diversity

Article

Host-Parasite Relationships of Quill Mites (Syringophilidae) and Parrots (Psittaciformes)

Natalia Marciniak-Musial [1,*], Maciej Skoracki [1], Jakub Z. Kosicki [2], Markus Unsöld [3] and Bozena Sikora [1,*]

1 Department of Animal Morphology, Faculty of Biology, Adam Mickiewicz University in Poznan, Uniwersytetu Poznanskiego 6, 61-614 Poznan, Poland
2 Department of Avian Biology and Ecology, Faculty of Biology, Adam Mickiewicz University in Poznan, Uniwersytetu Poznanskiego 6, 61-614 Poznan, Poland
3 Zoologische Staatssammlung München, Sektion Ornithologie, Münchhausenstr. 21, 81247 Munich, Germany
* Correspondence: natalia.marciniak@amu.edu.pl (N.M.-M.); bozena.sikora@amu.edu.pl (B.S.)

Abstract: The family Syringophilidae (Acari: Prostigmata) includes obligatory ectoparasites, which occupy feather quills from various parts of avian plumage, where they feed and reproduce. Our study was concerned with the global fauna of syringophilid mites associated with Psittaciformes, as well as host-parasite specificity and evolution. We assumed that the system composed of quill mites and parrots represents a model group that can be used in a broader study of the relationships between parasites and hosts. In total, we examined 1524 host individuals of parrots belonging to 195 species, 73 genera, and 4 families (which constitute ca. 50% of global parrot fauna) from all zoogeographical regions where Psittaciformes occur. Among them, 89 individuals representing 81 species have been infested by quill mites belonging to 45 species and 8 genera. The prevalence of host infestations by syringophilid mites varied from 2.8% to 100% (95% confidence interval (CI Sterne method) = 0.1–100). We applied a bipartite analysis to determine the parasite-host interaction, network indices, and host specificity at the species and whole network levels. The Syringophilidae-Psittaciformes network was composed of 24 mite species and 47 host species. The bipartite network was characterized by a high network level specialization $H2' = 0.98$, connectance $C = 0.89$, and high modularity $Q = 0.90$, with 23 modules, but low nestedness $N = 0.0333$. Moreover, we reconstructed the phylogeny of the quill mites on the generic level, and this analysis shows two distinct clades: *Psittaciphilus* (*Peristerophila* + *Terratosyringophilus*) (among Syringophilinae subfamily) and *Lawrencipicobia* (*Pipicobia* + *Rafapicobia*) (among Picobiinae). Finally, the distributions and host-parasite relationships in the system composed of syringophilid mites and parrots are discussed.

Keywords: Acari; biodiversity; parrots; Psittaciformes; quill mites; Syringophilidae

check for updates

Citation: Marciniak-Musial, N.; Skoracki, M.; Kosicki, J.Z.; Unsöld, M.; Sikora, B. Host-Parasite Relationships of Quill Mites (Syringophilidae) and Parrots (Psittaciformes). *Diversity* **2023**, *15*, 1. https://doi.org/10.3390/d15010001

Academic Editors: Joanna N. Izdebska, Leszek Rolbiecki and Dimitar Dimitrov

Received: 31 October 2022
Revised: 15 December 2022
Accepted: 15 December 2022
Published: 20 December 2022

1. Introduction

The study of parasitic organisms and their relationships to their hosts has, through the decades, enjoyed contributions from those who have studied parasites and parasitism from morphological, ecological, phylogenetical, physiological, and other standpoints [1]. Studying parasites in their own right is relatively simple, but the analyses of the interrelations between the parasite and its host requires a broad spectrum of biological disciplines [2]. As it increasingly happens in more sections of biological sciences, parasitologists are examining parasites and parasitism at all levels of organization, ranging from population and macro-ecological, to the micro-ecological levels [2].

The concept of the host-parasite relationship is an essential tenet in the study of parasitism because it provides the basis for understanding the manner in which the partners are tied to each other, both evolutionarily and ecologically [3,4]. As parasite-host relationships may constitute up to 75% of all species interactions in food webs [5], they are important at every level, up to entire ecosystems [6]. For this reason, precise indicators (including nestedness, specificity at the host and species level, connectance, and modularity) enhance the interpretation of the related communities [7,8].

Quill mites of the family Syringophilidae (Acariformes: Prostigmata: Cheyletoidea) are permanent and obligatory avian ectoparasites [9]. Syringophilid mites live, feed on, reproduce, and occupy various types of feathers of the avian plumage [9,10]. Their long and styletiform mobile digits of the chelicerae facilitate piercing the fibrous wall of the calamus and penetrating the interiors of quill feathers [10–12]. They are related to many orders of birds throughout the world. Based on their potential host species richness, Johnston and Kethley [13] noticed that all quill mite species permanently associated with birds could reach about 5000 species. Moreover, the distribution of quill mites includes all zoogeographical regions, which is correlated with their host distribution. Syringophilid mites are highly host-specific, and most known syringophilid species are mono- or oligoxenous parasites. To date, more than 400 species and 63 genera of quill mites have been described from about 670 bird species belonging to 27 orders of birds [14].

Although most of the work on the family deals with the morphology and systematics of these mites, recent studies focused on the non-taxonomical aspects, e.g., on anatomy [15–18], sexual selection [19], phylogeny [20–22], ecology [14,23–27]; and host-parasite relationships [22,28–30]. There are also an increasing number of papers with studies on trophic relationships in the host-parasite systems based on bipartite networks and some indices (e.g., nestedness, modularity, connectance). For quill mites, that research was conducted with the following host groups: passerines (Estrildidae [31], Nectariniidae [29]), cuckoos [28], and columbids [30,32]. The analysis of bipartite networks provides valuable information about the relationships between parasites and their hosts. In addition, they give a better understanding of their structure and impact on each other. Due to the syringophilid host- and habitat-specificity, they are a good model for the study of the ecological and evolutionary host-parasite relationships.

Parrots (Psittaciformes) are large and diverse bird order. This avian clade comprises about 390 living species belonging to four families: Strigopidae, Cacatuidae, Psittaculidae, and Psittacidae [33], which constitute three main lineages: Strigopoidea (New Zealand parrot), Psittacoidea (also called 'true parrots') and Cacatuoidea (cockatoos) [34]. The distribution of Psittaciformes is mainly related to the Southern Hemisphere, with ranges in Australasian, Oceanian, Oriental, Neotropical, and Afrotropical zoogeographical regions. They originated in Gondwana, with the Australasian region as the center of their radiation and distribution [35–37]. The most recent data indicate their closest affinity with passerines (Passeriformes), followed by falcons (Falconiformes). All three orders now form a single clade of Australaves [38,39] (belonging to the so-called Telluraves—core land birds [40]). The affinity between parrots and passerines is also confirmed by other studies on the evolution of modern Neoaves, which use different dating methods [38,41]. Parrots have the greatest diversity in South America and Australia. The superfamily Strigopoidea diverged from the other parrots around 82 mya when New Zealand broke off from Gondwana. In the Eocene, about 59 mya, Psittacoidea and Cacatoidea had a common ancestor. Finally, they diverged from each other at about 40.7 mya when Australia split off from western Antarctica and South America [42]. The families Psittaculidae and Psittacidae have been constituted into the superfamily clade of Psittacoidea [34,37]. Based on their complicated evolution history and poorly known relationship with mite parasites, parrots are a very interesting subject of examination regarding the infestation of quill mites.

In the present paper, we (1) summarized all taxonomic and locality records to create a worldwide distribution of quill mites associated with birds of the order Psittaciformes; (2) constructed a key to all species and genera of syringophilid mites parasitizing parrots; (3) described interactions and measured the specificity of quill mites and parrots at a global scale; (4) reconstructed the phylogeny of mites associated with parrots on a generic level, and finally (5) discussed the relationships between quill mite species and psittaciform birds.

2. Materials and Methods

2.1. Mite Material

In this study, we re-examined all syringophilid species described from birds of the order Psittaciformes. Mite material was examined mainly based on the syringophilid collection deposited in the Adam Mickiewicz University in Poznan, Department of Animal Morphology, Poznan, Poland. Other mite species were loaned from the collections deposited in different museums and institutions, i.e., Royal Museum for Central Africa, Tervuren, Belgium; Zoological Institute, Russian Academy of Science, St. Petersburg, Russia; Field Museum of Natural History, Chicago, IL, USA; National Autonomous University of Mexico (Universidad Nacional Autonoma de Mexico), Mexico City, Mexico.

2.2. Morphological Characters

The general morphological terminology for quill mites follows Skoracki [12] and Skoracki et al. [43]. The idiosomal setation follows Grandjean [44], as adapted for Prostigmata by Kethley [45]. The nomenclature of leg chaetotaxy follows that proposed by Grandjean [46]. All measurements are given in micrometers.

2.3. Prevalence

To describe the prevalence, we examined the bird collection (dry bird skins) housed in the Bavarian State Collection of Zoology, Munich, Germany, according to the methodology presented in Skoracki [12]. This bird collection was previously used as a donor of many mite species described and recorded in previous papers (e.g, Skoracki [12,47]; Skoracki et al. [43,48]; Skoracki & Hromada [49]; Marciniak et al. [50,51], Marciniak-Musial et al. [52]; Marciniak-Musiał & Sikora [53]). Descriptive statistics were computed using Quantitative Parasitology on the Web [54], with 95% confidence intervals (Sterne method).

2.4. Host Specificity

Terminology for the host specificity for particular mite species follows Caira et al. [55] and Skoracki et al. [43]. The division is based on host range and termed as: monoxenous species (parasite restricted to one host species), oligoxenous (more than one host, but restricted to one genus), mesostenoxenous (more than one genus of hosts, but restricted to one family), metastenoxenous (more than one family of hosts but restricted to one order), and polyxenous species (more than one order).

2.5. Host Scientific Names and Zoogeographical Regions

The common and scientific names of the birds follow Clements et al. [33]. Zoogeographic regions follow Holt et al. [56].

2.6. Bipartite Networks and Statistics

One way to represent the parasite-host interactions between quill mites and avian hosts is through the use of a 'bipartite' network. The 'bipartite' graph consists of rectangles representing compartment species, and the width is proportional to the sum of interactions involving that species. The number of interactions is shown by lines linking the species with different widths. To analyze patterns in the studied host-parasite-network, we used the 'bipartite' package available for R software [57]. The web was visualized by plotweb function. The number of quill mite species infesting each bird species was used as quantitative indices.

During our study, we prepared matrices where quill mite species are in the rows (parasites) and the bird species are (host) in the columns. Next, we calculated the following bipartite index: network specialization (H2′), nestedness (N), connectance (C), modularity (Q), and species specialization metrics (d′). Index of specialization at the species level (d′) measures interaction at the species level and refers to each quill mite species associated with parrots in the network [58]. Index of network specialization H2′ means the deviation of a species' realized number of interactions and that expected from each species' total number of interactions [59], with values ranging from 0 (implying low specialization) to 1 (suggesting high specialization). Nestedness describes how many interactions realized by specialists are a subset of those realized by generalists. The nestedness unit is the nestedness temperature T (0–100°). However, in this study, we used a binary system where metrics define as N = (100 − T)/100. It measures the departure from a perfectly nested interaction matrix [60]. In the range 0–1, value 1 implies maximum nestedness [61–63]. Connectance is understood as the proportion of possible links observed in the network, ranging from 0 to 1, where 0 suggests low connectance while approaching 1 means high connectance in the network [64]. Modularity is calculated as 'likelihood' implemented in computeModules in the bipartite library for R and has the same value meaning as Q (or M), given by Newman [65], Guimerà & Amaral [66], and is currently not supported by a library of QuanBiMo (Q) [67]. We evaluated 100 Q values (observed likelihood) [68] and compared them with 100 Q values coming from permutations for null models (null likelihood). Next, we also calculated the null.t.test ($p < 0.05$) to test a significant difference between the Q observed and Qnull values.

2.7. Mite Phylogeny

During the cladistic analysis, we examined relationships at the generic level, and OTUs (all operational units) were represented by taxonomic species, i.e., species related to parrots. Therefore, the character traits that appear as autapomorphies represent true synapomorphies for the genera. A total of nine OTUs representing all genera associated with psittaciform birds were included in our data matrix. Two species, i.e., a free living predator *Cheyletus eruditus* (Schrank, 1781) and quill-inhabiting predator *Cheletopsis norneri* (Poppe, 1888), both belonging to the sister family Cheyletidae, were used as the outgroups. In total, 56 unordered morphological characters were included in our data matrix (data matrix and morphological characters are supplemented (Figures S1 and S2). The data matrix was prepared in the NEXUS Data Editor 0.5.0 [69]. All characters were treated as unordered, and their states were polarized using outgroup comparison. The plesiomorphic state of each character was designated as '0', apomorphic as '1', and inapplicable as '-'. Reconstruction of phylogenetic relationships was performed with PAUP 4.0 [70]. The heuristic search option was used for maximum parsimony analysis. The delayed transformation option, which favors parallelism over reversal, was applied for a posteriori optimization of character states and tracing character changes in lineages.

2.8. Visualization of Host Phylogeny

A tree of the parrot species was constructed based on data and a consensus avian phylogenetic tool available from http://birdtree.org/ (accessed on 21 June 2022) [71], using the "Hackett All Species tree" with 1000 randomly generated trees. The most credible tree was then determined using the tool TreeAnnotator v1.8.2 in the software BEAST v1.8.2 Z [72]. The consensus tree was then graphically adjusted in FigTree v1.4.2 2 [73] (Andrew Rambaut, University of Edinburgh, UK; http://tree.bio.ed.ac.uk/software/figtree/ (accessed on 21 June 2022).

3. Results

3.1. The Species Richness of Syringophilid Mites Associated with Parrots

3.1.1. Subfamily Syringophilinae Lavoipierre, 1953

Mites of this subfamily occupy the quills of flight feathers, i.e., primaries, secondaries, rectrices, and wing and tail coverts. Mites of this subfamily differ from the Picobiinae ones by the presence of the rounded tibiotarsus of palps and fan-like proral setae of tarsuses I–IV.

The known Syringophilinae fauna from parrots comprises 28 species grouped in 5 genera, i.e., *Megasyringophilus* Fain, Bochkov & Mironov, 2000 (9 species), *Neoaulobia* Fain, Bochkov & Mironov, 2000 (11), *Peristerophila* Kethley, 1970 (3), *Psittaciphilus* Fain, Bochkov & Mironov, 2000 (2), and *Terratosyringophilus* Bochkov & Perez, 2002 (3). Syringophiline mites have been recorded on parrots belonging to all extant families, i.e., Cacatuidae, Psittacidae, Psittaculidae, and Strigopidae (Table 1).

Genus *Megasyringophilus* Fain, Bochkov & Mironov, 2000

This genus comprises large-sized syringophilids (total body length 950–1350), which are distinguished from the other genera by the combination of the following features in females: lateral hypostomal teeth are absent; the peritremes are M-shaped; the stylophore is rounded or slightly constricted posteriorly; the propodonotal shield is without pocket-like structures; the idiosoma and legs are with the full complement of smooth setae; legs I–IV are sub equal in thickness; the apodemes I are divergent, indistinctly fused to the apodemes II, and both apodemes are dissimilar in size and shape.

Currently, this genus comprises 11 species recorded in birds belonging to three orders; Accipitriformes, Psittaciformes, and Strigiformes [14], from the Afrotropical, Australian, Neotropical, Nearctic, Oriental, Oceanian, and Palearctic zoogeographical regions [47,74–80].

The *Megasyringophilus* fauna associated with parrots includes most of the described taxa of this genus and consists of nine species noted on representatives Cacatuidae, Psittaculidae, and Psittacidae.

Species included:

M. cacatua Glowska & Laniecka, 2013. Monoxenous parasite associated with Sulphur-crested Cockatoo *Cacatua galerita* (Latham) (Cacatuidae) from Australia [81].

M. cyanocephala Fain, Bochkov & Mironov, 2000. Oligoxenous species associated with psittaculid parrots of the genus *Psittacula* (Psittaculidae): Plum-headed Parakeet *P. cyanocephala* (Linnaeus), Alexandrine Parakeet *P. eupatria* (Linnaeus), and Rose-ringed Parakeet *P. krameri* (Scopoli) all host species from India [74,76].

M. dubinini Bochkov & Fain, 2003. Monoxenous parasite associated with Ornate Lorikeet *Saudareos ornatus* (Linnaeus) (Psittaculidae) from India [76].

M. eos Skoracki, 2005. Monoxenous parasite associated with Red Lory *Eos bornea* (Linnaeus) (Psittaculidae) from Indonesia [47].

M. geoffroyus Skoracki, 2005. Monoxenous parasite associated with Red-cheeked Parrot *Geoffroyus geoffroyi* (Bechstein) (Psittaculidae) from (Papua New Guinea) [47].

M. kethleyi Fain, Bochkov & Mironov, 2000. Mesostenoxenous parasite associated with parrots of the family Psittacidae: Jandaya Parakeet *Aratinga jandaya* (Gmelin) from Brazil, White-winged Parakeet *Brotogeris versicolurus* (St. Muller) from Brazil, and psittacid parrots of the genus *Eupsittula*: Orange-fronted Parakeet *E. canicularis* from Mexico, and Brown-throated Parakeet *E. pertinax* from Brazil [74,76,77].

M. platycercus Bochkov & Fain, 2003. Monoxenous parasite associated with Eastern Rosella *Platycercus eximius* (Shaw) (Psittaculidae) from Australia [76].

M. rhynchopsittae Bochkov & Perez, 2002. Monoxenous parasite associated with Thick-billed Parrot *Rhynchopsitta pachyrhyncha* (Swainson) (Psittacidae) from Mexico [75].

M. trichoglossus Fain, Bochkov & Mironov, 2000. Oligoxenous species associated with psittaculid parrots of the genus *Trichoglossus* (Psittaculidae): Olive-headed Lorikeet *T. euteles* (Temminck) from Indonesia, Scaly-breasted Lorikeet *T. chlorolepidotus* (Kuhl) from Australia, and unknown species *Trichoglossus* sp. from Papua New Guinea [47,74].

Genus *Neoaulobia* Fain, Bochkov & Mironov, 2000

The genus *Neoaulobia* comprises medium-sized syringophilids (total body length 430–730), exclusively associated with parrots. The females of the genus can be distinguished from other genera by the following combination of features: lateral hypostomal teeth are absent; the peritremes are M-shaped; the stylophore is slightly constricted posteriorly; the propodonotal shield is without pocket-like structures; the idiosoma is with the full complement of smooth setae; leg setae *dTIII–IV* or only *dTIII* are absent; legs I–IV are sub equal in thickness; the apodemes I are parallel and not fused to the apodemes II.

Currently, the *Neoaulobia* genus comprises 11 species recorded on members of the parrot families Cacatuidae, Psittaculidae, and Psittacidae in the Afrotropical, Australian, Oriental, Nearctic, and Neotropical regions [47,50,52,53,74–77,82].

Species included:

N. aratingae Fain, Bochkov & Mironov, 2000. Monoxenous parasite associated with Jandaya Parakeet *Aratinga jandaya* (Gmelin) (Psittacidae) from Brazil [74].

N. agapornis Fain, Bochkov & Mironov, 2000. Oligoxenous species associated with parrots of the genus *Agapornis* (Psittaculidae): Black-cheeked Lovebird *A. nigrigenis* Sclater from Zambia, Fischer's Lovebird *A. fischeri* (Reichenow) from Tanzania, Yellow-collared Lovebird *A. personatus* Reichenow from Tanzania, Rosy-faced Lovebird *A. roseicollis* (Vieillot) from Namibia, Black-winged Lovebird *A. taranta* (Stanley) from Ethiopia [74,76].

N. cacatui Marciniak, Skoracki & Hromada, 2019. Mesostenoxenous parasite associated with cockatoos (Cacatuidae): Yellow-tailed Black-Cockatoo *Calyptorhynchus funereus* (Shaw) from Australia, and Palm Cockatoo *Probosciger aterrimus* (Gmelin) from Papua New Guinea [50].

N. krafti Skoracki, 2005. Monoxenous parasite associated with Long-billed Corella *Cacatua tenuirostris* (Kuhl) (Cacatuidae) from Australia [47].

N. unsoeldi Marciniak-Musial & Sikora 2002. Mesostenoxenous parasite associated with psittacid parrots: Turquoise-fronted Parrot *Amazona aestiva* (Linnaeus) from Paraguay, Red-and-green Macaw *Ara chloropterus* Gray from Costa Rica, and Burrowing Parakeet *Cyanoliseus patagonus* (Vieillot) from Argentina [53].

N. mexicana Bochkov & Perez, 2002. Oligoxenous species associated with psittacid parrots of the genus *Eupsittula* (Psittacidae): Orange-fronted Parakeet *E. canicularis* from Mexico, and Brown-throated Parakeet *E. pertinax* from Brazil [75,76].

N. mironovi Bochkov & Perez, 2002. Monoxenous parasite associated with Lilac-crowned Parrot *Amazona finschi* Sclater (Psittacidae) from Mexico [75,77].

N. pseudeos Marciniak-Musial, Hromada & Sikora, 2022. Monoxenous parasite associated with Dusky Lory *Pseudeos fuscata* (Blyth) (Psittaculidae) from Papua New Guinea [52].

N. psittaculae Fain, Bochkov & Mironov, 2000. Monoxenous parasite associated with Plum-headed Parakeet *Psittacula cyanocephala* (Linnaeus) (Psittaculidae) from India [74].

N. puylaerti (Skoracki & Dabert 1999). Metastenoxenous parasite associated with Philippine Hanging-Parrot *Loriculus philippensis* (St. Muller) (Psittaculidae) from Philippines, Yellow-throated Hanging-Parrot *Loriculus pusillus* Gray (Psittaculidae) from Indonesia, and Senegal Parrot *Poicephalus senegalus* (Linnaeus) (Psittacidae) from Togo [47,82].

N. skorackii Marciniak-Musial, Hromada & Sikora, 2022. Monoxenous parasite associated with Eastern Rosella *Platycercus eximius* (Shaw) (Psittaculidae) from Australia [52].

Genus *Peristerophila* Casto, 1980

The *Peristerophila* genus comprises medium- or large-sized syringophilids (total body length in homeomorphic form of females 535–750; in heteromorphic form of females 800–1000), distinguished from other genera by the following combination of features: lateral hypostomal teeth are absent; the peritremes are M-shaped; the stylophore is rounded posteriorly; the propodonotal shield is without pocket-like structures; the propodonotal setae vi are absent; leg setae *dFII–IV* and *vsII* are absent; legs I are thicker than II–IV; and the apodemes I are parallel and fused to the apodemes II. It is worth adding that in this genus, two forms of females (homeomorphic and heteromorphic) are present [83].

The genus comprises 15 species recorded on the broadest host spectrum among quill mite genera, and it consists of representatives of the following bird orders, Accipitriformes, Bucerotiformes, Columbiformes, Falconiformes, and Psittaciformes from the Holarctic, Afrotropical, Neotropical, Oriental, Oceanian, and Saharo-Arabian regions [12,51,83–89].

The fauna associated with parrots includes three species noted on representatives of the parrot families Psittaculidae, Psittacidae, and Strigopidae. Within these three mite species, two are exclusively related to parrots [51,75], but one—*Peristerophila mucuya* Casto, 1980—has psittaciform and columbiform hosts.

Species included:

P. forpi (Bochkov & Perez, 2002). Monoxenous parasite associated with Mexican Parrotlet *Forpus cyanopygius* (Souancé) (Psittacidae) from Mexico [75].

P. mucuya Casto, 1980. Polixenous parasite associated with hosts of the orders Psittaciformes and Columbiformes. The following parrot species are hosts for this quill mite: White-winged Parakeet *Brotogeris versicolurus* (St. Muller) (Psittacidae) from Brazil [53,76], Gray-hooded Parakeet *Psilopsiagon aymara* (d'Orbigny) (Psittacidae) from South America [76], and Coconut Lorikeet *Trichoglossus haematodus* (Linnaeus) (Psittaculidae) from Indonesia [76]. The columbiform hosts for this mite species are given in the recent paper of Kaszewska et al. [88].

P. nestoriae Marciniak, Skoracki & Hromada, 2019. Monoxenous parasite associated with New Zealand Kaka *Nestor meridionalis* (Gmelin) from New Zealand [51].

Genus *Psittaciphilus* Fain, Bochkov & Mironov, 2000

The genus *Psittaciphilus* comprises medium-sized syringophilids (total body length 600–800), distinguished from other genera by the following combination of features in females: lateral hypostomal teeth are absent; the peritremes are M-shaped; the stylophore is constricted posteriorly; the propodonotal shield is with pocket-like structures; the propodonotal setae vi are absent; leg setae *dFII–IV* and *vsII* are absent; legs I thicker than II–IV; the apodemes I are divergent and not fused to the apodemes II.

Currently, this genus comprises four species recorded on birds belonging to two orders, Columbiformes and Psittaciformes. All species have been recorded only in the Neotropical region [53,74,76,90].

The fauna associated with parrots includes two species noted on host representatives of the family Psittacidae.

Species included:

P. amazonae Fain, Bochkov & Mironov, 2000. Oligoxenous species associated with psittaculid parrots of the genus *Amazona* (Psittacidae): Turquoise-fronted Parrot *A. aestiva* (Linnaeus) from Brazil, Orange-winged Parrot *A. amazonica* (Linnaeus) from Colombia, Yellow-crowned Parrot *A. ochrocephala* Berlepsch from Brazil [74,76].

P. fritschi Fain, Bochkov & Mironov, 2000. Monoxenous parasite associated with unidentified parrot (Psittacidae) from South America [Amazonia] [74].

Genus *Terratosyringophilus* Bochkov & Perez, 2002

This genus comprises large-sized syringophilids (total body length 1370–1850) distinguished from other genera by the following combination of features: lateral hypostomal teeth are absent; the peritremes are M-shaped; the stylophore is rounded posteriorly; the propodonotal shield is without pocket-like structures; the propodonotal setae vi are absent; leg setae *dFII* and *vsII* are absent, *dFIII–IV* are present but replaced ventrally; legs I–II are thicker than III–IV; the apodemes I are parallel and fused to the apodemes II.

Terratosyringophilus includes five species recorded from birds of the orders Psittaciformes and Columbiformes. They were noted in the Nearctic, Neotropical, Oceanian, and Oriental regions [47,75,76,91,92]. Currently, three species of this genus have been recorded from parrots belonging to the families Psittaculidae and Psittacidae.

Species included:

T. loricinus Bochkov & Fain, 2003. Mesostenoxenous parasite associated with parrots of the family Psittaculidae: Chattering Lory *Lorius garrulus* (Linnaeus) from Indonesia [Halmahera Isl.], and Coconut Lorikeet *Trichoglossus haematodus* (Linnaeus) from Indonesia [Sumbawa Isl.] [76].

T. pioni Bochkov & Perez, 2002. Monoxenous parasite associated with White-crowned Parrot *Pionus senilis* (Spix) (Psittacidae) from Mexico [75].

T. reichholfi Skoracki & Sikora, 2008. Monoxenous parasite associated with Black-capped Lory *Lorius lory* (Linnaeus) (Psittaculidae) from Papua New Guinea [91].

3.1.2. Subfamily Picobiinae Johnston & Kethley, 1973

Mites of this subfamily differ from the Picobiinae by the presence of the truncated tibiotarsus of palps and rod-like proral setae of tarsuses I–IV. In addition, they exclusively occupy the quills of contour feathers, with one exception to this rule—*Calamincola lobatus* Casto, 1977—a representative of the enigmatic and monotypic genus found in the quills of wing feathers [93].

The Picobiinae fauna known from parrots comprises three genera and 17 species, i.e., *Lawrencipicobia* Skoracki & Hromada, 2013 (7 species), *Pipicobia* Glowska & Schmidt, 2014 (5), and *Rafapicobia* Skoracki, 2011 (5). Picobiinae mites have been recorded on parrots belonging to all extant families, i.e., Cacatuidae, Psittacidae, and Psittaculidae (Table 1).

The analysis of picobiinae relationships with the avian hosts in research provided by Skoracki et al. [22] shows that Picobiinae genera form two distinct monophyletic clades: *Picobia*-generic group and *Neopicobia*-generic-group. The clade *Neopicobia*-generic group comprises six genera, including all the below mentioned genera associated with parrots.

Genus *Rafapicobia* Skoracki, 2011

This genus comprises small-sized picobiines (total body length 450–650) distinguished from other genera by the following combination of features: the hypostomal apex tapering; the opisthonotal and genital lobes are absent; the pseudanal series is represented by two pairs of setae; the genital series with one pair of setae; apodemes I are without thorn-like protuberances; solenidia *phi* (φ) on tibiae I are absent.

Currently, 19 representatives of the genus *Rafapicobia* are associated with five bird orders: Coraciiformes, Gruiformes, Passeriformes, Piciformes, and Psittaciformes [14,94,95]. They have been recorded in the Afrotropical, Nearctic, Neotropical, Palaearctic, and Sino-Japanese regions [43,48,49,82,96–99]. Among them, five species are known to parasitize parrots from a single family, Psittacidae.

Species included:

R. brotogeris (Fain, Bochkov & Mironov, 2000). Mesostenoxenous parasite associated with psittacid parrots: Andean Parakeet *Bolborhynchus orbygnesius* (Souancé) from Peru, Yellow-chevroned Parakeet *Brotogeris chiriri* (Vieillot) from Paraguay, Cobalt-winged parakeet *Brotogeris cyanoptera* (Pelzeln) from Brazil, Orange-chinned Parakeet *Brotogeris jugularis* (St. Muller) from Panama, White-winged Parakeet *Brotogeris versicolurus* (St. Muller) from Brazil, Northern Red-shouldered Macaw *Diopsittaca nobilis* (Linnaeus) from Surinam, Peach-fronted Parakeet *Eupsittula aurea* (Gmelin) from Brazil, Brown-throated Parakeet *Eupsittula pertinax* (Linnaeus) from Surinam, Monk Parakeet *Myiopsitta monachus* (Boddaert) from Argentina, Pileated Parrot *Pionopsitta pileata* (Scopoli) from Paraguay, Mountain Parakeet *Psilopsiagon* aurifrons (Lesson) from Peru, Grey-hooded Parakeet *Psilopsiagon aymara* (d'Orbigny) from Bolivia, Scarlet-fronted Parakeet *Psittacara wagleri* (Gray) from Venezuela, Painted Parakeet *Pyrrhura picta* (St. Muller) from Guyana, Blue-crowned Parakeet *Thectocercus acuticaudatus* (Vieillot) from Argentina [43,53,74].

R. pyrrhura Marciniak-Musial & Sikora, 2022. Oligoxenous species associated with parrots of the genus *Pyrrhura*: Green-cheeked Parakeet *P. molinae* (Massena & Souance) from Bolivia, Maroon-bellied Parakeet *P. frontalis* (Vieillot), and Pearly Parakeet *P. lepida* (Wagler) both from Brazil [53].

R. trinidadi Marciniak-Musial & Sikora, 2022. Monoxenous parasite associated with Lilac-tailed Parrotlet *Touit batavicus* (Boddaert) from Trinidad and Tobago [53].

R. valdiviana Marciniak-Musial & Sikora, 2022. Mesostenoxenous parasite associated with: Austral Parakeet *Enicognathus ferrugineus* (St. Muller) from Chile, and Burrowing Parrot *Cyanoliseus patagonus* (Vieillot) from Argentina [53].

R. xanthopterygius Marciniak-Musial & Sikora, 2022. Monoxenous parasite associated with Blue-winged *Forpus xanthopterygius* (von Spix) from Brazil [53].

Genus *Lawrencipicobia* Skoracki & Hromada, 2013

The genus *Lawrencipicobia* comprises medium-sized picobiines (total body length 630–860), and differs from other genera by the combination of the following features: the hypostomal apex is flat; the opisthonotal and genital lobes are absent; the pseudanal setal series with two pairs; the genital series with one pair of setae; the apodemes I are with small thorn-like protuberances; solenidia *phi* (φ) on tibiae I are present.

Presently, this genus includes seven species exclusively associated with parrots and recorded from birds of the families Cacatuidae, Psittacidae, and Psittaculidae. They have been noted in the Afrotropical, Australian, and Oriental regions [50,52,53,100].

Species included:

L. ararauna Marciniak-Musial & Sikora, 2022. Monoxenous parasite associated with Black-headed Parrot *Ara ararauna* (Linnaeus) (Psittacidae) from [53].

L. arini Marciniak-Musial & Sikora, 2022. Mesostenoxenous parasite associated with psittacid parrots: White-bellied Parrot *Pionites leucogaster* (Kuhl) (Psittacidae) from Brazil, Black-headed Parrot *Pionites melanocephalus* (Linnaeus) (Psittacidae) from Surinam, and Maroon-bellied Parakeet *Pyrrhura frontalis* (Vieillot) (Psittacidae) from Paraguay [53].

L. calyptorhyncha Marciniak, Skoracki & Hromada, 2019. Monoxenous parasite associated with Glossy Black-Cockatoo *Calyptorhynchus lathami* (Temminck) (Cacatuidae) from Australia [50].

L. eclectus Marciniak-Musial, Hromada & Sikora 2022. Monoxenous parasite associated with Eclectus Parrot *Eclectus roratus* (St. Muller) (Psittaculidae) from Papua New Guinea [52].

L. poicephali (Skoracki & Dabert, 2002). Oligoxenous species associated with parrots of the genus *Poicephalus* (Psittacidae): Senegal Parrot *P. senegalus versteri* Finsch from Cameroon, Cape Parrot *P. robustus* (Gmelin) from DR Congo, Rwanda, Zambia, Red-fronted Parrot *P. gulielmi* (Jardine) from DR. Congo, Tanzania, Kenya, Cameroon, Red-bellied Parrot *P. rufiventri* (Rüppell) from Somalia, Meyer's Parrot *P. meyeri* Cretzschmar from Zimbabwe, Rwanda, Kenya, Brown-necked Parrot *P. fuscicollis* Kuhl from Tanzania, Brown-headed Parrot *P. cryptoxanthus* (Peters) from Tanzania [100,101].

L. sulphurea Marciniak, Skoracki & Hromada, 2019. Monoxenous parasite associated with Yellow-crested Cockatoo *Cacatua sulphurea* (Gmelin) (Cacatuidae) from Indonesia [51].

L. touiti Marciniak-Musial & Sikora, 2022. Monoxenous parasite associated with Golden-tailed Parrotlet *Touit surdus* (Kuhl) (Psittacidae) from Brazil [53].

Genus *Pipicobia* Glowska and Schmidt, 2014

This genus comprises small-sized picobiines (total body length 430–690), distinguished from other genera by the following combination of features: the hypostomal apex is tapering; the opisthosomal and genital lobes are absent; each pseudanal and genital setal series is represented by one pair; apodemes I are with small thorn-like protuberances; solenidia *phi* (φ) on tibiae I are absent.

Members of this genus are known to parasitize birds of the orders Psittaciformes and Passeriformes and have been recorded in the Afrotropical, Australian, and Palearctic regions [47,102–104]. The *Pipiobia* fauna associated with parrots comprises five species recorded on birds from a single family Psittaculidae.

Species included:

P. cyclopsitta Marciniak-Musial, Hromada & Sikora, 2022. Monoxenous parasite associated with Double-Eyed Fig-Parrot *Cyclopsitta diophthalma* (Hombron & Jacquinot) Papua New Guinea [48,52]

P. fuscata Marciniak-Musial, Hromada & Sikora, 2022. Monoxenous parasite associated with Dusky Lory *Pseudeos fuscata* (Blyth) from Papua New Guinea [52].

P. tahitiana Marciniak-Musial, Hromada & Sikora, 2022. Monoxenous parasite associated with Blue Lorikeet *Vini peruviana* (St. Muller) from Tahiti [French Polynesia] [52].

P. malherbi Marciniak-Musial, Hromada & Sikora, 2022. Monoxenous parasite associated with Malherbe's Parakeet *Cyanoramphus malherbi* Souance from New Zealand [52].

P. glossopsitta (Skoracki, Glowska & Sikora, 2008). Oligoxenous species associated with psittaculid parrots of the genus *Parvipsitta* (Psittaculidae): Purple-Crowned Lorikeet *P. porphyrocephala* (Dietrichsen), and Little Lorikeet *P. pusilla* (Shaw), both from Australia [48,52].

Table 1. Quill mite species of the family Syringophilidae parazitising birds of the order Psittaciformes with their distribution.

Quill Mite Species	Host Species	Host Family	Distribution	References
Subfamily **Syringophilinae** Lavoipierre, 1953				
Genus ***Megasyringophilus*** Fain, Bochkov & Mironov, 2000				
M. cacatua Glowska & Laniecka, 2013	*Cacatua galerita* (Latham)	Cacatuidae	Aust. (Australia)	[81]
M. cyanocephala Fain, Bochkov & Mironov, 2000	*Psittacula cyanocephala* (Linnaeus) *	Psittaculidae	Orie. (India)	[74]
	Psittacula eupatria (Linnaeus)	Psittaculidae	Orie. (India)	[76]
	Psittacula krameri (Scopoli)	Psittaculidae	Orie. (India)	[76]
M. dubinini Bochkov & Fain, 2003	*Saudaeeos ornatus* (Linnaeus)	Psittaculidae	Orie. (India)	[76]
M. eos Skoracki, 2005	*Eos bornea* (Linnaeus)	Psittaculidae	Orie. (Indonesia)	[47]
M. geoffroyus Skoracki, 2005	*Geoffroyus geoffroyi* (Bechstein)	Psittaculidae	Ocea. (Papua New Guinea)	[47]
M. kethleyi Fain, Bochkov & Mironov, 2000	*Aratinga jandaya* (Gmelin) *	Psittacidae	Neot. (Brazil)	[74]
	Brotogeris versicolurus (St. Muller)	Psittacidae	Neot. (Brazil)	[76]
	Eupsitulla canicularis (Linnaeus)	Psittacidae	Near. (Mexico)	[77]
	Eupsittula pertinax (Linnaeus)	Psittacidae	Neot. (Brazil)	[76]
M. platycercus Bochkov & Fain, 2003	*Platycercus eximius* (Shaw)	Psittaculidae	Austr. (Australia)	[74]
M. rhynchopsittae Bochkov & Perez, 2002	*Rhynchopsitta pachyrhyncha* (Swainson)	Psittacidae	Near. (Mexico)	[75]
M. trichoglossus Fain, Bochkov & Mironov, 2000	*Trichoglossus* sp.	Psittaculidae	Ocea. (Papua New Guinea)	[74]
	Trichoglossus chlorolepidotus (Kuhl)	Psittaculidae	Austr. (Australia)	[47]
	Trichoglossus euteles (Temminck)	Psittaculidae	Orie. (Indonesia)	[47]
Genus ***Neoaulobia*** Fain, Bochkov & Mironov, 2000				
N. agapornis Fain, Bochkov & Mironov, 2000	*Agapornis nigrigenis* * Sclater	Psittaculidae	Afro. (Zambia)	[74]
	Agapornis fischeri (Reichenow)	Psittaculidae	Afro. (Tanzania)	[76]
	Agapornis personatus Reichenow	Psittaculidae	Afro. (Tanzania)	[76]
	Agapornis roseicollis (Vieillot)	Psittaculidae	Afro. (Namibia)	[76]
	Agapornis taranta (Stanley)	Psittaculidae	Afro. (Ethiopia)	[76]
N. aratingae Fain, Bochkov & Mironov, 2000	*Aratinga jandaya* (Gmelin)	Psittacidae	Neot. (Brazil)	[74]
N. cacatui Marciniak, Skoracki & Hromada, 2019	*Calyptorhynchus funereus* * (Shaw)	Cacatuidae	Austr. (Australia)	[50]
	Probosciger aterrimus (Gmelin)	Cacatuidae	Ocea. (Papua New Guinea)	[50]
N. krafti Skoracki, 2005	*Cacatua tenuirostris* (Kuhl)	Cacatuidae	Austr. (Australia)	[47]
N. mexicana Bochkov & Perez, 2002	*Eupsittula canicularis* * (Linnaeus)	Psittacidae	Near. (Mexico)	[75]
	Eupsittula pertinax (Linnaeus)	Psittacidae	Neot. (Brazil)	[76]
N. mironovi Bochkov & Perez, 2002	*Amazona finschi* Sclater	Psittacidae	Near. (Mexico)	[75,77]
N. pseudeos Marciniak-Musial, Hromada & Sikora, 2022	*Pseudeos fuscata* (Blyth)	Psittaculidae	Ocea. (Papua New Guinea)	[52]
N. psittaculae Fain, Bochkov & Mironov, 2000	*Psittacula cyanocephala* (Linnaeus)	Psittaculidae	Orie. (India)	[74]
N. puylaerti (Skoracki & Dabert 1999)	*Loriculus philippensis* (St. Muller)	Psittaculidae	Orie. (Philippines)	[47]
	Loriculus pusillus Gray	Psittaculidae	Orie. (Indonesia)	[47]
	Poicephalus senegalus (Linnaeus)	Psittacidae	Afro. (Togo)	[82]
N. skorackii Marciniak-Musial, Hromada & Sikora, 2022	*Platycercus eximius* (Shaw)	Psittaculidae	Austr. (Australia)	[52]
N. unsoeldi Marciniak-Musial & Sikora 2002	*Amazona aestiva* (Linnaeus)	Psittacidae	Neot. (Paraguay)	[53]
	Ara chloropterus Gray	Psittacidae	Pana. (Costa Rica)	[53]
	Cyanoliseus patagonus * (Vieillot)	Psittacidae	Neot. (Argentina)	[53]
Genus ***Peristerophila*** Kethley, 1970				
P. forpi (Bochkov & Perez, 2002)	*Forpus cyanopygius* (Souancé)	Psittacidae	Near. (Mexico)	[75]
P. mucuya Casto, 1980	*Brotogeris versicolurus* (St. Muller)	Psittacidae	Neot. (Brazil)	[53,76]
	Psilopsiagon aymara (d'Orbigny)	Psittacidae	Neot. (South America)	[76]
	Trichoglossus haematodus (Linnaeus)	Psittaculidae	Orie. (Indonesia: Sumbawa Isl.)	[76]
	Columbina minuta ** Linnaeus	Claravinae	Neot. (Paraguay)	[88]
	Columbina passerina *,** Linnaeus	Claravinae	Neot. (Colombia, Surinam); Near. (USA)	[84,89]
	Columbina squammata ** (Lesson)	Claravinae	Neot. (Brazil, Paraguay)	[76,88]
	Columbina talpacoti ** (Temminck)	Claravinae	Neot. (Brazil, Surinam, Trinidad and Tobago); Pala. (Monaco)	[88,89]
	Geophaps plumifera ** Gould	Claravinae	Aust. (Australia)	[76]

Table 1. *Cont.*

Quill Mite Species	Host Species	Host Family	Distribution	References
Genus ***Peristerophila*** Kethley, 1970				
P. mucuya Casto, 1980	*Metriopelia ceciliae* ** (Lesson)	Claravinae	Neot. (Peru)	[88]
	Metriopelia melanoptera ** (Molina)	Claravinae	Neot. (Argentina)	[88]
P. nestoriae Marciniak, Skoracki & Hromada, 2019	*Nestor meridionalis* (Gmelin)	Strigopidae	Austr. (New Zealand)	[51]
Genus ***Psittaciphilus*** Bochkov & Mironov, 2000				
P. amazonae Fain, Bochkov & Mironov, 2000	*Amazona aestiva* (Linnaeus)	Psittacidae	Neot. (Brazil)	[76]
	Amazona amazonica * (Linnaeus)	Psittacidae	Neot. (Colombia)	[74]
	Amazona ochrocephala Berlepsch	Psittacidae	Neot. (Brazil)	[49]
P. fritschi Fain, Bochkov & Mironov, 2000	unidentified parrot	Psittacidae	Neot. (South America [Amazonia])	[70]
Genus ***Terratosyringophilus*** Bochkov & Perez, 2002				
T. loricinus Bochkov & Fain, 2003	*Lorius garrulus* * (Linnaeus)	Psittaculidae	Orie. (Indonesia: Halmahera Isl.)	[72]
	Trichoglossus haematodus (Linnaeus)	Psittaculidae	Orie. (Indonesia: Sumbawa Isl.)	[72]
T. pioni Bochkov & Perez, 2002	*Pionus senilis* (von Spix)	Psittacidae	Near. (Mexico)	[75]
T. reichholfi Skoracki & Sikora, 2008	*Lorius lory* (Linnaeus)	Psittaculidae	Ocea. (Papua New Guinea)	[91]
Subfamily **Picobiinae** Johnson & Kethley, 1973				
Genus ***Lawrencipicobia*** Skoracki & Hromada, 2013				
L. ararauna Marciniak-Musial & Sikora, 2022	*Ara ararauna* (Linnaeus)	Psittacidae	Neot. (Brazil)	[53]
L. arini Marciniak-Musial & Sikora, 2022	*Pionites leucogaster* * (Kuhl)	Psittacidae	Neot. (Brazil)	[53]
	Pionites melanocephalus (Linnaeus)	Psittacidae	Neot. (Surinam)	[53]
	Pyrrhura frontalis (Vieillot)	Psittacidae	Neot. (Paraguay)	[53]
L. calyptorhyncha Marciniak, Skoracki & Hromada, 2019	*Calyptorhynchus lathami* (Temminck)	Cacatuidae	Austr. (Australia)	[50]
L. eclectus Marciniak-Musial, Hromada & Sikora 2022	*Eclectus roratus* (St. Muller)	Psittaculidae	Ocea. (Papua New Guinea)	[52]
L. poicephali (Skoracki & Dabert, 2002)	*Poicephalus senegalus versteri* * Finsch	Psittacidae	Afro. (Cameroon)	[100]
	Poicephalus robustus (Gmelin)	Psittacidae	Afro. (DR Congo, Rwanda, Zambia)	[101]
	Poicephalus gulielmi (Jardine)	Psittacidae	Afro. (DR. Congo, Tanzania, Kenya, Cameroon)	[101]
	Poicephalus rufiventri (Rüppell)	Psittacidae	Afro. (Somalia)	[101]
	Poicephalus meyeri Cretzschmar	Psittacidae	Afro. (Zimbabwe, Rwanda, Kenya)	[101]
	Poicephalus fuscicollis Kuhl	Psittacidae	Afro. (Tanzania)	[101]
	Poicephalus cryptoxanthus (Peters)	Psittacidae	Afro. (Tanzania)	[101]
L. sulphurea Marciniak, Skoracki & Hromada, 2019	*Cacatua sulphurea* (Gmelin)	Cacatuidae	Orie. (Indonesia)	[50]
L. touiti Marciniak-Musial & Sikora, 2022	*Touit surdus* (Kuhl)	Psittacidae	Neot. (Brazil)	[53]
Genus ***Pipicobia*** Glowska & Schmidt, 2014				
P. cyclopsitta Marciniak-Musial, Hromada & Sikora, 2022	*Cyclopsitta diophthalma* (Hombron & Jacquinot)	Psittaculidae	Ocea. (Papua New Guinea)	[52]
P. fuscata Marciniak-Musial, Hromada & Sikora, 2022	*Pseudeos fuscata* (Blyth)	Psittaculidae	Ocea. (Papua New Guinea)	[52]
P. glossopsitta (Skoracki, Glowska & Sikora, 2008)	*Parvipsitta porphyrocephala* * (Dietrichsen)	Psittaculidae	Austr. (Australia)	[48]
	Parvipsitta pusilla (Shaw)	Psittaculidae	Austr. (Australia)	[52]
P. malherbi Marciniak-Musial, Hromada & Sikora, 2022	*Cyanoramphus malherbi* Souancé	Psittaculidae	Austr. (New Zealand)	[52]
P. tahitiana Marciniak-Musial, Hromada & Sikora, 2022	*Vini peruviana* (St. Muller)	Psittaculidae	Ocea. (Tahiti [French Polynesia])	[52]

Table 1. *Cont.*

Quill Mite Species	Host Species	Host Family	Distribution	References
Genus ***Rafapicobia*** Skoracki, 2011				
R. brotogeris (Fain, Bochkov & Mironov, 2000)	*Brotogeris cyanoptera* * (Pelzeln)	Psittacidae	Neot. (Brazil)	[43,53,74]
	Brotogeris chiriri (Vieillot)	Psittacidae	Neot. (Paraguay)	[53]
	Brotogeris jugularis (St. Muller)	Psittacidae	Pana. (Panama)	[53]
	Brotogeris versicolurus (St. Muller)	Psittacidae	Neot. (Brazil)	[53]
	Bolborhynchus orbygnesius (Souancé)	Psittacidae	Neot. (Peru)	[53]
	Diopsittaca nobilis (Linnaeus)	Psittacidae	Neot. (Surinam)	[53]
	Eupsittula pertinax (Linnaeus)	Psittacidae	Neot. (Surinam)	[53]
	Eupsittula aurea (Gmelin)	Psittacidae	Neot. (Brazil)	[53]
	Myiopsitta monachus (Boddaert)	Psittacidae	Neot. (Argentina)	[53]
	Pionopsitta pileata (Scopoli)	Psittacidae	Neot. (Paraguay)	[53]
	Psilopsiagon aymara (d'Orbigny)	Psittacidae	Neot. (Bolivia)	[53]
	Psilopsiagon aurifrons (Lesson)	Psittacidae	Neot. (Peru)	[53]
	Psittacara wagleri (Gray)	Psittacidae	Neot. (Venezuela)	[53]
	Pyrrhura picta (St. Muller)	Psittacidae	Neot. (Guyana)	[43]
	Thectocercus acuticaudatus (Vieillot)	Psittacidae	Neot. (Argentina)	[53]
R. pyrrhura Marciniak-Musial & Sikora, 2022	*Pyrrhura molinae* * (Massena & Souancé)	Psittacidae	Neot. (Bolivia)	[53]
	Pyrrhura lepida (Wagler)	Psittacidae	Neot. (Brazil)	[53]
	Pyrrhura frontalis (Vieillot)	Psittacidae	Neot. (Brazil)	[53]
R. trinidadi Marciniak-Musial & Sikora, 2022	*Touit batavicus* (Boddaert)	Psittacidae	Neot. (Trinidad and Tobago)	[53]
R. valdiviana Marciniak-Musial & Sikora, 2022	*Enicognathus ferrugineus* * (St. Muller)	Psittacidae	Neot. (Chile)	[53]
	Cyanoliseus patagonus (Vieillot)	Psittacidae	Neot. (Argentina)	[53]
R. xanthopterygius Marciniak-Musial & Sikora, 2022	*Forpus xanthopterygius* (von Spix)	Psittacidae	Neot. (Brazil)	[53]

Zoogeographical regions: Afro.—Afrotropical; Aust.—Australian, Near.—Nearctic, Neot.—Neotropical, Ocea.—Oceanian, Orie.—Oriental, Pala.—Palaearctic, Pana.—Panamanian, Sa-Arab.—Saharo-Arabian, Si-Jap.—Sino-Japanese (according to Holt et al. [52]). *—type host; **—host from order Columbiformes. Locality established based on the host distribution.

3.1.3. Key to the Syringophilid Subfamilies, Genera, and Species Associated with Parrots (the Morphological Terminology and Chaetotaxy follow Skoracki [12])

1. Tibiotarsus of palps rounded on distal margin. Prorals setae p' and p'' multiserrate, fan-like . . . subfamily **Syringophilinae** Lavoipierre, 1953 . . . 2
   – Tibiotarsus of palps truncate on distal margin. Prorals setae p' and p'' with two minute tines, rod-like . . . subfamily **Picobiinae** Johnston & Kethley, 1973 . . . 28
2. Propodonotal setae *vi* absent . . . 3
   – Propodonotal setae *vi* preset . . . 9
3. Setae *dFIII-IV* absent . . . 4
   – Setae *dFIII-IV* present, but placed ventrally . . . genus ***Terratosyringophilus*** Bochkov & Perez 2002 . . . 7
4. Setae *ve* and *si* situated at same transverse level. Pocket-like structures in anterior part of propodonotum present . . . genus ***Psittaciphilus*** Fain, Bochkov & Mironov, 2000 . . . 5
   – Setae *ve* situated anterior to *si*. Pocket-like structures in anterior part of propodonotum absent . . . genus ***Peristerophila*** Kethley, 1970 . . . 6
5. Lengths of setae *ve* and *si* 83–101 and 18–22, respectively . . . ***Ps. fritschi*** Fain, Bochkov & Mironov, 2000
   – Lengths of setae *ve* and *si* 110–123 and 30–47, respectively . . . ***Ps. amazonae*** Fain, Bochkov & Mironov, 2000
6. Propodonotal shield divided into 3 sclerites . . . ***Pe. mucuya*** Casto, 1980
   – Propodonotal shield entire . . . ***Pe. nestoriae*** Marciniak, Skoracki & Hromada, 2019
7. Setae *si* at least two times longer than *ve* . . . ***T. reicholfi*** Skoracki & Sikora, 2008
   – Setae *si* less than 1.3 times longer than *ve* . . . 8

8. Setae *ve* and *si* shorter than 200 . . . ***T. loricinus*** Bochkov & Fain, 2003
   – Setae *ve* and *si* longer than 340 . . . ***T. pioni*** Bochkov & Perez, 2002
9. Leg setae *dTIII* absent. Apodemes I parallel . . . ***Neoaulobia*** Fain, Bochkov & Mironov, 2000 . . . 10
   – Leg setae *dTIII* present. Apodemes I divergent . . . ***Megasyringophilus*** Fain, Bochkov & Mironov, 2000 . . . 20
10. Setae *dTIV* absent . . . 11
    – Setae *dTIV* present . . . 15
11. Setae *ve* distinctly longer than *vi* . . . 12
    – Setae *vi* and *ve* subequal in length . . . 13
12. Each lateral branch of peritremes with 7 chambers . . . ***N. pseudeos*** Marciniak-Musial, Hromada & Sikora, 2022
    – Each lateral branch of peritremes with 3 chambers . . . ***N. agapornis*** Fain, Bochkov & Mironov, 2000
13. Bases of setae *d1* situated close to anterior margin of hysteronotal shield. Each medial branch of peritremes with 3–5 chambers. Length of setae *vi* 70–105 . . . ***N. mironovi*** Bochkov & Perez, 2002
    – Bases of setae *d1* situated far from anterior margin of hysteronotal shield. Each medial branch of peritremes with 1–2 chambers. Length of setae *vi* 20–50 . . . 14
14. Lateral branch of peritremes with 5–6 chambers. Lengths of setae *d1*, *e2* and *f2* 25–45, 40–57 and 50–65, respectively . . . ***N. mexicana*** Bochkov & Perez, 2002
    – Lateral branch of peritremes with 4 chambers. Lengths of setae *d1*, *e2* and *f2* 74–105, 120–166 and 70–115, respectively . . . ***N. aratingae*** Fain, Bochkov & Mironov, 2000
15. Hysteronotal shield not fused to pygidial shield . . . 16
    – Hysteronotal shield fused to pygidial shield . . . 18
16. Lengths of stylophore 250–260. Bases of setae *d1* situated distant from anterior margin of hysteronotal shield . . . ***N. krafti*** Skoracki, 2005
    – Lengths of stylophore 140–160. Bases of setae *d1* are situated close to anterior margin of hysteronotal shield . . . 17
17. Each lateral branch of peritremes with 3 chambers. Stylophore and coxal fields punctate. Setae *g2* 36–52 long . . . ***N. cacatui*** Marciniak, Skoracki & Hromada, 2019
    – Each lateral branch of peritremes with 4 chambers. Stylophore and coxal fields apunctate. Setae *g2* 13–23 long . . . ***N. skorackii*** Marciniak-Musial, Hromada & Sikora, 2022
18. Each lateral branch of peritremes with 2–3 chambers. Bases of setae *d1* situated distant from anterior margin of hysteronotal shield. Stylophore 125–136 long . . . ***N. unsoeldi*** Marciniak-Musial & Sikora, 2022
    – Each lateral branch of peritremes with 4 chambers. Bases of setae *d1* situated close to anterior margin of hysteronotal shield. Stylophore 160–196 long . . . 19
19. Hysteronotal shield apunctate; bases of setae *e2* situated near lateral margins of this shield . . . ***N. puylaerti*** (Skoracki & Dabert, 1999)
    – Hysteronotal shield punctate in posterior part; bases of setae *e2* situated on this shield . . . ***N. psittaculae*** Fain, Bochkov & Mironov, 2000
20. Tarsal claws of legs III and IV without basal angles . . . 21
    – Tarsal claws of legs III and IV with basal angles . . . 24
21. Stylophore constricted posteriorly . . . 22
    – Stylophore rounded posteriorly . . . 23

22. Setae *ve* about 4 times longer than *vi*. Length of setae *g1* 115–130. Hysteronotal shield well sclerotized . . . ***M. geoffroyus*** Skoracki, 2005
    – Setae *ve* twice as long as *vi*. Length of setae *g1* 50. Hysteronotal shield weakly sclerotized or absent . . . ***M. cyanocephala*** Fain, Bochkov & Mironov, 2000
23. Length ratio of setae *vi*:*ve* 1:5. Setae *g2* twice shorter than *ag1*. Hysteronotal shield present . . . ***M. cacatua*** Glowska & Laniecka, 2013
    – Length ratio of setae *vi*:*ve* 1:2.3. Setae *g2* long, subequal to *ag1*. Hysteronotal shield absent . . . ***M. platycercus*** Bochkov & Fain, 2003
24. Hypostomal apex without median protuberances . . . ***M. dubinini*** Bochkov & Fain, 2003
    – Hypostomal apex with 1–3 pairs of median protuberances . . . 25
25. Setae tc' and tc'' of the legs III–IV subequal in length . . . ***M. trichoglossus*** Fain, Bochkov & Mironov, 2000
    – Setae tc'' of the legs III–IV distinctly longer than tc' of legs III–IV . . . 26
26. Hysteronotal shield absent . . . 27
    – Hysteronotal shield well-developed . . . ***M. rhynchopsittae*** Bochkov & Perez, 2002
27. Setae *se* situated posterior to level of setae *c2*. Bases of setae *d1* situated equidistant between setae *d2* and *e2*. Setae *ag1* longer than *g2* . . . ***M. eos*** Skoracki, 2005
    – Setae *se* situated anterior to level of setae *c2*. Bases of setae *d1* situated closer to *d2* than to *e2*. Setae *ag1* and *g2* subequal in length . . . ***M. kethleyi*** Fain, Bochkov & Mironov, 2000
28. Solenidion *phi* on tibia I present . . . ***Lawrencipicobia*** Skoracki & Hromada, 2013 . . . 29
    – Solenidion *phi* on tibia I absent . . . 35
29. Hysteronotal shield absent . . . 30
    – Hysteronotal shield present and reduced to two small sclerites surrounding bases of setae *d1* . . . 32
30. Bases of setae *c1* situated posterior to *se*. Two pairs of pseudanal setae (*ps*) present . . . ***L. poicephali*** (Skoracki & Dabert, 2002)
    – Bases of setae *c1* and *se* situated at same transverse level. One pair of pseudanal setae (*ps*) present . . . 31
31. Agenital shield absent. Setae *g1* setiform and 20 long . . . ***L. sulphurea*** Marciniak, Skoracki & Hromada, 2019
    – Agenital shield present as two narrow plates above bases of *ag1*. Setae *g1* as microsetae and 10 long . . . ***L. calyptorhyncha*** Marciniak, Skoracki & Hromada, 2019
32. Posterior end of apodemes I without small thorn-like protuberances . . . ***L. eclectus*** Marciniak-Musial, Hromada & Sikora, 2022
    – Posterior end of apodemes I with small thorn-like protuberances . . . 33
33. Propodonotal shield without striae in middle part. Setae *c1* and *se* situated at same transverse level. Coxal felds III–IV and alveoles surrounding bases of setae *ag1* with minute punctuations . . . ***L. arini*** Marciniak-Musial & Sikora, 2022
    – Propodonotal shield with striae in middle part. Setae *c1* situated posterior to *se*. Coxal felds III–IV and alveoles surrounding bases of setae *ag1* apunctate . . . 34
34. Pygidal shield weakly sclerotized with indistinct margins. Setae *ve* situated slightly posterior to *vi*. Lengths of setae *c1*, *d1* and *ag3* 184–217, 134–148 and 182–216, respectively . . . ***L. ararauna*** Marciniak-Musial & Sikora, 2022
    – Pygidal shield well sclerotized with clearly visible margins. Setae *vi* and *ve* situated at same transverse level. Lengths of setae *c1*, *d1* and *ag3* 307, 186 and 261, respectively . . . ***L. touiti*** Marciniak-Musial & Sikora, 2022
35. Two pairs of pseudanal setae (*ps1*, *ps2*) present . . . ***Rafapicobia*** Skoracki, 2011 . . . 36

– One pair of pseudanal setae (*ps1*) present . . . ***Pipicobia*** Glowska & Schmidt, 2014 . . . 40

36. Agenital plates absent . . . 37
   – Agenital plates as two longitudinal sclerites . . . 38
37. Bases of setae *c1* and *se* situated at same transverse level. Length of setae *ag2* and *4c* 5 and 75, respectively . . . ***R. brotogeris*** (Fain, Bochkov & Mironov, 2000)
   – Bases of setae *c1* situated anterior to *se*. Length of setae *ag2* and *4c* 18–23 and 120–154, respectively . . . ***R. valdiviana*** Marciniak-Musial & Sikora, 2022
38. Each medial branch of peritremes with 4–6 chambers. Setae *f2* subequal or slightly (1.2–1.5 times) longer than *f1* . . . 39
   – Each medial branch of peritremes with 6–7 chambers. Setae *f2* about 2–3.5 times longer than *f1* . . . ***R. trinidadi*** Marciniak-Musial & Sikora, 2022
39. Stylophore 111–118 long . . . ***R. xanthopterygius*** Marciniak-Musial & Sikora, 2022
   – Stylophore 136–143 long . . . ***R. pyrrhura*** Marciniak-Musial & Sikora, 2022
40. Agenital shield present as two longitudinal sclerites with *ag1* situated on posterior margin of shield . . . ***P. cyclopsitta*** Marciniak-Musial, Hromada & Sikora, 2022
   – Agenital shield absent . . . 41
41. Anterior margin of pygidial shield reaching level of seate *e2* . . . ***P. glossopsitta*** (Skoracki, Glowska & Sikora, 2008)
   – Anterior margin of pygidial shield not reaching level of seate *e2* . . . 42
42. Length of setae *ve* 60–80 . . . 43
   – Length of setae *ve* 35–50 . . . ***P. fuscata*** Marciniak-Musial, Hromada & Sikora, 2022
43. Pygidial shield apunctate. Propodonotal shield weakly sclerotized, striae visible . . . ***P. malherbi*** Marciniak-Musial, Hromada & Sikora, 2022
   – Pygidial shield punctate. Propodonotal shield well developed and without striae . . . ***P. tahitiana*** Marciniak-Musial, Hromada & Sikora, 2022

3.2. Prevalence

In this study, we investigated a total of 1524 host individuals belonging to 195 species (50% of the global parrot fauna on the species level), 73 genera (76% of the global parrot fauna on the generic level), and four families of the order Psittaciformes (100% of the global parrot fauna on the family level). Among them, 89 individuals representing 46 species have been infested by quill mites belonging to the following genera: *Megasyringophilus* Fain, Bochkov & Mironov, 2000 (9 species), *Neoaulobia* Fain, Bochkov & Mironov, 2000 (11 species), *Peristerophila* Kethley, 1970 (3 species), *Psittaciphilus* Fain, Bochkov & Mironov, 2000 (2 species), *Terratosyringophilus* Bochkov & Perez, 2002 (3 species) (subfamily Syringophilinae), *Lawrencipicobia* Skoracki & Hromada, 2013 (7 species), *Pipicobia* Glowska & Schmidt, 2014 (5 species), and *Rafapicobia* Skoracki, 2011 (5 species) (subfamily Picobiinae) (Table 2 and Tables S1 and S3).

The index of prevalence (IP) of host species from Psittaciformes ranges from 2.8% to 100% (IP = 100 in 8 cases); the 95% confidence intervals (the Sterne method) varied from 0.1 to 100 (Table 2). We grouped host species into four classes according to the prevalence index:

Low IP 1–25%—*Eupsitulla aurea*, *Forpus xanthopterygius*, *Amazona aestiva*, *Pyrrhura frontalis*, *Thectocercus acuticaudatus*, *Brotogeris versicolurus*, *Myiopsitta monachus*, *Pseudeos fuscata*, *Eclectus roratus*, *Diopsittaca nobilis*, *Psittacara wagleri*, *Brotogeris chiriri*, *Cyanoliseus patagonus*, *Enicognathus ferrugineus*, *Eupsitulla pertinax*, *Pionopsitta pileata*, *Parvipsitta porphyrocephala*, *Pionites melanocephalus*, *Touit batavicus*, *Pyrrhura molinae*, *Poicephalus cryptoxanthus*, *Poicephalus gulielmi*, *Pionites leucogaster*, *Poicephalus meyeri*, *Poicephalus robustus*, *Bolborhynchus orbygnesius*, *Nestor meridionalis*, and *Touit surdus*.

Middle IP 26–50%—*Poicephalus rufiventris*, *Brotogeris juglaris*, *Cacatua sulphurea*, *Calyptorhynchus funereus*, *Cyclopsitta diophthalma*, *Parvipsitta pusilla*, *Poicephalus fuscicollis*, *Amazona ochrocephala*, *Brotogeris cyanoptera*, *Platycercus eximius*, and *Psilopsiagon aymara*.

High IP 51–75%—None.

Extremely high 76–100%—*Ara ararauna*, *Ara chloropterus*, *Calyptorhynchus lathami*, *Cyanoramphus malherbi*, *Probosciger aterrimus*, *Psilopsiagon aurifrons*, *Pyrrhura lepida*, and *Vini peruviana*.

In our material, 58 host species (257 individuals) were not infested by the syringophilid mites (excluded from Table 2), i.e.,

Cacatuidae: *Callocephalon fimbriatum* (Grant) [N = 1].

Psittaculidae: *Agapornis fischeri* Reichenow [N = 6], *A. lilianae* Shelley [N = 2], *A. nigrigenis* Sclater [N = 1], *A. personatus* Reichenow [N = 1], *A. taranta* Stanley [N = 4], *A. pullarius* (Linnaeus) [N = 3], *Aprosmictus erythropterus* (Gmelin) [N = 3], *A. jonquillaceus* (Vieillot) [N = 6], *Barnardius zonarius* (Shaw) [N = 3], *Chalcopsitta atra* (Scopoli) [N = 3], *Ch. duivenbodei* (Dubois) [N = 7], *Charmosyna placentis* (Temminck) [N = 2], *Coracopsis nigra sibilans* Milne-Edwards & Oustalet [N = 2], *Coracopsis vasa comorensis* (Peters) [N = 2], *Cyanoramphus auriceps* (Kuhl) [N = 1], *Eos bornea* (Linnaeus) [N = 2], *Eos squamata* (Boddaert) [N = 1], *Forpus xanthops* (Salvin) [N = 4], *Geoffroyus geoffroyi* (Bechstein) [N = 33], *Geoffroyus heteroclitus* Bonaparte [N = 1], *Geoffroyus simplex* (Meyer) [N = 1], *Loriculus aurantiifrons* Schlegel [N = 1], *L. galgulus* Linnaeus [N = 2], *L. philippensis* (Müller) [N = 2], *L. pusillus* Gray [N = 6], *L. stigmatus* (Müller) [N = 1], *L. vernalis* (Sparrman) [N = 2], *Lorius domicella* (Linnaeus) [N = 1], *Lorius garrulous* (Linnaeus) [N = 1], *Lorius hypoinochrous* Gray [N = 5], *Lorius lory* (Linnaeus) [N = 20], *Glossopsitta concinna* (Shaw) [N = 4], *Melopsittacus undulates* (Shaw) [N = 4], *Micropsitta bruijnii* (Salvadori) [N = 1], *M. keiensis* (Salvadori) [N = 3], *M. pusio* (Sclater) [N = 2], *Polytelis anthopeplus* Lear [N = 1], *Prioniturus luconensis* Steere [N = 2], *P. mada* Hartert [N = 1], *P. platurus* (Vieillot) [N = 3], *Psittinus cyanurus* Forster [N = 4], *Psittaculirostris edwardsii* (Oustalet) [N = 12], *Psittacula alexandri* (Linnaeus) [N = 7], *P. cyanocephala* (Linnaeus) [N = 8], *P. eupatria* (Linnaeus) [N = 1], *P. himalayana* (Lesson) [N = 1], *P. longicauda* (Boddaert) [N = 12], *P. krameri* (Scopoli) [N = 8], *Psitteuteles versicolor* (Lear) [N = 1], *Psittrichas fulgidus* (Lesson) [N = 5], *Saudareos ornatus* (Linnaeus) [N = 2], *Tanygnathus magalorhynchos* (Boddaert) [N = 3], *T. sumatranus* (Raffles) [N = 3], *Trichoglossus haematodus* (Linnaeus) [N = 32], *Vini australis* (Gmelin) [N = 2].

Strigopidae: *Nestor notabilis* Gould [N = 1], *Strigops habroptila* Gray [N = 1].

Table 2. Host species infested by quill mites with habitat and the index of prevalence (IP) and 95% confidence interval (CI, Sterne's method).

Host Species		Exa.	Inf.	IP; CI	Mite Species	Habitat
Amazona aestiva	Turquoise-fronted Parrot	25	1	4 (0.2–19.6)	*Ne. unsoeldi*	covert
Amazona ochrocephala	Yellow-crowned Parrot	2	1	50 (2.5–97.5)	*Ps. amazonae*	covert
Ara ararauna	Chestnut-fronted Macaw	1	1	100 (5.0–100)	*La. ararauna*	contour
Ara chloropterus	Red-and-green Macaw	1	1	100 (5.0–100)	*Ne. unsoeldi*	covert
Bolborhynchus orbygnesius	Andean Parakeet	4	1	25 (1.3–75.1)	*Ra. brotogeris*	contour
Brotogeris chiriri	Yellow-chevroned Parakeet	20	2	10 (1.8–32.0)	*Ra. brotogeris*	contour
Brotogeris cyanoptera	Cobalt-winged Parakeet	2	1	50 (2.5–97.5)	*Ra. brotogeris*	contour
Brootgeris juglaris	Orange-chinned Parakeet	7	2	28.6 (5.3–65.9)	*Ra. brotogeris*	contour
Brotogeris versicolurus	White-winged Parakeet	42	2	4.8 (0.9–16.3)	*Ra. brotogeris*	contour
		42	2	4.8 (0.9–16.3)	*Pe. mucucya*	covert
Cacatua sulphurea	Yellow-crested Cockatoo	3	1	33.3 (1.7–86.5)	*La. sulphurea*	contour
Calyptorhynchus funereus	Yellow-tailed Black-Cockatoo	3	1	33.3 (1.7–86.5)	*Ne. cacatui*	covert
Calyptorhynchus lathami	Glossy Black-Cockatoo	1	1	100 (5.0–100)	*La. calyptorhychus*	contour
Cyanoliseus patagonus	Burrowing Parakeet	9	1	11.1 (0.6–44.4)	*Ra. valdiviana*	contour
		9	1	11.1 (0.6–44.4)	*Ne. unsoeldi*	covert
Cyanoramphus malherbi	Malherbe's Parakeet	1	1	100 (5.0–100)	*Pi. malherbi*	contour
Cyclopsitta diophthalma	Double-eyed Fig-Parrot	3	1	33.3 (1.7–86.5)	*Pi. cyclopsitta*	contour
Diopsittaca nobilis	Red-shouldered Macaw	11	1	9.1 (0.5–40.5)	*Ra. brotogeris*	contour
Eclectus roratus	Eclectus Parrot	26	2	7.7 (1.4–24.6)	*La. eclectus*	contour
Enicognathus ferrugineus	Austral Parakeet	9	1	11.1 (0.6–44.4)	*Ra. valdiviana*	contour
Eupsitulla aurea	Peach-fronted Parakeet	36	1	2.8 (0.1–14.8)	*Ra. brotogeris*	contour

Table 2. *Cont.*

Host Species		Exa.	Inf.	IP; CI	Mite Species	Habitat
Eupsitulla pertinax	Brown-throated Parakeet	18	2	11.1 (2.0–33.0)	*Ra. brotogeris*	contour
Forpus xanthopterygius	Blue-winged Parrotlet	33	1	3 (0.2–16.1)	*Ra. xanthopterygius*	contour
Parvipsitta porphyrocephala	Purple-crowned Lorikeet	4	1	12.5 (1.3–75.1)	*Pi. glossopsitta*	contour
Parvipsitta pusilla	Little Lorikeet	3	1	33.3 (1.7–86.5)	*Pi. glossopsitta*	contour
Myiopsitta monachus	Monk Parakeet	18	1	5.6 (0.3–27.1)	*Ra. brotogeris*	contour
Nestor meridionalis	New Zealand Kaka	4	1	25 (1.3–75.1)	*Pe. nestoriae*	contour
Pionites leucogaster	White-bellied Parrot	5	1	20 (1.0–65.7)	*La. arini*	contour
Pionites melanocephalus	Black-headed Parrot	8	1	12.5 (0.6–5.0)	*La. arini*	contour
Pionopsitta pileata	Pileated Parrot	9	1	11. 1 (0.6–44.4)	*Ra. brotogeris*	contour
Platycercus eximius	Eastern Rosella	2	1	50 (2.5–97.5)	*Ne. skoracki*	covert
Poicephalus cryptoxanthus	Brown-headed Parrot	11	2	18.2 (3.3–50.0)	*La. poicephali*	contour
Poicephalus flavifrons	Yellow-fronted Parrot	1	0	-	*La. poicephali*	contour
Poicephalus fuscicollis	Brown-necked Parrot	9	3	33.3 (9.8–67.7)	*La. poicephali*	contour
Poicephalus gulielmi	Red-fronted Parrot	38	7	18.4 (8.8–34.0)	*La. poicephali*	contour
Poicephalus meyeri	Meyer's Parrot	48	11	22.9 (12.9–37.4)	*La. poicephali*	contour
Poicephalus robustus	Cape Parrot	30	7	23.3 (11.2–41.6)	*La. poicephali*	contour
Poicephalus rueppellii	Rüppell's Parrot	1	0	-	*La. poicephali*	contour
Poicephalus rufiventris	Red-bellied Parrot	11	3	27.3 (7.9–59.6)	*La. poicephali*	contour
Poicephalus senegalus	Senegal Parrot	11	0	-	*La. poicephali*	contour
Probosciger aterrimus	Palm Cockatoo -	1	1	100 (5.0–100)	*Ne. cacatui*	covert
Pseudeos fuscata	Dusky Lory	16	1	6.2 (0.3–30.5)	*Pi. fuscata*	contour
		16	1	6.2 (0.3–30.5)	*Ne. pseudeos*	covert
Psilopsiagon aurifrons	Mountain Parakeet	1	1	100 (5.0–100)	*Ra. brotogeris*	contour
Psilopsiagon aymara	Gray-hooded Parakeet	2	1	50 (2.5–97.5)	*Ra. brotogeris*	contour
Psittacara wagleri	Scarlet-fronted Parakeet	11	1	9.1 (0.5–40.5)	*Ra. brotogeris*	contour
Pyrrhura lepida	Pearly Conure	1	1	100 (5.0–100)	*Ra. pyrrhura*	contour
Pyrrhura molinae	Green cheeked Parakeet	6	1	16.7 (0.9–58.9)	*Ra. pyrrhura*	contour
Pyrrhura frontalis	Maroon-bellied Parakeet	50	2	4 (0.7–13.7)	*Ra. pyrrhura*	contour
		50	2	4 (0.7–13.7)	*La. arini*	contour
Thectocercus acuticaudatus	Blue-crowned Parakeet	24	1	4.2 (0.2–20.4)	*Ra. brotogeris*	contour
Touit surdus	Golden-tailed Parrotlet	4	1	25 (1.3–75.1)	*La. touiti*	contour
Touit batavicus	Lilac-tailed Parrotlet	8	1	12.5 (0.6–50)	*Ra. trinidadi*	contour
Vini peruviana	Blue Lorikeet	1	1	100 (5.0–100)	*Pi. tahitiana*	contour

Exa.—number of individual host species examined during study; Inf.—number of host individuals infested by quill mites; IP—prevalence index given in (%); CI—confidence interval (Sterne method); "-" —unknown prevalence for infested hosts.

3.3. Host-Specificity of the Quill Mites

Based on the analyzed mite material (see Table 1), we classified all syringophilids associated with parrots into the following host specificity groups:

Monoxenous parasites (28 species): Subfamily Syringophilinae: *Megasyringophilus cacatua*, *Me. dubinini*, *Me. eos*, *Me. geoffroyus*, *Me. platycercus*, *Me. rhynchopsittae*, *Neoaulobia aratingae*, *Ne. krafti*, *Ne. mironovi*, *Ne. pseudeos*, *Ne. psittaculae*, *Ne. skorackii*, *Peristerophila forpi*, *Pe. nestoriae*, *Psittaciphilus fritschi*, *Terratosyringophilus pioni*, *Te. reichholfi*. Subfamily Picobiinae: *Lawrencipicobia ararauna*, *La. calyptorhyncha*, *La. eclectus*, *La. sulphurea*, *La. touiti*, *Pipicobia cyclopsitta*, *Pi. fuscata*, *Pi. tahitiana*, *Pi. malherbi*, *Rafapicobia trinidadi*, *Ra. xanthopterygius*.

Oligoxenous parasites (8 species): Subfamily Syringophilinae: *Megasyringophilus cyanocephala*, *Me. trichoglossus*, *Neoaulobia agapornis*, *Ne. mexicana*, *Psittaciphilus amazonae*. Subfamily Picobiinae: *Pipicobia glossopsitta*, *Rafapicobia pyrrhura*, *Lawrencipicobia poicephali.*

Mesostenoxenous parasites (6 species): Subfamily Syringophilinae: *Megasyringophilus kethleyi*, *Neoaulobia cacatui*, *Ne. unsoeldi*, *Terratosyringophilus loricinus*. Subfamily Picobiinae: *Lawrencipicobia arini*, *Rafapicobia valdiviana.*

Metastenoxenous parasites (2 species): Subfamily Syringophilinae: *Neoaulobia puylaerti.* Subfamily Picobiinae: *Rafapicobia brotogeris*.

Polyxenous parasites (1 species): Subfamily Syringophilinae: *Peristerophila mucuya*.

3.4. Bipartite Network Analysis

Fifty one quill mite-parrot associations were observed between 24 species of quill mites and 47 species of parrots (Figure 1). The Syringophilidae–Psittaciformes antagonistic bipartite network had a high value of connectance (C = 0.89). The specialization is high (H2′ = 0.98), but with a low degree of nestedness (N = 0.033). The comparison between H2′ and null model values showed significant differences (mean for null model = 0.078; t = −8.970, $p < 0.0001$). The specialization on the species-level (d′) is ranged between 0.84–1 (see Tables 3 and 4).

Table 3. Host specificity of quill mite species of the subfamily Syringophilinae with the value of d′ index.

Specificity	d′	Quill Mites	Hosts Spectrum
Monoxenous	-	*Megasyringophilus cacatua*	*Cacatua galerita*
	-	*Megasyringophilus dubinini*	*Trichoglossus ornatus*
	-	*Megasyringophilus eos*	*Eos bornea*
	-	*Megasyringophilus geoffroyus*	*Geoffroyus geoffroyi*
	-	*Megasyringophilus platycercus*	*Platycercus eximius*
	-	*Megasyringophilus rhynchopsittae*	*Rhynchopsitta pachyrhyncha*
	-	*Neoaulobia aratingae*	*Aratinga jandaya*
	-	*Neoaulobia krafti*	*Cacatua tenuirostris*
	-	*Neoaulobia mironovi*	*Amazona finschi*
	0.84	*Neoaulobia pseudeos*	*Pseudeos fuscata*
	-	*Neoaulobia psittaculae*	*Psittacula cyanocephala*
	1	*Neoaulobia skorackii*	*Platycercus eximius*
	-	*Peristerophila forpi*	*Forpus cyanopygius*
	1	*Peristerophila nestoriae*	*Nestor meridionalis*
	-	*Psittaciphilus fritschi*	unidentified parrot
	-	*Terratosyringophilus pioni*	*Pionus senilis*
	-	*Terratosyringophilus reichholfi*	*Lorius lory*
Oligoxenous	-		*Psittacula cyanocephala*
	-	*Megasyringophilus cyanocephala*	*Psittacula eupatria*
	-		*Psittacula krameri*
	-		*Trichoglossus* sp.
	-	*Megasyringophilus trichoglossus*	*Trichoglossus euteles*
	-		*Trichoglossus chlorolepidotus*
	-		*Agapornis nigrigenis*
	-		*Agapornis fischeri*
	-	*Neoaulobia agapornis*	*Agapornis personatus*
	-		*Agapornis roseicollis*
	-		*Agapornis taranta*
	-	*Neoaulobia mexicana*	*Eupsittula canicularis*
	-		*Eupsittula pertinax*
	-		*Amazona aestiva*
	-	*Psittaciphilus amazonae*	*Amazona amazonica*
	1		*Amazona ochrocephala*
Mesostenoxenous	-		*Aratinga jandaya*
	-	*Megasyringophilus kethleyi*	*Brotogeris versicolurus*
	-		*Eupsitulla canicularis*
	-		*Eupsittula pertinax*
	1	*Neoaulobia cacatui*	*Calyptorhynchus funereus*
			Probosciger aterrimus
			Amazona aestiva
	0.97	*Neoaulobia unsoeldi*	*Ara chloropterus*
			Cyanoliseus patagonus
	-	*Terratosyringophilus loricinus*	*Lorius garrulous*
	-		*Trichoglossus haematodus*

Table 3. *Cont.*

Specificity	d′	Quill Mites	Hosts Spectrum
Polixenous	-	*Neoaulobia puylaerti*	*Loriculus philippensis*
	-		*Loriculus pusillus*
	-		*Poicephalus senegalus*
	0.84	*Peristerophila mucuya*	*Brotogeris versicolurus*
	-		*Psilopsiagon aymara*
	-		*Trichoglossus haematodus*
	-		*Columbina minuta* *
	-		*Columbina passerine* *
	-		*Columbina squammata* *
	-		*Columbina talpacoti* *
	-		*Metriopelia ceciliae* *
	-		*Metriopelia melanoptera*
	-		*Streptopelia decaocto* *

d′—index measured specialization at species level; *—hosts species belonging to order Columbiformes.

Table 4. Host specificity of quill mite species the subfamily Picobiinae with the value of d′ index.

Specificity	d′	Quill Mites	Hosts Spectrum
Monoxenous	1	*Lawrencipicobia ararauna*	*Ara ararauna*
	1	*Lawrencipicobia calyptorhyncha*	*Calyptorhynchus lathami*
	1	*Lawrencipicobia eclectus*	*Eclectus roratus*
	1	*Lawrencipicobia sulphurea*	*Cacatua sulphurea*
	1	*Lawrencipicobia touiti*	*Touit surdus*
	1	*Pipicobia cyclopsitta*	*Cyclopsitta diophthalma*
	0.84	*Pipicobia fuscata*	*Pseudeos fuscata*
	1	*Pipicobia tahitiana*	*Vini peruviana*
	1	*Pipicobia malherbi*	*Cyanoramphus malherbi*
	1	*Rafapicobia trinidadi*	*Touit batavicus*
	1	*Rafapicobia xanthopterygius*	*Forpus xanthopterygius*
Oligoxenous	1	*Pipicobia glossopsitta*	*Parvipsitta porphyrocephala* *Parvipsitta pusilla*
	0.99	*Rafapicobia pyrrhura*	*Pyrrhura molinae* *Pyrrhura lepida* *Pyrrhura frontalis*
	1	*Lawrencipicobia poicephali*	*Poicephalus senegalus versteri* *Poicephalus robustus* *Poicephalus gulielmi* *Poicephalus rufiventri* *Poicephalus meyeri* *Poicephalus fuscicollis* *Poicephalus cryptoxanthus*
Mesostenoxenous	0.98	*Lawrencipicobia arini*	*Pionites leucogaster* *Pionites melanocephalus* *Pyrrhura frontalis*
	0.91	*Rafapicobia valdiviana*	*Enicognathus ferrugineus* *Cyanoliseus patagonus*
	0.99	*Rafapicobia brotogeris*	*Brotogeris cyanoptera* *Brotogeris chiriri* *Brotogeris jugularis* *Brotogeris versicolurus* *Bolborhynchus orbygnesius* *Diopsittaca nobilis* *Eupsittula pertinax* *Eupsittula aurea* *Myiopsitta monachus* *Pionopsitta pileata*

Table 4. *Cont.*

Specificity	d′	Quill Mites	Hosts Spectrum
Mesostenoxenous	0.99	*Rafapicobia brotogeris*	*Psilopsiagon aymara* *Psilopsiagon aurifrons* *Psittacara wagleri* *Pyrhurra picta* *Thectocercus acuticaudatus*

d′—index measured specialization on species level.

The prevalence, understood as the strength of the interaction between both sides, is illustrated in the graph as the thickness of the interaction between parasites and hosts. To make it easier to read the bipartite graph, each type of the quill mites genus is marked with a different color: *Neoaulobia*—pink, *Peristerophila*—green, *Psittaciphilus*—purple, *Lawrencipicobia*—yellow, *Pipicobia*—blue, and *Rafapicobia*—red (see Figure 1).

Ectoparasitic specialization (d′) to their hosts was placed into two categories:

d′ = 0.80–0.99 for 8 quill mite species: *Peristerophila mucuya* (0.84), *Neoaulobia pseudeos* (0.84), *Pipicobia fuscata* (0.84), *Rafapicobia valdiviana* (0.91), *Neoaulobia unsoeldi* (0.97), *Lawrencipicobia arini* (0.98), *Rafapicobia pyrrhura* (0.99), *Rafapicobia brotogeris* (0.99).

d′ = 1 for 16 quill mites species: *Lawrencipicobia ararauna*, *Lawrencipicobia calyptorhyncha*, *Lawrencipicobia eclectus*, *Lawrencipicobia poicephali*, *Lawrencipicobia sulphurea*, *Lawrencipicobia touiti*, *Neoaulobia cacatui*, *Neoaulobia skorackii*, *Peristerophila nestoriae*, *Pipicobia cyclopsitta*, *Pipicobia glossopsitta*, *Pipicobia malherbi*, *Pipicobia tahitiana*, *Psittaciphilus amazonae*, *Rafapicobia trinidadi*, *Rafapicobia xanthopterygius*.

The highest value is observed for sixteen quill mites species from six genera (see above: d′ = 1), whereas for three of eight quill mites species with the lowest value d′ = 0.84 (*Peristerophila mucuya*, *Neoaulobia pseudeos*, *Pipicobia fuscata*).

W registered high modularity (likelihood = 0.90), presenting 23 modules sorted into three types of modules: (A) single-host (one quill mite species associated with one host species), (B) multi-host (one quill mite species connected with more the one host species), and (C) multi-parasites (more than one quill mite species associated with one host species) (Figure 2).

A. Single-host module: (module number: 4) parasite: *Neoaulobia skorackii*—[host: *Platycercus eximius*], (5) *Peristerophila mucuya*—[*Brotogeris versiculorus*], (6) *Peristerophila nestoriae*—[*Nestor meridionalis*], (7) *Psittaciphilus amazonae*—[*Amazona ochrocephala*], (8) *Lawrencipicobia ararauna*—[*Ara ararauna*], (10) *Lawrencipicobia calyptorhyncha*—[*Calypt orhynchus lathami*], (11) *Lawrencipicobia eclectus*—[*Eclectus roratus*], (13) *Lawrencipicobia sulphurea*—[*Cacatua sulphurea*], (14) *Lawrencipicobia touiti*—[*Touit surdus*], (15) *Pipicobia cyclopsitta*—[*Cyclopsitta diophthalma*], (16) *Pipicobia tahitiana*—[*Vini peruviana*], (17) *Pipicobia malherbi*—[*Cyanoramphus malherbi*], (21) *Rafapicobia trinidadi*—[*Touit batavicus*], (23) *Rafapicobia xanthopterygius*—[*Forpus xanthopterygius*].
B. Multi-host module: (1) parasite *Neoaulobia cacatui*—[hosts: *Calyptorhynchus funereus*, *Probosciger aterrimus*], (2) *Neoaulobia unsoeldi*—[*Amazona aestiva*, *Ara chloropterus*], (9) *Lawrencipicobia arini*—[*Pionites leucogaster*, *Pi. melanocephalus*, *Pyrrhura frontalis*], (12) *Lawrencipicobia poicephali*—[*Poicephalus senegalus*, *Po. robustus*, *Po. gulielmi*, *Po. rufiventris*, *Po. meyeri*, *Po. fuscicollis*, *Po. cryptoxanthus*], (18) *Pipicobia glossopsitta*—[*Parvipsitta porphyrocephala*, *Pa. pusilla*], (19) *Rafapicobia brotogeris*—[*Brotogeris cyanoptera*, *Br. chiriri*, *Br. jugularis*, *Br. versicolurus*, *Bolborhynchus orbygnesius*, *Diopsittaca nobilis*, *Eupsittula pertinax*, *Eu. aurea*, *Myiopsitta monachus*, *Pionopsitta pileata*, *Psilopsiagon aymara*, *Ps. aurifrons*, *Psittacara wagleri*, *Pyrhurra picta*, *Thectocercus acuticaudatus*], (20) *Rafapicobia pyrrhura*—[*Pyrrhura molinae*, *Py. lepida*, *Py. frontalis*], (22) *Rafapicobia valdiviana*—[*Enicognathus ferrugineus*, *Cyanoliseus patagonus*].
C. Multi-parasite module: (3) parasites: *Neoaulobia pseudeos*, *Pipicobia fuscata*—[host: *Pseudeos fuscata*].

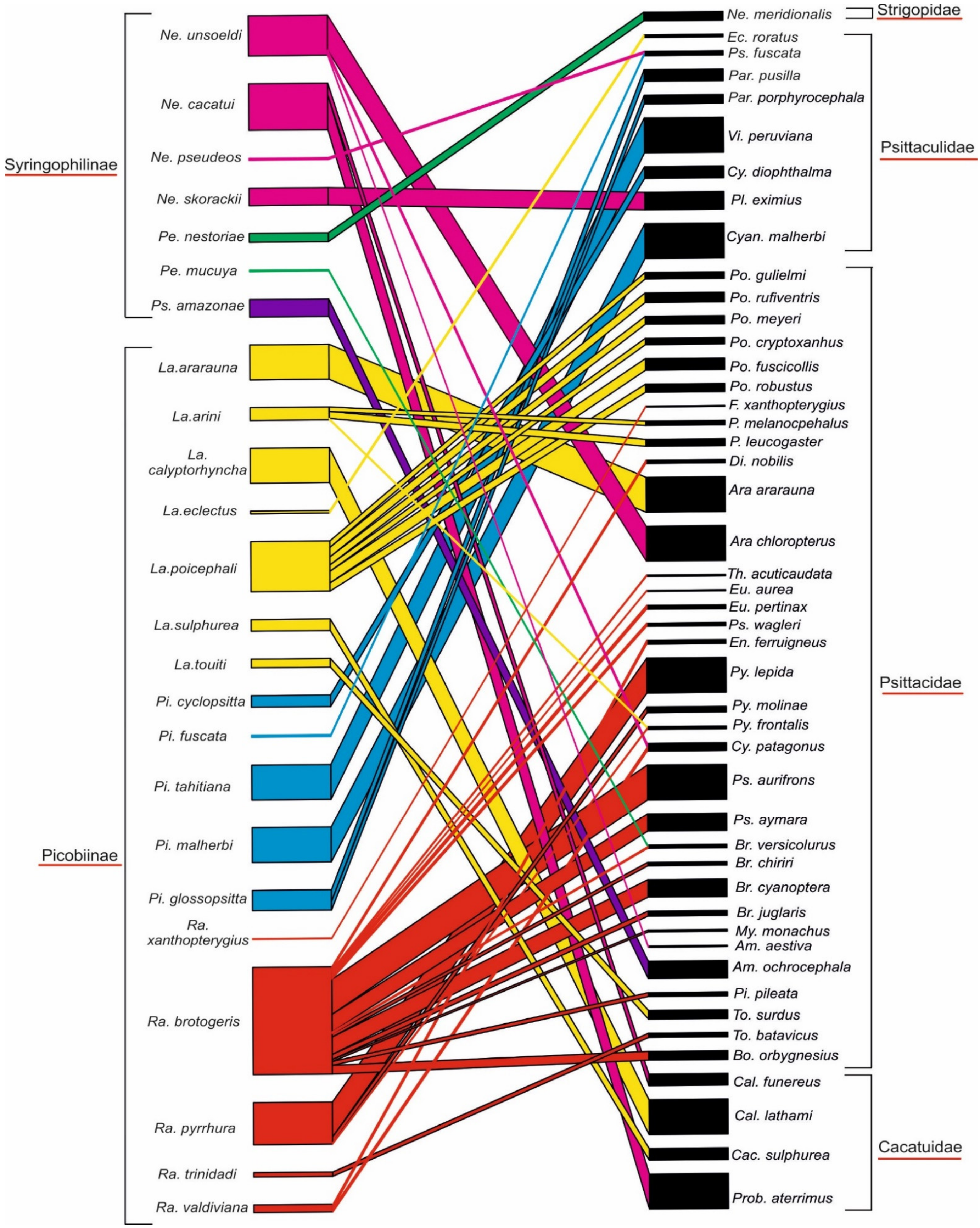

Figure 1. Bipartite network graph of interactions between quill mite species (**left**) and their parrot hosts (**right**).

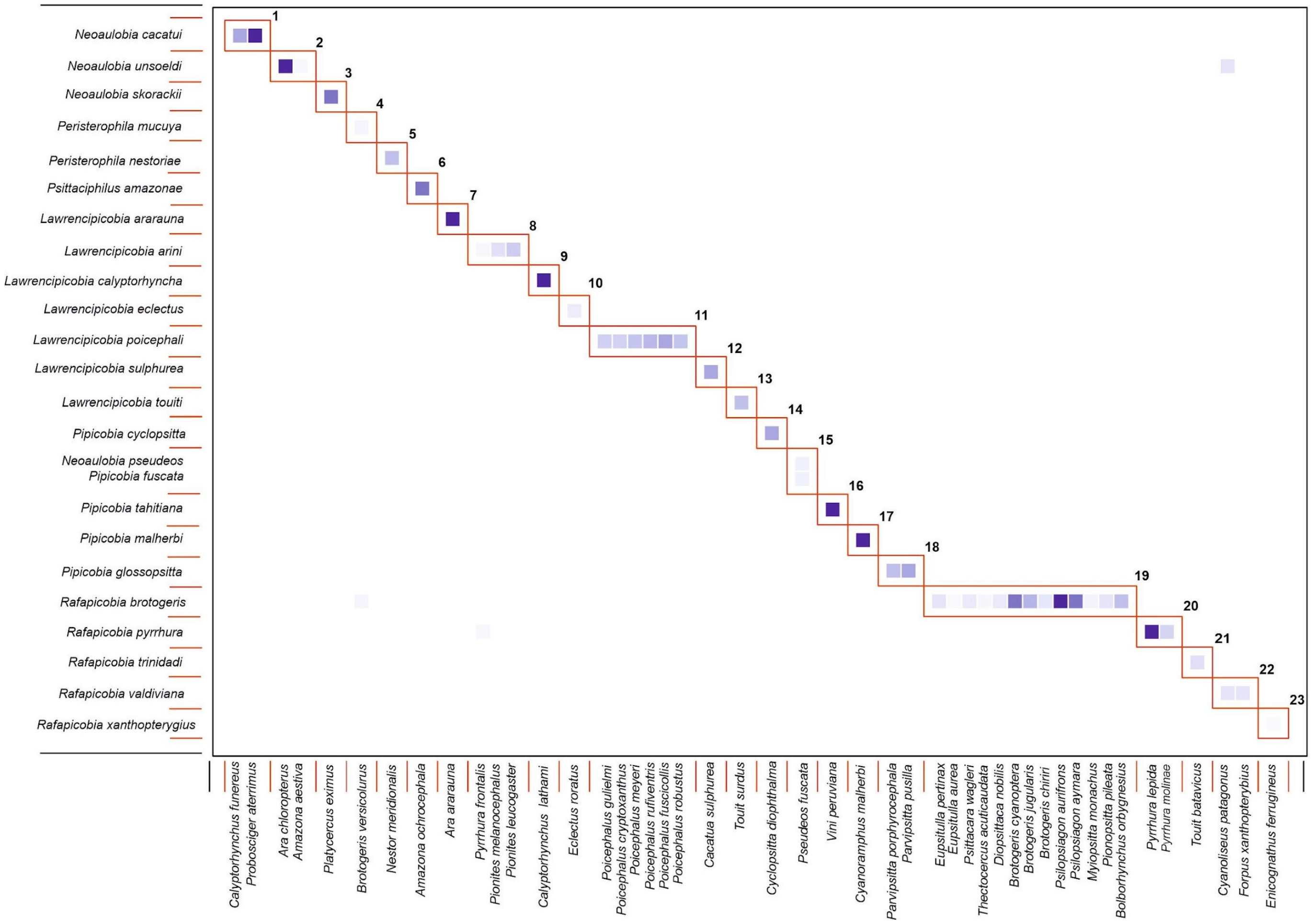

Figure 2. Modules of the quill mites–parrot communities. Modules 1–23, generated for quill mites species and parrots. The intensity of the colors of the squares indicates the strength of the interaction between particular parasite species (vertical axis) and their host species (horizontal axis).

3.5. Co-Infestation of the Quill Mites

The analysis of the host spectrum and preferred habitat showed three various patterns of co-infestation (Table 5):

A. **"Syr + Pic"**—quill mite species belonging to the different Syringophilidae subfamilies and inhabiting the same host species but different habitats, i.e., members of Syringophilinae in quills of flight feathers and members of Picobiinae in quills of contour feathers.

Host: *Cyanoliseus patagonus* parasitized by *Neoaulobia unsoeldi* (subfamily: Syringophilidae; habitat: wing coverts) and by *Rafapicobia valdiviana* (subfamily: Picobiinae; habitat: contours);
Host: *Poicephalus senegalus* parasitized by *Neoaulobia puylaerti* (Syr; wing cov.) + *Lawrencipicobia poicephali* (Pic; con.);
Host: *Pseudeos fuscata* parasitized by *Neoaulobia pseudeos* (Syr; wing cov.) + *Pipicobia fuscata* (Pic; con.);
Host: *Psilopsiagon aymara* parasitized by *Peristerophila mucuya* (Syr; wing cov.) + *Rafapicobia brotogeris* (Pic; con.).

B. **"Syr + Syr + Pic"**—another, more extensive above mentioned variant of co-infestation was observed when one host species was infested by two species of the subfamily Syringophilinae occupying flight feathers, but restricted to coverts or secondaries, and by the species of Picobiinae found in quills of contour feathers.

Host: *Brotogeris versicolurus* parasitized by *Megasyringophilus kethleyi* (Syr; sec.) + *Peristerophila mucuya* (Syr; wing cov.) + *Rafapicobia brotogeris* (Pic; con.);

Host: *Eupsitulla pertinax* parasitized by *Megasyringophilus kethleyi* (Syr; sec.) + *Neoaulobia mexicana* (Syr; wing cov.) + *Rafapicobia brotogeris* (Pic; con.).

C. **"Syr + Syr"**—this configuration only includes representatives of the subfamily Syringophilinae which were found in the different habitats of the flight feathers on the same host species.

Host: *Amazona aestiva* parasitized by *Neoaulobia unsoeldi* (Syr; wing cov.) + *Psittaciphilus amazonae* (Syr; tail cov.);

Host: *Aratinga yandaya* parasitized by *Megasyringophilus kethleyi* (Syr; sec.) + *Neoaulobia aratinga* (Syr; wing cov.);

Host: *Eupsitulla canicularis* parasitized by *Megasyringophilus kethleyi* (Syr; sec.) + *Neoaulobia mexicana* (Syr; wing cov.);

Host: *Platycercus eximius* parasitized by *Megasyringophilus platycercus* (Syr; sec.) + *Neoaulobia skorackii* (Syr; wing cov.).

D. **"Pic + Pic"**—this configuration includes different quill mites species belonging to the subfamily Picobiinae, and inhabiting the same niche on the same host species.

Host: *Pyrrhura frontalis* parasitized by *Lawrencipicobia arini* (Pic; con.) + *Rafapicobia pyrrhura* (Pic; con.).

Table 5. Host species infested by two or more syringophilid species with the notation of the habitat preference.

Hosts	Quill Mites	Subfamily	Habitat
Amazona aestiva	*Neoaulobia unsoeldi* *Psittaciphilus amazonae*	S S	w.cov. t.cov.
Aratinga yandaya	*Megasyringophilus kethleyi* *Neoaulobia aratinga*	S S	sec. w.cov.
Brotogeris versiculorus	*Megasyringophilus kethleyi* *Peristerophila mucuya* *Rafapicobia brotogeris*	S S P	sec. w.cov. con.
Cyanoliseus patagonus	*Neoaulobia unsoeldi* *Rafapicobia valdiviana*	S P	w.cov. con.
Eupsitulla canicularis	*Megasyringophilus kethleyi* *Neoaulobia mexicana*	S S	sec. w.cov.
Eupsitulla pertinax	*Megasyringophilus kethleyi* *Neoaulobia mexicana* *Rafapicobia brotogeris*	S S P	sec. w.cov. con.
Platycercus eximius	*Megasyringophilus platycercus* *Neoaulobia skorackii*	S S	sec. w.cov.
Poicephalus senegalus	*Neoaulobia puylaerti* *Lawrencipicobia poicephali*	S P	w.cov. con.
Pseudeos fuscata	*Neoaulobia pseudeos* *Pipicobia fuscata*	S P	w.cov. con.
Psilopsiagon aymara	*Peristerophila mucuya* *Rafapicobia brotogeris*	S P	w.cov. con.
Psittacula cyanocehala	*Megasyringophilus cyanocephala* *Neoaulobia psittaculae*	S S	sec. w.cov.
Pyhrrura frontalis	*Lawrencipicobia arini* *Rafapicobia pyrhurra*	P P	con. con.

P—Picobiinae; S—Syringophilinae; con.—contour feathers; w.cov.—wing coverts; t.cov.—tail coverts; sec.—secondaries.

3.6. Zoological Distribution of Quill Mites Species Associated with Parrots

Data presented in Table 1, indicate that syringophilid mites associated with parrots are present in the following zoogeographical regions: Neotropical, Nearctic, Panamanian, Afrotropical, Oriental, Australasian, and Oceanian (Table 6).

In the particular regions, we noted the following genera with the number of quill mites species:

- **Neotropical**: *Megasyringophilus* (4), *Neoaulobia* (3), *Peristerophila* (1), *Psittaciphilus* (2), *Terratosyringophilus* (1), *Lawrencipicobia* (3), *Rafapicobia* (5);
- **Nearctic**: *Megasyringophilus* (2), *Neoaulobia* (2), *Peristerophila* (1), *Terratosyringophilus* (1);
- **Panamanian**: *Neoaulobia* (1), *Rafapicobia* (1);
- **Afrotropical**: *Neoaulobia* (2), *Lawrencipicobia* (1);
- **Oriental**: *Megasyringophilus* (4), *Neoaulobia* (2), *Peristerophila* (1); *Terratosyringophilus* (1), *Lawrencipicobia* (1);
- **Oceanian**: *Megasyringophilus* (2), *Neoaulobia* (2), *Terratosyringophilus* (1), *Lawrencipicobia* (1), *Pipicobia* (3);
- **Australasian**: *Megasyringophilus* (3), *Neoaulobia* (3), *Peristerophila* (1), *Lawrencipicobia* (1), *Pipicobia* (2).

Among all 45 quill mites species associated with parrots, 37 of them were noted only from one zoogeographical region:

- **Nearctic**: *Megasyringophilus rhynchopsittae*, *Neoaulobia mironovi*, *Peristerophila forpi*, *Terratosyringophilus pioni*;
- **Neotropical**: *Neoaulobia aratingae*, *Psittaciphilus amazonae*, *Ps. fritschi*, *Lawrencipicobia ararauna*, *La. arini*, *La. touiti*, *Rafapicobia pyrrhura*, *Ra. trinidadi*, *Ra. valdiviana*, *Ra. xanthopterygius*;
- **Afrotropical**: *Neoaulobia agapronis*, *Lawrencipicobia poicephali*;
- **Australasian**: *Megasyringophilus cacatua*, *Me. platycercus*, *Neoaulobia krafti*, *Ne. skorackii*, *Peristerophila nestoriae*, *Lawrencipicobia calyptorhyncha*, *Pipicobia malherbi*, *Pi. glossopsitta*;
- **Oriental**: *Megasyringophilus cynaocephala*, *Me. dubinini*, *Me. eos*, *Neoaulobia psittaculae*, *Terratosyringophilus loricinus*, *Lawrencipicobia sulphurea*;
- **Oceanian**: *Megasyringophilus geoffroyus*, *Neoaulobia pseudeos*, *Terratosyringophilus reichlofi*, *Lawrencipicobia eclectus*, *Pipicobia cyclopsitta*, *Pi. fuscata*, *Pi. tahitiana*.

Eight quill mite species were recorded from more than one zoogeographical region:

- **Oriental** + Afrtotropical: *Neoaulobia puylaerti*;
- **Neotropical** + **Panamanian**: *Neoaulobia unsoeldi*, *Rafapicobia brotogeris*;
- **Neotropical** + **Nearctic**: *Megasyringophilus kethleyi*, *Neoaulobia mexicana*;
- **Neotropical** + **Oriental**: *Peristerophila mucuya*;
- **Oceanian** + **Australasian**: *Neoaulobia cacatui*;
- **Oriental** + **Oceanian** + **Australasian**: *Megasyringophilus trichoglossus*.

Table 6. Distribution of syringophilids associated with parrots in the zoogeographical regions.

	Zoogeographical Region						
Quill Mites Species	Neot.	Near.	Pana.	Afro.	Orie.	Ocean.	Austra.
Me. cacatua							■
Me. cyanocephala					■		
Me. dubinini					■		
Me. eos					■		
Me. geoffroyus						■	
Me. kethleyi	■	■					
Me. platycercus							■
Me. rhynchopsittae		■					

Table 6. *Cont.*

	Zoogeographical Region						
Quill Mites Species	Neot.	Near.	Pana.	Afro.	Orie.	Ocean.	Austra.
Me. trichoglossus					■	■	■
Ne. aratingae	■						
Ne. agapornis				■			
Ne. cacatui						■	■
Ne. krafti							■
Ne. unsoeldi	■		■				
Ne. mexicana	■	■					
Ne. mironovi		■					
Ne. pseudeos						■	
Ne. psittaculae					■		
Ne. puylaerti				■	■		
Ne. skorackii							■
Pe. forpi		■					
Pe. mucuya	■				■		
Pe. nestoriae							■
Ps. amazonae	■						
Ps. fritschi	■						
Te. loricinus					■		
Te. pioni		■					
Te. reichholfi						■	
La. araraunae	■						
La. arini	■						
La. calyptorhyncha							■
La. eclectus						■	
La. poicephali				■			
La. sulphurea					■		
La. touiti	■						
Pi. cyclopsitta						■	
Pi. fuscata						■	
Pi. tahitiana						■	
Pi. malherbi							■
Pi. glossopsitta							■
Ra. brotogeris	■		■				
Ra. pyrrhura	■						
Ra. trinidadi	■						
Ra. valdiviana	■						
Ra. xanthopterygius	■						

Zoogeographical regions: Afro.—Afrotropical, Aust.—Australasian, Near.—Nearctic, Neot.—Neotropical, Ocea.—Oceanian, Orie.—Oriental, Pala.—Palaearctic, Pana.—Panamanian, Sa-Arab.—Saharo-Arabian, Si-Jap.—Sino-Japanese (according to Holt et al. [56]). Filling with black color - confirms the presence of a given species of quill mite in a given area.

3.7. Phylogenetic Relationship of the Genera Associated with Parrots

The analysis under equal weights resulted in one most parsimonious tree (MPT) shown in Figure 3. Number of characters—56 (Figures S1 and S2), number of parsimony informative characters—46, tree length (L) = 69, consistency index (CI) = 0.841, retention index (RI) = 0.861, rescaled consistency index (RC) = 0.724, homoplasy index (HI) = 0.259.

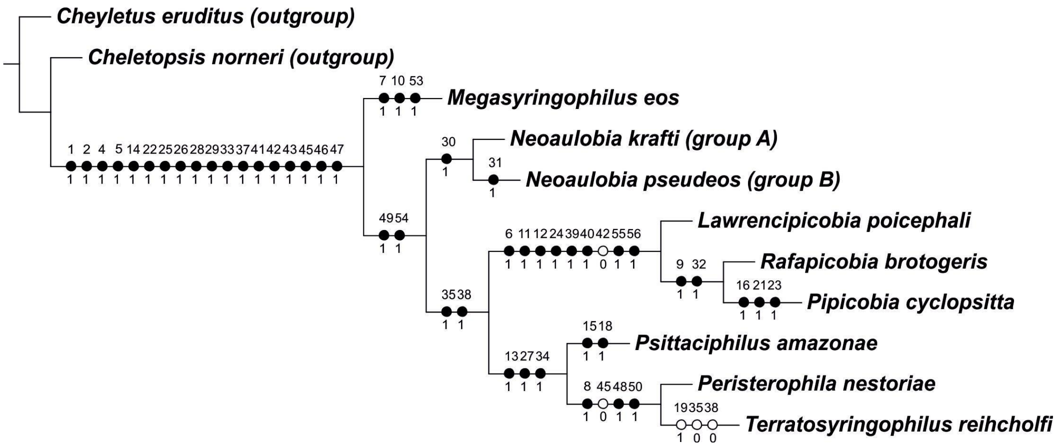

Figure 3. Phylogenetic tree of the syringophilid genera associated with parrots.

4. Discussion

4.1. Species Richness and Phylogenetic Relationship of Quill Mites Associated with Psittaciformes Birds

Despite intensive taxonomic research provided on quill mites in recent years, our knowledge of the extent ofSyringophilidae biodiversity is still far from satisfactory. Currently, more than 400 species and 63 genera of these mites have been described from about 670 bird species belonging to 27 orders of birds [14]. However, these numbers show that the actual species richness of syringophilids is only a small part of their taxonomical diversity because the broad spectrum of the avian hosts is still largely unexplored. In addition, most taxonomic studies were conducted on mite species collected from randomly selected (or found) birds and, with few exceptions, did not focus on detailed studies of the syringophilid fauna associated with particular groups of birds. These exceptions are, for example, research on quill mite fauna associated with birds of the genus *Estrilda* [31], family Nectariniidae [29], Cuculidae [28], Cacatuidae [50], Psittaculidae [52], Psittacidae [53], or recently studied avian order Columbiformes [30].

The fauna of quill mites related to parrots comprises 45 species belonging to five genera, *Megasyringophilus*, *Neoaulobia*, *Psittaciphilus*, *Peristerophila*, and *Terratosyringophilus* representing the subfamily Syringophilinae and three genera, *Lawrencipicobia*, *Pipicobia*, and *Rafapicobia*, representing subfamily Picobiinae (see Table 1; Figures 3–5).

The genera *Megasyringophilus* and *Neoaulobia* comprise large and medium-sized syringophilids occupying quills of wing feathers and represent basal lineages to all remaining syringophilid genera involved in the analysis (Figure 3). These genera are common on all parrot families except the family Strigopidae, suggesting that these genera were already present in a common ancestor before the split of the main phylogenetic lines of parrots, i.e., Psittacoidea and Cacatoidea in the Eocene (about 59 mya). It is worth noting that the absence of *Neoaulobia* and *Megasyringophilus* on the small group (only four species) of New Zealand parrots (Strigopidae) can be a result of the too-small sample of examined birds of this family. In the present study, we examined only four specimens of *Nestor meridionalis* (see Table 2), and we cannot exclude that future research on quill mites associated with strigopids bring records of these mite genera also on birds of the family Strigopidae.

In contrast to *Neoaulobia*, which host distribution is restricted exclusively to Psittaciformes, the representatives of *Megasyringophilus*, except parrots, were also recorded on raptor birds, i.e., *Megasyringophilus dalmas* Skoracki & Unsoeld, 2016 collected from a representative of owls, *Megascops choliba* (Strigidae) from Venezuela and *M. aquilus* Skoracki et al., 2010 from accipitrids (Accipitridae) of the genera *Aquila*, *Accipiter*, *Buteo*, *Clanga*, and *Hieraaetus* [78,80] (Figure 4). The presence of this genus on phylogenetically not closely related avian orders, Psittaciformes, Strigiformes, and Accipitriformes, is probably an example of the horizontal transfers (host switch) between prey and predator. In the literature, there are two similar examples of the exchange of quill mite fauna between predator and prey, i.e., the mite species *Syringophilopsis kirgizorum* Bochkov et al. found on finches of the genus *Carduelis* (Passeriformes: Fringillidae) but also found on the Tawny Owl *Strix aluco* Linnaeus (Strigidae) [105], and the mite *Peristerophila columbae* Casto known from the domestic pigeon *Columba livia*, but also recorded on the Red-tailed Hawk *Buteo jamaicensis* (Accipitriformes: Accipitridae) [106].

The following three syringophiline genera associated with parrots form phylogenetically closely related lineages *Psittaciphilus* + (*Peristerophila* + *Terratosyringophilus*) (Figure 3). This monophyletic clade is also known as *Psittaciphilus*-generic-group assigned by Bochkov & Perez [75]. The species of these genera are found inside the quills of wing coverts (*Peristerophila*, *Terratosyringophilus*) or tail coverts (*Psittaciphilus*). The genera *Terratosyringophilus* (five species) and *Psittaciphilus* (four species), except parrots, share their species also with pigeons and doves (Columbiformes). In contrast, *Peristerophila* (currently comprising 14 species) is associated, excepting parrots and columbiform birds, also with raptors Accipitriformes and Falconiformes, and the other two non-passerine avian orders, i.e., Bucerotiformes, and Coraciiformes (Figure 4). The presence of representatives of *Terratosyringophilus* and *Psittaciphilus* on parrots and pigeons is problematic, because recent molecular studies indicate that these two avian clades are phylogenetically not closely related; Psittaciformes belongs to the clade Australaves, whereas Columbiformes to distant Columbaves [38,39,107]. Similarly, a broad host spectrum of *Peristerophila*, represented by not related avian orders, suggests factors other than co-evolutionary processes.

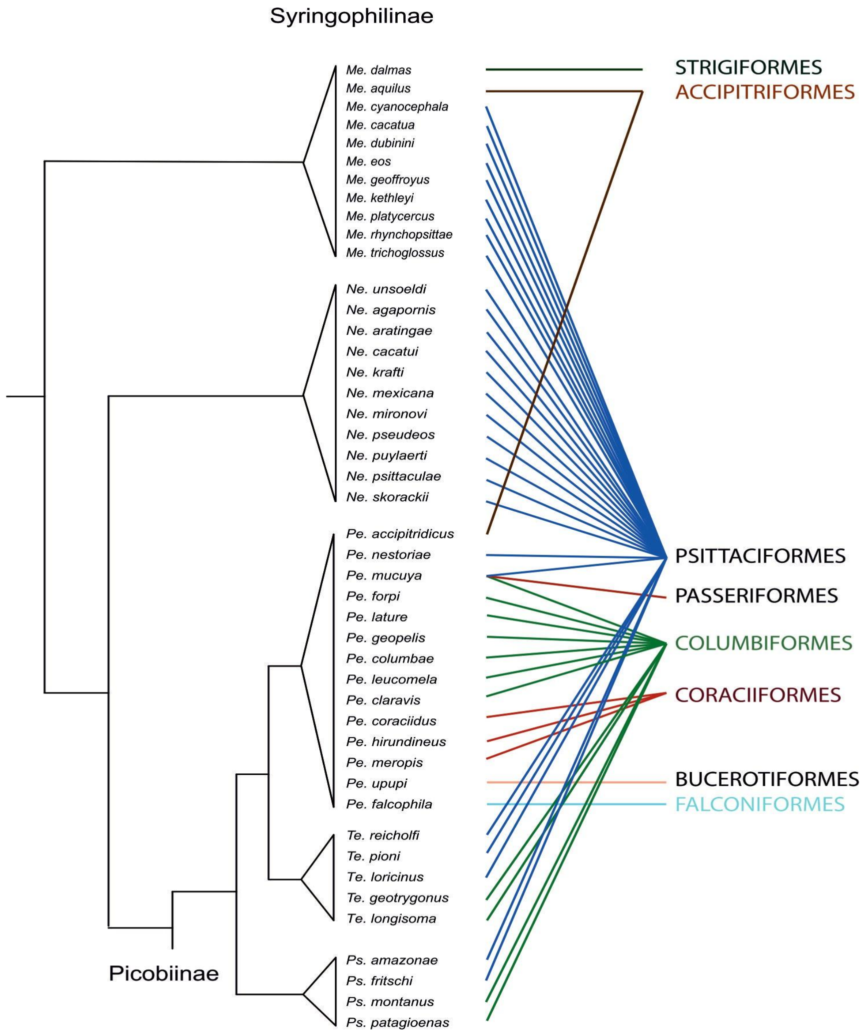

Figure 4. Host association of the species in the particular genera of the subfamily Syringophilinae recorded from parrots.

The Psittaciformes-related picobiine genera *Lawrenicipicobia*, *Pipicobia*, and *Rafapicobia*, belong to the monophyletic *Neopicobia*-generic-group in the subfamily Picobiinae [22]. Among representatives of this clade, the genus *Lawrencipicobia*, the sister clade to the other two genera, is exclusively associated with parrots and is present on all parrot families except Strigopidae (Figure 5). On the other hand, the genus *Pipicobia* infests only old world parrots (Psittaculidae), but is also recorded on passerines (Passeriformes) which are phylogenetically closely related to Psittaciformes (both orders belong to the Australaves clade) [38]. The *Rafapicobia* species associated with parrots are limited only to the Neotropical psittacines, but this genus is also known from closely related passerines (Passeriformes). Additionally, *Rafapicobia* was also noted on hosts from the orders Coraciiformes and Piciformes, which belong to the sister clade Coraciimorphae [38,98]. The host spectrum comprising four closely related avian orders (Psittaciformes + Passeriformes + Piciformes + Coraciiformes—all of them belong to the Telluraves, core landbirds [40]) suggests co-evolutionary events, but surprisingly, this genus was recently also recorded on several hosts of the distant order Gruiformes [98] which indicates that also horizontal transfers took place in this parasite-host system. In conclusion, the quill mites-parrots system is a composition of the co-evolutionary processes that undoubtedly take place, e.g., in genera exclusively associated with parrots—*Neoaulobia*, *Lawrencipicobia*, as well as horizontal transmission to unrelated hosts clades, e.g., genera *Megasyringophilus*, *Rafapicobia*.

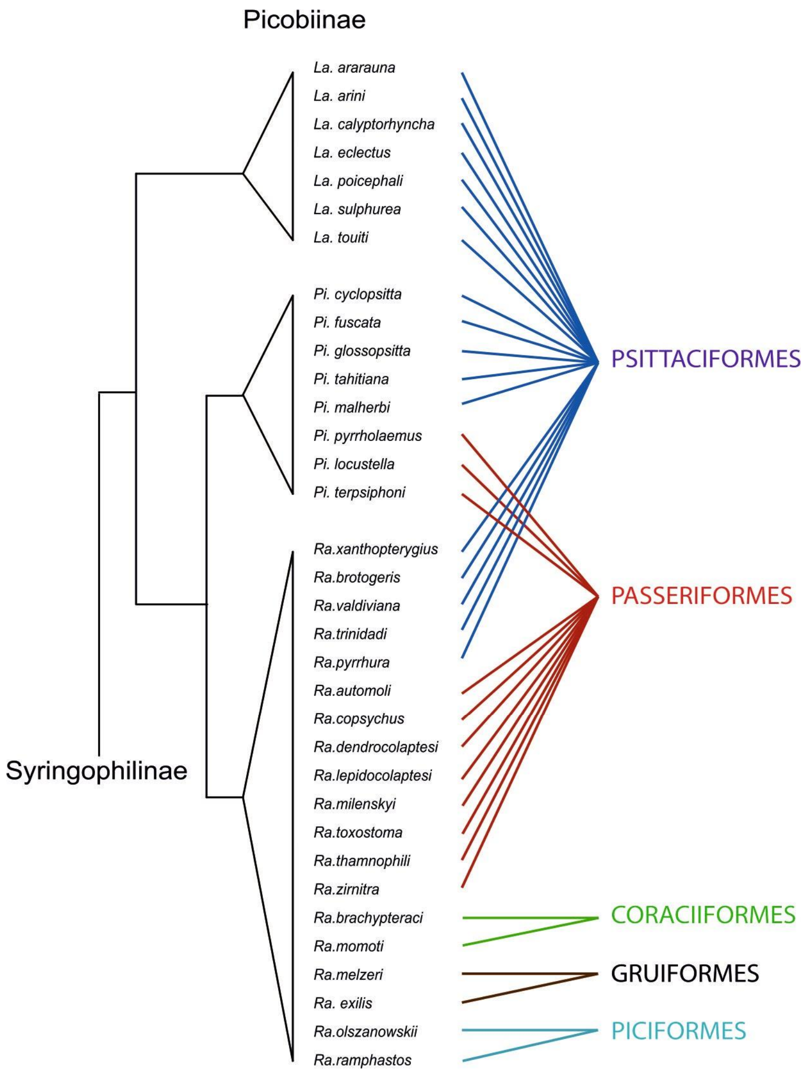

Figure 5. Host association of the species in the particular genera of the subfamily Picobiinae recorded from parrots.

4.2. Species Richness and Phylogenetic Relationship of Quill Mites Associated with Psittaciformes Birds

Although the quill mite fauna includes genera found on unrelated host groups (see above), at the species level, most syringophilid species are restricted to one host species (monoxenous parasites; 63%). The species associated with phylogenetically closely related host species belonging to the same genus (oligoxenous parasites; 18%) or family (mesostenoxenous parasites; 17%) are a minority. The marginal part of the syringophilid fauna associated with parrots are the species infesting more or less but not closely related host species (metastenoxenous parasites; 1% or polixenous parasites; 1%) (Table 7). The proportion of monoxenous quill mite species in relation to the rest is not unique to the fauna associated with parrots. A similar ratio is typical for all other genera of the family Syringophilidae, which is evidence of a long-term and close relationship with their hosts [12,30,36]. Additionally, except for horizontal transmission, we cannot exclude that *Neoaulobia puylaerti* and *Peristerophila mucuya*, which are metastenoxenous and polixenous parasites, respectively, are, in fact, represented by cryptic species. Although we do not yet have evidence of this, future molecular research will clear up the doubts on this topic.

Table 7. Host specificity of quill mites associated with parrots.

Genus and Number of Species	Monoxenous Parasites	Oligoxenous Parasites	Mesostenoxenous Parasites	Metastenoxenous Parasites	Polixenous Parasites
Megasyringophilus (9)	6	2	1	-	-
Neoaulobia (11)	6	2	2	1	-
Peristerophila (3)	2	-	-	-	1
Terratosyringophilus (3)	2	-	1	-	-
Psittaciphilus (2)	1	1	-	-	-
Lawrencipicobia (7)	5	1	1	-	-
Pipicobia (5)	4	1	-	-	-
Rafapicobia (5)	2	1	2	-	-
Total (45)	28 (63%)	8 (18%)	7 (15%)	1 (2%)	1 (2%)

4.3. Quill Mites and Their Habitat-Specificity

Feathers and their various types are interesting examples of a living environment for many parasitic and commensal species that can coexist in such a habitat. J.B. Kethley was the first to give (but without exact examples) a short note that “adaptations restrict mites to specific conditions so that some genera are limited to specific feather tracts” and, consequently, one host species can by parasitized by three or even four different genera occupying different habitats (types of feathers) [9]. Later on, Schmäschke et al. [108] observed the co-infestation of two species, *Syringophilopsis turdi* and *Syringophiloidus* sp., on Fieldfare *Turdus pilaris* (Passeriformes: Turdidae), as well as *Syringophilopsis kirgizorum* and *Syringophiloidus* sp. found on European greenfinch *Chloris chloris* (Passeriformes: Fringillidae). In the paper of Skoracki et al. [109], the authors showed not only different patterns of observed co-infestation, but they noted also the niches occupied by quill mites, e.g., *Syringophilipsis kirgizorum* (primaries) + *Torotrogla gaudi* (secondaries) on Chaffinch *Fringilla coelebs* (Fringillidae); *Syringophiloidus presentlis* (secondaries) + *Picobia sturni* and *Aulonastus buczekae* (contour feathers) on Common Starling *Sturnus vulgaris* (Sturnidae).

Until recently, the multi-infestations by quill mites have been observed only in passeriform birds. However, interesting results on habitat specificity were also obtained by Kaszewska-Gilas et al., who observed several cases of the multi-infestation on columbiform birds [30]. The authors distinguish two patterns of the multi-infestations, i.e., “*Syr-Pic pattern*”, where the quill mites belonging to two subfamilies Syringophilinae and Picobiinae occupy the same host species or individual; and “*Syr-Syr pattern*”, where the quill mites belong to the same subfamily, Syringophilinae and are present on the same host species.

In our study, we found 12 examples of multi-infestation in three different patterns: *Syr-Pic*, *Syr-Syr*, and, for the first time, *Pic-Pic*, where both components belong to the same subfamily, Picobiinae, and are recorded from the same host species or individual.

In the first *Syr-Pic* configuration, members of Syringophilinae inhabit mainly quills of secondaries, wing or tail coverts, and rectrices (Tables 2 and 5), while representatives of Picobiinae exclusively inhabit contour feathers. However, within the *Syr-Pic* group, we distinguished two variants. The first one is when one host species is infested by two quill mite species that occupy different types of feathers, e.g., *Neoaulobia unsoeldi* (covert) + *Rafapicobia valdiviana* (contour) on Burrowing Parrot *Cyanoliseus patagonus*; *Neoaulobia puylaerti* (covert) + *Lawrencipicobia poicephali* (contour) on Senegal Parrot *Poicephalus senegalus*; *Neoaulobia pseudeos* (covert) + *Pipicobia fuscata* (contour) on Dusky Lory *Pseudeos fuscata*; *Peristerophila mucuya* (covert) + *Rafapicobia brotogeris* (contour) on Grey-hooded Parakeet *Psilopsiagon aymara*. The second one is more diverse, and comprises two different species of the subfamily Syringophilinae and a representative of the subfamily Picobiinae on the same host. This configuration was observed, e.g., *Megasyringophilus kethleyi* (secondary) + *Peristerophila mucuya* (covert) + *Rafapicobia brotogeris* (contour) from White-winged Parakeet *Brotogeris versicolurus*; *Megasyringophilus kethleyi* (secondary) + *Neoaulobia mexicana* (covert) + *Rafapicobia brotogeris* (contour) from Brown-throated Parakeet *Eupsitulla pertinax*.

For *Syr-Syr pattern*, in all four observed cases, representatives of the subfamily infested the same host, but also with the restriction to the different types of feathers, e.g., *Neoaulobia unsoeldi* (wing covert) + *Psittaciphilus amazonae* (tail covert) on Turquoise-fronted Amazon *Amazona aestiva*.

For *Pic-Pic pattern*, we found only one case, when two quill mites species, *Lawrencipicobia arini* and *Rafapicobia pyrrhura*, infested the same host species and occupied the same type of habitat—quills of contour feathers.

Generally, various species of quill mites avoid occurrence in the same niche, because niche separation is one of the parts of natural selection. Thanks to this, the competing species try using different hosts or microhabitats [110]. This happens because the competition for the same resources, understood as occupying the same niche and using the same resources, ends when one competitor displaces the other and, thus, leads to his extinction [111–113]. The phenomenon of separation of the niche is common and well-documented among many ectoparasitic mites, but these relationships remain poorly studied among Syringophilidae. Our results confirm that the family Syringophilidae is characterized by a high degree of specificity to occupy a niche as it was previously postulated [9,30,108,109,114]. Kethley & Johnston [115], Casto [11], Grossi & Proctor [25], Skoracki et al. [27] postulated that the habitat specificity is also a result of the preference of quill mites to the specific parameters of the quills—their volume and quill-wall thickness. It should also be noted, however, habitat represented by contour feathers comprises more or less morphologically uniform feathers; the particular sectors of the contour plumage do not have to be infected by syringophilids with the same frequency, and, in fact, mites choose a specific place on the host body, e.g., the feathers on the belly are more often infested than the feathers on the neck or back.

4.4. Prevalence

The prevalence index (IP) provides information about the strength of the relationship between a given host species and the parasite. A crucial role in determining the prevalence of infested hosts in the environment is the number of examined bird individuals and the number of examined feathers [25,27]. The previous studies on the distribution of the quill mites on their hosts showed that the highest values of prevalence are for birds kept in crowded conditions, e.g., 75% for domestic hens *Gallus gallus domesticus* (N = 1500) [116] and 82% (N = 492) for house sparrows *Passer domesticus* [117]. When analyzing farm birds or highly gregarious hosts, these high prevalence values are understandable. However, the prevalence for wild and non-social birds is much lower and rarely exceeds 45%, e.g., 7.3% for the rock ptarmigans *Lagopus muta* (N = 1209) [24]; 7.3% for the boreal owls *Aegolius* *funereus* (N = 55) [27]; 3.5% for the great grey shrike *Lanius excubitor* (N = 508) [118]; 42.9% for the ovenbirds *Seiurus aurocapilla* (N = 21) [25].

The only analysis of the infestation of parrots was carried out by Jardim et al. [119]. Their research was mainly concerned with parrots held captive in Brazil. During this study, authors examined 30 species of New World parrots and syringophilid mites were found on three of them, i.e., *Aratinga aurea* (IP = 9.1%; N = 11), *Brotogeris chirri* (IP = 7.7%; N = 13), and *Pionopsitta pilleata* (IP = 20%; N = 5).

In our study, most of the host species belong to the first group, for which the prevalence is low and not exceeds 25%, e.g., 2.8% for *Eupsitulla aurea* (N=36), 3% for *Forpus xanthopterygius* (N = 33), 4% for *Amazona aestiva* (N = 25), 4% for *Pyrrhura frontalis* (N = 50), 4.8% *Brotogeris versicolurus* (N = 42) (see Table 2). To this group also belong parrots with evident higher prevalence, e.g., birds of the genus *Poicephalus*—18.4% for *P. gulielmi* (N = 38); 22.9% for *P. meyeri* (N = 48), or 23.3% for *P. robustus* (N = 30). The second group of hosts, where IP is medium (26–50%), includes 11 host species, whereas none of them belong to the group of hosts with high IP (51–75%). However, in our material there are parrots with IP = 100% (eight species), but these results are affected by the small sample size of study specimens.

The studies on the infestation of the host populations were provided on bird material originated from various sources: (i) from the ornithological collection (dry bird skins, frozen or alcohol preserved specimens) deposited in the museum or other scientific institutions [26,27,29–31,114,120]; (ii) from birds examined during fieldworks [24,109,113,114], and (iii) from birds kept in the zoological gardens [119] or farms [23,116,121,122]. Considering that not every feather on the host is infected (see [25,27]), it is important that the analyzed host sample, apart from the sufficiently large number of tested specimens, also includes the largest possible number of examined feathers, or all, if we want to know the border of the habitat. Of course, the second condition is impossible to realize during research on museum and live bird material. In estimating the prevalence, the age and sex of the tested hosts and the sampling season are also important. We are aware that our results are estimates that show, at least approximately, the degree of the infestation of the host population. However, this does not change the fact that it is worthwhile to investigate further the strength of the relationships mentioned in the prevalence index and simultaneously continue research toward the study of habitat specificity.

4.5. Analyses of the Bipartite Network of Quill Mite–Parrots Communities

The bipartite network and some indices, such as nestedness, connectance, etc., are part of an ecological approach which provides interesting information about biological systems, i.e., host-parasite relationships for communities of quill mites and birds. Networks are good tools for illustrating and describing the interactions inside of various types of communities, their relationships, and ecological connections [7]. Although for many years this type of research has mainly focused on mutualistic relationships at the plant-animal level, such as pollinators, seed spreading, and others [57,123–125], we can use this type of analysis to study parasite-host relationships. The bipartite analyses are read as a graph that illustrates links between two trophic levels, but, above all, quantify indices such as host specificity in parasites and provide a topological description [8,123].

Until now, analyses at the level of host-parasite were conducted for relationships among quill mites and sunbirds (Passeriformes: Nectariniidae) [29], estrildids (Passeriformes: Estrildidae) [31], and pigeons and doves (Columbiformes: Columbidae) [30,32].

Our investigation was intended to determine binary indices such as: network specialization (H2′), nestedness (N), modularity (Q), species specialization metrics (d′ index), and connectance (C). Each of these indices provides the following information: the number of interactions, the level of sharing partners, the degree of compartmentalization of the networks, and network-level specialization [58,126,127].

The indicators used in our research (i.e., nestedness, modularity, and connectance) allow a better understanding of the relationships occurring between species in the network, which are correlated and depend on each other, which has been shown in previous studies provided by Fortuna et al. [63], Pavlopoulos et al. [62] and Olesen et al. [128].

Connectance illustrates a relationship between parasitic species and individual hosts. A high index means non-random infestation and a stable community. This has been proven, e.g., by Devictor's analyses concerned with the conservation and protection of biodiversity demonstrate that high C-value is characteristic for more stable communities, while low C-value can be an indicator of an ecological threat [129]. Moreover, when the network loses or gains generalists, the value of the connectance may decrease [129,130]. A high value of the connectance indicator was observed in many other networks, i.e., food webs, plant–herbivores–parasitoids in the forest or plant–pollinator [131–133].

Nestedness is one of the most important indicators, and values higher and closer to 1 means that the structure of the studied network is non-random, more diverse, and complex [61]. Nestedness interacts with modularity [128], and their correlation depends on network connectance [63]. On the other hand, a trend towards the ecological network to divided into modules is known as modularity [63]. Delmas et al. [134] indicate that the modules should be stable, thanks to which the organisms within them have a limited ability to spread beyond their structure. Modularity interacts with nestedness [128] and their correlation depends on network connectance [63]. Moreover, Fortuna et al. showed that the complex dependence between nestedness and modularity has clear potential to temper or augment the different connotation of the two patterns [63].

Our results confirm that there is a high specialization between syringophilid mites and parrots, on both the network- and the species-level. Our network pattern is characterized by a high values of: connectance (C = 0.89), H2′ (H2′ = 0.98), and modularity (Q = 0.90) with 23 modules. Specialization on the species-level (d′) is also high and ranged between 0.84–1. By contrast to these, the value of nestedness index is low (N = 0.033).

The connectance, modularity, and network specialization results were similar to those obtained by Kaszewska-Gilas et al. [30] in a study of syringophilids and doves and pigeons as well as ectoparasitic flies of the family Streblidae (Hippoboscoidea) and bat hosts from the tropical dry forest [125]. The values of examined features have the following qualities for:

- Network specialization (H2′) = 0.98 (in our study), (H2′) = 0.93 (in quill mites-columbid birds network [30]), and (H2′) = (in Hippoboscoidea-bats network [125]);
- Conncetance (C) = 0.89 (in our study), (C) = 0.90 (in quill mites-columbid birds network [30]), and (C) = 0.30 (in Hippoboscoidea-bats network [125]);
- Modularity (Q) = 0.90 (in our study), (Q) = 0.83 (quill mites-columbid birds network [30]), (Q) = 0.7 (in Hippoboscoidea-bats network [125]);
- Nestedness (N) = 0.033 (in our study), (N) = 0.908 (in quill mites-columbid birds network [30]), but in the study of Duran et al. the nesttednes has not been examined [125].

The high similarity C-index of the ecological network of quill mites and columbids and psittacids, as opposed to flies-bats value (C)=0.30, can be related to sampled and net-work size—the syringophilds and their bird hosts were more numerous. In the quill mites–parrots and quill mites–doves networks, the proportion of specialized species is comparably high, and much higher than in the bat–fly network. As in the case of Kaszewska-Gilas et al. [30] and their networks of quill mites-doves with a high C-index value, we also hypothesize that the higher the index of C-value is observed, the hosts-parasites systems are older and more stable.

Our network has a high value of modularity (Q = 0.90) and consists of 23 modules. Within these modules there were three types of elements: single-host, multi-host, multi-parasite modules. The most common adjustment is single-host item. Thus, a strong interaction with the host species was observed for 14 single-host modules. The next seven modules were multi-host; among them module number "19" has the highest number of hosts. Only one of them was a multi-parasite module (see module number "3" with *Neoaulobia pseudeos* and *Pipicobia fuscata* related to *Pseudeos fuscata*). This multi-parasite community contains two species from the genera: *Neoualobia* (Syringophilinae) and *Pipicobia* (Picobiinae), which interact with one host species. Although *Neoaulobia* and *Pipicobia* are not the sister caldes and represent two subfamilies of Syringophilidae, their coexistence on one host species—the Dusky lory *Pseudeos fuscata* from the Australian region, which was a center of diversity and diversification of parrots during the Gondwanaland rifting [35–37], could be a result of the phylogenetic relationship between particular quill mites and their hosts.

According to research of Bascompte et al., a higher nestedness index determines the complexity of the network [63], which was confirmed in the quill mites-columbid birds relationships (N = 0.908) [30], our study shows that nestedness index between Syringophilidae and parrots is very low (N) = 0.033.

Although nestedness and modularity are correlated, Fortuna et al. also observed that the most highly connected communities inclined to demonstrate only one of these two properties [63]. This trend seems to be observed in our study. The bipartite network associated with Syrongophilidae and Psittaciformes favored modularity, with a high value in contrast to a very low amount of nestedness.

5. Conclusions

Before we began the current research, the number of fauna from Syringophilidae associated with parrots was 26 species. We examined the feathers of 1524 parrot specimens belonging to 195 species and our analysis was concerned with 50% of all known species of parrots distributed in the Australian, Afrotropical, Neotropical, Oriental and Oceanian regions. After completing the study and analyzing all available acarological material, this fauna contained 45 species of quill mites belonging to 8 syringophilid genera, infesting 81 parrot species. A full key to the identification of all currently known species and genera of quill mites occurring on parrots are also a part of this publication.

Mites of the subfamily Syringophilinae are found on parrots of the families: Strigopidae, Cacatuiae, Psittaculidae, and Psittacidae. In contrast, species of the subfamily Picobiinae infested representatives of the families Cacatuidae, Psittaculidae, and Psittacidae. They still have not been seen from the from Strigopidae family. Parrot-associated Syringophilidae mites, similar to the whole family, are highly host-specific. They are mainly monoxenous (63%) and mesostenoxenous (18%) parasites, as well as mesostenoxenous (15%), metastenoxenous (2%) and polixenous (2%) parasites. The analysis of the host spectrum and preferred habitat showed three various patterns of co-infestation. The prevalence of host infestations by syringophilid mites varied from 2.8% to 100% (95% confidence interval (CI Sterne method) = 0.1–100).

The zoogeographical distribution of quill mites coincides with the distribution of their hosts, and suggest a high level of endemism both of individual parrot and syringophilid species. The greatest species richness of Syringophilidae is found in the Austrolasian (center of biodiversity of the families: Cacatuidae and Psittaculidae) and Neotropical (center of biodiversity of the family Psittacidae) regions.

The Syringophilidae-Psittaciformes bipartite network was composed of 24 mite species and 47 host species. The bipartite network was characterized by a high network level specialization $H2' = 0.98$, connectance $C = 0.89$, and high modularity $Q = 0.90$, with 23 modules, but low nestedness $N = 0.0333$.

The analysis of phylogeny of the quill mites on the generic level shows two distinct clades: *Psittaciphilus* (*Peristerophila* + *Terratosyringophilus*) (among Syringophilinae subfamily) and *Lawrencipicobia* (*Pipicobia* + *Rafapicobia*) (among Picobiinae).

Our results are interesting and certainly give deeper insight into the relationship between Syringophilidae mites and parrots. As syringophilid mites form a sizable part of the parasite world, the results of the described research will significantly contribute to the basic knowledge of parasitology, biogeography, phylogeny, and evolution of parasites and their hosts. In the future, these results may also be used by epidemiologists and bird conservation organizations in their research. Someday, perhaps they will help ornithologists to finalize the family tree of birds.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d15010001/s1, Figure S1: Characters; Figure S2: A data matrix; Table S1: The degree of Syringophilidae examination for each Psittaciformes family.

Author Contributions: Conceptualization, N.M.-M.; methodology, N.M.-M., M.S., J.Z.K., M.U. and B.S.; investigation, N.M.-M., M.S., J.Z.K., M.U. and B.S.; data curation, N.M.-M.; formal analysis, N.M.-M., M.S., J.Z.K. and B.S.; writing—original draft preparation, N.M.-M.; writing—review and editing, N.M.-M., M.S. and B.S.; supervision, N.M.-M., M.S. and B.S.; project administration, N.M.-M.; funding acquisition, N.M.-M. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by POWR.03.02.00-00-I006/17 and by Dean of Faculty Biology, Adam Mickiewicz University.

Institutional Review Board Statement: Not applicable.

Data Availability Statement: Data is available upon request from the corresponding authors.

Acknowledgments: We thank Stefan Friedrich and Roland Melzer (SNSB-ZSM—Arthropoda Varia) for their help during our studies in the Bavarian State Collection of Zoology. We also thank anonymous reviewers for their critical review of the manuscript.

Conflicts of Interest: The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or in the decision to publish the results.

References

1. Cheng, C.T. *General Parasitology*, 2nd ed.; Academic Press: Orlando, FL, USA, 1986; p. 827.
2. Trager, W. *Living Together. The Biology of Animal Parasitism*; Plenum Press: New York, NY, USA, 1986; p. 467.
3. Crofton, H.D. A quantitative approach to parasitism. *Parasitology* **1971**, *62*, 179–193. [CrossRef]
4. Crofton, H.D. A model for host-parasite relationships. *Parasitology* **1971**, *63*, 343–364. [CrossRef] [PubMed]
5. Dobson, A.; Lafferty, K.D.; Kuris, A.M.; Hechinger, R.F.; Jetz, W. Homage to Linneaus: How many parasites? How many hosts? *Proc. Natl. Acad. Sci. USA* **2008**, *105*, 11482–11489. [CrossRef] [PubMed]
6. Kissling, W.D.; Schleuning, M. Multispecies interactions across trophic levels at macroscales: Retrospective and future directions. *Ecography* **2015**, *38*, 346–357. [CrossRef]
7. Poulin, R. Network analysis shining light on parasite ecology and diversity. *Trends Parasitol.* **2010**, *26*, 492–498. [CrossRef] [PubMed]
8. Araújo, W.S.; Kollár, J. First characterization of a highly specialized ecological network composed by gall-inducing mites and their host plants. *Int. J. Acarol.* **2019**, *45*, 223–226. [CrossRef]
9. Kethley, J.B. A revision of the family Syringophilidae (Prostigmata: Acarina). *Contrib. Am. Entomol. Inst.* **1970**, *5*, 1–76.
10. Kethley, J.B. Population regulation in quill mites (Acari: Syringophilidae). *Ecology* **1971**, *52*, 1113–1118. [CrossRef]
11. Casto, S.D. Quill wall thickness and feeding of *Syringophiloidus minor* (Berlese) (Acarina: Syringophilidae). *Ann. Entomol. Soc. Am.* **1974**, *67*, 824. [CrossRef]
12. Skoracki, M. Quill mites (Acari: Syringophilidae) of the Palaearctic region. *Zootaxa* **2011**, *2840*, 1–414. [CrossRef]
13. Johnston, D.E.; Kethley, J.B. A numerical phenetic study of the quill mites of the family Syringophilidae (Acari). *J. Parasitol.* **1973**, *59*, 520–530. [CrossRef]
14. Zmudzinski, M.; Skoracki, M.; Sikora, B. An Updated Checklist of Quill Mites of the Family Syringophilidae (Acariformes: Prostigmata). 2021. Available online: https://sites.google.com/site/syringophilidae/v2021 (accessed on 10 June 2022).
15. Filimonova, S.A. The ultrastructural investigation of the midgut in the quill mite *Syringophilopsis fringilla* (Acari, Trombidiformes: Syringophilidae). *Arthropod Struct. Dev.* **2009**, *38*, 303–313. [CrossRef] [PubMed]
16. Filimonova, S.A. Morpho-functional variety of the coxal glands in cheyletoid mites (Prostigmata). I. Syringophilidae. *Arthropod Struct. Dev.* **2016**, *45*, 356–367. [CrossRef] [PubMed]
17. Filimonova, S.A.; Mironov, S.V. Functional morphology of the gnathosoma in the quill mite *Syringophilopsis fringilla* Fritsch (Acari: Prostigmata: Syringohpilidae). *Zool. Anz.* **2010**, *249*, 165–180. [CrossRef]
18. Leonovich, S.A.; Filimonova, S.A. The quill mite *Syringophilopsis fringilla* (Fritsch) (Acari: Trombidiformes: Syringophilidae): The structure of sensory organs providing feeding of the parasite in the feather quill. *Entmol. Rev.* **2017**, *97*, 383–394. [CrossRef]
19. Rózsa, L.; Moldovan, E. Relationship between body size and sexual size dimorphism in syringophilid quill mites. *Parasitol. Res.* **2022**, *121*, 891–898. [CrossRef]
20. Hendricks, S.A.; Flannery, M.E.; Spicer, G.S. Cophylogeny of Quill Mites from the Genus *Syringophilopsis* (Acari: Syringophilidae) and their North American Passerine Hosts. *J. Parasitol.* **2013**, *99*, 827–834. [CrossRef]
21. Skoracki, M.; Glowska, E.; Bochkov, A.V. Phylogeny of quill mites of the family Syringophilidae (Acari: Prostigmata) based on their external morphology. *Eur. J. Entomol.* **2013**, *110*, 663–675. [CrossRef]

22. Skoracki, M.; Sikora, B.; Jerzak, L.; Hromada, M. *Tanopicobia* gen. nov., a new genus of quill mites, its phylogenetic placement in the subfamily Picobiinae (Acariformes: Syringophilidae) and picobiine relationships with avian hosts. *PLoS ONE* **2020**, *15*, e0225982. [CrossRef]
23. Pires, E.O.; Daemon, E. Biological and ecological aspects of quill mites, parasites of domestic hen *Gallus gallus domesticus* (Aves, Phasianidae) from rusting breeding locations in the municipality of Juiz de Fora, Minas Gerais, Brasil. *Rev. Bras. Zoociencias* **2007**, *9*, 95–102.
24. Skirnisson, K.; Nielsen, Ó.K. Quill mite infestation of rock ptarmigan *Lagopus muta* (Aves: Phasianidae) in relation to year and host age, sex, body condition, and density. *Parasitol. Res.* **2019**, *118*, 2643–2650. [CrossRef] [PubMed]
25. Grossi, A.; Proctor, H. The distribution of quill mites (*Betasyringophiloidus seiuri*) among flight feathers of the ovenbird (*Seiurus aurocapilla*). *J. Parasitol.* **2020**, *106*, 82–89. [CrossRef] [PubMed]
26. Skoracki, M.; Kosicki, J.Z.; Sikora, B.; Töpfer, T.; Hušek, J.; Unsöld, M.; Hromada, M. The Occurrence of Quill Mites (Arachnida: Acariformes: Syringophilidae) on Bee-Eaters (Aves: Coraciiformes: Meropidae: *Merops*) of Two Sister Clades. *Animals* **2021**, *11*, 3500. [CrossRef]
27. Skoracki, M.; Kosicki, J.Z.; Kwieciński, Z. Distribution of the parasitic mite *Bubophilus aegolius* sp. n. (Acariformes: Syringophilidae) on the Boreal Owl *Aegolius funereus* (L) (Strigiformes: Strigidae) and the low effectiveness of infestation. *Eur. Zool. J.* **2021**, *88*, 352–362. [CrossRef]
28. Hromada, M.; Klimovicova, M.; Unsold, M.; Skoracki, M. Host-parasite relationships in the system composed by cuckoos and quill mites. *Syst. Appl. Acarol.* **2016**, *21*, 528–536.
29. Skoracki, M.; Hromada, M.; Zmudzinski, M.; Unsoeld, M.; Sikora, B. Parasitic quill mites of the family Syringophilidae (Acariformes: Prostigmata) associated with Sub Saharan Sunbirds (Passeriformes: Nectariniidae): Species composition and host-parasite relationships. *J. Med. Entomol.* **2018**, *55*, 1464–1477. [CrossRef]
30. Kaszewska-Gilas, K.; Kosicki, J.Z.; Hromada, M.; Skoracki, M. Global Studies of the Host-Parasite Relationships between Ectoparasitic Mites of the Family Syringophilidae and Birds of the Order Columbiformes. *Animals* **2021**, *11*, 3392. [CrossRef] [PubMed]
31. Skoracki, M.; Hromada, M.; Prevuznakova, P.; Wamiti, W. Mites of the family Syringophilidae (Acariformes: Cheyletoidea) parasitizing waxbills of the genus *Estrilda* (Passeriformes: Estrildidae). *Syst. Appl. Acarol.* **2019**, *24*, 1799–1808.
32. Kaszewska, K.; Skoracki, M.; Hromada, M. A review of the quill mites of the genus *Gunabopicobia* Skoracki and Hromada (Acariformes: Prostigmata: Syringophilidae) associated with birds of the order Columbiformes. *Int. J. Acarol.* **2018**, *44*, 288–299. [CrossRef]
33. Clements, J.F.; Schulenberg, T.S.; Iliff, M.J.; Roberson, D.; Fredericks, T.A.; Sullivan, B.L.; Wood, C.L. The eBird/Clements Checklist of Birds of the World. 2021. Available online: http://www.birds.cornell.edu/clementschecklist/download/v2021 (accessed on 25 May 2022).
34. Joseph, L.; Toon, A.; Schirtzinger, E.; Wright, T.; Schodde, R. A revised nomenclature and classifcation for family-group taxa of parrots (Psittaciformes). *Zootaxa* **2012**, *3205*, 26–40. [CrossRef]
35. de Kloet, R.; de Kloet, S. The evolution of the spindlin gene in birds: Sequence analysis of an intron of the spindlin W and Z gene reveals four major divisions of the Psittaciformes. *Mol. Phylogen. Evol.* **2005**, *36*, 706–721. [CrossRef] [PubMed]
36. Tavares, E.S.; Baker, A.J.; Pereira, S.L.; Miyaki, C.Y. Phylogenetic relationships and historical biogeography of Neotropical parrots (Psittaciformes: Psittacidae: Arini) inferred from mitochondrial and nuclear DNA sequences. *Syst. Biol.* **2006**, *55*, 454–470. [CrossRef]
37. Wright, T.F.; Schirtzinger, E.E.; Matsumoto, T.; Eberhard, J.R.; Graves, G.R.; Sanchez, J.J.; Capelli, S.; Müller, H.; Scharpegge, J.; Chambers, G.K.; et al. A multilocus molecular phylogeny of the parrots (Psittaciformes): Support for a Gondwanan origin during the Cretaceous. *Mol. Biol. Evol.* **2008**, *25*, 2141–2156. [CrossRef]
38. Prum, R.O.; Jacob, S.B.; Dornburg, A.; Field, D.J.; Townsend, J.P.; Lemmon, E.M.; Lemmon, A.R. A comprehensive phylogeny of birds (Aves) using targeted next-generation DNA sequencing. *Nat. Lett.* **2015**, *15697*, 569–573. [CrossRef] [PubMed]
39. Kimball, R.T.; Oliveros, C.H.; Wang, N.; White, N.D.; Barker, F.K.; Field, D.J.; Ksepka, D.T.; Chesser, R.T.; Moyle, R.G.; Braun, M.J.; et al. A phylogenomic super tree of birds. *Diversity* **2019**, *11*, 109. [CrossRef]
40. Yuri, T.; Kimball, R.T.; Harshman, J.; Bowie, R.C.; Braun, M.J.; Chojnowski, J.L.; Han, K.L.; Hackett, S.J.; Huddleston, C.J.; Moore, W.S.; et al. Parsimony and model-based analyses of indels in avian nuclear genes reveal congruent and incongruent phylogenetic signals. *Biology* **2013**, *2*, 419–444. [CrossRef]
41. Claraumnt, S.; Cracraft, J. A new time tree reveals Earth history's imprint on the evolution of modern birds. *Sci. Adv.* **2015**, *1*, e1501005. [CrossRef]
42. White, N.E.; Phillips, M.J.; Gilbert, T.P.; Alfaro-Núñez, A.; Willerslev, E.; Mawson, P.R.; Spencer, P.B.S.; Bunce, M. The evolutionary history of cockatoos (Aves: Psittaciformes: Cacatuidae). *Mol. Phylogenet. Evol.* **2011**, *59*, 615–622. [CrossRef]
43. Skoracki, M.; Sikora, B.; Spicer, G.S. A review of the subfamily Picobiinae Johnston and Kethley, 1973 (Acariformes: Prostigmata: Syringophilidae). *Zootaxa* **2016**, *4113*, 1–95. [CrossRef]
44. Grandjean, F. Les Segments Post-Larvaires de L'hystérosoma Chez Les Oribates (Acariens). *Bull. Soc. Zool. Fr.* **1939**, *64*, 273–284.
45. Kethley, J.B. Acarina: Prostigmata (Actinedida). In *Soil Biology Guide*; Dindal, D.L., Ed.; John Wiley & Sons: New York, NY, USA, 1990; pp. 667–756.
46. Grandjean, F. Observations Sur Les Acariens de La Famille Des Stigmaeidae. *Arch. Sci. Phys. Nat.* **1944**, *26*, 103–131.
47. Skoracki, M. A review of the quill mites (Acari: Syringophilidae) parasitizing parrots (Aves: Psittaciformes) with description of three new species. *Acarina* **2005**, *13*, 127–136.

48. Skoracki, M.; Glowska, E.; Sikora, B. Four new species of the quill mite genus *Picobia* Haller (Acari: Syringophilidae) parasitizing birds in the Australian Region. *Zootaxa* **2008**, *1961*, 58–68. [CrossRef]
49. Skoracki, M.; Hromada, M. A review of picobiine mites (Acari: Syringophilidae: Picobiinae) parasitising African birds. *Folia Parasitol.* **2013**, *60*, 192–212. [CrossRef]
50. Marciniak, N.; Skoracki, M.; Hromada, M. Quill mites of the family Syringophilidae (Acariformes: Prostigmata) associated with Cockatoos (Psittaciformes: Cacatuidae). *Zootaxa* **2019**, *4565*, 190–200. [CrossRef]
51. Marciniak, N.; Skoracki, M.; Hromada, M. *Peristerophila nestoriae*, a new species of quill mite of the family Syringophilidae (Acariformes: Prostigmata) parasitizing New Zealand Kaka *Nestor meridionalis* (Gmelin) (Psittaciformes: Strigopidae). *N. Z. J. Zool.* **2019**, *46*, 348–352. [CrossRef]
52. Marciniak-Musial, N.; Hromada, M.; Sikora, B. Taxonomic diversity of the quill mites of the family Syringophilidae (Acariformes: Prostigmata) associated with old world parrots (Psittaciformes: Psittaculidae). *J. Med. Entomol.* **2022**, *55*, 213–232. [CrossRef]
53. Marciniak-Musial, N.; Sikora, B. Quill Mites of the Family Syringophilidae (Acariformes: Prostigmata) Associated with the New World and African Parrots (Psittaciformes: Psittacidae) With the Description of Eight New Species. *J. Med. Entomol.* **2022**, *5*, 1562–1588. [CrossRef]
54. Reiczigel, J.; Marozzi, M.; Fábián, I.; Rózsa, L. Biostatistics for parasitologists—A primer to Quantitative Parasitology. *Trends Parasitol.* **2019**, *35*, 277–281. [CrossRef]
55. Caira, J.N.; Jensen, K.; Holsinger, K.I. On a new index of host specificity. In *Taxonomie, Écologie et Évolution des Metazoaires Parasites*; Combes, C., Jourdane, J., Eds.; Presses Universitaires de Perpignan: Perpignan, France, 2003; pp. 161–201.
56. Holt, B.G.; Lessardb, J.P.; Borregaard, M.K.; Fritz, S.A.; Araújo, M.B.; Dimitrov, D.; Fabre, P.H.; Graham, C.H.; Graves, G.R.; Jønsson, K.A.; et al. An update of Wallace's zoogeographic regions of the world. *Science* **2013**, *339*, 74–78. [CrossRef]
57. Dormann, F.; Gruber, B.; Fründ, J. Introducing the bipartite package: Analysing ecological networks. *R News* **2008**, *8*, 1–11.
58. Blüthgen, N.; Menzel, F.; Bliithgen, N. Measuring specialization in species interaction networks. *BMC Ecol.* **2006**, *9*, 6–9.
59. Blüthgen, N. Why network analysis is often disconnected from community ecology: A critique and an ecologist's guide. *Basic Appl. Ecol.* **2010**, *11*, 185–195. [CrossRef]
60. Atmar, W.; Patterson, B.D. The measure of order and disorder in the distribution of species in fragmented habitat. *Oecologia* **1993**, *96*, 373–382. [CrossRef]
61. Bascompte, J.; Jordano, P.; Melia, C.J.; Olesen, J.M. The nested assembly of plant–animal mutualistic networks. *Proc. Natl. Acad. Sci. USA* **2003**, *100*, 9383–9387. [CrossRef]
62. Pavlopoulos, G.A.; Kontou, P.I.; Pavlopoulou, A.; Bouyioukos, C.; Markou, E.; Bagos, P.G. Bipartite graphs in systems biology and medicine: A survey of methods and applications. *GigaScience* **2018**, *7*, giy014. [CrossRef]
63. Fortuna, M.A.; Stouffer, D.B.; Olesen, J.M.; Jordano, P.; Mouillot, D.; Krasnov, B.R.; Poulin, R.; Bascompte, J. Nestedness versus modularity in ecological networks: Two sides of the same coin? *J. Anim. Ecol.* **2010**, *79*, 811–817. [CrossRef]
64. Blüthgen, N.; Fründ, J.; Vázquez, D.P.; Menzel, F. What do interaction network metrics tell us about specialization and biological traits. *Ecology* **2008**, *89*, 3387–3399. [CrossRef]
65. Newman, M.E.J.; Barabási, A.L.; Watts, D.J. *The Structure and Dynamics of Networks*; Princeton University Press: Princeton, NJ, USA, 2006; p. 592.
66. Guimera, R.; Amaral, L.A.N. Functional cartography of complex metabolic networks. *Nature* **2005**, *433*, 895–900. [CrossRef]
67. Dormann, C.F.; Strauss, R. A method for detecting modules in quantitative bipartite networks. *Methods Ecol. Evol.* **2014**, *5*, 90–98. [CrossRef]
68. Carstensen, D.W.; Sabatino, M.; Morellato, L.P.C. Modularity, pollination systems, and interaction turnover in plant-pollinator networks across space. *Ecology* **2016**, *97*, 1298–1306. [CrossRef] [PubMed]
69. Page, R.D.M. *NDE, NEXUS Data Editor 0.5.0*; University of Glasgow: Glasgow, UK, 2001.
70. Swofford, D.L. *PAUP*. Phylogenetic Analysis Using Parsimony (and Other Methods), Version 4*; Sinauer Associates: Sunderland, MA, USA, 2002.
71. Jetz, W.; Thomas, G.H.; Joy, J.B.; Hartmann, K.; Mooersm, O.A. The global diversity of birds in space and time. *Nature* **2012**, *491*, 444–448. [CrossRef]
72. Drummond, A.J.; Rambaut, A. BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evol. Biol.* **2007**, *7*, 214. [CrossRef]
73. Rambaut, A. FigTree v1.4.4. 2018. Available online: http://tree.bio.ed.ac.uk/software/5figtree/ (accessed on 25 May 2022).
74. Fain, A.; Bochkov, A.V.; Mironov, S.V. New genera and species of quill mites of the family Syringophilidae (Acari: Prostigmata). *Bull. Inst. R. Sci. Nat. Belg.* **2000**, *70*, 33–70.
75. Bochkov, A.V.; Perez, T.M. New quill mites of the family Syringophilidae (Acari: Cheyletoidea) parasitizing Mexican parrots. *Belg. J. Entomol.* **2002**, *4*, 145–159.
76. Bochkov, A.V.; Fain, A. New and little known species of the family Syringophilidae (Acari: Cheyletoidea) from parrots (Aves: Psittaciformes). *Acarina* **2003**, *11*, 37–44.
77. Skoracki, M. Quill mites (Acariformes: Syringophilidae) associated with birds of Mexico. *Zootaxa* **2017**, *4282*, 179–191. [CrossRef]
78. Skoracki, M.; Lontkowski, J.; Stawarczyk, T. New taxa of the parasitic quill mites associated with accipitrid birds indicating close relationship of falconid birds to Psittaci-Columbi clade. *J. Nat. Hist.* **2010**, *44*, 1203–1214. [CrossRef]
79. Skoracki, M.; Unsoeld, M.; Marciniak, N.; Sikora, B. Diversity of quill mites of the family Syringophilidae (Acari: Prostigmata) parasitizing owls (Aves: Strigiformes) with remarks on the host-parasite relationships. *J. Med. Entomol.* **2016**, *53*, 815–826. [CrossRef]

80. Zmudzinski, M.; Unsoeld, M.; Knee, W.; Skoracki, M. New host records for parasitic mites of the family Syringophilidae from accipitriform birds (Aves: Accipitriformes). *Ann. Parasitol.* **2015**, *61*, 291–293.
81. Glowska, E.; Laniecka, I. Two new quill mite species (Prostigmata: Syringophilidae) parasitizing Australian birds. *Zootaxa* **2013**, *3670*, 385–390. [CrossRef] [PubMed]
82. Skoracki, M.; Dabert, J. New species of Syringophilidae (Acari: Prostigmata) from African birds. *Genus* **1999**, *10*, 523–527.
83. Skoracki, M.; Hromada, M.; Kaszewska, K.; Sikora, B. Females of the quill mite genera *Peristerophila* and *Castosyringophilus* (Acariformes: Syringophilidae) are two morphological forms: Ontogenetic and population evidences. *Syst. Appl. Acarol.* **2020**, *25*, 1803–1820.
84. Casto, S.D. A new quill mite (Acarina: Syringophilidae) from the ground dove. *Southwest. Entomol.* **1980**, *5*, 1–5.
85. Skoracki, M.; Hromada, M.; Kaszewska, K.; Unsoeld, M. *Peristerophila falcophila* sp. nov., a new species and first record of quill mites (Acariformes: Syringophilidae) parasitizing birds of the order Falconiformes. *Acta Parasitol.* **2018**, *63*, 744–749. [CrossRef]
86. Kaszewska, K.; Kavetska, K.; Skoracki, M. Two new species of quill mites of the family Syringophilidae (Acariformes: Cheyletoidea) associated with treronine doves (Columbiformes: Columbidae: Treroninae). *Zootaxa* **2014**, *3846*, 293–300. [CrossRef]
87. Klimovičová, M.; Peter, M.; Kahure, N.; Hromada, M. A review of quill mites (Acari: Syringophilidae) parasitising Kenyan birds. *Zootaxa* **2014**, *3857*, 571–580. [CrossRef]
88. Kaszewska, K.; Skoracki, M.; Kosicki, J.Z.; Hromada, M. New species and records of the quill mites of the genus *Peristerophila* Kethley, 1970 (Acariformes: Syringophilidae) associated with pigeons and doves (Aves: Columbiformes). *Zootaxa* **2020**, *4878*, 349–361. [CrossRef]
89. Skoracki, M.; Glowska, E. Quill mites (Acari: Syringophilidae) associated with columbiform birds. *Genus* **2008**, *19*, 151–160.
90. Kaszewska, K.; Skoracki, M. Two new quill mite species of the genus *Psittaciphilus* Fain, Bochkov & Mironov, 2000 (Acariformes: Syringophilidae) associated with pigeons and doves (Columbiformes: Columbidae). *Syst. Parasitol.* **2018**, *95*, 953–958.
91. Skoracki, M.; Sikora, M. *Terratosyringophilus reichholfi*, a new species of quill mites parasitizing the black-capped lory *Lorius lory* (L.) in New Guinea. *Spixiana* **2008**, *31*, 195–198.
92. Casto, S.D. A new syringophilid mite from the white-winged dove. *Tex. J. Sci.* **1979**, *31*, 225–229.
93. Casto, S.D. *Cuculiphilus lobatus* gen. n., sp. n. representing a new subfamily of quill mites (Acarina: Syringophilidae) from the groove-billedani, *Crotophaga sulcirostris* (Cuculiformes: Cuculidae). *Southwest. Nat.* **1977**, *22*, 169–176. [CrossRef]
94. Skoracki, M.; Hromada, M.; Sikora, B. Quill mites of the family Syringophilidae (Acariformes: Prostigmata) parasitizing coraciiform birds (Aves: Coraciiformes). *Zootaxa* **2020**, *4802*, 169–181. [CrossRef] [PubMed]
95. Skoracki, M.; Zmudzinski, M.; Sikora, B. *Rafapicobia olszanowskii*, a New Species of Syringophilid Mite (Acariformes: Syringophilidae) from *Semnornis ramphastinus* (Piciformes: Semnornithidae). *Annal. Zool.* **2020**, *70*, 449–452. [CrossRef]
96. Sikora, B.; Fajfer, M.; Skoracki, M. Quill mites (Acari: Syringophilidae) from mimid birds (Aves: Mimidae). *Zootaxa* **2011**, *3027*, 29–38. [CrossRef]
97. Skoracki, M.; Solarczyk, P. New picobiin mites (Acari: Syringophilidae: Picobiinae) associated with woodcreeper birds (Passeriformes: Dendrocolaptidae). *Zootaxa* **2012**, *3406*, 59–66. [CrossRef]
98. Skoracki, M.; Unsoeld, M.; Skorupski, M.; Kavetska, K. Syringophilid mites associated with the rails (Aves: Rallidae) and a key to the species of the genus *Rafapicobia* Skoracki, 2011. *Syst. Parasitol.* **2014**, *88*, 227–232. [CrossRef]
99. Glowska, E.; Laniecka, I.; Milensky, C.M. Two new picobiin mite species (Acari: Cheyletoidea: Syringophilidae) parasitizing passerine birds in Guyana. *Acta Parasitol.* **2015**, *60*, 488–493. [CrossRef]
100. Skoracki, M.; Dabert, J. A review of parasitic mites of the family Syringophilidae (Acari, Prostigmata) from African birds, with descriptions of four new species. *Acta Parasitol.* **2002**, *47*, 137–146.
101. Skoracki, M.; Sikora, B.; Hromada, M. First record of quill mites (Acariformes: Syringophilidae: Picobiinae) living in the quill walls of parrots. *J. Med. Entomol.* **2019**, *5*, 1610–1613. [CrossRef] [PubMed]
102. Skoracki, M.; Bochkov, A.V.; Wauthy, G. Revision of the quill mites of the genus *Picobia* Haller,1878 (Acari: Syringophilidae) with notes on their host-parasites relationships. *Insect Syst. Evol.* **2004**, *35*, 155–176. [CrossRef]
103. Skoracki, M.; Glowska, E. Two new species of the genus *Picobia* Haller (Acari: Syringophilidae) from Australian and Indonesian passeriform birds. *N. Z. J. Zool.* **2008**, *35*, 281–286. [CrossRef]
104. Glowska, E.; Schmidt, B.K. New quill mites (Cheyletoidea: Syringophilidae) parasitizing the black-headed paradise flycatcher *Terpsiphone rufventer* (Passeriformes: Monarchidae) in Gabon. *Zootaxa* **2014**, *3786*, 57–64. [CrossRef] [PubMed]
105. Nattress, B. Horizontal transmission of *Syrngophilopsis kirgizorum* (Acari: Cheyletoidea: Syringophilidae). *Acarina* **2011**, *19*, 270.
106. Casto, S.D. Host records and observations of quill mites (Acarina: Syringophilidae) from Texas birds. *Southwest. Entomol.* **1976**, *1*, 155–160.
107. Jarvis, E.D.; Mirarab, S.; Aberer, A.J.; Li, B.; Houde, P.; Li, C.; Ho, S.Y.W.; Faircloth, B.C.; Nabholz, B.; Howard, J.T.; et al. Whole-genome analyses resolve early branches in the tree of life of modern birds. *Science* **2014**, *346*, 1320–1331. [CrossRef]
108. Schmaschke, R.; Sachse, M.; Eulenberger, K.; Schone, R. Quill mites–Little Known Parasites of Birds. Verhandlungsbericht des 41. *Int. Symp. Über Die Erkrank. Der Zoo–Und Wildtiere* **2003**, *41*, 127–133.
109. Skoracki, M.; Michalik, J.; Sikora, B. Prevalence and habitat preference of quill mites (Acari, Syringophilidae) parasitizing forest passerine birds in Poland. *Acta Parasitol.* **2010**, *55*, 188–193. [CrossRef]
110. Huang, L.Q.; Guo, X.G.; Wu, D.; Zhou, D.H. Distribution and ecological niches of gamasid mites (Acari: Mesostigmata) on small mammals in Southwest China. *Psyche* **2010**, *934508*, 1–12. [CrossRef]

111. MacArthur, R.H.; Levins, R. The limiting similarity, convergence and divergence of coexisting species. *Am. Nat.* **1967**, *101*, 377–385. [CrossRef]
112. Amarasekare, P. Competitive coexistence in spatially structure environments: A synthesis. *Ecol. Lett.* **2003**, *6*, 1109–1122. [CrossRef]
113. Gonzalez-Acuna, D.; Venzal, J.M.; Keirans, J.E.; Robbins, R.G.; Ippi, S.; Guglielmone, A.A. New host and locality records for the *Ixodes auritulus* (Acari: Ixodidae) species group, with a review of host relationships and distribution in the Neatropical Zoogeographic Region. *Exp. Appl. Acarol.* **2005**, *37*, 147–156. [CrossRef] [PubMed]
114. Skoracki, M.; Hebda, G. Quill mites (Acari: Syringophilidae) from *Aegithalos caudatus* (Passeriformes: Aegithalidae). *Zootaxa* **2004**, *691*, 1–6. [CrossRef]
115. Kethley, J.B.; Johnston, D.E. Resource tracking patterns in bird and mammal ectoparasites. *Misc. Publ. Entomol. Soc. Amer.* **1975**, *9*, 227–236.
116. Rebrassier, R.E.; Martin, E.D. *Syringophilus bipectinatus* a quill mite of poultry. *Science* **1932**, *76*, 128. [CrossRef]
117. Casto, S.D. The effect of the postjuvenal molt in the House Sparrow on infestations of the quill mite, *Syringophiloidus minor* (Berlese) (Acarina: Syringophilidae). *J. Med. Entomol.* **1975**, *12*, 23–27. [CrossRef]
118. Skoracki, M.; Hromada, M.; Tryjanowski, P. Description of a new species of quill mite *Syringophiloidus weiszii* sp. n. (Acari, Prostigmata, Syringophilidae) from Great Grey Shrike *Lanius excubitor*. *Acta Parasitol.* **2001**, *46*, 30–34.
119. Jardim, C.C.; Cunha, L.M.; Do Carmo Rezende, L.; Teixeira, C.M.; Silva Martins, N.R.; Oliveira, P.R.; Leite, R.C.; Faccini, J.L.H.; Leite, R.C. Quill mites in Brazilian psittacine birds (Aves: Psittaciformes). *J. Zoo Wildl. Med.* **2012**, *43*, 511–516. [CrossRef]
120. Skoracki, M.; Hromada, M.; Sikora, B. *Castosyringophilus meropis* sp. n. (Acariformes: Syringophilidae)—A new quill mite species parasitising the world population of *Merops apiaster* Linnaeus (Coraciiformes: Meropidae). *Folia Parasitol.* **2017**, *64*, 24. [CrossRef]
121. Skirnisson, K.; Palsdottir, G.R. Past and present status of poultry parasites in Iceland. *Icel. Agric. Sci.* **2020**, *33*, 3–14. [CrossRef]
122. Gritsenko, E.F. The biology and ecology of the quill mite Syringophilus bipectinatus Heller, 1880. In *Proceedings of the 3rd International Congress of Acarology*; Milan, D., Rosicky, B., Eds.; Czechoslovak Academy of Sciences: Prague, Czech Republic, 1973; pp. 515–516.
123. Poulin, R. Parasite biodiversity revisited: Frontiers and constraints. *Int. J. Parasitol.* **2014**, *44*, 581–589. [CrossRef] [PubMed]
124. Landi, P.; Minoarivelo, H.O.; Brännström, A.; Hui, C.; Dieckmann, U. Complexity and stability of ecological networks: A review of the theory. *Popul. Ecol.* **2018**, *60*, 319–345. [CrossRef]
125. Durán, A.; Saldaña-Vázquez, R.; Graciolli, G.; Peinado, L. Specialization and Modularity of a Bat Fly Antagonistic Ecological Network in a Dry Tropical Forest in Northern Colombia. *Acta Chiropt.* **2019**, *20*, 503–510. [CrossRef]
126. Dormann, C.F.; Fründ, J.; Blüthgen, N.; Gruber, B. Indices, graphs and null models: Analysing bipartite ecological networks. *Open Ecol. J.* **2009**, *2*, 7–24. [CrossRef]
127. Thebault, E.; Fontaine, C. Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science* **2010**, *329*, 853–856. [CrossRef]
128. Olesen, J.M.; Bascompte, J.; Dupont, Y.L.; Jordano, P. The modularity of pollination networks. *Proc. Natl. Acad. Sci. USA* **2007**, *104*, 19891–19896. [CrossRef]
129. Devictor, V.; Julliard, R.; Jig, F. Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. *Oikos* **2008**, *117*, 507–514. [CrossRef]
130. Heleno, R.; Devoto, M.; Pocock, M. Connectance of species interaction networks and conservation value: Is it any good to be well connected? *Ecol. Indic.* **2012**, *14*, 7–10. [CrossRef]
131. Briand, F. Environmental control of food web structure. *Ecology* **1983**, *64*, 253–263. [CrossRef]
132. Memmott, J.; Waser, N.M. Integration of alien plants into a native flower pollinator visitation web. *Proc. R. Soc. Lond. Ser. B-Biol. Sci.* **2002**, *269*, 2395–2399. [CrossRef] [PubMed]
133. Heleno, R.H.; Lacerda, I.; Ramos, J.A.; Memmott, J. Evaluation of restoration effectiveness: Community response to the removal of alien plants. *Ecol. Appl.* **2010**, *20*, 1191–1203. [CrossRef] [PubMed]
134. Delmas, E.; Besson, M.; Brice, M.H.; Burkle, L.A.; Dalla Riva, G.V.; Fortin, M.J.; Gravel, D.; Guimarães, P.R., Jr.; Hembry, D.H.; Newman, E.A.; et al. Analysing ecological networks of species interactions. *Biol. Rev.* **2018**, *94*, 16–36. [CrossRef] [PubMed]