host specificity categories: *Molothrus-specific*, *Molothrus-alien*, and *Multi-host mites* (Table 1). This arrangement of host specificity was supported by multiple lines of evidence. Here we used the same data and categories to explore the geographic distribution of those mites.

Geographic distribution of mites on the Shiny Cowbird

We performed a bipartite network analysis to investigate the geographic distribution of the recorded feather mite species in the biomes Amazon, Caatinga, Cerrado, Atlantic Forest, and Pampa in Brazil, and Chaco in Argentina and Paraguay (Morrone 2014). Brazilian biomes are mostly characterized by the phytophysiognomies, the fauna, and average climatic condition of geographic regions, creating a uniform separation of regions in Brazil based on their biotic properties (Coutinho 2006). Those aspects certainly influence the avifauna distribution, and likely their feather mite community and distribution in Brazil. Therefore, it is expected that non-specific cowbird feather mite communities (*Molothrus-alien*) are shaped according to local distributions of bird species serving as foster parents for the shiny cowbird (Bodrati & Fraga 2010; Colina et al. 2016; Louder et al. 2015).

A network analysis was done by clustering the shiny cowbird mite records (by species) on nodes connected to single nodes representing the biomes in which they were recorded. Mite and biome nodes were connected by edges representing the connection strength (edge thickness is proportional to the number of total mite records per biome) (Figure 5). The network was created and explored in Gephi 0.9.2 (Bastian et al. 2009). To identify biogeographic patterns, we also performed a community detection analysis (modularity) using the same software with default settings (Barberán et al. 2012; Carstensen et al. 2012; Economo et al. 2015). A modularity analysis estimates sub-network clusters based on the strength of the connecting nodes, separating groups (modules) of nodes based on their proximity and distance. The quality of the estimated modules is computed as the Q index (modularity), with higher values indicating more connections (edges) within an estimated module than between modules (Newman 2006). Only mites assigned to the *Molothrus-alien* and *Multi-Host Parasite* categories were included in the Networks analysis since the remaining *Molothrus-specific* mites were evenly distributed across the biomes (as expected), resulting in a weaker network modularity (Q = 0.17) (Supplementary File 10 and 11). The single exception was *Trouessartia* sp.6 (*Molothrus-specific*), which was absent in the Pampa biome, and therefore was included in the analysis. In total, 84 hosts were used in the network analyses (65 carrying *Molothrus-alien* and *Multi-host* + 19 carrying *Trouessartia* sp. 6).

A modularity analysis also provides a way to visualize the distribution of the recorded mites across the modules by using the normalized degree (z) and among module connectivity (r) indexes (Carstensen et al. 2012; Economo et al. 2015). The former (z) indicates the frequency of each mite species across regions considering all its module connections (for example, high values may point to a range expansion), whereas the latter (r) represents how evenly a mite species is spread across the modules (low values=not even distribution across modules, high values=even). To calculate those indexes we considered the modules estimated in the Gephi analysis. We also considered connections of species i across all modules (Economo et al. 2015). For each mite species the normalized degree (z) was calculated by the fraction of all connections of species i across all modules (here as the total number of host specimens each mite species was recorded) by the mean degree (K_m) of its respective module (the number of edges divided by the number of nodes of a module). The among module connectivity (r) was calculated as $r_i = 1 - \sum_m (P_{im})^2$, where m represents the modules and P_{im} is the fraction of the number of occurrences of species i in a given module by the total number of records of this species in all modules (Economo et al. 2015). When a species is recorded only in a single module its r score is 0 (Figure 6). Finally, to visualize patterns of modularity, we plotted results of our Gephi modularity analysis onto a map of South America using QGis 3.12 (QGIS.org) (Figure 7).

We also performed an additional modularity estimation for the same dataset using the package "Bipartite" in R, which uses an improved algorithm to calculate the modularity accounting for the connection's weight (Beckett 2016) (Supplementary File 12); and a heatmap, which allows a complete visualization of the whole dataset (each bird and mite record) across the biomes, using the package 'heatmap.plus' in R with the hierarchical clustering algorithm *ward.D2* (Figure 8).

RESULTS

Feather mite diversity

A total of 146 shiny cowbirds specimens were inspected for feather mites, 22 captured in the wild, 10 from washes, and 114 from museum bird skins. Of these, 7 bird individuals lacked any mites, and 139 individuals had mites (Supplementary File 2). Of the group of birds harboring mites, there were 365 mite records having confidence scores 1-2, representing 29 mite morphospecies (12 genera, 8 families), including 13 named species (Supplementary File 2). In the specificity categories, 5 species were recognized in the *Molothrus-specific* category (*Amerodectes molothrus*, *Proctophyllodes molothrus*, *Trouessartia* sp.6, *Mesalgoides* sp.1, and *Xolalgoides* sp.1), 5 species in the Multi-host mite category, and 18 species in Molothrus-alien (Figure 9, 10, 11, 12).

Geographic Distribution vs. Host Specificity Categories

Cumulative abundances (the total number of mite specimens) and the number of biomes were statistically different in *Molothrus-specific* vs *Molothrus-alien* or *Multi-host Parasite* categories ($p < 0.05$), but not in *Molothrus-alien* vs *Multi-host mites* (Supplementary File 3). Furthermore, abundances of each mite species plotted against mites' geographic distribution indicate that highly abundant and evenly distributed taxa across biomes are likely to be *Molothrus-specific* species, while less abundant and non-evenly distributed taxa are likely to originate from foster parents (*Molothrus-alien*) or be *Multi-host mites* (Figure 5; 8; Supplementary File 11).

Our data strongly indicate a positive relationship between host specificity vs high prevalence and even geographic distributions for *Molothrus-specific* mites; while foster parent mites (*Molothrus-alien*) are likely to have lower prevalence and less even geographic distribution (Figure 7; Supplementary Files 11).

Geographic Module Analyses

Spatial distribution of mites on shiny cowbirds was analyzed using networks and two modularity analyses. For this analysis we have excluded the *Molothrus-specific* mites with the exception of *Trouessartia* sp. 6. The modularity analysis clustered the network`s nodes into modules based on the number of records in each biome (Figure 5). Four modules with a modularity score of 0.402 were detected: Module 1 (purple – biome Amazon); Module 2 (blue – Caatinga); Module 3 (orange – biomes Cerrado and Atlantic Forest) and Module 4 (green – biomes Chaco and Pampa) (Figure 5, 7). The modularity score (Q = 0.402) match with the suggested value to consider a network modular (0.4) (Beckett 2016). The "bipartite" modularity analysis retrieved almost the same module composition retrieved in Gephi, except for the placement of the species *Microlichus* cf. *americanus* in the module 2 (Caatinga) instead of module 3 (Atlantic Forest + Cerrado) (Supplementary File 12). For comparison, a modularity analysis was carried out including all categories for *Molothrus*-mites (Supplementary File 10). This comparative analysis resulted in three modules with weak modularity score (Q = 0.17), which suggests a low support for the established modules, i.e., a

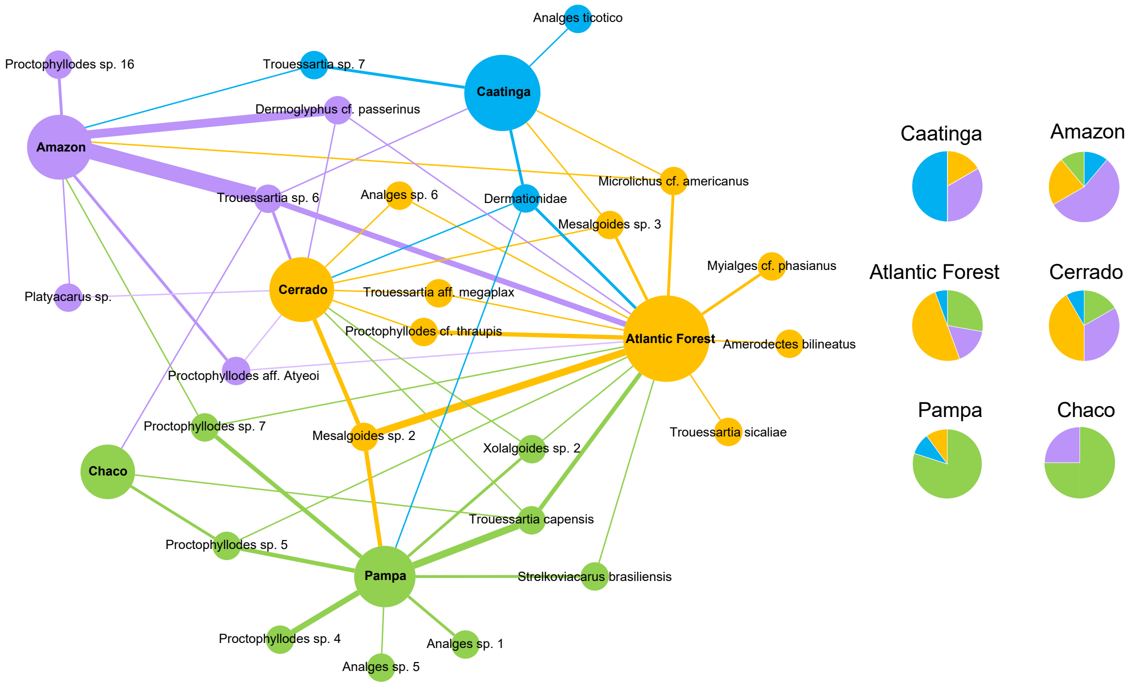


Figure 5. Networks of *Molothrus-alien*, *Trouessartia* sp. 6 (*Molothrus-specific*) and *Multi-Host Parasite* feather mite species (smaller nodes) and 6 biomes (larger nodes). The thickness of the edges (connectors) indicates the number of mite records per host. Networks modules (represented by unique colors) were established by a modularity analysis, clustering and separating nodes according to their similarity. The pie charts indicate the modularity composition of the mite species recorded in each biome.

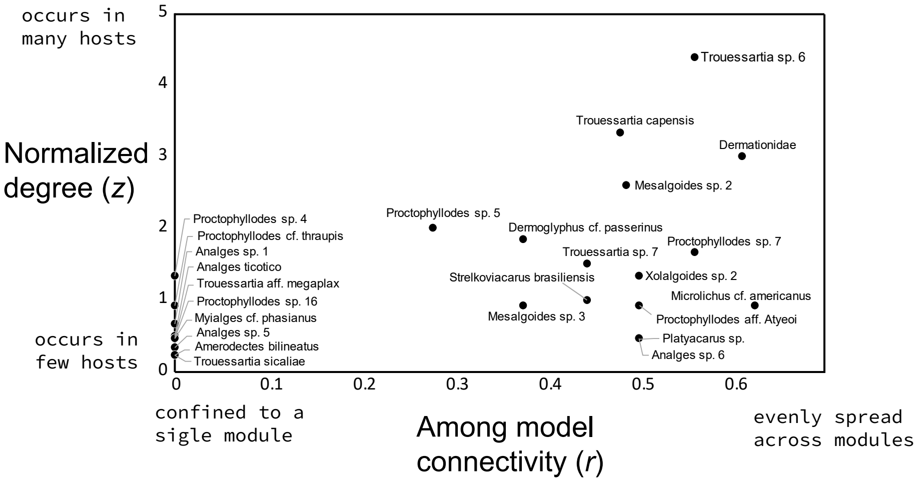


Figure 6. Normalized degree (z) and among module connectivity (r) calculated based on the modules as found by our network analysis (see Figure 5) for *Molothrus-specific*, *Multi-host* mites and the *Molothrus-specific* species *Trouessartia* sp. 6.

randomized association among the modules caused by *Molothrus-specific* mite categories (Supplementary File 10).

Of the species included in the analysis (n=25), 10 were exclusively found within one module, although some, such as *Trouessartia* aff. *megaplax* and *Proctophyllodes* cf. *thraupis*, were recorded on more than one biome (Figure 5, 6). Other species, such as *Dermoglyphus* cf. *passerines*, despite having connections in more than one module, were strong associated with a particular biome (in this case, the Amazon). Additional noteworthy cases include the mite species of the genus *Analges*, all recorded in a single module. Overall, the biome connections by the network modules also presented a geographic accuracy, connecting biomes known for sharing biotic properties with transition zones (i.e. ecotones) (Coutinho 2006).

DISCUSSION

Here we tested the hypothesis of association among the host specificity, the transmission route, and the geographic distribution in symbionts using feather mites from the shiny cowbird (*M. bonariensis*) as model systems. The peculiarities of this system allowed for a precise distinction of the transmission route and the specificity nature of feather mites – feather mite species with high abundance and prevalence on host populations are specific to shiny cowbirds (*Molothrus-specific*), and transmitted solely through a horizontal line of acquisition; whereas mites with low prevalence and abundance were acquired mainly through vertical transmissions from the shiny cowbird’s foster parents (*Molothrus-alien*).

Our results suggest a connection between host specificity and geographic distribution of feather mites on shiny cowbirds. *Molothrus-specific* mite species were evenly distributed along with their host distribution, while *Molothrus-alien* and *Multi-host* mite species were patchy distributed (Figure 7; Supplementary File 11). Regarding the transmission, mite species presenting an even distribution in shiny cowbirds are the ones transmitted horizontally between conspecific contacts between cowbirds (*Molothrus-specific*), while mites patchy distributed are the ones acquired vertically from the shiny cowbird’s foster parents (*Molothrus-alien*).

Recent studies indicate that the diversity and the geographic distribution in vane-dwelling feather mites is strongly shaped by biotic factors, i.e., by the host diversity and the host specificity (Doña et al. 2018; Gusmão et al. 2020). Our results coincide with those

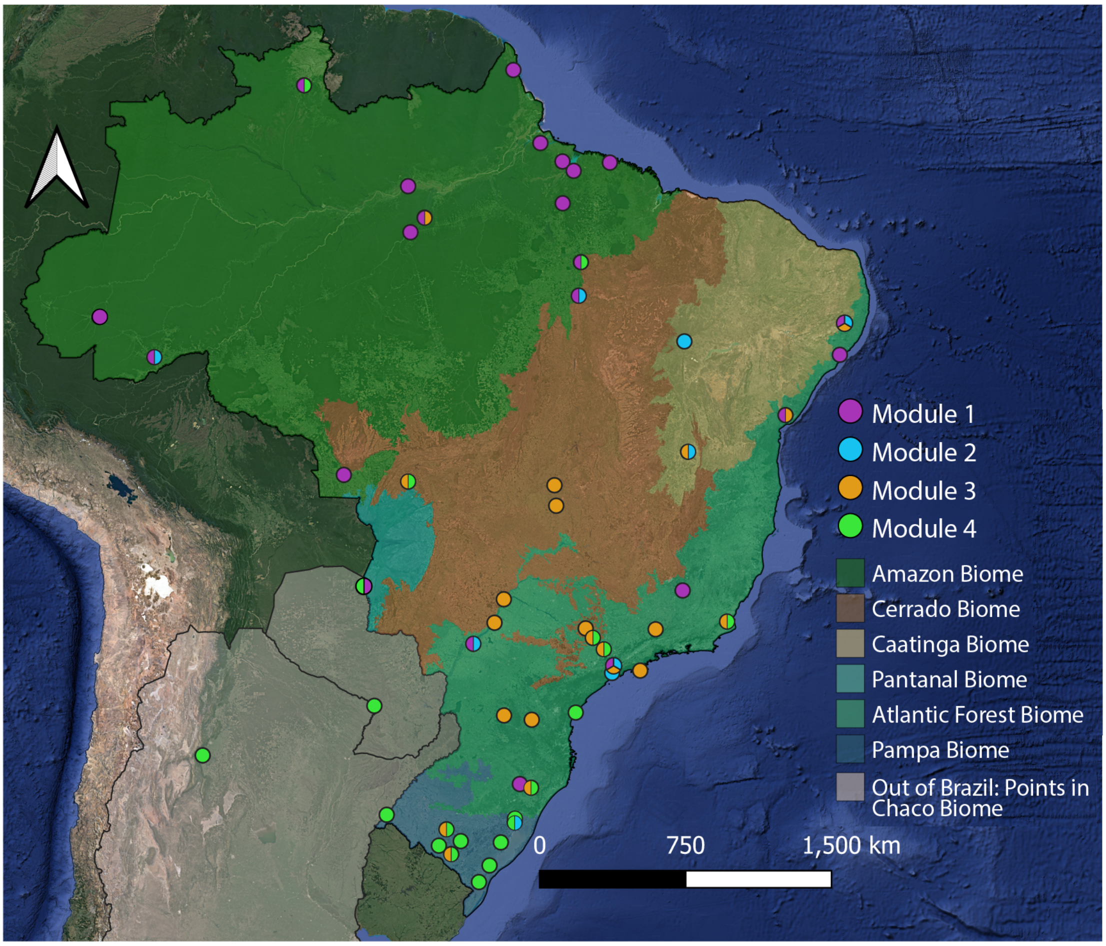


Figure 7. Geographic of shiny cowbirds sampled holding feather mites from the specificity categories *Molothrus-alien*, and *Multi-host* mites, and for the *Molothrus-specific* species *Trouessartia* sp. 6. Each point (solid or pie-chart) represents a single sampled shiny cowbird specimen; single-colored points represent shiny cowbirds with mite communities composed of geographically restricted species (single-module mites), while multi-colored pie-charts represent cowbirds holding mites from different geographic modularities.

findings as we found a strong host-dependent distribution of *Molothrus-specific* mites on shiny cowbirds in Brazil. Therefore, our data also indicates that the property of the transmission method (either vertical or horizontal) has likely low impact over the host specificity in these symbionts, as it was expected that a strict horizontal transmission would reduce the diversity of host specific symbionts (Vas et al. 2013), or reduce the dispersion potential of symbionts on their host populations. Instead, despite the apparent low impact over the mite specificity, horizontal transmissions were essential for the transmission of *Molothrus-specific* mites in this system, and therefore, for their homogenized geographic distribution.

Even though these evidences were discovered using a brood parasitic system as a model, it can reasonably be extended to regular bird-feather mite systems. It is unlikely that different feather mite lineages (the five *Molothrus-specific* species) on a single host species would converge and develop unique adaptations favoring horizontal transmissions. Instead, despite the apparent low mobility, feather mites in general may present properties that turn horizontal transmissions not a rare but a frequent event. This assumption have been suggested in many cophylogenetic, molecular, and ecological studies, which found that feather mites are more active symbionts on their hosts (Labrador et al. 2021), with multiple host switch events along their coevolutionary history (Dabert 2004; Klimov et al. 2017; Matthews et al. 2018a). The presence of straggler mites on unusual hosts on passerines in Spain also support that feather mites in general present a higher rate of horizontal transmission, even among interspecific hosts (Doña et al. 2019). However, the host biology cannot be completely excluded, as it may also explain the patterns observed in our study. The shiny cowbird is a gregarious species known to form huge seasonal flocks for short migrations, feeding, and roosting (Linz et al. 2017; Soler 2017). This constant aggregation between shiny cowbird individuals may favor horizontal transmissions in this host in particular, explaining the even geographic distribution of specific feather mite species. The influence of the host biology (gregarious or solitary) over their symbiont community is yet to be tested for feather mites.

Given the host specificity and the transmission importance for feather mite’s distribution, it would be expected the same pattern of even distribution found on shiny cowbirds in other bird-mite systems. In fact, studies recording differences on feather mite community of geographically separated host populations (either latitudinal or altitudinal), found evidences for abiotic factors impacting their distribution, especially humidity (precipitation) and temperature (Grossi & Proctor 2021; Meléndez et al. 2014). Contrarily, we did not find direct evidences of abiotic factors impacting the distribution of feather mites on shiny cowbirds in Brazil. Nonetheless, our modularity analysis showed that except for the *Molothrus-specific* mite species *Trouessartia* sp. 6, the almost uniform distribution of *Molothrus-specific* mites could also be an indicative of a near uniform distribution of shiny cowbirds in Brazil, which in turn can be a reflect of a recent expansion of this host.

The distribution of *Trouessartia* sp. 6 appears to be restricted (either in prevalence and abundance) to the northern regions in Brazil – more precisely to the Amazon and the Northeast portion of the Atlantic Forest biomes (Supplementary File 11). This mite species was especially collected from birds deposited at the Museu Paraense Emílio Goeldi (MPEG, Belém, Pará), which counts with a vast bird collection from the northern Brazilian regions. Therefore, shiny cowbird skins from this museum are specifically from the subspecies found on these regions, namely *Molothrus bonariensis riparius* Griscom & Greenway, 1937, and to a lesser extend to *M. bonariensis minimus* Dalmas, 1900. This indicates a partition among the feather mite community on shiny cowbird mites in Brazil based on their subspecies, where southern shiny cowbird populations lack any specific mites from the genus *Trouessartia,* whereas the northern subspecies hold *Trouessartia* sp. 6. A few abundance and prevalence of *Trouessartia* sp. 6 was collected from samples belonging to the shiny cowbird subspecies *M. bonariensis bonariensis* (Gmelin, JF, 1789) from other museums in Brazil. However, these samples could actually represent cases of contamination from the northern shiny cowbird subspecies due to their low abundance (Supplementary File 2). On top of that, when comparing the mite community from Brazil with recent records from 47 shiny cowbirds from Chile (Mena et al. 2020), it is possible to recognize that none of the *Proctophyllodes* species recorded in Chile match with the *Proctophyllodes molothrus* recognized here as *Molothrus-specific* and widely recorded in Brazil (Supplementary File 11) (Pedroso & Hernandes 2021). Additionally, no mites adapted to live on down feathers (e.g., genera *Mesalgoides* and *Xolalgoides*), were recorded on Chilean cowbirds. Down feather mites are usually rare and difficult to collect from live birds in the field, however, 20 of the 47 examined shiny cowbirds in the Chilean study were dead birds, which allows for a more complete screening for feather mites by using methodologies such as the washing technique. Therefore, shiny cowbirds from Chile could indeed also lack the presence of the down feather mites *Mesalgoides* sp. 1 and *Xolalgoides* sp. 1 of *Molothrus-specific* mites widely recorded in Brazil (Supplementary File 11).

Notoriously, the differences observed between Brazilian and Chilean populations of shiny cowbirds might give clues about the colonization of this bird in Chile (Marín 2000).

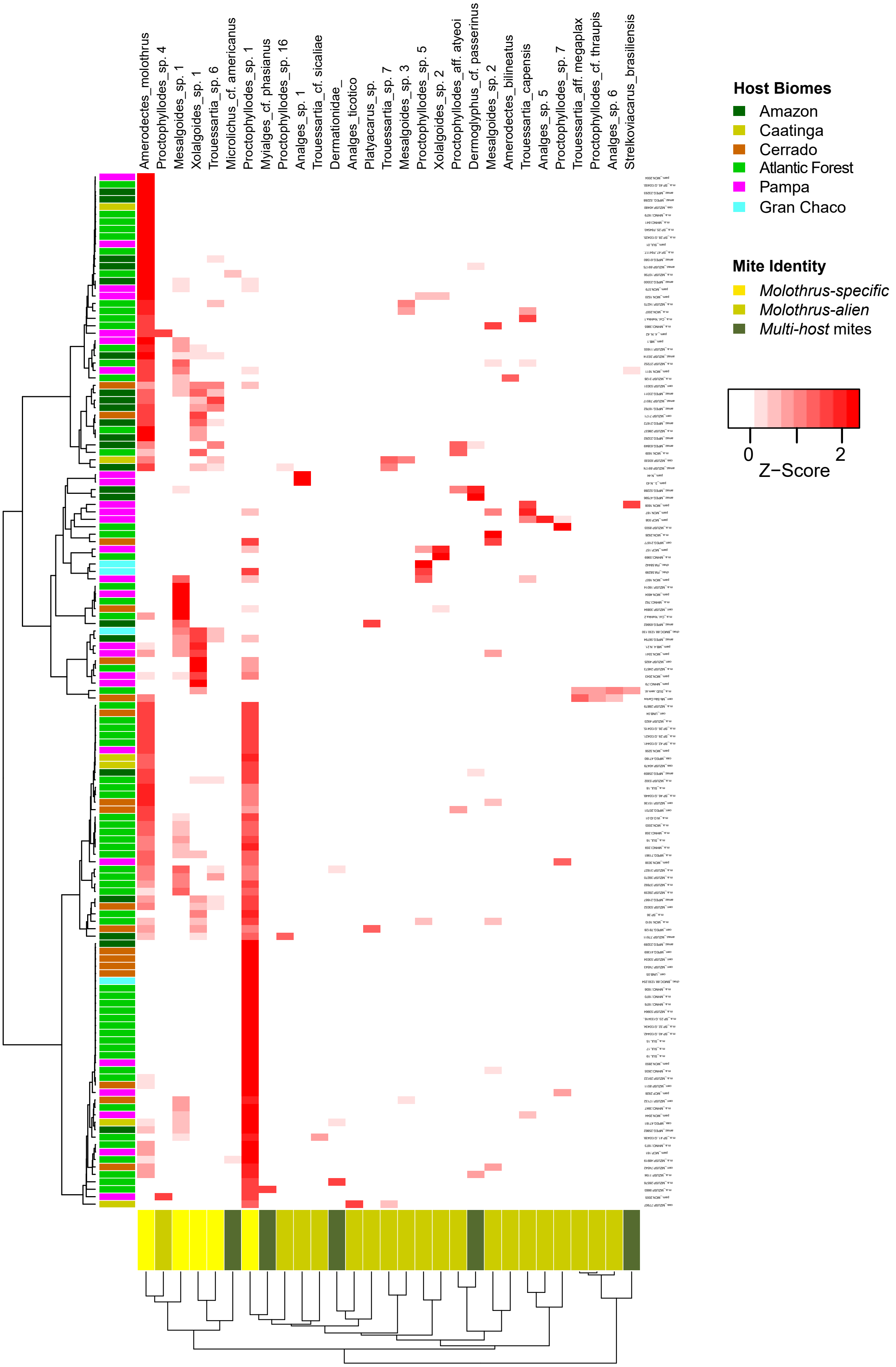


Figure 8. Heatmap with normalized abundances of mite species recorded on individual shiny cowbirds. Mite specificity categories (for the mite species) and biomes of occurrence (for the shiny cowbirds) are highlighted. The R package heatmap.plus with the hierarchical clustering algorithm ward.D2 was used to generate this heatmap.

Marín (2000) suggested that the shiny cowbird was likely introduced in Chile from specimens from Argentina as it was a popular cage bird in early 1900’s, from where it spread to other regions of the country. The Chilean cowbirds population might have passed by founder effects (or missing the boat) where few bird individuals were responsible for originating the current Chilean populations, and those few hosts were potentially free of some of the common specific feather mite community usually found on cowbirds (Paterson et al. 1999). A second hypothesis is based on secondary extinctions, where some of the specific mites failed to disperse along with their hosts in Chile, or went extinct as a result of a natural selection due to the Chilean cold and dry climate. Both hypotheses seems reasonable since drops in feather mite diversity were observed along a altitudinal and climatic gradient in passerines in Spain (Meléndez et al. 2014), and founder effects in pigeons from Canada (Grossi & Proctor 2021).

It is interesting that a similar system is found in the Australian brush-turkey *Alectura lathami* (Galliformes: Megapodiidae), where eggs are incubated under warm substrates and hatchings live independent from parent’s provisions. Therefore, similar to cowbirds, vertical transmission of ectosymbionts via parental care is not possible in this system (Jones et al. 1995). Yet, brush-turkeys have a specific and rich feather mite fauna (Atyeo 1992; Proctor & Jones 2004). Their acquisition of feather mites appears to occur gradually, with older birds presenting a richer mite fauna than younger birds. Copulation is probably the main route for mite intraspecific transmission, along with transfers via agonistic interactions, roosting aggregations, and phoresy on hippoboscid flies (Proctor and Jones, 2004). More interesting, mites associated with bush-turkeys also presented some levels of geographic structure among host populations. However, in this case, past cases of host contacts and host isolation better explain the observed pattern of mite distribution.

Our network analysis showed that *Trouessartia* sp. 6 (the weakest species from the *Molothrus-specific* category) was the single mite species having connections with all established modules, but with a higher intensity in the Amazon biome and no records for the extreme South (Pampa biome) (Figure 5). This is indicative that this species could indeed be a *Molothrus-specific* mite but with a peculiar geographic configuration. This pattern is also clear in the graph of the normalized degree (z) and the among module connectivity indexes (r) (Figure 6), where *T.* sp. 6 is an outlier based on high number of occurrences and as a near outlier in evenness and among module distribution (Figure 6). It is noteworthy that different classes of feather mites may present different transmission potential, i.e., vane dweller-feather mites are better dispersers among hosts than mites living on the other microhabitats

(Dabert et al. 2015; Dabert & Mironov 1999; Grossi & Proctor 2021). This pattern is also presented in our data (exception of the vane-dwelling species *Trouessartia* sp. 6), where the most prevalent and abundant mite species on shiny cowbirds were the vane dwelling *Amerodectes molothrus* and *Proctophyllodes molothrus* (Supplementary File 10).

Although *Trouessartia* sp. 6 is a *Molothrus-specific* mite that simply does not occur on its host in the South (or occurs at very low prevalence) for different reasons, our network analysis also shows patterns in mite distributions near-coinciding with the shiny cowbird host usage, which can be variable across its range (Bodrati & Fraga 2010; King 1973; Colina et al. 2016; Sick 1997). For example, there is a tendency of mites from *Z. capensis* and other icterid birds (except for *P.* aff. *atyeoi*) to be concentrated in the south (Chaco and Pampa biomes) (Module 4 – green), whereas thraupid mites were more frequent in the Southeastern Atlantic Forest (Module 3 – orange) (Supplementary File 13). These findings coincide with bird distribution, as the Pampa biome is a plain wetland area, and a suitable environment for Icteridae birds; while some species of thraupids, specifically *T. sayaca*, are well adapted to urban environments, which is concentrate in the Southeastern Atlantic Forest in Brazil (Batisteli et al. 2019; Linz et al. 2017).

We identified 42 mite records (out of 66) which could originate from foster parents of the shiny cowbird (Supplementary File 4). One such species, *Trouessartia sicaliae* Hernandes, 2014, was also sampled from *Sicalis* spp., common hosts of *Molothrus bonariensis* (Figure 2). Other mite records included mites from tanagers (*Thraupis* spp.) – *Proctophyllodes* cf. *thraupis*, *Trouessartia* aff. *megaplax* and *Amerodectes bilineatus* (Berla, 1958)) – probably from the sayaca tanager *Thraupis sayaca* (L., 1766) as this species is commonly found in urban areas throughout Brazil, and have been recorded as a host of *M. bonariensis* in the same region (Batisteli et al. 2019). Furthermore, at least four cowbird museum samples could be assigned to the rufous-collared sparrow *Zonotrichia capensis* (Passerellidae) as the source of mites, due to the presence of *Trouessartia capensis* Berla, 1959, *Analges ticotico* Pedroso and Hernandes, 2018 and *Proctophyllodes carmenmirandae* Pedroso and Hernandes 2021. The rufous-collared sparrow is well known as one of the main hosts for the shiny cowbird parasitism in urban environments in Brazil (Fraga 1978; King 1973; Sick 1997). The remaining records could not be assigned to any specific bird species, due to insufficient feather mite information from the Neotropics (Pedroso & Hernandes 2016; Valim et al. 2011). Interestingly, we recorded both *Proctophyllodes* species (here as *P.* sp. 4 and *P.* sp. 5) recently recorded on *M. bonariensis* from Chile by Mena et al. (2020) (sp. 1 and sp. 2 in this study, respectively), as well as mites related to other Icteridae birds such as *Proctophyllodes* aff. *atyeoi* Černý, 1974.

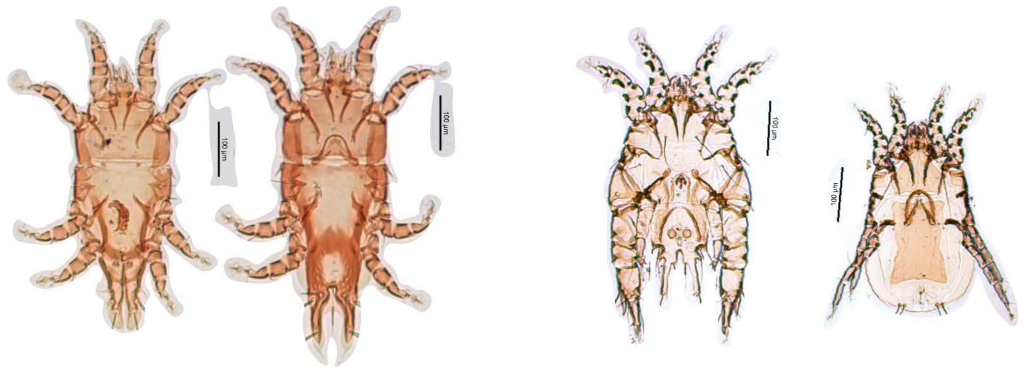
CONCLUSION

Based on the patterns of host specificity and transmission of feather mites on the shiny cowbirds, we identified the host specificity as the most important feature responsible for defining the geographic distribution of *Molothrus-specific* mites. The gregarious host ecology explains the connection of even geographic distribution with horizontal transmissions for these *Molothrus-specific* mites. For *Molothrus-alien* feather mites, differences in regional preferences of host selection by shiny cowbirds better explain the observed scattered pattern of distribution. Yet, different shiny cowbird subspecies and populations may also present slightly different assemblage of feather mites, here demonstrated by the species *Trouessartia* sp. 6, and by the comparison with shiny cowbird populations from Chile. Lastly, further studies are necessary to understand some peculiarities of this system, including sampling more hosts from live birds to investigate the presence of hidden molecular structure of feather mites among different shiny cowbird populations, as well as the dynamics of persistence of *Molothrus-alien* mites.

1. *Amerodectes molothrus*

2. *Proctophyllodes molothrus*

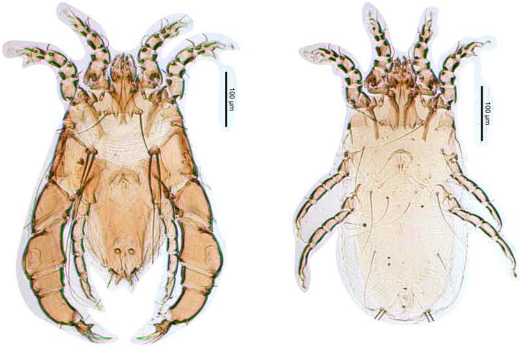
3. *Xolalgoides* sp. 1



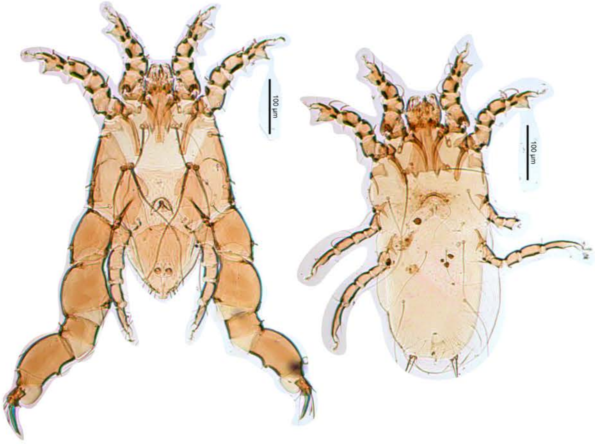
4. *Trouessartia* sp. 6

5. *Mesalgoides* sp. 1

Figure 9. Feather mites recorded on *Molothrus bonariensis* in the present work. Figures 1, 2, 3, 4, and 5 are classified in the *Molothrus-specific* specificity category. Mites on the left = males; mites on the right = females.

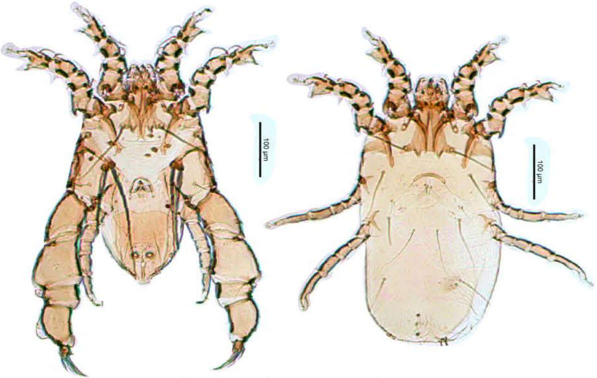


1. *Analges* sp. 1

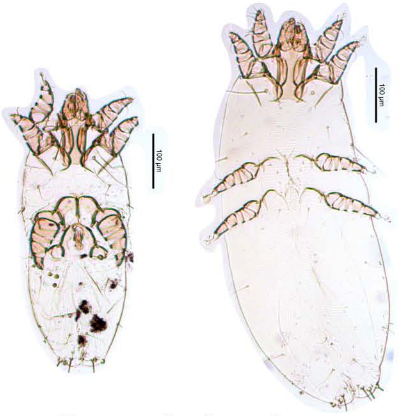


2. *Analges ticotico*

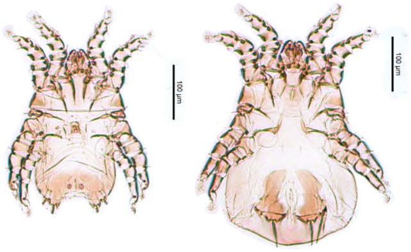
3. *Analges* sp. 6



4. *Analges* sp. 5



5. *Dermoglyphus* cf. *passerinus*

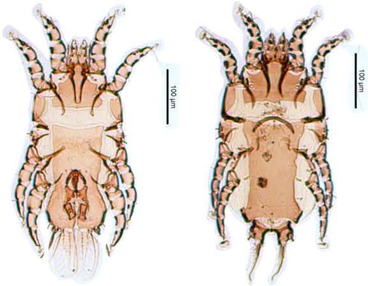


6. *Strelkoviacarus brasiliensis*

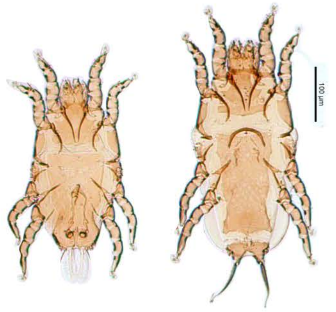
7. Dermationidae

8. *Metamicrolichus* cf. *phasianus*

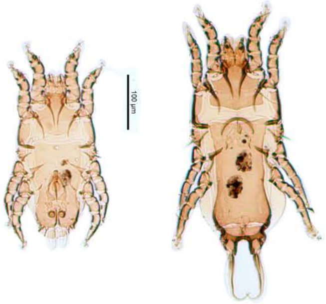
Figure 10. Feather mites recorded on *Molothrus bonariensis* in the present work. Figures 1, 2, 3, 4 are classified in the *Molothrus-alien* specificity category. Figures 5, 6, 7, and 8 are classified in the *Multi-host* mite category. Mites on the left = males; mites on the right = females.



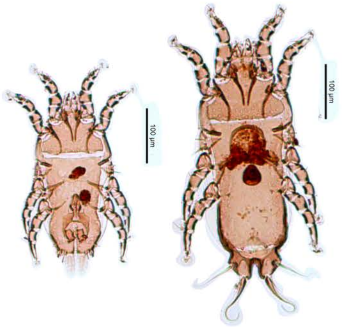
1. *Proctophyllodes* sp. 4



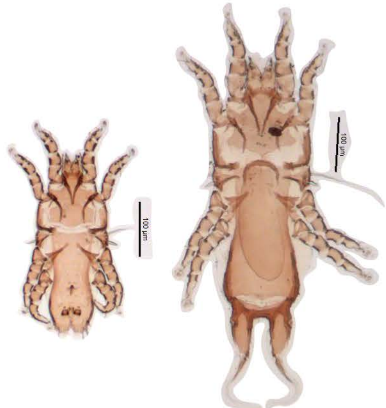
2. *Proctophyllodes* sp. 5



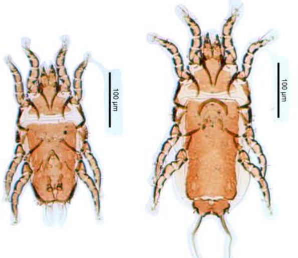
3. *Proctophyllodes carmenmirandae*



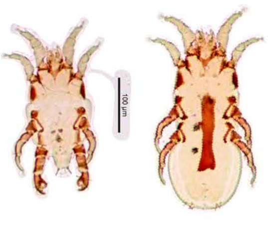
4. *Proctophyllodes* sp. 13



5. *Platyacarus* sp.

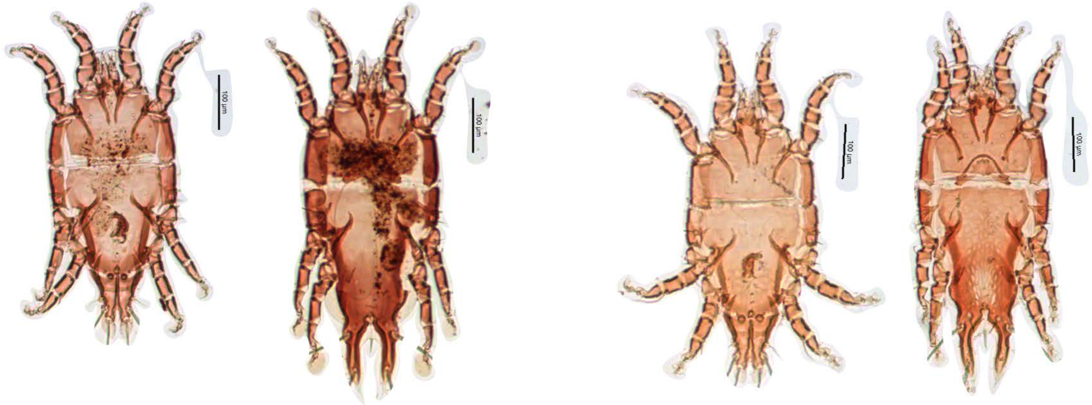


6. *Proctophyllodes* sp. 16



7. *Xolalgoides* sp. 2

Figure 11. Feather mites recorded on *Molothrus bonariensis* in the present work. Figures 1, 2, 3, 4, 5, 6, and 7 are classified in the *Molothrus-alien* specificity category. Mites on the left = males; mites on the right = females.

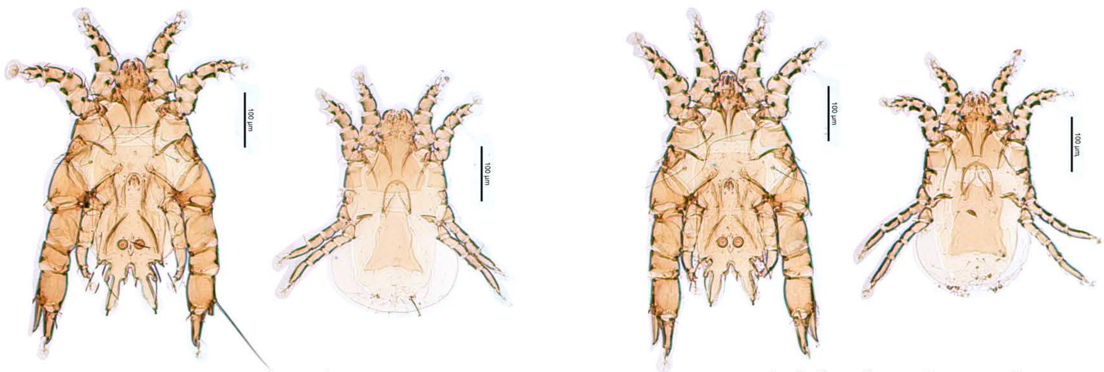


1. *Trouessartia* aff. *megaplax*

2. *Trouessartia* sp. 7

3. *Trouessartia capensis*

4. *Trouessartia sicaliae*



5. *Mesalgoides* sp. 2

6. *Mesalgoides* sp. 3

Figure 12. Feather mites recorded on *Molothrus bonariensis* in the present work. Figures 1, 2, 3, 4, 5, and 6 are classified in the *Molothrus-alien* specificity category. Mites on the left = males; mites on the right = females.

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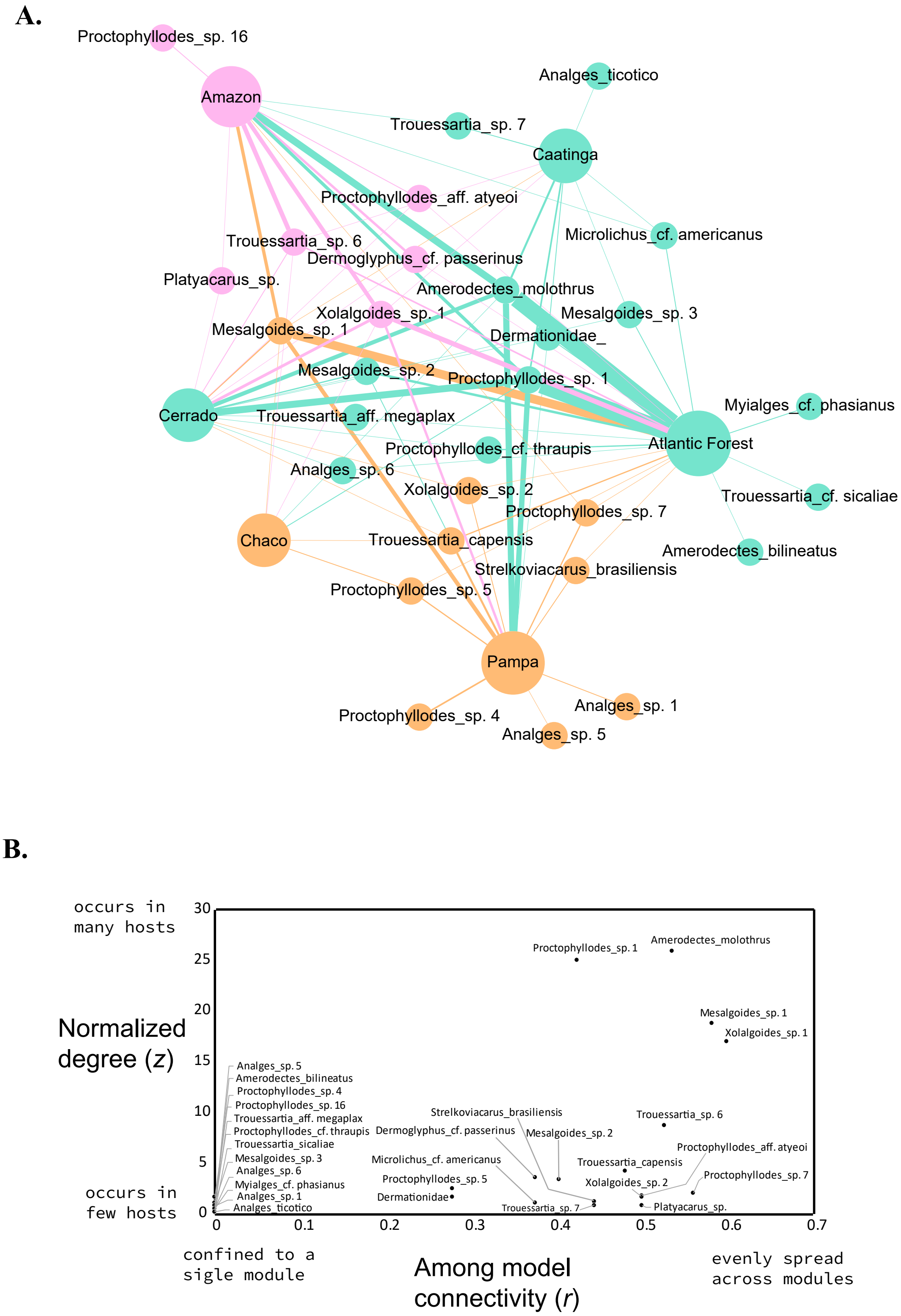
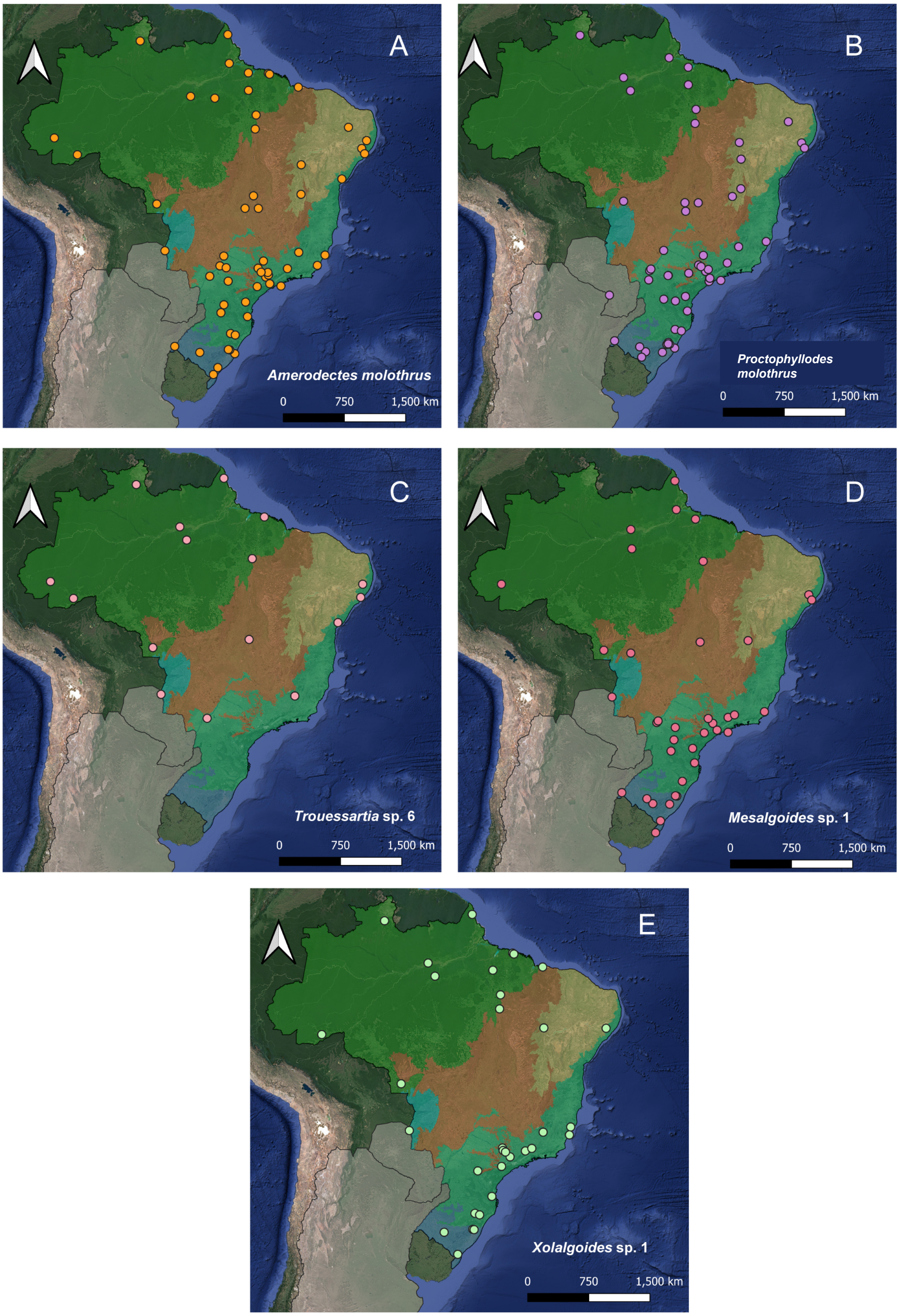
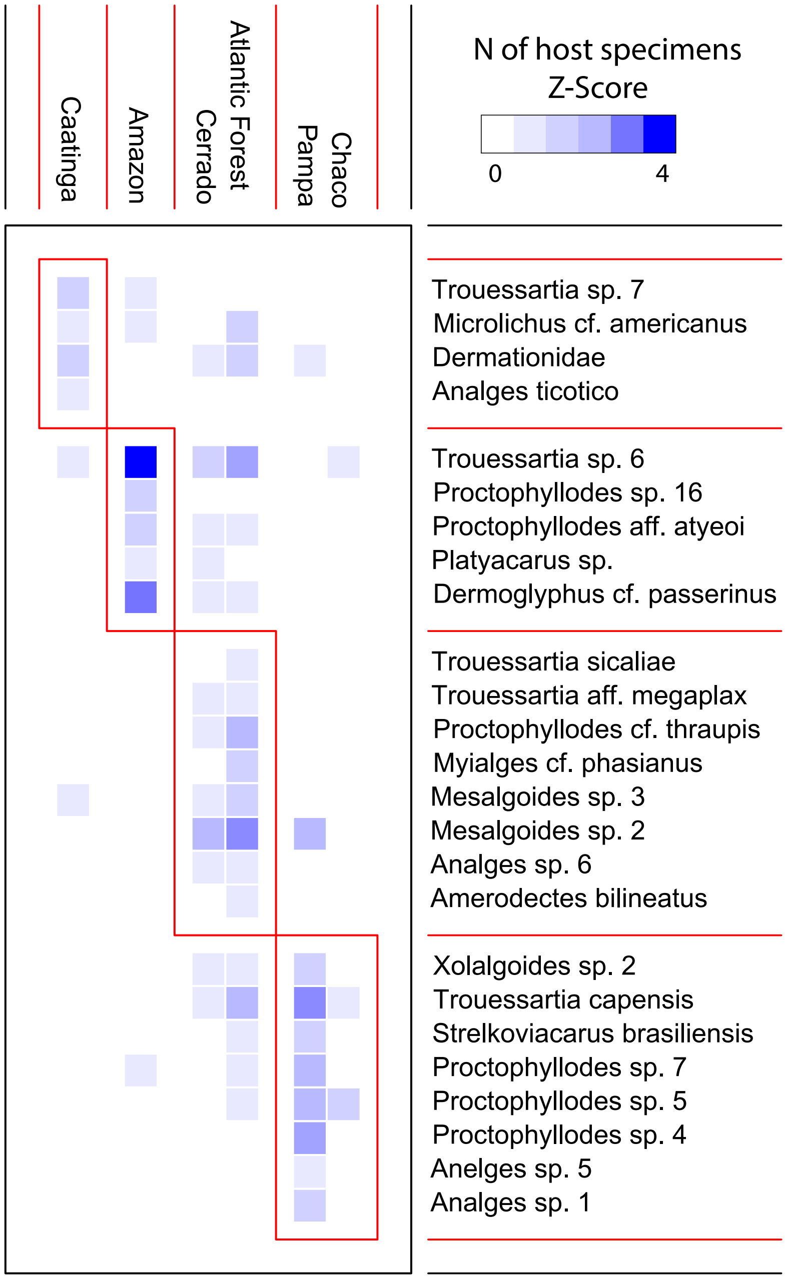


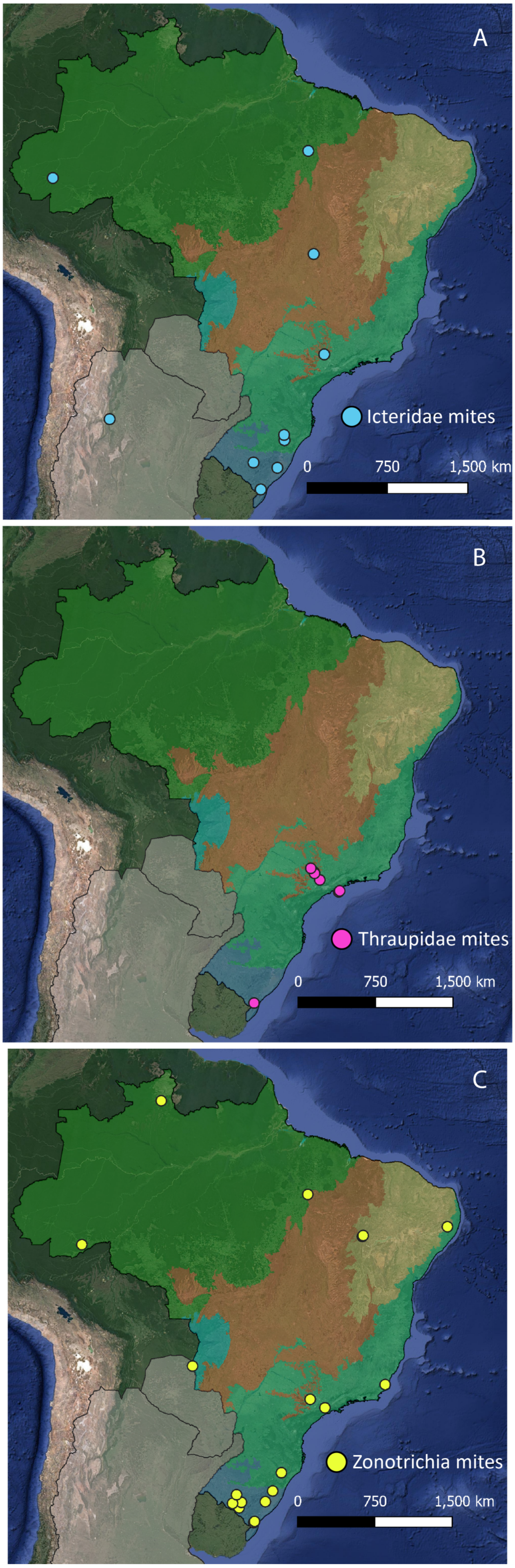
Supplementary File 10. A. - Network analysis including all feather mite specificity categories (smaller nodes) and 6 Brazilian biomes (larger nodes). The thickness of the edges indicates the number of mite records per host. Networks modules (represented by unique colors) were established by a modularity analysis clustering and separating nodes according to their similarity. In this analysis the modularity presented a low Q index (0.17), meaning low support for the established modules. **B.** - Normalized degree (z) and among module connectivity (r) calculated based on the modules found in the network modularity found in A.



Supplementary File 11. Geographic distribution of *Molothrus-specific* mites: A - *Amerodectes molothrus*; B - *Proctophyllodes molothrus*; C - *Trouessartia* sp. 6; D - *Mesalgoides* sp. 1; and E - *Xolalgoides* sp. 1.



Supplementary File 12. Modularity estimation of the *Molothrus-alien*, *Trouessartia* sp. 6 (*Molothrus-specific*) and *Multi-Host Parasite* feather mites in the R package bipartite.



Supplementary File 13. Distribution of *Molothrus-alien* mites putative associated with: A - Icteridae hosts; B - Thraupidae hosts; and C - with the rufous-collared sparrow *Zonotrichia capensis*.

PUBLISHED MANUSCRIPTS

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An unexpected finding of mammal mites (Psoroptidia: Sarcoptoidea) on a bird

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Short note

ABSTRACT

The psoroptidian mite *Myocoptes musculinus* (Koch, 1844) is the most common species of the family Myocoptidae (Sarcoptoidea), along with its main host, the house mouse *Mus musculus* Linnaeus. The present article reports the first recorded confirmation of *M. musculinus* on a bird – the tropical screech-owl *Megascops choliba* (Vieillot). Finding myocoptid mites on a non-rodent host is an additional case of predator-prey contamination.

Keywords horizontal transfer; contamination; ectoparasites; Strigiformes; Myocoptidae; *Myocoptes*

Introduction

Mites of the family Myocoptidae Gunther, 1942 (Astigmata: Psoroptidia: Sarcoptoidea) are permanent ectoparasites associated with rodents (Mammalia: Rodentia) (Bochkov 2010; OConnor 2009). These mites are specialized to live on the skin of their hosts, except for the genus *Trichoecius* Canestrini, 1899, which is specialized for living on fur (Bochkov 2010; Fain 1970; Fain *et al.* 1970). Currently 6 genera and more than 60 myocoptid species have been recognized (Bochkov 2010; Bochkov *et al.* 2016; Bochkov and OConnor 2017; Fain 1970; Fain *et al.* 1970). The genus *Myocoptes* Claparède, 1869 is the most diverse in this family, comprising 23 described species (Bochkov 2010; Bochkov and OConnor 2017), including *Myocoptes musculinus* (Koch, 1844) the most common species, distributed worldwide along with its main host, the house mouse *Mus musculus* Linnaeus, 1758 (Rodentia: Muridae). This mite is also the main cause of the myocoptic mange in laboratory white mice around the world (Rice *et al.* 2013).

The two myocoptids recorded on non-rodent hosts are likely contaminations: *M. ictonyx* Fain, 1970 was described from the striped polecat *Ictonyx striatus* (Perry, 1810) (Carnivora: Mustelidae) from Africa (Fain *et al.* 1970), and *M. musculinus* was also recorded on the spotted-tailed quoll *Dasyurus maculatus* (Kerr, 1792) (Marsupialia: Dasyuridae) from Australia (Vilcins *et al.* 2008). Samples recovered from these hosts were scarce and both species are known to prey on rodents (Bochkov 2010; Vilcins *et al.* 2008; Fain *et al.* 1970).

In the present study we report the finding of *M. musculinus* on a bird, the tropical screech-owl *Megascops choliba* (Vieillot, 1817) (Aves: Strigidae) in Brazil.

Materials and methods

During September of 2015 a tropical screech owl *Megascops choliba* was kept in captivity after being attacked and injured by a dog in Mogi Mirim, São Paulo State, Brazil. The owl was fed daily with live white mice (*Mus musculus*). After a month, the bird died and was taken to the Acari laboratory of the São Paulo State University (UNESP) in Rio Claro, where it was washed for ectoparasites following the technique described by Clayton and Walther (1997). The recovered mites were put in 30% lactic acid for 24 hours, then mounted on microscopic

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Two new feather mite species of the family Analgidae (Acariformes: Analgoidea) from the Rufous-collared Sparrow *Zonotrichia capensis* (Müller, 1776) (Passeriformes: Passerellidae)

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Abstract

Two new feather mite species of the family Analgidae are described from the Rufous-collared Sparrow, *Zonotrichia capensis* (Müller, 1776) (Passeriformes: Passerellidae), from Brazil: *Analges ticotico* **sp. nov.** (Analginae) and *Strelkoviacarus brasiliensis* **sp. nov.** (Anomalginae). *Analges ticotico* **sp. nov.** is characterized by the heteromorphic males having three short and rounded spines on the inner margin of femur III, the anterior margin of adanal shield convex, the hysteronotal shield with the anterior margin sinuous, and the terminal lamella rectangular. *Strelkoviacarus brasiliensis* **sp. nov.** is characterized by the anterior ends of the adanal shields being convergent and encompassing the bases of setae *ps3* in males, and by the strongly convex median extension of the prodorsal shield and short dorsal setae *vi*, *c2*, *d2* and *e2* in females. These species represent the first records of corresponding feather mite genera in Brazil.

Key words: Acariformes, Analgidae, *Analges*, *Strelkoviacarus*, *Zonotrichia*, host-associations, Brazil

Introduction

The feather mite family Analgidae Trouessart & Mégnin, 1884 (Astigmata: Analgoidea) was one of the first suprageneric taxa of feather mites created by Trouessart & Mégnin (1884). The name of the first feather mite genus *Analges* Nitzsch, 1818 means *no pain*, a characteristic which can be generally attributed to most families of feather mites due to their harmless influence on their bird hosts (Mégnin & Trouessart 1884; Gaud & Atyeo 1996). However, some analgids such as several *Megninia* species have been recorded causing distinct harm to *Gallus gallus domesticus* (Linnaeus, 1758) and leading to economic losses in the poultry industry (Gaud & Atyeo 1996; Tucci *et al.* 2005). Analgidae is also one of the most diverse and widespread feather mite families, including currently about 180 species in 34 genera arranged into seven subfamilies and recorded from a wide range of bird orders, including kiwis (Apterygiformes), New World vultures (Cathartiformes), rails (Gruiformes: Rallidae), pigeons (Columbiformes), cuckoos (Cuculiformes), gallinaceus birds (Galliformes), passerines (Passeriformes), and hummingbirds and swifts (Apodiformes) (Gaud & Atyeo 1982, 1996). These mites inhabit mainly the downy feathers that cover the body and the coverts of the wings, while the skin surface is infected in cases when the mite population on a host individual becomes extremely numerous. The most characteristic morphological adaptations to these habitats are represented by spines and hook-like apophyses on the two anterior pairs of legs, which enable them to grasp the soft barbules, and many long dorsal and ventral setae on the body, apparently allowing better orientation among barbules of downy feathers (Gaud & Atyeo 1996; Dabert & Mironov 1999).

Despite the broad distribution and great variety of hosts, only eleven named analgid mites have been unequivocally recorded from Brazilian birds: 7 species of the subfamily Megniniinae recorded from the bird orders Columbiformes, Gruiformes and Galliformes; 2 species of Protalginae from Apodiformes; and 2 species of Analginae, a subfamily restricted to Passeriformes (Gaud & Atyeo 1982, 1996; Valim *et al.* 2011; Pedroso & Hernandes 2016). The record of *Megninia constricta* Trouessart, 1899 (Analgidae: Megniniinae) on *Aratinga*

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Two new feather mites of the genus *Proctophyllodes* Robin (Acariformes: Proctophyllodinae) from passerines in Brazil

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Abstract

Proctophyllodes Robin (Proctophyllodidae: Proctophyllodinae) is a widely distributed feather mite genus, which most species show high level of specificity to their bird hosts. We describe two new species of this genus from passerines commonly found in urban environments in Brazil: *Proctophyllodes molothrus* **sp. nov.** from the Shiny Cowbird *Molothrus bonariensis* (Gmelin) (Icteridae), and *P. carmenmirandae* **sp. nov.** from the Rufous-collared Sparrow *Zonotrichia capensis* (Statius Müller) (Passerellidae). The former is similar to *P. egglestoni* Spory and differs from it in having a unique shape of opisthosomal lobes in females; *P. carmenmirandae* is closer to *P. tiaris* Atyeo & Braasch and differs in having a relatively longer adeagus in males and setae *h1* situated on soft tegument between hysteronotal and lobar shields in females.

Keywords: Feather mites, *Molothrus bonariensis*, *Zonotrichia capensis*, Icteridae, Passerellidae, Analgoidea, symbionts, Systematics, host-association

Introduction

Among the most diverse genera of feather mites (Astigmata: Analgoidea and Pterolichoidea) (Oconnor 1984), *Proctophyllodes* Robin, 1868 (Analgoidea: Proctophyllodidae: Proctophyllodinae) currently includes nearly 180 named species (Atyeo & Braasch 1966; Hernandes *et al.* 2017; Mironov 2012, 2017; Mironov *et al.* 2017; Mironov 2019; Mironov & OConnor 2014; Wang *et al.* 2014; Yamasaki *et al.* 2018). A high specificity and co-diversification of feather mites with their hosts renders this number only as a small fraction of the *Proctophyllodes* total richness, as these mites are predominantly found on passerines of the suborder Passeri (oscine birds), which represent around 78% of the ca. 5000 passerine species in the world (Clements *et al.* 2019; Klimov *et al.* 2017b). Notwithstanding, *Proctophyllodes* species have also been recorded on Tyranni (suboscine) passerines, as well as on few avian hosts of the orders Charadriiformes, Apodiformes, and Piciformes, although these represent events of host switch from oscine passerines with further speciation (Atyeo & Braasch 1966; Černý 1974; Klimov *et al.* 2017b). Philips (2000) and Atyeo and Braasch (1966) also recorded *Proctophyllodes* species on birds from the orders Strigiformes and Falconiformes, however, these records were only temporary transfers by predatory-prey interaction, not representing valid host associations (Gaud 1992; Pedroso & Hernandes 2018a). Due to the large number of species, the genus *Proctophyllodes* was arbitrarily divided into 12 artificial groups to facilitate species delimitation (Atyeo & Braasch 1966; Gaud & Fain 1990; Mironov 2012; Mironov & Kopij 1996). Recently, monophyly of most of these groups was confirmed by molecular phylogenetic studies (Klimov *et al.* 2017a, b).

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Scientific Note

Genetic variation is predominantly structured by geography rather than host in feather mites (Acariformes: Sarcoptiformes) associated with tanagers (Aves: Thraupidae) in Brazil

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Abstract. Feather mites are the most common ectosymbionts on birds. These obligatory symbionts are mainly transmitted during their host's parental care, which creates high host specificity. Due to this intimate relationship, it is thought that their geographic distribution is restricted by their host distribution, or that a host species harbors the same mite composition across its whole range. However, our knowledge regarding the geographic distribution of feather mites remains scarce, with only a few studies indicating disconnections between mite and host distributions, especially in widespread hosts. Here, we investigate the feather mites distribution on four tanager species, three widespread – *Thraupis sayaca* (L.), *T. palmarum* (Wied), and *Stilpnia cayana* (L.) from Northern and Southern Brazil; and the Amazonian *T. episcopus* (L.). Feather mites were identified using the molecular barcode marker COX-1 using K2P genetic distances. We found a strong genetic structure between Northern and Southern populations of tanagers of more than 10%, even among conspecific hosts. Therefore, the mite distribution on Brazilian tanagers is predominantly shaped by geography rather than by host species. These features in turn reflect historical horizontal transmissions among the hosts, suggesting a high potential for frequent host switches in these symbionts.

Keywords: cryptic species, biogeography, symbionts, coevolution, Psoroptidia.

Analgoidean feather mites (Sarcoptiformes: Analgoidea) are the most abundant ectosymbionts associated with passerine birds (Aves: Passeriformes) (Gaud & Atyeo 1996). These mites have high levels of host specificity and most mite species are found on a single or closely related host species. In addition, different mites species can co-exist in different microhabitats of the same host individual (Dabert & Mironov 1999). Despite being common and abundant avian ectosymbionts, many aspects of the feather mite ecology remain underexplored. One such aspect is their geographic distribution with respect to their host ranges. Does a feather mite distribution mirror that of its host? Does a host species have the same set of feather mites across its whole distribution? Only a few studies addressed those questions; in general they indicate that the feather mite assemblage on a bird species may be affected by climatic variables, such as humidity and temperature (Grossi & Proctor 2021; Meléndez et al. 2014); or reflect vicariance due to historical isolation of host populations (Dabert & Mironov 1999).

In ubiquitous hosts spread by humans, such as rock pigeons, *Columba livia* Gmelin, 1789 and domestic chickens, *Gallus gallus domesticus* (L., 1758), mite assemblages apparently change in new localities, indicating that some mite species have been acquired in recent events of interaction with native and phylogenetically similar host species (Gaud 1992). As for feather mites on naturally widespread host species, *i.e.* generalist hosts with high adaptive plasticity, a molecular identification of mites is often required to investigate their patterns of distribution, either for a proper identification of different mite haplotypes across different localities, as for the identification of potential cryptic species (Doña et al. 2015). Notwithstanding, assessing the geographic distribution of symbionts is a background needed to measure their dispersal potential and their specificity level. Yet, almost no effort has been made to properly understand the patterns of distribution of these symbionts, especially in the Neotropics, where many feather mite species are yet to be named (Valim et al. 2011; Pedroso & Hernandes 2016). Our knowledge is especially scarce for Brazil, a country with various landscapes and one of the richest bird faunas in the World (Pacheco et al. 2021). Therefore, here we investigate the preliminary distribution of feather mites on tanagers (Thraupidae Cabanis, 1847), comparing samples from Brazilian Northern and Southern territories.

Feather mites were collected from four common and widespread tanager species: *Thraupis sayaca* (L., 1766), *T. palmarum* (Wied, 1821), *Stilpnia cayana* (L., 1766) from both Northern and Southern territories of Brazil, and the Amazonian *T. episcopus* (L., 1766). Birds were captured using mist nets in: Amazon Forest (AMF), Northeast Atlantic Forest (NAF), and Southeast Atlantic Forest (SAF) (Tab. 1). Feather mites were collected by plucking infested feathers (permit MMA/SISBIO 57944), then their DNA was extracted and a barcode gene, the mitochondrial cytochrome oxidase subunit-1 (COX-1) was sequenced following the protocols, primers, and parameters described in Klimov & OConnor (2008). A Maximum Likelihood phylogenetic tree was inferred using RaxML, also using sequences from previous studies, including samples of mites on tanagers from Mexico (Klimov et al. 2017). Mite's exoskeletons (vouchers) were slide-mounted for morphological identification using Hoyer's Medium (Gaud & Atyeo 1996). All specimens were deposited at the Department of Ecology and Zoology of the Universidade Federal de Santa Catarina (ECZ-UFSC).

Two species delimitation criteria based on the COX-1 were also performed – (i) a distance based delimitation using the Kimura-two-parameter (K2P) distance calculated in the R package 'ape' 5.3 (Paradis