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Taxonomy and evolution of quill mites of the family Syringophilidae (Acariformes: Prostigmata) parasitising columbiform birds (Aves: Columbiformes)

Taksonomia i ewolucja dutkowych roztoczy z rodziny Syringophilidae (Acariformes: Prostigmata) pasożytujących na ptakach gołębiowych (Aves: Columbiformes)

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„Jeśli widzę dalej, to tylko dlatego że stoję na ramionach olbrzymów”

Isaac Newton 1667

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STRESZCZENIE

Znajomość różnorodności gatunkowej pasożytów związanych z poszczególnymi grupami żywicieli ma kluczowe znaczenie w badaniach nad układem pasożyt-żywiciel i ich historii ewolucyjnej. Pasożytnictwo permanentne jest jednym z najbardziej intrygujących rodzajów pasożytnictwa, badania nad tego typu pasożytami mogą pomóc lepiej zrozumieć interakcje i relacje w układach antagonistycznych. Przedmiotem badań w mojej pracy doktorskiej była acarofauna obligatoryjnych oraz wysoce specyficznych ektopasożytniczych roztoczy należących do rodziny Syringophilidae pasożytujących na ptakach z rzędu Columbiformes. Gołębiowe były jedną z najsłabiej przebadanych grup ptaków pod kątem występowania roztoczy dutkowych oraz wzajemnych relacji w układzie pasożyt-żywiciel.

W ramach pracy doktorskiej podjęto następujące cele: 1) zbadanie różnorodności taksonomicznej Syringophilidae z możliwie szerokiego spektrum potencjalnych żywicieli należących do ptaków gołębiowych reprezentujących trzy klady oraz pochodzących ze wszystkich krain zoogeograficznych; 2) zbadanie interakcji w układzie pasożyt-żywiciel m. in. określenie prewalencji, specyficzności żywicielskiej i topicznej roztoczy dutkowych związanych z ptakami gołębiowymi; 3) ustalenie relacji filogenetycznych na poziomie rodzajowym Syringophilidae pasożytujących na ptakach gołębiowych. Prezentowana praca doktorska składa się z części taksonomicznej oraz części poświęconej zagadnieniom specyficzności żywicielskiej, interakcjom w układzie pasożyt-żywiciel oraz powiązań filogenetycznych pomiędzy poszczególnymi rodzajami w obrębie Syringophilidae.

Podczas badań przebadano 112 gatunków ptaków należących do rzędu Columbiformes. Stwierdzono obecność 25 gatunków roztoczy dutkowych pasożytujących na 65 gatunkach ptaków. Opisano 16 nowych dla wiedzy gatunków dutkowców, będących przedstawicielami następujących rodzajów: *Meitingsunes* (*M. chalcophas, M. turacoenas M. lengai, M. ptilinopus*), *Peristerophila* (*P. lature, P. geopelis, P. leucomela*), *Psittaciphilus* (*P. montanus, P. patagioenas*) oraz *Gunabopicobia* (*G. claravis, G. geotrygoni, G. masalaje, G. metriopelia, G. lathami, G. leptotila, G. verraruxi*).

Badania taksonomiczne prowadzone były na przedstawicielach wszystkich krain zoogeograficznych, w których występują ptaki gołębiowe. Syringophilidae stwierdzono w nowych regionach zoogeograficznych tj.: Oceania (Papua Nowa Gwinea, Indonezja) oraz kraina Australijska (Australia), poszerzając tym samym wiedzę na temat światowego rozmieszczenia tychże roztoczy na przedstawicielach Columbiformes.

W ramach pracy doktorskiej określono prewalencję dla każdego zainfekowanego gatunku żywicielskiego. Indeks prewalencji oscylował między 4.2%–100%. Otrzymane wyniki pozwoliły na scharakteryzowanie stopnia powiązań pomiędzy poszczególnymi gatunkami pasożytów i ich żywicielami. Na podstawie przeprowadzonej analizy specyficzności żywicielskiej stwierdzono 8 gatunków monoksenicznych, 5 gatunków oligoksenicznych, 8 mesostenokseniczych, 3 metastenoksenicznych oraz 1 polikseniczny.

Ponadto zaobserwowano ko-infestację kilku gatunków roztoczy na 11 gatunkach ptaków gołębiowych. Stwierdzono występowanie następujących wzorców multiinfestacji: Syringophilinae-Syringophilinae (*Syr-Syr*) oraz Syringophilinae-Picobiinae (*Syr-Pic*), w których czynnikiem rozdzielającym pasożyty była zasiedlana nisza. Tylko w jednym przypadku odnotowano zasiedlanie tego samego typu piór, przez dwa odrębne gatunki dutkowców, jednakże nie zaobserwowano w żadnym z przypadków występowania dwóch różnych gatunków w obrębie tej samej dutki.

Kolejnym celem pracy doktorskiej było zbadania interakcji w układzie pasożyt-żywiciel. Przeprowadzono analizę sieci dwudzielnych składających się ze wszystkich dotychczas poznanych gatunków Syringophilidae infestujących ptaki z rzędu Columbiformes. Otrzymana sieć charakteryzowała się następującymi wartościami współczynników: *specjalizacja na poziomie sieciowym* H2=0.93, *połączeń* C=0.90, *zagnieżdżenia* N=0.908 oraz *modularności* Q=0.83. Architektura sieci – Syringophilidae-Columbiformes, wskazuje iż roztocze dutkowe pasożytujące na ptakach gołębiowych tworzą wysoce specyficzny układ o silnej dominacji gatunków wyspecjalizowanych na rzecz pasożytów o szerszym spektrum żywicielskim. Wykazano także tworzenie w ramach sieci 20 modułów (klastrów), które podzielono na 3 grupy: A) skupiające jeden gatunek pasożyta i związany z nim gatunek żywicielski, B) jeden gatunek pasożyta zasiedlający wiele gatunków żywicielskich, C) dwa lub więcej gatunków Syringophilidae skupionych wokół kilku gatunków żywicielskich. Na podstawie otrzymanych wyników stwierdzono, że roztocze dutkowe tworzą trwałe związki pomiędzy żywicielami z niską tendencją do losowej zmiany żywiciela, na co wskazują słabe interakcje poza zajmowanymi klastrami.

W ramach prac badawczych przeprowadzono analizę filogenetyczną opartą na cechach morfologicznych, która wykazała występowanie dwóch odrębnych kladów w obrębie podrodziny Syringophilinae, tj. *Meitingsunes-Psittaciphilus* oraz *Peristerophila-Terratosyringophilus*.

ABSTRACT

The knowledge of parasite diversity associated with particular groups of hosts is crucial to the study of the parasite-host system and its evolutionary history. Permanent parasitism is one of the most intriguing types of parasitism. The study of such parasites can help to better understand interactions and relationships in the antagonistic systems. The subject of research in my doctoral dissertation was the acarofauna of obligatory and highly specific ectoparasitic mites belonging to the family Syringophilidae, parasitizing birds of the order Columbiformes. Pigeons have been one of the least studied groups of birds for the presence of quill mites and their parasite-host interactions.

The following objectives were discussed as part of my dissertation: 1) to investigate the taxonomic diversity of Syringophilidae from the broadest possible spectrum in terms of their potential hosts belonging to the Columbiformes that represent three clades and come from all zoogeographic zones, 2) to investigate the interactions in the host-parasite system, i.e., to determine the prevalence, host and topical specificity of quill mites associated with pigeons, 3) to establish phylogenetic relationships on the generic level of Syringophilidae parasitizing pigeon birds. The dissertation consists of a taxonomic section as well as a section on the issues connected to host specificity and parasite-host interactions

During the study, 112 species of birds belonging to the order Columbiformes were examined. The presence of 25 species of quill mites was found parasitizing 65 species of birds. The study describes 16 new species of the Syringophilidae, representing the following genera: *Meitingsunes* (*M. chalcophas, M. turacoenas M. lengai*, *M. ptilinopus*), *Peristerophila* (*P. lature*, *P. geopelis*, *P. leucomela*), P*sittaciphilus* (*P. montanus*, *P. patagioenas*) and *Gunabopicobia* (*G. claravis, G. geotrygoni, G. masalaje, G. metriopelia, G. lathami, G. leptotila*, *G. verraruxi*).

Taxonomic studies were carried out on representatives of all zoogeographic zones in which doves and pigeons are present. Syringophiliidae were found in new zoogeographic zones, i.e. Papua New Guinea, Indonesia, and Australia, thus increasing the knowledge of the global distribution of these mites on the Columbiform representatives.

The dissertation determined the prevalence of each infected host species. The index of prevalence oscillated between 4.2 % to 100 %. The obtained results allowed us to characterize the degree of association between the particular species of parasites and their hosts. Based upon the analysis of host specificity, 8 monoxenous species, 5 oligoxenous species, 8 mesostenoxenous species, 3 metastenoxenous, and 1 polixenous were found. In addition, co-infestation phenomena were observed on 11 species of pigeon. The following multi-infestation patterns have been found: Syringophilinae-Syringophilinae (Syr-Syr) and Syringophilinae-Picobiinae (Syr-Pic). The factor separating the parasites was the inhabited niche. Only one case notes the inhabitation of the same feather type by two distinct species of quill mice. However, no case notes the presence of the two species within the same quill.

Another goal of the dissertation was to study host-parasite interactions. An analysis of the bipartite network has taken into account all known species of Syringophiliidae which were associated with the birds from the order Columbiformes. The obtained bipartite network was characterized by the following factors: *specialization on network level* – H2=0.93, *connectance* – C=0.90, *nesting* – N=0.908, and *modularity* – Q=0.83. The architecture of the Syringophilidae-Columbiformes network indicates that the quill mites parasitizing doves and pigeons form a highly specific system, with a strong dominance of specialized species in favor of parasites with a broader host spectrum. The network also allowed to indicate 20 modules (clusters) which were then divided into three groups, namely: (A) clustering one parasite species and its associated host species (B) one parasite species inhabiting multiple hosts species, (C) two or more Syringophilidae species clustered around several host species. The results indicate that quill mites form permanent relationships between hosts, with a low tendency to randomly change hosts, as indicated by weak interactions outside the occupied clusters.

As a part of the research, a phylogenetic analysis based on morphological characteristics was carried out and revealed the presence of two distinct clades within the subfamily Syringophilinae: *Meitingsunes-Psittaciphilus* and *Terratosyringophilus-Peristerophila*.

WPROWADZENIE

Roztocze należące do rodziny Syringophilidae (Acariformes: Prostigmata) to obligatoryjne ektopasożyty, infestujące wyłącznie ptaki. Roztocze te, nazywane również dutkowcami, odżywiają się tkanką otaczająca dutkę pióra, przebijając jej włóknistą ścianę długimi i sztyletowatymi chelicerami (Casto 1974a, Kethley 1970, 1971). Ich mikrohabitat stanowią dutki różnych typów piór: lotki I, II, III-cio rzędowe, sterówki, pokrywy skrzydeł I, II, III-cio rzędowe, pokrywy pod- i nadogonowe oraz pióra konturowe. W dutkach przebiega cały ich rozwój oraz reprodukcja (Skoracki 2011). Rodzina ta dzieli się na dwie podrodziny Syringophilinae Lavoipierre, 1953 i Picobiinae Johnson i Kethley, 1975, które różnią się między sobą licznymi cechami morfologicznymi. Przedstawiciele podrodziny Syringophilinae mają zaokrąglone tibiotarsusy palp oraz wachlarzowate proralne szczeciny tarsusów *p'* i *p"* odnóży I-IV , podczas gdy u Picobiinae tibiotarsusy palp są ścięte, a szczeciny *p'* i *p"* są prętowate (Skoracki 2011). Ponadto, u przedstawicieli Picobiinae obserwujemy występowanie samic fyzogastrycznych, charakteryzujących się silnym rozrostem opistosomy. Młodociane formy Syringophilinae mają dobrze wykształcone szczeciny ciała oraz odnóży, natomiast u Picobiinae szczeciny nimf są słabo wykształcone. Roztocze te różnią się także preferencjami zasiedlanych mikrohabitatów. Przedstawiciele Syringophilinae infestują zróżnicowane typy piór głównie skrzydeł i ogona, natomiast Picobiinae zasiedlają wyłącznie pióra konturowe (Skoracki i in. 2004). Roztocze dutkowe to pasożyty permanentne, ich cały cykl życiowy realizowany jest w dutce pióra, za wyjątkiem krótkiego okresu poświęconemu dyspersji. Infestacja odbywa się na dwa sposoby i jest zsynchronizowana z cyklem dobowym żywicieli. Po pierwsze, do zarażenia dochodzi podczas lęgów w wyniku transmisji pionowej, kiedy to roztocze przechodzą z osobników rodzicielskich na osobniki młodociane. Po drugie, transmisja roztoczy odbywa się podczas sezonowego pierzenia, podczas którego roztocze infestują nowo rozwijające się pióra tego samego gospodarza (Kethley 1971; Kethley i Johnston 1975). Formą dyspersyjną są wyłącznie zapłodnione samice, które opuszczają pióro poprzez naturalny otwór *superior umbilicus*. Zapłodniona samica (założycielka kolonii) trafiając do dutki zaczyna składać jaja; pierwsze z nich jest haploidalne i z niego rozwija się samiec, natomiast kolejne są diploidalne z których rozwijają się samice (Kethley 1971; Casto 1974b).

Badania taksonomiczne nad rodziną Syringophilidae rozpoczęto już pod koniec XIX wieku kiedy to Heller opisał pierwszy gatunek dutkowca – *Syringophilus bipectinatus* Heller, 1880, ale to właśnie szczególnie dynamiczne studia w ostatnim dziesięcioleciu w sposób istotny przyczyniły się do lepszego poznania tej grupy zwierząt. Obecnie światowa fauna roztoczy dutkowych reprezentowana jest przez 403 gatunki należące do 63 rodzajów (podrodzina Syringophilinae – 51; podrodzina Picobiinae 12) (Zmudzinski i in. 2021). Syringophilidae znane są z ptaków należących do 27 rzędów, co stanowi ponad 65% wszystkich wytyczanych rzędów w obrębie Aves. Notowane były na ptakach pochodzących ze wszystkich krain zoogeograficznych za wyjątkiem Antarktydy i Arktyki. Biorąc pod uwagę bogactwo gatunkowe ptaków, jako potencjalnych żywicieli dla roztoczy z rodziny

Syringophilidae, szacuje się, że rodzina ta może liczyć blisko 5000 gatunków (Johnston i Kethley 1973). Wyraźnie więc widać, że stopień zbadania różnorodność gatunkowej tychże pasożytów jest wciąż niewystarczający. Mimo wieloletnich badań na fauną Syringophilidae oraz stwierdzenia występowania dutkowców na ponad 670 gatunkach żywicielskich, w dalszym ciągu wiele rzędów ptaków pozostaje niedostatecznie zbadanych pod kątem współegzystujących z nimi pasożytów. Szczególnie brakuje badań prowadzonych pod kątem poznania rzeczywistego spektrum żywicielskiego w obrębie konkretnej grupy (rodzaju, rodziny, rzędu) ptaków wraz z identyfikacją relacji w układzie pasożyt-żywiciel.

Przedmiotem badań w mojej pracy doktorskiej była akarofauna Syringophilidae związanych z ptakami z rzędu gołębiowych (Columbiformes). Ptaki te były jedną z najsłabiej poznanych grup żywicielskich dla tych roztoczy. Przedstawiciele tego rzędu zamieszkują szereg zróżnicowanych ekologicznie siedlisk, spotykane są niemal na wszystkich kontynentach za wyjątkiem Antarktydy (Gibbs i in. 2001). Columbiformes to monofiletyczny rząd ptaków obejmujący ponad 320 gatunków zgrupowanych w 49 rodzajach, należących do jednej rodziny Columbidae. Rodzina Columbidae dzieli się trzy podrodziny: a) Columbinae, obejmującą gołębiowe Starego i Nowego Świata, B) Claravinae, do której należą nieduże gołębie Neotropikalne oraz C) Raphinae, do której zaliczane są taksony Afro-Eurazjatyckie oraz Australijskie. Zakłada się, że przedstawiciele rzędu Columbiformes oddzieliły się od Apodiformes (Krótkonogie) i Caprimulgiformes (Lelkowate) w Kredzie, przed masowym wymieraniem. Radiacja współczesnych gołębiowych przypada na wczesny Eocen do środkowego Miocenu (Pereira i in. 2007). Uważa się, że przodkowie wszystkich współcześnie żyjących gołębiowych zasiedlali Gondwanę (najprawdopodobniej z obecnego regionu Neotropiku), kiedy to Afryka i Indie już oddaliły się od wspólnej masy lądowej, którą tworzyły Antarktyda-Austarlia-Ameryka Południowa. Badania molekularne oraz filogenetyczne wykazały, iż przedstawiciele podrodziny Columbinae zasiedlały krainę Orientalną co najmniej raz, natomiast reprezentanci podrodziny Claravinae osiem razy. Kraina Afrotropikalna zasiedlana była co najmniej cztery razy przez przedstawicieli Raphinae. Biorąc pod uwagę ostatniego wspólnego przodka w krainie Afrotropikalnej oraz taksonów w krainie Orientalnej, przypuszcza się, że zasiedlanie tych krain następowało przez Australazję (Gibbs i in. 2001; Pereira i in. 2007; Clements i in. 2019; Kretschmer i in. 2020).

Przed podjęciem badań w ramach pracy doktorskiej, światowa akarofauna Syringophilidae związanych z ptakami gołębiowymi obejmowała zaledwie 9 gatunków zgrupowanych w 5 rodzajach należących do dwóch podrodzin: Syringophilinae i Picobiinae. W obrębie podrodziny Syringophilinae były to następujące rodzaje: *Meitingsunes*, *Peristerophila*, *Castosyringophilus* oraz *Terratosyringophilus*.

Rodzaj *Meitingsunes* Skoracki i Głowska, 2010, charakteryzuje się gładkim, pozbawionym wyrostków szczytem hypostomu oraz rozbieżnymi apodemami I, niezrośniętymi z apodemami II. Rodzaj ten obejmował łącznie cztery gatunki: 1) *M. aldwelles* Głowska i Skoracki, 2010 opisany z *Geotrygon frenata* z krainy Neotropikalnej (Kolumbia); 2) *M. columbicus* Skoracki, 2011, notowany na przedstawicielach rodzaju *Columba – C.*

oeans (gatunek typowy), *C. livia* oraz *C. palumbus* i stwierdzany z Palearktyki (Kazachstan, Polska, Rosja); 3) *M. tympanistria* (Skoracki i Dabert, 2002) opisany z *Turtur tympanistria* z krainy Afrotropikalnej (Togo); 4) *M. zenadourae* (Clark, 1964) notowany na ptakach gołębiowych należących do dwóch rodzajów – *Columba*: *C. livia* z Nearktyki (USA) oraz *Zenaida*: *Z. macroura* (gatunek typowy) i *Z. asiatica*, oba gatunki żywicielskie pochodzące z Nearktyki (USA) oraz *Z. auriculata* z krainy Neotropikalnej (Argentyna). Przedstawiciele rodzaju *Meitingsunes* zasiedlają głównie ptaki z rzędu Columbiformes, za wyjątkiem *M. caprimulgus* Skoracki, Kaszewska, Unsoeld, Skorupski, 2015, który stwierdzony został na *Chordeiles minor* należącym do rzędu Lelkowych (Caprimulgiformes).

Rodzaj *Peristerophila* Kethley, 1970, wyodrębniono na podstawie następujących cech morfologicznych: braku szczecin propodonotalnych – *vi*, braku szczecin odnóży *dFII, dFIII, dFIV* i *vs'II*. Ponadto przedstawiciele tego rodzaju charakteryzują się obecnością dimorficznych samic: homeo.- i heteromorficznych różniących się między sobą długością i stopniem sklerotyzacji ciała a także długością poszczególnych szczecin (Skoracki i in. 2020). Rodzaj ten obejmował łącznie pięć gatunków zasiedlających ptaki z rzędu Gołąbiowych (Columbiformes), Sokołowych (Falconiformes), Szponiastych (Accipitriformes), Dzioborożcowatych (Bucerotiformes), Kraskowatych (Coraciiformes) oraz Papugowych (Psittaciformes). Fauna dutkowców z tego rodzaju pasożytujących na ptakach z rzędu gołębiowych reprezentowana była przez trzy gatunki: *P. columbae* (Hirst, 1920), infestujący dwa gatunki żywicielskie: *C. livia* (gatunek typowy), notowany z krainy Nearktycznej (USA), Orientalnej (Indie), Palearktycznej (Wielka Brytania, Polska, Turcja) oraz krainy Saharo-Arabskiej (Iran). Kolejnym gatunkiem żywicielskim był *Streptopelia decaocto* z krainy Saharo-Arabskiej (Jordania). Następnym przedstawicielem rodzaju *Peristerophila* był gatunek opisany z *Claravis pretiosa* – *P. claravis* Skoracki i Glowska, 2008, z krainy Neotropikalnej (Boliwia). Gatunkiem o najszerszym spektrum żywicielskim był *P. mucuya* Casto, 1980, infestujący zarówno ptaki z rzędu Gołębiowych oraz ptaki z rzędu Papugowych. Spektrum żywicielskie obejmowało następujących przedstawicieli ptaków gołębiowych: *Columbina passerina* (gatunek typowy), Nearktyka (USA), *C. squammata* oraz *C. talpacoti* oba gatunki żywicielskie pochodziły z krainy Neotropikalnej (Brazylia), *Metriopelia melanoptera* z krainy Neotropikalnej (Argentyna) oraz *Streptopelia decaocto* z krainy Saharo-Arabskiej (Jordania). W spektrum żywicielskim gatunku *Peristerophila mucuya* znaleźli się także przedstawiciele z rzędu Papugowych: *Brotogeris versicolurus* oraz *Psilopsiagon aymara* oba gatunki notowane z krainy Neotropikalnej (Brazylia) i *Trichoglossus haematodus* notowany z krainy Orientalnej (Indonezja).

Rodzaj *Castosyringophilus* Bochkov i Perez, 2002 został ustanowiony i wyodrębniony z rodzaju *Peristerophila* Kethley, 1970 na podstawie następujących cech różnicujących: u samic z rodzaju *Castosyringophilus* podstawy szczecin *se* usytuowane są poniżej podstaw szczecin *c1*; apodemy I są 1.1–1.2 razy dłuższe od gnatosomy; nogi I pary są 1.5 razy dłuższe od nóg II pary. Samice należące do rodzaju *Peristerophila* w przeciwieństwie do samic z rodzaju *Castosyringophilus*, charakteryzują się położeniem szczecin *se* i *c1* na tym samym poziomie; apodemy I są nieznacznie krótsze od gnatosomy, natomiast nogi I pary są dłuższe

1.1 – 1.2 razy od nóg II pary (Bochkov i Perez 2002). Rodzaj ten reprezentowany był przez cztery gatunki*:* 1) *C. mucuya* (Casto, 1980) opisany z *Columbina passerina* (gatunek typowy) z rzędu Golębiowych, 2) *C. forpi* Bochkov i Perez, 2002, opisany z ptaków należących do rzędu Papugowych, 3) *C. claravis* Glowska i Skoracki, 2008 zasiedlający ptaki z rzędu Gołębiowch oraz 4) *C. meropis* Skoracki, Hromada i Sikora, 2017 infestujący ptaki z rzędu Kraskowatych. Na podstawie badań porównawczych z zakresu ontogenezy i morfologii przeprowadzonych na wielu infrapopulacjach roztoczy dutkowych z gatunku *Peristerophila hirundineus* Skoracki, Hromada, Kaszewska, Sikora, 2020, rodzaj *Castosyringophilus* został synonimizowany z rodzajem *Peristerophila*. Autorzy wykazali obecność samic dimorficznych: formy homeomorficzne odpowiadały cechami morfologicznym obserwowanymi u *Peristerophila* oraz samic heteromorficznych, które charakteryzowały się cechami obecnymi u *Castosyringophilus* (Skoracki i in. 2020). Zjawisko dimorficznych samic u roztoczy z rodziny Syringophilidae było obserwowane również w rodzajach: *Stibarokris* Kethley, 1970 (Glowska i in. 2014); *Chenophila* Kethley, 1970 (Skoracki i Zawierucha 2016). Przeprowadzone badania nie potwierdziły wcześniejszych hipotez dotyczących dyspersyjnych funkcji samic homeomorficznych, ponieważ założycielkami nowych populacji były zarówno formy homeomorficzne jak również heteromorficzne.

Rodzaj *Terratosyringophilus* Bochkov i Perez, 2002, odróżnia się od innych rodzajów wentralnym położeniem szczecin odnóży *dFIII* i *dFIV*. Roztocze należące do tego rodzaju zasiedlają ptaki należące do rzędu Columbiformes oraz Psittaciformes. Ptaki gołębiowe infestowane były przez dwa gatunki *T. geotrygonus* Skoracki and Glowska, 2008, opisany z *Geotrygon linearis* (gatunek typowy) z krainy Neotropikalnej (Wenezuela) oraz *T. longisoma* (Casto, 1979) infestujący przedstawicieli rodzaju *Zenaida*: *Z. macroura* oraz *Z. asiatica* oba z Nearktyki (USA). Przedstawiciele rodzaju *Terratosyringophilus* infestujące ptaki papugowe obejmują dwa gatunki *T. loricinus* Bochkov and Fain, 2003 opisany z *Trichoglossus haematodus* kraina Orientalna (Indonezja) oraz *T. reichholfi* Skoracki, Sikora, 2008 z Oceanii (Nowa Gwinea).

Rodzaj *Psittaciphilus* Fain, Bochkov and Mironov, 2000, charakteryzuje się usytuowaniem szczecin *si* oraz *se* na tym samym poziomie oraz długimi terminalnymi szczecinami. Dotychczas roztocze te notowane były wyłącznie z ptaków z rzędu Papugowych. Rodzaj ten obejmował dwa gatunki: *P. amazonae* Fain, Bochkov and Mironov, 2000 infestujący *Amazona amazonica* (gatunek typowy) stwierdzony z krainy Neotropikalnej (Kolumbia) oraz *P. fritschi* Bochkov and Mironov, 2000 gatunek typowy nieznany.

W podrodzinie Picobiinae, reprezentowanej przez 12 rodzajów, tylko przedstawiciele rodzaju *Gunabopicobia* Skoracki i Hromada, 2013 zasiedlają ptaki z rzędu Columbiformes. Rodzaj *Gunabopicobia* wyodrębniony został na podstawie następujących cech morfologicznych: szczeciny *vi* usytuowane są nad szczecinami *ve*, szczyt hypostomu zaopatrzony w boczne wyrostki, brak kolcowatych wyrostków na apodemach I. Rodzaj ten obejmował jeden gatunek – *G. zumpti* (Lawrence, 1959). Stwierdzony został z ptaków gołębiowych należących do następujących rodzajów: *Streptopelia* – *S. capicola* (gatunek typowy), *S. senegalensis* oba gatunki opisane z krainy Afrotropikalnej (RPA), *S. semitorquata*, kraina Afrotropikalna (Etiopia); rodzaj *Columba* – *C. speciosa* z krainy Neotropikalnej (Brazylia) *C. delegorguei* z krainy Afrotropikalnej (Tanzania), *C. livia* Nearktyka (USA), Palearktyka (Polska); rodzaj *Patagioenas* – *P. picazuro* z krainy Neotropikalnej (Brazylia) oraz rodzaj *Zenaida* – *Z. macroura* Nearktyka (USA) (*wszystkie rekordy wraz z referencjami zamieszczone zostały w Tabeli 1*).

Zważywszy na fakt, niewielkiego stopnia poznania akarofauny Syringophilidae związanej z ptakami gołębiowymi, cele badawcze podjęte w ramach pracy doktorskiej, ukierunkowane były szczególnie na taksonomię dutkowców. Wyniki tych badań z kolei umożliwiły podjęcie interpretacji ekologicznych i filogenetycznych.

Pierwszym celem pracy doktorskiej było zbadanie różnorodności taksonomicznej Syringophilidae z możliwie szerokiego spektrum potencjalnych żywicieli należących do ptaków gołębiowych reprezentujących trzy klady oraz pochodzących ze wszystkich krain zoogeograficznych. Drugim celem było zbadanie interakcji w układzie pasożyt-żywiciel m. in. określenie prewalencji, specyficzności żywicielskiej i topicznej roztoczy dutkowych związanych z ptakami gołębiowymi. Trzecim celem było ustalenie relacji filogenetycznych na poziomie rodzajowym Syringophilidae pasożytujących na ptakach gołębiowych.

Taksonomiczna część mojej rozprawy doktorskiej składa się z cyklu sześciu publikacji poświęconych różnorodności gatunkowej oraz rozmieszczeniu Syringophilidae pasożytujących na ptakach z rzędu Columbiformes. Pod kątem występowania roztoczy dutkowych przebadanych zostało 112 gatunków należących do 28 rodzajów potencjalnych żywicieli co stanowi 57% wyodrębnionych rodzajów w tym rzędzie ptaków. Próba obejmowała przedstawicieli z następujących krain zoogeograficznych: Neotropikalnej, Nearktyki, Afrotropikalnej, Saharo-Arabskiej, Palearktyki, Orientalnej, Oceanii oraz krainy Australijskiej, co stanowi niemal wszystkie krainy (za wyjątkiem krainy Madagaskarskiej oraz wysp Pacyfiku) w których występują Columbiformes. Na podstawie analizy taksonomicznej wykazano, iż ptaki gołębiowe infestowanie były przez 25 gatunków roztoczy dutkowych z rodziny Syringophilidae, należących do następujących rodzajów: *Meitingsunes*, *Peristerophila*, *Psittaciphilus, Gunabopicobia*. Roztocze te stwierdzone zostały łącznie na 65 gatunkch ptaków gołębiowych będących przedstawicielami wszystkich podrodzin w obrębie Columbiformes.

Wykazano infestowanie ptaków gołębiowych przez wcześniej opisane gatunki roztoczy dutkowych tj.: *Meitingsunes columbicus* Skoracki, 2011; *M. zenadurae* (Clark, 1964), *M. tympanistria* (Skoracki i Dabert, 2012), *Peristerophila columbae* (Hirst, 1920) *P. claravis* (Skoracki i Glowska, 2008), *P. mucuya* Casto, 1980 oraz *Gunabopicobia zumpti* (Lawrence, 1959). Spektrum żywicielskie dla tych gatunków poszerzono o szereg nowych żywicieli, w tym także o przedstawicieli rodzajów wcześniej niezbadanych pod kątem występowania Syringophilidae tj. *Leptotila*, *Patagioenas*, *Oena*, *Treron*, *Leucosarcia*, *Caloenas*, *Ducula*, *Ptilinopus*, *Ocyphas*, *Turacoena*, *Macropygia*, *Gallicolumba*, *Chalcophas* (*Tabela 1*). Na uwagę zasługują dwa gatunki dutkowców: *Peristerophila claravis* oraz

Meitingsunes colmbicus. Dotychczas *P. claravis* opisywany był z ptaków gołębiowych należących do rodzaju *Columbina* z podrodziny Claravinae. Podczas analiz stwierdzono, iż roztocze te infestują także monotypowy gatunek Turkaweczkę czarnogardłą (*Oena capensis*) należący do podrodziny Raphinae. W przypadku *M. columbicius*, gatunek ten wykazywany był wyłącznie z przedstawicieli rodzaju *Columba* należących do podrodziny Columbinae. Podczas badań odnotowano, że gatunek ten infekował także przedstawiciela gołębiowych z podrodziny Raphinae – Trerona żółtobrzychego (*Treron waalia*). Obecność tych gatunków na żywicielach z dwóch różnych podrodzin wskazuje na szerszą specyficzność żywicielską niż dotychczas sądzono, a w przypadku *M. columbicus* rozmieszczenie zoogeograficzne poszerzone zostało także o krainę Afrotropikalną (zestawienie nowych żywicieli oraz lokalizacji zaprezentowano w Tabeli *Roztocze dutkowe z rodziny Syringophilidae związane z ptakami z rzędu Columbiformes*).

Ponadto opisałam wraz ze współautorami 16 nowych dla wiedzy gatunków, których szczegółowe diagnozy wraz z rycinami i kluczami przedstawione zostały w części taksonomicznej rozprawy doktorskiej. Dla roztoczy dutkowych z rodzaju *Meitingsunes* były to cztery gatunki: *M. chalcophas* Kaszewska, Skoracki and Kavetska, 2016, *M. turacoenas* Kaszewska, Skoracki and Kavetska, 2016 **(Kaszewska i in. 2016. *Zootaxa*)**, *M. lengai* Kaszewska, Skoracki, Hromada, 2020; *M. ptilinopus* Kaszewska, Skoracki, Hromada, 2020 **(Kaszewska i in. 2020. *International Journal of Acarology*)**. Gatunki te stwierdzone zostały po raz pierwszy na ptakach gołębiowych występujących w krainach: Orientalnej, Oceanii, Australii. Jak dotąd reprezentanci tego rodzaju notowani byli z krain Neotropikalnej, Palearktycznej oraz Afrotropikalnej. Otrzymane wyniki wykazały, że *Meitingsunes* jest najbogatszym w gatunki rodzajem roztoczy dutkowych związanych z gołębiowymi w obrębie podrodziny Syringophilinae i liczy osiem gatunków zasiedlających łącznie 25 gatunków żywicielskich. Przedstawiciele tego rodzaju występują w następujących krainach zoogeograficznych: Neotropikalnej, Nearktycznej, Palearktycznej, Afrotropikalnej, Orientalnej, Oceanii, Australijskiej.

W obrębie rodzaju *Peristerophila*, opisane zostały następujące gatunki: *P. lature* Kaszewska, Kavetska, Skoracki, 2014 (**Kaszewska i in. 2014. *Zootaxa***), *P. geopelis* Kaszewska, Skoracki, Kosicki, Hromada, 2020; *P. leucomela* Kaszewska, Skoracki, Kosicki, Hromada, 2020 (**Kaszewska i in. 2020. *Zootaxa***). Pierwsze dwa są ściśle związane z ptakami gołębiowymi z podrodziny Raphinae natomiast gatunek *P. leucomela* został opisany z *Columba leucomela* należącego do podrodziny Columbinae. Wszystkie nowo opisane gatunki zasiedlały gołębiowe występujące w Indonezji, Papui Nowej Gwinei oraz Australii. Rodzaj *Peristerophila* obejmuje obecnie 6 gatunków roztoczy dutkowych pasożytujących głównie na przedstawicielach podrodziny Raphinae.

Rodzaj *Gunabopicobia*, który jest jedynym taksonem z podrodziny Picobiinae infestującym ptaki z rzędu Columbiformes, reprezentowany był przed podjęciem badań przez jeden gatunek *Gunabopicobia zumpti* (Lawrence, 1959). Opisywany był z licznych gatunków żywicielskich należących do rodzaju *Columba* i *Sterptopelia* występujących w Palearktyce, Nearktyce oraz Afrotropiku. Podczas prac badawczych w ramach dysertacji zostało opisanych siedem nowych dla wiedzy gatunków: *G. masalaje* Kaszewska, Kavetska and Skoracki, 2014 (**Kaszewska i in. 2014. *Zootaxa***), *G. claravis* Kaszewska, Skoracki and Hromada, 2018, *G. geotrygoni* Kaszewska, Skoracki and Hromada, 2018, *G. metriopelia* Kaszewska, Skoracki and Hromada, 2018, *G. lathami* Kaszewska, Skoracki and Hromada, 2018, *G. leptotila* Kaszewska, Skoracki and Hromada, 2018, *G. verraruxi* Kaszewska, Skoracki and Hromada, 2018 (**Kaszewska i in. 2018. *International Journal of Acarology***) infestujące łącznie 16 gatunków gołębiowych. Roztocze te zasiedlały żywicieli należących z podrodzin: Columbinae (rodzaje *Leptotila*, *Geotrygon*), z podrodziny Claraviinae (rodzaje *Claravis*, *Metriopelia*) oraz Raphinae (rodzaje *Caloeans*, *Ducula*, *Leucosarcia* i *Ptilinopus*). Rodzaj *Gunabopicobia* reprezentowany jest przez osiem gatunków roztoczy dutkowych, których spektrum żywicielskie obejmuje łącznie 24 gatunki ptaków gołębiowych ze wszystkich podrodzin oraz ze wszystkich krain zoogeograficznych w których występują Columbiformes (za wyjątkiem krainy Madagaskarskiej).

Podczas badań stwierdzono po raz pierwszy infestację ptaków gołębiowych przez reprezentantów rodzaju *Psittaciphilus*. Gatunki należące do tego rodzaju dotychczas opisywane były z ptaków należących do rzędu Papugowych. Stwierdzono występowanie dwóch nowych gatunków: *Psittaciphilus montanus* Kaszewska, Skoracki, 2018 oraz *Psittaciphilus patagioenas* Kaszewska, Skoracki, 2018. *P. montanus* opisany został z Błyskotka rdzawego *Geotrygon montana*, natomiast *P. patagioenas* opisany został z Gołąbczaka pręgosternego *Patagioenas fasciata* (gatunek typowy) oraz z Gołąbczaka łuskowanego *Patagioenas speciosa* (**Kaszewska i Skoracki 2018. *Systematic Parasitology***). Wykazanie przedstawicieli *Psittaciphilus* na ptakach gołębiowych dołącza ten rodzaj do wyznaczonej przez Bochkov i Perez 2002, grupy blisko spokrewnionych roztoczy dutkowych zasiedlających wspólnie papugowe i gołębiowe. W grupie tej oprócz wcześniej wymienionego rodzaju zalicza się również rodzaje *Peristerophila* oraz *Terratosyringophilus*. (Zestawienie nowych gatunków wraz z żywicielami zaprezentowano w Tabeli *Roztocze dutkowe z rodziny Syringophilidae związane z ptakami z rzędu Columbiformes*).

Druga część pracy doktorskiej dotyczy badań nad specyficznością żywicielską i topiczną oraz interakcjach w obserwowanym układzie między Syringophilidae i ptakami z rzędu Columbiformes. Przedstawiam także rezultaty analizy filogenetycznej dla roztoczy dutkowych na poziomie rodzajowym.

Specyficzność żywicielska obejmuje różnorodność i zakres gatunków żywicielskich, które pasożyt może zainfekować i jest uważana za kluczową miarę potencjału pasożyta (Welles i Clark 2019). Specyficzność żywicielska pasożytów odzwierciedla na przykład szerokość nisz ekologicznych, a co za tym idzie pozycję i rolę pasożyta w biosferze. Ponadto cecha ta określa prawdopodobieństwo, że pasożyt z powodzeniem może infestować nowych żywicieli, po wprowadzeniu na nowy obszar geograficzny (Poulin i Mouillot 2003). Nieliczne badania poświęcone analizie interakcji między Syringophilidae i ich żywicielami jak dotąd koncentrowały się na akarofaunie dutkowców związanych z ptakami z rzędu Wróblowych, np. Nectariniidae oraz Estrildidae (Skoracki i in. 2018, 2019). Podjęte analizy w ramach pracy doktorskiej są pierwszymi tego typu analizami dla Syringophilidae związanych z ptakami nie-wróblowymi (Non-Passeriformes). W celu określenia specyficzności hostalnej oraz ustalenia interakcji w układzie pasożyt-żywiciel dla Syringophilidae związanych z ptakami z rzędu Columbiformes, przeprowadzono analizę specyficzności żywicielskiej oraz zbadano prewalencję i wykonano analizę sieci dwudzielnych.

Wyniki badań faunistycznych prowadzonych w ramach dysertacji pozwoliły na oszacowanie kręgu żywicieli oraz określenie specyficzności żywicielskiej dla poszczególnych gatunków roztoczy dutkowych infestujących Columbiformes. W analizach zostały użyte następujące rangi specyficzności od bardzo wąskiej do szerokiej: monokseniczność (pasożyt infestuje tylko jednego żywiciela); oligokseniczność (pasożyt infestuje żywicieli należących do tego samego rodzaju); mesostenokseniczność (pasożyt infestuje żywicieli należących do tej samej podrodziny); metastenokseniczność (pasożyt infestuje żywicieli należących do różnych podrodzin); poliksenicznosć (pasożyt infestuje żywicieli należących do różnych rzędów) (Caira i in. 2003).

Wśród wszystkich Syringophilidae pasożytujących na ptakach gołębiowych odnotowano osiem gatunków monoksenicznych. W grupie tej dominowali przedstawiciele rodzaju *Gunabopicobia*. Oligokseniczne roztocze dutkowe reprezentowane były przez cztery gatunki dutkowców należących do podrodziny Syringophilinae z następujących rodzajów: *Meitingsunes, Psittaciphilus* oraz *Terratosyringophilus*. W obrębie Picobiinae zanotowano jeden gatunek, który infestował żywicieli z tego samego rodzaju – *Gunabopicobia geotrygoni*. Grupa mesostenokseniczna obejmowała łącznie osiem gatunków dutkowców z rodzajów: *Meitingsunes* (2 gatunki), *Peristerophila* (3 gatunki) (podrodzina Syringophilinae) oraz *Gunabopicobia* (podrodzina Picobiinae) (3 gatunki). Gatunki metastenokseniczne to roztocze należące do dwóch rodzajów *Meitingsunes* (2 gatunki) oraz *Peristerphila* (1 gatunek) (podrodz. Syringophilinae). Najszerszą specyficzność żywicielską – poliksenicznosć, zaobserwowano dla gatunku *Peristerophila mucuya*. Gatunek ten infestuje zarówno ptaki gołębiowe jak również żywicieli z rzędu papugowych, np. *Brotogeris versicolurus*, *Psilopsiagon aymara*, *Trichoglossus haematodus* (Bochkov i Fain 2003). Podczas badań *P. mucuya*, został stwierdzony na trzech nowych gatunkach żywicielskich należących do rzędu Columbiformes: *Columbina minuta*, *Metriopelia ceciliae*, *M. melanoptera.* W celu porównania poszczególnych gatunków z danej kategorii kseniczności obliczony został indeks specyficzności (d'), który mierzy interakcję pasożyta z szeregiem potencjalnych żywicieli (puli gatunków żywicielskich) w całym obserwowanym układzie pasożyt-żywiciel (Blüthgen i Menzel 2006). Stwierdzono, iż roztocze infestujące więcej niż jednego żywiciela miały wysoki wskaźnik specyficzności co świadczy o nieprzypadkowym infekowaniu żywicieli.

Podczas badań wykazano, że 11 gatunków żywicielskich infestowanych było przez co najmniej dwa odrębne gatunki roztoczy dutkowych. Zaobserwowane zostały następujące wzorce ko-infestcji dla roztoczy dutkowych:

1) wzorzec *Syr-Pic* (roztocze należące do dwóch różnych podrodzin Syringophilinae i Picobiinae infestujące różne typy piór), np.: *Geotrygon montanus* infestowany przez *Gunabopicobia geotrygoni* (pióra konturowe) oraz *Meitingsunes zenadourae* (pióra pokrywowe)
2) wzorzec *Syr-Syr* (roztocze należące do tej samej podrodziny, ale infestujące róże typy piór) np. *Columba palumbus* infestowany przez *Meitingsunes columbicus* (lotki II-rzędowe) oraz *Peristerophila columbae* (pokrywy skrzydeł)

Dla dwóch gatunków *Peristerophila columbae* i *Psittaciphilus patagioenas* zaobserwowano ko-infestację tego samego żywiciela przez roztocze z tej samej podrodziny. Oba gatunki infestowały pokrywy skrzydeł gołębia z gatunku *Patagioenas speciosa*. W żadnym z badanych przypadków jednak nie zaobserwowano dwóch różnych gatunków roztoczy w jednej infekowanej dutce pióra. Prezentowane wyniki badań wykazały, iż czynnik niszy odgrywa istotną rolę przy unikaniu konkurencji o zasoby pomiędzy pasożytami, które współdzielą gatunek żywicielski. Unikanie konkurencji poprzez rozdzielenie nisz zwiększa szansę na sukces zarażenia nowego mikrohabitatu i założenia kolonii wewnątrz infekowanej dutki.

Kolejnym punktem pracy było zbadanie interakcji w układzie Syringophilidae-Columbiformes. Do zwizualizowania i scharakteryzowania powiązań pomiędzy pasożytami i ich żywicielami została wykonana analiza sieci dwustronnych „bipartite". Sieci używane są do przedstawiania dowolnego typu relacji pomiędzy partnerami tworzącymi dany układ (Poulin 2010). Dostarczają narzędzi pozwalających badać np. specyficzność układu, interakcje pomiędzy gatunkami. W badaniu zostały użyte współczynniki pozwalające na określenie: specjalizacji na poziomie układu pasożyt-żywiciel – współczynnik H2' (wartość 0 oznacza niską specjalizację interakcji w sieci, 1 oznacza wysoką specjalizację interakcji w sieci (Blüthgen 2010)); proporcji obserwowanych interakcji realizowanych w ramach sieci do wszystkich możliwych – współczynnik C (wartość C bliska 1 wskazuje na wysoka liczbę powiązań w sieci) (Blüthgen i Menzel 2006) oraz zagnieżdżenie – współczynnik N (mierzy ile interakcji realizowanych przez specjalistów stanowi podzbiór interakcji realizowanych przez generalistów, gdzie 0 oznacza brak zagnieżdżenia, 1 oznacza maksymalne zagnieżdżenie) (Dromann et al. 2009), oraz współczynnik modułowość – Q, jest miarą struktury sieci, który mierzy siłę podziału sieci na moduły (Olesen i in. 2007, Newman 2006). Moduły definiuje się jako podsystemy nienakładających się i silnie oddziaływujących ze sobą gatunków w obrębie klastra (Stouffer i Bascompte 2010, 2011).

Sieć obrazująca powiązania w układzie Syringophilidae-Columbiformes charakteryzowała się wysokimi wartościami współczynnika H2'=0.93 oznaczającym, że obserwowana sieć dwudzielna charakteryzuje się wysokim stopniem specjalizacji, biorąc pod uwagę liczbę zrealizowanych interakcji danego gatunku pasożytniczego z pulą dostępnych żywicieli. Stwierdzono, iż sieć dwudzielna była zagnieżdżona N=0.908, co oznacza, że roztocze dutkowe o wąskiej specyficzności hostalnej (monokseniczne), infekowali gatunki ptaków gołębiowych będących w spektrum żywicielskim pasożytów o szerokiej specyficzności. Wśród gatunków monoksenicznych zaobserwowano podzbiory dla następujących przedstawicieli Syringophilidae: *Gunabopicobia leptotila* – notowany na *Leptotila verreauxi*, który jest jednym z żywicieli *Meitingsunes zenadourae* będącym gatunkiem dutkowców o szerokim spektrum żywicielskim (gat. metastenokseniczny), *Meitingsunes adwelles* zasiedla wyłącznie żywiciela z gatunku *Geotrygon frenata*, który jest także żywicielem dla *M. zenadourae* (gat. mesostenokseniczny), *Gunabopicobia claravis* gatunek dutkowca występujący na *Claravis pretiosa*, który infekowany jest także przez *P. claravis* (gat. mesostenokseniczny), *Gunabopicobia metriopelia* infestuje *Metripelia melanoptera*, który jest także żywicielem dla *Peristerophila mucuya* (gat. poliikseniczny), *Psittaciphilus montanus* opisany z żywiciela *Geotrygon montana*, który jest także gospodarzem dla *Gunabopicobia geotrygoni* oraz *Terratosyringophilus geotrygonus* infestujący wyłącznie *Geotrygon montana*, który jest żywicielem dla *Gunabopicobia geotrygoni* (gat. oligokseniczny). Dwa monokseniczne gatunki roztoczy dutkowych– *Meitingsunes chalcophas* zasiedlającym *Chalcophas indica* oraz *Peristerophila leucomela* infekującym *Columba leucomela* nie tworzyły podzbiorów. Na podstawie analizy spektrum żywicielskiego podzbiorów stwierdzić można, iż dutkowce silnie wyspecjalizowane zasiedlają gospodarzy o szerokim zasięgu występowania tworzących liczne populacje. Uważa się, że infekowanie gospodarzy o zwiększonej podatności na pasożyty zmniejsza ryzyko koekstynkcji (McQuaid i Britton 2013). Ponadto badania prowadzone przez McQuaid i Britton 2013 wykazały, że zagnieżdżenie w układach antagonistycznych tj. pasożyt-żywiciel jest wynikiem zachodzących procesów koewolucji. Zjawisko koewolucji u wyspecjalizowanych pasożytów ptaków jest notowane dla wielu grup systematycznych w tym także dla roztoczy. Wartość zagnieżdżenia w prezentowanych badaniach wskazuje na zachodzące procesy koewolucyjne.

Indeks połączeń charakteryzował się wysoką wartością C=0.90, wskazując na dużą liczbę potencjalnych interakcji w układzie pasożyt-żywiciel. Poszczególne gatunki dutkowców wchodziły w liczne interakcje z gospodarzami. W sieci dominowały gatunki Syringophilidae mające więcej niż jednego żywiciela (gatunki oligokseniczne (5 gat.), mesostenoksenicze (8 gat.), metastenoksenicze (3 gat.), polikseniczne (1 gat.) podczas gdy grupa gatunków monoksenicznych obejmowała ośmiu reprezentantów tej rodziny. Biorąc pod uwagę powiązania filogenetyczne pomiędzy żywicielami, Syringophilidae wchodzące w liczne interakcje z gospodarzami, zasiedlają gatunki blisko ze sobą spokrewnione, co oznacza że interakcje z żywicielami nie są losowe. Wyniki analizy sieciowej wykazały, że roztocze dutkowe pasożytujące na ptakach gołębiowych tworzą wysoce wyspecjalizowany i nieprzypadkowy układ pasożyt-żywiciel. Roztocze dutkowe wchodziły głównie w interakcje z gatunkami żywicielskimi należącymi do tego samego rodzaju lub tej samej podrodziny.

Wykonano także analizę modularności w celu określenia: tendencji tworzenia modułów, zgrupowań w ramach sieci oraz identyfikacji kluczowych żywicieli. Stwierdzono w obrębie sieci, 20 modułów (zgrupowań, klastrów), które podzielono na następujące typy: A) moduły składające się z jednego gatunku pasożytniczego oraz jednego gatunku żywicielskiego, B) moduły zbudowane z jednego gatunku pasożyta związanego z wieloma gatunkami żywicielskimi oraz C) moduły w skład których wchodziły liczne gatunki pasożytnicze skupione w obrębie grupy żywicieli. Wykazano, iż w obserwowanym układzie pasożyt-żywiciel dochodzi do tworzenia zgrupowań z silnymi interakcjami wewnątrz każdego modułu i słabymi relacjami poza klastrami. Wskaźnik modułowości Q wynosił 0.83. Identyfikacja modułów pozwala na wyłonienie kluczowych żywicieli dla danej grupy Syringophilidae i ich potencjał do infekowania kolejnych gospodarzy.

W ramach pracy doktorskiej przeprowadzona została analiza filogenetyczna roztoczy z rodziny Syringophilidae zasiedlających ptaki gołębiowe na poziomie rodzajowym. Analizę filogenetyczną wykonano na podstawie jakościowych cech morfologicznych reprezentantów rodzajów: *Peristerophila*, *Meitingsunes*, *Terratosyringophilis*, *Psittaciphilus* (podrodz. Syringophilinae) oraz *Gunabopicobia* (podrodz. Picobiinae). Analiza oparta była o 26 cech jakościowych opisujących: a) obecność lub brak szczecin tj: *vi*, *g1*, szczecin odnóży: *vs* (II), *df* (II-III), *vF* (III), *l'R I*, *e1*, *ps3*; b) obecność lub brak struktur tj. palczaste wyrostki hypostomu, struktury kieszeniowe na tarczy propodonotalnej, apodem III i IV pary; c) kształtu: peritrem, końcowej części styloforu, odnóży I pary, dystalnej części chelicer oraz szczecin *p'* oraz *p";* d) ornamentacji tarcz i szczecin; e) pozycji szczecin *ve* oraz *si*; f) występowania zjawiska fyzogastrii; g) występowania zjawiska bimorfizmu samic. Liczba cech parsymonicznych – 19, indeks spójności (CI) = 0.9, indeks retencji (RI) = 0.9, indeks homoplazji (HI) = 0.1. Na podstawie przeprowadzonych badań stwierdzono, iż w obrębie podrodziny Syringophilinae występują dwa klady: A – *Peristerophila*+*Terratosyringophilus* oraz B *Meitingsunes*+*Psittaciphilus*. Cechy synapomorficzne wspierające wyodrębniony klad *Peristerophila*+*Terratosyringophilus* to: obecność palcowatych wyrostków na szczycie hypostomu, apodamy I są równoległe, obecność dimorficznych samic. Drugi klad *Meitingsunes*+*Psittaciphilus*, wyodrębniony na podstawie synapomorficznych cech tj: zwężone zakończenie styloforu. Klad A – *Peristerophila-Terratosyringophilus* obejmuje łącznie osiem gatunków (*P. columbae, P. geopelis, P. lature, P. mucuya, P. claravis, P. leucomela, T. geotrygonus, T. longisoma*), które zasiedlają przedstawicieli gołębiowych ze wszystkich trzech podrodziny Columbinae, Claravinae oraz Raphinae. Roztocze dutkowe z rodzaju *Peristerophila* infestowały gatunki żywicielskie z trzech podrodzin: Columbinae (z rodzaju *Columba*, *Geotrygon*, *Patagioenas*, *Streptopelia*); Claravinae (z rodzaju *Columbina*, *Metriopelia*, *Claravis*); Raphinae (*Oena*, *Geopelia*, *Ocyphas*, *Ducula*, *Ptilinopus*). Przedstawiciele rodzaju *Terratosyringophilus* notowani byli wyłącznie na ptakach gołębiowych z rodzaju Columbinae (*Geotrygon*, *Zenaida*). Klad B – *Meitingsunes-Psittaciphilus* obejmuje łącznie 10 gatunków roztoczy dutkowych (*M. adwelles, M. columbicus, M. chalcophas, M. lengai, M. ptilinopus, M. turacoenas, M. tympanistria, M. zenadourae, P. montanus, P. patagioenas*) zasiedlających żywicieli należących do podrodzin Columbinae oraz Raphinae. Roztocze dutkowe z rodzaju *Meitingusnes* notowane bylo na żywicielach z podrodziny Columbinae (*Columba*, *Streptopelia*, *Macropygia*, *Turacoena*, *Geotrygon*, *Leptotila*, *Patagioenas*, *Zenaida*) oraz Raphinae (*Chalcophas*, *Gallicolumba*, *Ptilinopus*, *Turtur* oraz *Treron*). Przedstawiciele rodzaju *Psittaciphilus* notowani byli wyłącznie na ptakach gołębiowych z podrodziny Columbinae (*Geotrygon*, *Patagioenas*).

Występowanie roztoczy z rodziny Syringophilidae na przedstawicielach wszystkich podrodzin wyznaczanych w obrębie rzędu gołębiowych świadczyć może o ich długiej i wspólnej historii (**Kaszewska-Gilas i in. 2021 *Animals***).

Podsumowanie

Badania w ramach pracy doktorskiej poszerzyły wiedzę na temat różnorodności gatunkowej oraz spektrum żywicielskiego ektopasożniczych roztoczy z rodziny Syringophilidae pasożytujących na ptakach z rzędu Columbiformes. Przeprowadzone analizy prewalencji, specyficzności żywicielskiej i topicznej, sieci dwudzielnych oraz filogenetycznej, pozwoliły na lepsze zrozumienie relacji w badanym układzie pasożyt-żywiciel. Uzyskane wyniki pozwalają stwierdzić, iż roztocze dutkowe pasożytujące na ptakach gołębiowych to bogata i różnorodna część acarofauny Syringophilidae. Roztocze te stwierdzone zostały na przedstawicielach Columbiformes występujących we wszystkich krainach zoogeograficznych, a w ich spektrum żywicielskim znaleźli się przedstawiciele wszystkich wytyczanych podrodzin w obrębie tego rzędu żywicielskiego. Analizy sieci dwudzielnych wykonane w ramach pracy doktorskiej wykazały, że obserwowany układ Syringphilidae-Columbiformes charakteryzuje się wysokim stopniem specyficzności i nielosowym wchodzeniem w interakcje. Otrzymane wyniki pozwoliły na wytypowanie kluczowych żywicieli dla pasożyta i jego potencjału do zarażania innych gatunków żywicielskich.

INTRODUCTION

Mites belonging to the family Syringophilidae (Acariformes: Prostigmata) are obligatory ectoparasites infesting only birds. Those mites, also called quill mites, feed on the live tissue of their hosts by piercing the fibrous wall of the calamus with long, styliform mobile digits of the chelicerae (Casto 1974a; Kethley 1970, 1971). Syringophilids inhabit various types of plumage ex: primaries, secondaries, alularies, coverts, tail feathers, and body feathers, where they live and reproduce (Skoracki 2011). The family Syringophilidae is divided into two subfamilies: Syringophilinae Lavoipierre 1953 and Picobiinae Jonhson i Kethley 1975, which differ in numerous morphological characteristics. Members of the subfamily Syringophilinae have rounded tibiotarsus palps and fan-shaped preoral tarsus setae *p′* and *p″* of legs I-IV. While in Picobiinae mites, the tibiotarsus palps is truncate and the *p′* and *p″* setae are rod-shaped (Skoracki 2011). Furthermore, in representatives of Picobiinae, we observe the presence of physogastric females, characterized by strong growth of the opisthosoma. Immature stages of Syringophilinae have well-developed setae of body and legs, while Picobiinae's immature stages of chaetotaxy are reduced to small spinose structures. These mites also differ in their preference for inhabited microhabitats. Quill mites, belonging to the family Syringophilinae, occupied various parts of plumage ex.: covert feathers, and tail, while Picobiinae inhabits exclusively contour feathers (Skoracki et al. 2004).

Quill mites are permanent ectoparasites, their entire life cycle is carried out in the quill feather, except for a short period of dispersion. The infestation occurs in two ways and is synchronized with the host's daily cycle. Firstly, it occurs during the breeding season in the spring, as a result of vertical transmission when mites pass from parent birds onto the plumage of juvenile nestlings (nestling passage). Secondly, infestation occurs when mites invade newly developed feathers on the same host individual during the fall molt (molting passage) (Kethley 1971; Kethley and Johnston 1975). The dispersal form is exclusively fertilized females which leave the feather through the natural opening of the superior umbilicus. The fertilized female (colony founder) arriving at the quill begins to lay eggs; the first one is haploid and the male develops from it, while the rest is diploid and thus females develop from them (Casto 1974b; Kethley 1971).

Taxonomic studies on the family Syringophiidae have already started in the late 19th century, when Heller described the first species of the quill mites – *Syringopphilus bipectinat*e Heller, 1880 but it is for the particularly dynamic study over the last decade that has significantly contributed to a better understanding of this group of animals. Nowadays, the world's fauna of quill mites is represented by 403 species belonging to 63 genera (Syringophilinae subfamily – 51; Picobiinae subfamily 12) (Zmudzinski et al. 2020). Syringophiidae were described from birds belonging to 27 orders, accounting for more than 65% of all delineated orders within Aves. They have been recorded on birds from all zoogeographic regions except Antarctica and the Arctic. Considering the species richness of birds as potential hosts for mites of the family Syringophilidae, it is estimated that the family may number close to 5,000 species (Johnston & Kethley 1973). Therefore, the degree of examination of the species diversity of these parasites is still insufficient. Despite many years of research on the Syringophilidae and the finding of quill mites associated with more than 670 host species, many orders of birds remain underresearched for co-existing parasites. In particular, there is a lack of research conducted to identify the actual host spectrum within a specific group (genus, family, order) of birds, along with the identification of the host-parasite relationship.

The subject of the doctoral dissertation was the acarofauna of Syringophilidae related to birds of the Columbiformes order. These birds were one of the least known host groups for these mites. Members of the bird order occupy various ecologically diverse habitats, which are found in almost all zoogeographically areas except Antarctica (Gibbs et al. 2001). Columbiformes is a monophyletic group of birds, comprising more than 320 species, grouped in 49 genera, belonging to a single family Columbidae. This order is divided into three sub-families: (A) the Columbidae comprising the doves and pigeons of the Old World and New World, (B) the Claravinae, which includes the small Neotropical pigeons, (C) Raphinae, which includes the Afro-Eurasian and Australian taxa. It is assumed that representatives of the order Columbiformes diverged from outgroups such as Apodiformes and Caprimulgiformes in the Cretaceous before the mass extinction that marks the end of this period. The radiation of the modern genera of Columbiformes started in the Early Eocene to the Middle Miocene (Pereira, 2007)The ancestors of all modern pigeons are believed to have originated in Gondwana (most likely in the present Neotropics region), when Africa and India had already moved away from the common landmass that was Antarctica-Australia-South America. Molecular and phylogenetic studies have shown that representatives of the subfamily Columbinae colonized the Oriental land at least once, while representatives of the subfamily Claravinae colonized it eight times. Afrotropical was colonized at least four times by representatives of the subfamily Raphinae. Taking into account the last common ancestor of the Afrotropical and Oriental taxa, it is presumed that the colonization of the Oriental and Afrotropical lands occurred by Australasia (Gibbs et al. 2001, Pereira et al. 2007; Clements et al. 2019; Kretschmer et al. 2020).

Prior to the research, the world’s fauna of Syringophilidae related to pigeon birds had consisted of as little as nine species of quill mites grouped into five genera belonging to two sub-families: Syringophiliae and Picobiinae. The following genera were within the subfamily Syringophilinae: *Meitingsunes*, *Peristerophila*, *Castosyringophilus*, and *Terratosyringophilus* have been noted from Columbiformes.

According to Skoracki and Głowska, the genus Meitingsunes is characterized by smooth, without median protuberances hypostome apex, apodemes leg I divergent and not fused with apodemes II (2010). Genus *Meitingsues* include in total four species: 1) *M. aldwelles* Głowska and Skoracki, 2010, described from *Geotrygon frenata*. from Neotropical (Colombia); 2) *M. columbicus* Skoracki, 2011, noted from hosts belonging to *Columba – C.*

oeans (type species), *C. livia*, and *C. palumbus* (Skoracki, 2011). *M. columbicius* was recorded from Palearctic (Kazakhstan, Poland, Russia); 3) *M. tympanistria* (Skoracki and Dabert, 2002), typically host species is *Turtur tympanistria* from Afrotrotropikal (Togo) (Skoracki and Dabert, 2002); 4) *M. zenadourae* (Clark, 1964) host spectrum for this quill mites species included doves from two genera – *Columba*: *C. livia* noted from z Nearctic (USA) and genus *Zenaida*: *Z. macroura* (type species) and *Z. asiatica*, both hosts species recorded form Neotropical (Argentina). Members of *the Meitingsunes* genus infected mainly birds from the Columbiformes order, however, except for one case – *M. caprimulgus* Skoracki, Kaszewska, Unsoeld, Skorupski, 2015 described from *Chordeiles minor* belonging to order Caprimulgiformes (Skoracki et al. 2015).

Genus *Peristerophila* Kethley, 1970 was derived from the following morphological characteristics: absence of propodonotal setae – *vi*, absent legs setae; *dFII*, *dFIII*, *dFIV*, and *vs'II*. Moreover, this genus is characterized by the presence of dimorphic females: homeo- and heteromorphic. Morphotypes of the females differ by body and setae length and also the level of sclerotization of the body (Skoracki et al., 2020). This genus encompasses five species of infected hosts from differential orders: Accipitriformes, Columbiformes, Falconiformes, Buceratiformes, Coraciiformes, and Psittaciformes. The fauna of quill mites species belonging to this genus and associated with doves and pigeons have been represented by the following parasitic species: *P. columbae* (Hirst, 1920), recorded from two hosts species: *C. livia* (type species) from Nearctic (USA), Oriental (India), Palearctic (UK, Poland, Turkey), Saharo-Arabian (Iran) and *Streptopelia decaocto* from Saharo-Arabian (Jordan). The next species of the genus *Peristerophila* was – *P. claravis* Skoracki and Glowska, 2008, associated with *Claravis pretiosa* from the Neotropical (Bolivia). Quill mites species *P. mucuya* Casto, 1980 has been noted from numerous hosts spectrum belonging to two orders Columbiformes as well Psittaciformes. Hosts spectrum of this quill mites species encompasses the following doves and pigeons hosts: *Columbina passerina* (type species), Nearctic (USA), *C. squammata*, and *C. talpacoti* oba both species from Neotropical (Brasilia), *Metriopelia melanoptera* from Neotropical (Argentina) and *Streptopelia decaocto* from Saharo-Arabian (Jordan). *Peristerophil*a *mucuya* has been noted also from members of Psittaciformes birds – *Brotogeris versicolurus* and *Psilopsiagon aymara* both species derive from the Neotropical area (Brazil) and *Trichoglossus haematodus* from Oriental (Indonesia).

Based on differential characters, the genus *Castosyringophilus* Bochkov and Perez has been excluded from the genus *Peristerophila* Kethley, 1970. Females of *Castosyringophilus* have bases of setae *se* situated anterior to bases of setae *c1*: apodemes I are 1.1–1.2 longer than the gnathostoma; legs I pairs are 1.5 times longer than legs of II pair. Females of *Peristerophila* setae *se* and *c1* are situated at the same level; apodems I are distinctly shorter than gnathosoma, legs I 1.1 – 1.2 longer than legs II. Those genera have been represented by four species: 1) *C. mucuya* (Casto, 1980) associated with *Columbina passerina* (type host), 2) *C. claravis* Glowska and Skoracki, 2008 infected *Claravis pretiosa* (Glowska and Skoracki 2008), both species have been described from birds belonging to Columbiformes, 3) *C. forpi* Bochkov and Perez, 2002 associated with birds from order Passeriformes and 4) *C. meropis*

Skoracki, Hromada and Sikora, 2017 infected Coraciiformes. Moreover, based on comparative studies of ontogenesis and morphology performed on the many infrapopulation of *Peristerophila hirundinesu*, the genus *Castosyringophilus* has been synonymized with the genus *Peristerophila* (Skoracki, Hromada, Kaszewska and Sikora 2020). Authors of this research indicated the presence of dimorphic females the homeomorphic forms which have a similar morphological feather as *Peristerophila* observed, while heteromorphic forms were similar to *Castosyringophilus* (Skoracki et al. 2020). The phenomenon of female dimorphism in mites of the family Syringophilidae has been also observed in the genus *Stibaroksis* Kethley, 1970 (Glowska et al. 2014) and *Chenophila* Kethley, 1970 (Skoracki and Zawierucha 2016). The study did not confirm previous hypotheses regarding the dispersive functions of homeomorphic females, as both homeomorphic and heteromorphic females were the new population founders.

Genus *Terratosyringophilus* Bochkov and Perez, 2002 different from other quill mites genera by the following characteristics: setae *dFIII* and *dFIV* are situated ventrally. Mites belonging to this genus have been associated with birds from two distinctly orders Columbiformes and Psittaciformes. Birds from order Columbiformes have been infected by two parasitic species *T. geotrygonus* Skoracki and Glowska, 2008 described *Geotrygon linearis* (type hosts) from Neotropical area (Wenezuela) and *T. longisoma* (Casto, 1979) infected members of genus *Zenaida*: *Z. macroura* and *Z. asiatica* both from Nearktic (USA). Next species *T. loricinus* Bochkov and Fain, 2003 and *T. reichholfi* Skoracki and Sikora, 2008 described from *Lorius garrulus* (type species) *Trichoglossus haematodus* and *Lorius lory* respectively from Indonesian and Oceanian.

Genus *Psittaciphilus* Fain, Bochkov and Mironov, 2000 characterized by situated bases of setae *si* and *se* at the same transverse level and long terminal setae. Until now, quill mites of this genus have been described only as birds belonging to parrots. According to Fain, Bochkov and Mironov, 2000 and *P. fritschi* Bochkov and Mironov, 2000, P. amazonae has been described from Neotropical (Colombia) from *Amazona amazonica* (type species).

Subfamily Picobiinae is represented by 12 genera, and only one genus – *Gunabopicobia* Skoracki and Hromada, 2013 includes quill mites species associated with birds from the order Columbiformes. Genus *Gunabopicobia* is characterized by the following morphologic features: setae *vi* are situated anterior to setae *ve*, hypostome apex with shoulders, thorn-like protuberances on apodemes I absent. Those genera included only one species – *G. zumpti* (Lawrence 1959), recorded from numerous doves and pigeon species, belonging to the following genera: *Streptopelia – S. capicola* (type species), *S. senegalensis* both species described from Afrotropical zone (RPA), *S. semitorquata*, from Afrotropical (Ethiopia); genus *Columba – C. speciosa* from Neotropical (Brazil) *C. delegorguei* from Afrotropical (Tanzania), *C. livia* Nearctic (USA), Palearktic (Poland); genus *Patagioenas – P. picazuro* from Neotropical (Brazil) and genus *Zenaida – Z. macroura* Nearctic (USA) (All records and references are listed in Table. *Quill mites from family Syringophilidae associated with birds from order Columbiformes*).

Given the fact that little is known about acarofauna Syringophilidae connected to pigeons, the research objectives undertaken within the framework of this dissertation exclusively focused on the taxonomy of quill mites. Furthermore, the results of the research enabled a take on ecological and phylogenetic interpretations.

The first aim of the dissertation was to explore the taxonomic diversity of Syringophilidae from the broadest possible spectrum of potential hosts that belong to pigeons and represent three subfamilies and occupy all zoogeographical zones. The second aim was to investigate interactions in the host-parasite system i.e. to determine the prevalence, host, and topical specificity of the quill mites connected to pigeons. The third aim was to determine the phylogenetic relation between Syringophilidae genera which parasitize pigeons.

The taxonomic part of my doctoral dissertation consists of a series of six publications devoted to the species diversity and the worldwide distribution of Syringophiidae mites associated with birds from the order Columbiformes. Therefore, 112 birds were examined for the presence of quill mites. Moreover, the birds belong to 28 genera of potential hosts which marks up 57% of all recognized genera in the order Columbiformes. The sample consisted of representatives from the following zoogeographic regions: Neotropical, Nearctic, Afrotropical, Saharo-Arabian, Palearctic, Oriental, Oceanian, and Australian. These are almost all regions in which Columbiformes are present except for Madagascar's land and the Pacific islands. Based on the taxonomic analysis, the examined birds were infested by 25 species of Syringophilidae which belong to the following genera: *Meitingsunes*, *Peristerophila*, *Psittaciphilus*, *Gunabopicobia*. In total, quill mites have been found on 65 doves and pigeons which were representatives of all subfamilies within the family Columbiformes.

The following species of quill mites had been previously documented as infesting pigeons: *Meitingsunes columbicus* Skoracki, 2011; *M. zenadurae* (Clark, 1964), *M. tympanistria* (Skoracki and Dabert, 2012), *Peristerophila columbae* (Hirst, 1920) *P. claravis* (Skoracki and Glowska, 2008), *P. mucuya* Casto, 1980 and *Gunabopicobia zumpti* (Lawrence, 1959). The host spectrum for Syringophilidae species has been extended to numerous new hosts, including representatives of genera previously examined for the presence of quill mites ex. *Leptotila*, *Patagioenas*, *Oena*, *Treron*, *Leucosarcia*, *Caloenas*, *Ducula*, *Ptilinopus*, *Ocyphas*, *Turacoena*, *Macropygia*, *Gallicolumba*, *Chalcophas* (*Tabele 1*). For example, *Peristerophila claravis* was described as pigeon species belonging to the genus *Columbina* of the subfamily Claravinae. During the analysis, these quill mite species were also associated with the Namaqua dove (*Oena capensis*) belonging to the subfamily Raphinae. Until now, *M. columbicus* was recorded exclusively from the members of the genus *Columba* belonging to the sub-family Columbinae. During the study, *M. columbicus* has been also noted from pigeons belonging to the subfamily Raphinae – Bruce's green pigeon (*Treron waalia*). The presence of these two species on hosts from two different sub-families indicates a greater specificity of the host than previously thought. For species *M. columbicus* the zoogeographic distribution was also extended to the Afrotropical region (*a summary of the new hosts and locations is presented in Table 1*).

I described together with the co-authors 16 new species of syringophilid mites. The morphologically diagnoses and keys are presented in the taxonomic section of the doctoral dissertation. In the genus *Meitingunes*, four species: *M. chalcophas* Kaszewska, Skoracki and Kavetska, 2016, *M. turacoenas* Kaszewska, Skoracki and Kavetska, 2016 **(Kaszewska et al., 2016. *Zootaxa*)**, *M. lengai* Kaszewska, Skoracki, Hromada, 2020; *M. ptilinopus* Kaszewska, Skoracki, Hromada, 2020 **(Kaszewska et al., 2020. *International Journal of Acarology*)** were described. These species have been found for the first time on pigeons in the Oriental, Oceanian, and Australian. So far, representatives of the genus *Meitingsunes* have been noted from the Neotropical, Palearctic and Afrotropical zones. Acquired results have shown that *Meitingsanes* is the most diverse genus of quill mites connected to the subfamily Syringophilinae and the genus counts for eight species inhabiting 25 host species. Members of Meitingsanes are present in the following zoogeographic region: Neotropics, Nearctic, Palearctic, Afrotropic, Oriental, Oceanian, and Australian regions.

Within the genus *Peristerophila*, the following species have been described: *P. lature* Kaszewska, Kavetska, Skoracki, 2014 (**Kaszewska et al., 2014. *Zootaxa***), *P. geopelis* Kaszewska, Skoracki, Kosicki, Hromada, 2020; *P. leucomela* Kaszewska, Skoracki, Kosicki, Hromada, 2020, (**Kaszewska et al., 2020. *Zootaxa***). The first two quill mites species infected closely related doves and pigeons from the subfamily Raphinae, while the species *P. leucomela* was described from the *Columba leucomela*, from the subfamily Columbinae. All the new species were described from: Indonesia, Papua New Guinea, and Australia. Genus *Peristerophila* currently comprises six species of quill mites which are mainly associated with members of the sub-family Raphinae. The genus of *Gunabopicobia* is the only genus from the Picobiinae subfamily associated with the birds from the genus Columbiformes. Before the Ph.D. study, this genus was represented by only one species – *Gunabopicobia zumpti* (Lawrence, 1959). It was described by numerous host species of the genus *Columba* and *Streptopelia* recorded from Palearctic, Nearctic, and Afrotropical zoogeographical zone. Seven new species of the genus *Gunabopicobia* were described: *G. masalaje* Kaszewska, Kavetska and Skoracki, 2014 (**Kaszewska et al., 2014. *Zootaxa***), *G. claravis* Kaszewska, Skoracki and Hromada, 2018, *G. geotrygoni* Kaszewska, Skoracki and Hromada, 2018, *G. metriopelia* Kaszewska, Skoracki and Hromada, 2018, *G. lathami* Kaszewska, Skoracki and Hromada, 2018, *G. leptotila* Kaszewska, Skoracki and Hromada, 2018, *G. verraruxi* Kaszewska, Skoracki and Hromada, 2018 (**Kaszewska et al., 2018. *International Journal of Acarology***), associated in total with 16 hosts species. Those mites have been recorded from hosts belonging to the following subfamily: Columbinae (genera: *Leptotila*, *Geotrygon*), subfamily Claraviinae (genera: *Claravis, Metriopelia*), and also from subfamily Raphinae (genera: *Caloeans, Ducula*, *Leucosarcia*, and *Ptilinopus*). During the research, the infestation of pigeon birds by representatives of the genus *Psittaciphilus* was found for the first time. To this time, quill mites belonging to the genus *Psittaciphilus* have been described only in birds belonging to the order Psittaciformes. Two new species *Psittaciphilus montanus* Kaszewska, Skoracki, 2018 and *Psittaciphilus patagioenas* Kaszewska and Skoracki, 2018 were described. *P. montanus* has been noted from *Geotrygon montana* while *P. patagioenas* has been recorded from two hosts species: *Patagioenas fasciata* (type species) and *Patagioenas speciosa* (**Kaszewska and Skoracki 2018. *Systematic Parasitology***). Genus *Psittaciphilus* has been found inhabiting both parrots and pigeons. Therefore, the genus was added to the group of closely related quill mites designated by Bochkov and Perez 2002. The group also consists of the genera *Peristerophila* and *Terratosyringophilus* (*a summary of the new species and host species is presented in Table 1*).

The second part of this dissertation concerns research on the host and topical specificity, as well as patterns of interactions within the system between Syringophilidae and Columbiformes. I also present the results of the phylogenetic analysis of quill mites at the generic level.

Host specificity encompasses the range and diversity of host species, that a parasite can infect. Moreover, it is considered a crucial marker of a parasite's potential to change hosts and trigger disease outbreaks (Welles and Clark 2019). The host specificity of parasites illustrates the width of ecological niches and parasites' role and position in the biosphere. Furthermore, the marker assesses the likelihood of a parasite to successfully infest new hosts once introduced to a new geographical area (Poulin and Mouillot 2003). Until now, few studies devoted to the analysis of interactions between Syringophilidae and their hosts have focused on acarofauna of quill mites associated with birds from the order Passeriformes, e.g. Nectarniidae and Estrildae (Skoracki et al. 2018, 2019). The analyses undertaken in the framework of this research are the first of their kind, connecting Syringophilidae to Non-Passeriform birds. I carried out host specificity analysis, measured the prevalence index, and performed the bipartite network analyses to determine host specificity and describe the interactions in the parasite-host system for Syringophilidae connected to birds of the order Columbiformes. The results of the faunistic study made it possible to estimate the host spectrum and determine host specificity for particular quill mites infesting Columbiformes.

The following specificity ranges from very narrow to broad were used in the analyses: Monoxenous (the parasite infest only one host); oligoxenous (the parasite infests host species belonging to the same genera); mesostenoxenous (the parasite infests hosts belonging to the same sub-family); metastenoxenous (parasite infests hosts belonging to the same order); polixenous (parasite infest hosts species from different orders). Among all Syringophilidae parasitizing pigeons, eight species were monoxenous. Within this group, the most numerous were representatives of the genus *Gunabopicobia*. The group of oligoxenous species comprised four species of representatives of the subfamily Syringophilinae belonging to the genera *Meitingsunes*, *Psittaciphilus,* and *Terratosyringophilus*. Within *Picobiinae* one species, *Gunabopicobia geotrygoni* was recorded to infest hosts from the same genus– *Geotrygon.* Mesostenoxenous. The mesostenoxenic group in total included eight syringophilids species from the following genera: *Meitingsunes* (2 species), *Peristerophila* (3 species) (subfam. Syringophilinae), and *Gunabopicobia* (subfam. Picobiinae) (3 species).

Metastenoxenous were represented by quill mites belonging to two genera *Meitingsunes* (2 species) and *Peristerphila* (1 species) (sub-fam. Syringophilinae). *Peristerophila mucuya* (sub-fam. Syringophilinae) was described as being polygynous, meaning its host specificity is broad. Those species infest pigeons as well as hosts from the order Psittaciformes, e.g. *Brotogeris versicolurus*, *Psilopsiagon aymara*, *Trichoglossus haematodus* (Bochkov and Fain, 2003). During the study, the species *P. mucuya* was found in three new host species belonging to the order Columbiformes: *Columbina minuta*, *Metriopelia ceciliae*, and also *M. melanoptera.* To compare individual species in a given xenicity category, a specificity index (d') was calculated, which measures the interaction of the parasite with a range of potential hosts (pools of host species) across the observed parasite-host system (Blüthgen and Menzel 2006). It was found that mites infesting more than one host had a high specificity index, which indicates non-accidental host infestation.

The study shows that 11 host species were infested by at least two separate species of quill mites. The following co-infestation patterns have been observed:

1. *Syr-Pic* pattern (mites belonging to two subfamilies Syringophilinae and Picobiinae infesting different types of plumage), e.g. *Geotrygon montanus* infected by *Gunabopicobia geotrygoni* (contour feathers) and *Meitingsunes zenadourae* (covert feathers).
2. *Syr-Syr* pattern (mites belonging to the same subfamily but infecting different types of feathers, e.g. *Columba palumbus* infected by *Meitingsunes columbicus* (secondaries) and *Peristerophila columbae* (covert feathers).

Peristerophila columbae and *Psittaciphilus patagioenas* are species of quill mites that belong to the same subfamily and they have been observed to infest the same host species. Both syringophilids species infested the covert feathers of a pigeon from the species *Patagioenas speciose.* On one hand, none of the examined samples showed the presence of two different species of quill mites infecting one quill. On the other hand, the results of the study show that the niche is a factor that plays an important role in avoiding competition for resources between the parasites which do share the host species. Separating the niche increases the chance of successfully infecting a new microhabitat and establishing a new colony inside the infected quill while avoiding competition.

The next point of the study was to explore interactions within the Syringophiidae-Columbiformes system. For that purpose, an analysis of the "bipartite" networks has been carried out to help visualize and characterize the links between parasites and their hosts. The networks are used to represent any type of interaction between partners on the net (Poulin 2010). They provide rates to explore e.g. the specificity of the host-parasite system, and interactions between the species. For the study, indexes have been assigned to determine the specialization of interactions at the network level –index *H2'*(value 0 means low specialization of network interaction, 1 means high specialization of network interaction (Blüthgen 2010)); the proportion of interactions realized within the network – *connectance index* C (value close to 1 indicates a high number of links(Blüthgen and Menzel 2006));

nesting – index N, it indicates how many interactions realized by specialists make up a subset of those realized by generalists (value equal 0 means no nesting, 1 means maximal nesting (Almeida-Neto et al. 2008, Canard et al. 2015, Dromann et al. 2009). Last but not least, a factor of modularity, marked by index Q, is the measure of the network's structure and it measures the force at which the network breaks into modules (Olesen et al. 2007, Newman 2006). Modules are defined as subsystems of non-overlapping and highly interacting species within a cluster (Stouffer and Bascompte 2010, 2011).

Taking into account the number of interactions between the parasitic species and the pool of available hosts, the network Syringophiidae-Columbiformes has high values of H2'=0.93 which means that the network observed is highly specialized. The bipartite network was found to be nested at N=0.908, which means, that the quill mites with narrow host specificity (monoxenous) infected pigeons which are also a part of the host spectrum of parasites with broad host specificity. Within monoxenous species the following subset of Syringophilidae representatives have been observed: *Gunabopicobia leptotila* – recorded from *Leptotila verreauxi*, which is one of the host species for *Meitingsunes zenadourae*, those quill mites share the broad host spectrum (metastenoksenous); *Meitingsunes adwelles* infects exclusively the host species – *Geotrygon frenata*, which is one of the host species for *Meitingsunes zenadourae* (metastenoxsenous); *Gunabopicobia claravis* quill mites are associated with *Claravis pretiosa*, which is also infected by *P. claravis* (mesostenoksenous); *Gunabopicobia metriopelia* infects *Metripelia melanoptera*, which is a host for *Peristerophila mucuya* (polyxenous); *Psittaciphilus montanus* described from the host species – *Geotrygon montana*, is also infected by *Gunabopicobia geotrygoni* (oligoxenosu species) as well as *Terratosyringophilus geotrygonus* (monoxenous species). Two monoxenous quill mite species – *Meitingsunes chalcophas* infecting *Chalcophas indica* and *Peristerophila leucomela* occupying *Columba leucomela* do not form any subsets. Based on the analysis of the host subsets' spectrum, we draw the conclusion that highly specialized quill mites, with narrow host specificity, occupy large-scale and population-rich host species. Infecting hosts with increased susceptibility to parasites lowers the risk of co-extinction (McQuaid and Britton, 2013). In addition, studies conducted by McQuaid and Britton 2013 show that nesting in antagonistic systems, i.e. the parasite-host system, is a result of co-evolution. The phenomenon of co-evolution in specialized avian parasites is present in many systematic groups, including mites. The value of nesting in the presented studies indicates that the co-evolutionary process takes place.

The connectance index was set at C=0.90 indicating a large number of potential interactions in the host-parasite system. Particular species of quill mites had numerous interactions with numerous host species. While a group of monoxenous species included eight representatives of the Syringophilidae family, the network was dominated by species that infect more than one host, namely: 8 mesostenoxenous species, 5 oligoxenous species, 3 metastenoxenous, 1 polixenous. Considering phylogenetic relationships between pigeon species, Syringophilidae interact with their hosts in numerous ways and inhabit closely related species which means that interactions with their hosts do not occur at random. The results of the network analysis show that the quill mites parasitizing pigeons create a highly specialized and non-coincidental host-parasite system. Quill mites interact mainly with host species belonging to the same genus or subfamily.

Furthermore, as a part of the dissertation, a modular analysis was carried out to identify the tendency for module developments, and clustering within the network, as well as to identify the key hosts. Within the network, 20 modules (clusters) have been identified and divided into the following types: (A) modules consisting of one parasitic species and one host species, (B) modules composed of one parasite species associated with several host species, and (C) modules comprising several parasitic species grouped within the host group. It was shown that in the observed host-parasite system, clustering occurs with strong interactions within each module and weak relationships outside the clusters. The Q modularity index was 0.83. Identification of modules allows for the determination of the key hosts for each group of Syringophilidae and their potential to infect new host species.

Phylogenetic analysis of Syringophilidae associated with Columbiformes was conducted at the generic level as part of the dissertation. The analysis was performed based on the qualitative morphological features of the following genera: *Peristerophila*, *Meitingsunes*, *Terratosyringophilis*, *Psittaciphilus* (Syringophilinae), and also *Gunabopicobia* (Picobiinae). The analysis was based on 26 qualitative characteristics describing the following: a) presence or absence of setae, i.e. *vi*, *g1*, legs setae: *vs* (II), *df* (II – III), *vF* (III), *l'R I*, *e1*, *ps3*; b) presence or absence of structures: finger-like protuberances of hypostome, pocket-like structure on propodonotal fields, apodem III – IV; c) the shape of peritrems, stylophor, legs I pairs, distal part of cheliceral and setae *p'* and *p''*; d) ornamentation of shields and setae; e) position of *ve* and *si* setae, f) presence or absence of the physogastric phenomena; g) presence or absence of female dimorphism. The number of parsimony characteristics – 19, cohesion index (CI)=0.9, retention index (RI)=0.9, homoplasy index (HI)=0.1, Goloboff-fits (G-fit) index = 18.25. Based on the study, it was concluded that there are two clades within the subfamily Syringophilinae: A *Peristerophila*+*Terratosyringophilus* and B *Meitingsunes*+*Psittaciphilus*. Synapomorphic features supporting the identification of *the Peristerophila*+*Terratosyringophilus* clade were: the presence of finger-like protuberances situated on the apex of the hypostome, parallel apodemes I, the presence of dimorphic females. The second clad *Meitingsunes*+*Psittaciphilus* were distinguished based on such synapomorphic features: stylophone constricted posteriorly, lineal-shaped. Clad A – *Peristerophila-Terratosyringophilus* includes eight quill mite species (*P. columbae, P. geopelis, P. lature, P. mucuya, P. claravis, P. leucomela, T. geotrygonus, T. longisoma*), all of which infect pigeons belonging to three subfamilies, namely: Columbinae, Claravinae, and Raphinae. Quill mites from the genus *Peristerophila* infected host species belonging to the following three subfamilies: Columbinae (from genus *Columba*, *Geotrygon*, *Patagioenas*, *Streptopelia*), Claravinae (from genus *Columbina*, *Metriopelia*, *Claravis*), Raphinae (from genus *Oena*, *Geopelia*, *Ocyphas*, *Ducula*, *Ptilinopus*). Representatives of the genus Terratosyringophilus were recorded only on pigeon birds of the genus Columbinae (Geotrygon, Zenaida). Clade B – *Meitingsunes-Psittaciphilus* includes a total of 10 species of quill mites (*M. adwelles, M. columbicus, M. chalcophas, M. lengai*, *M. ptilinopus, M. turacoenas, M. tympanistria, M. zenadourae, P. montanus, P. patagioenas*) inhabiting hosts belonging to the subfamilies Columbinae and Raphinae. Quill mites of the genus Meitingusnes were recorded on hosts of the subfamilies: Columbinae (from the genus *Columba*, *Streptopelia*, *Macropygia*, *Turacoena*, *Geotrygon*, *Leptotila*, *Patagioenas*, *Zenaida*) and Raphinae (from genus *Chalcophas*, *Gallicolumba*, *Ptilinopus*, *Turtur,* and *Treron*). Members of the genus *Psittaciphilus* have been recorded on hosts belonging to the subfamily Columbinae (from the genus *Geotrygon*, *Patagioenas*). The presence of mites of the family Syringophilidae on representatives of all subfamilies delineated by the order Columbiformes testifies to their long and shared history **Kaszewska-Gilas et al., 2021, Animals.**

Conclusions

The dissertation research has expanded knowledge of the species diversity and host spectrum of ectoparasitic mites of the family Syringophilidae parasitizing birds of the order Columbiformes. Carried out the analyses of prevalence, host and topical specificity, bipartite networks, and phylogenetics allowed us to better understand the relationships in the parasite-host system that was under study. Quill mites associated with pigeons are a rich and diverse part of the family Syringophilidae. Quill mite species were found in all zoogeographic zones occupied by Columbiformes, and their host spectrum includes representatives of all designated sub-families within this host order. Bipartite network analyses performed as part of the dissertation showed that the observed Syringphilidae-Columbiformes system is characterized by a high degree of specificity and non-random interaction. The results obtained allowed the selection of key hosts for the parasite and its potential to infect other, possibly new host species.

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ROZPRAWA DOKORSKA

DOCTORAL DISSERTATION

Lista publikacji wchodzących w skład dysertacji / *List of orginal publications*

I. **Kaszewska K**., Kavetska K., Skoracki M. 2014. Two new species of quill mites of the family Syringophilidae (Acariformes: Cheyletoidea) associated with treroninae doves. *Zootaxa*, 293 – 300.

II. **Kaszewska K**., Skoracki M., Kavetska K. 2016. Two new *Meitingsunes* species (Acari: Syringophilidae) from Indonesian doves Columbiforms: Columbidae. *Zootaxa*, 4109 (4): 479 – 486.

III. **Kaszewska K**., Skoracki M., Hromada M. 2018. A review of the quill mites of the genus *Gunabopicobia* Skoracki and Hromada (Acariformes: Prostigmata: Syringophilidae) associated with birds of the order Columbiformes. *International Journal of Acarology*, 1945 (3892):1 – 12.

IV. **Kaszewska K**., Skoracki M. 2018. Two new quill mite species of the genus *Psittaciphilus* Fain, Bochkov & Mironov, 2000 (Acariformes: Syringophilidae) associated with pigeons and doves (Columbiformes: Columbidae). *Syst. Parasitol*, 95:953 – 958.

V. **Kaszewska K**., Skoracki M., Hromada M. 2020. The mites of the genus *Meitingsunes* Glowska and Skoracki (Acariformes: Syringophilidae) associated with pigeons and doves (Aves: Columbiformes): taxonomic studies with description of two new species. *International Journal of Acarology*, 46 (6): 439 – 445.

VI. **Kaszewska K**., Skoracki M., Kosicki ZK., Hromada M. 2020. New species and records of the quill mites of the genus *Peristerophila* Kethley, 1970 (Acariformes: Syringophilidae) associated with pigeons and doves (Aves: Columbiformes). *Zootaxa*, 4878 (2): 349 – 361.

VII. **Kaszewska K**., Kosicki Z.J, Hromada M., Skoracki M., 2021. Global studies on the host-parasite relationship between ectoparasitic mites of the family Syringophilidae and birds of the order Columbiformes. *Animals* 11, 3392: 1 – 32

I

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Two new species of quill mites of the family Syringophilidae (Acariformes: Cheyletoidea) associated with treronine doves (Columbiformes: Columbidae: Treroninae)

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Abstract

Two new species of quill mites (Acariformes: Syringophilidae) associated with doves of the subfamily Treroninae (Columbiformes: Columbidae) from the Oceanian realm are described: *Gunabopicobia masalaje* **sp. nov.** from six avian host species, *Ptilinopus iozonus* Gray (type host) *Ducula pistrinaria* (Bonaparte), *D. rosacea* (Temminck), *D. rufigaster* (Quoy and Gaimard), *D. spilorrhoa* (Gray), *D. luctuosa* (Temminck), and *Peristerophila lature* **sp. nov.** also from six host species *Ducula luctuosa* (type host), *D. spilorrhoa*, *Ptilinopus jambu* Gmelin, *P. melanospilus* Salvadori, *P. porphyreus* Temminck, *P. regina* Swainson. Additionally, *Treron waalia* (Meyer) is noted as a new host species for *Meitingsunes columbicus* Glowska and Skoracki, 2010.

Key words: Acari, Syringophilidae, ectoparasites, Columbiformes, Treroninae

Introduction

The family Syringophilidae Lavoipierre (Acariformes: Prostigmata: Cheyletoidea) includes permanent and highly specialized mono- or stenoxenous ectoparasites, infesting feather quills (Kethley 1970; Skoracki 2011). This taxonomically specious family with about 320 species grouped in 60 genera is distributed on a broad spectrum of hosts belonging to 23 orders, both from neoganthous and paleognathous birds (Skoracki 2011; Skoracki *et al*. 2012; Glowska & Schmidt 2014).

Until now, the fauna of syringophilid mites associated with columbiform birds included 11 species of six genera: *Castosyringophilus* Bochkov and Perez, 2002, *Columbiphilus* Kivagnov and Sharafat, 1995, *Gunabopicobia* (Lawrence, 1958), *Meitingsunes* Glowska and Skoracki, 2010, *Peristerophila* Kethley, 1970, and *Terratosyringophilus* Bochkov and Perez, 2002. Up to now, the quill mite fauna has been recorded only from birds of the subfamily Columbinae belonging to nine genera and 19 species (Lawrence 1958; Kivganov and Sharafat 1995; Bochkov and Perez 2002; Glowska and Skoracki 2010; Skoracki *et al*. 2012; Skoracki and Hromada 2013).

In this paper we give descriptions of two new species, *Gunabopicobia masalaje* **sp. nov.** and *Peristerophila lature* **sp. nov.**, associated with several dove-species from the genera *Ptilinopus* and *Ducula* (Columbidae, Treroninae). Additionally, *Treron waalia* (Meyer) is noted as a new host species for *Meitingsunes columbicus* Glowska and Skoracki, 2010.

Material and methods

The material used in the present study was collected from dry bird skins housed in the ornithological collection of the Bavarian State Collection of Zoology (ZSM), Munich, Germany. Mites were extracted with sharp, fine tweezers through a longitudinal cut made in the quill. Before mounting, mites were softened and cleared in Nessbitt's

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solution at room temperature for 24 hours. Then, mites were mounted on slides in Faure's medium and examined under an Olympus BH-2 light microscope with differential interference contrast optics. Drawings were made with the aid of a camera lucida. All measurements are given in micrometres. Range of lengths of paratypes is given in brackets following the holotype data. In the descriptions below the idiosomal setation follows Grandjean (1939) as adapted for Prostigmata by Kethley (1990). The nomenclature of leg chaetotaxy follows Grandjean (1944). The morphological terminology follows that proposed by Skoracki (2011).The scientific names of the birds follow Clements *et al*. (2013). Specimen depositories are cited using the following abbreviations: AMU—A. Mickiewicz University, Department of Animal Morphology, Poznan, Poland; ZISP—Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia; ZSM—Bavarian State Collection of Zoology, Munich, Germany.

Systematics

Family Syringophilidae Lavoipierre

Subfamily Picobiinae Johnston and Kethley

Genus *Gunabopicobia* Skoracki and Hromada

Gunabopicobia masalaje sp. nov.

(Figs. 1–3)

Description. FEMALE, holotype. Total body length 470 (470–493 in 8 paratypes). *Gnathosoma*. Hypostomal apex truncate with pair of small and blunt-ended shoulders (Fig. 2A). Each medial branch of peritremes with 6–7 chambers, each lateral branch with 5–6 chambers (Fig. 2B). Length of stylophore 195 (190–210). Distal end of movable cheliceral digit dentate, each with 3 teeth (Fig. 2A), proximal end smooth (Fig. 2D). *Idiosoma*. Propodonotal shield divided into 3 sclerites: pair of narrow, densely punctate, bearing bases of setae *vi*, *ve*, *si* and *se*; and large apunctate central sclerite, bearing setae *c1* bases. Length ratio of setae *vi*:*ve*:*si* 1:2.5–2.7:2.6–2.8. Setae *d2* about twice as long as *e2*. Pygidial and hysteronotal shields absent. Length ratio of setae *f1*:*f2* 1:1.2–1.6. Setae *f1* and *f2* located at same transverse level. Setae *h1* 1.8 times longer than *f1*. Agenital and genital plates absent. Length ratio of setae *ag1*:*ag2*:*ag3* 2.8–3.5:1:3.6–4. Setae *3c* about 4 times longer than *3b.* Cuticular striations as in figs 1A, B. *Legs.* Antaxial and paraxial claw members of legs III and IV dissimilar in size and shape. Setae *tc"* of legs III and IV slightly (1.2 times) longer than *tc'III–IV.* Solenidia of legs I as in fig. 2C. *Lengths of setae*: *vi* 60 (50–65), *ve* 150 (150–185), *si* 160 (150–170), *se* 255 (250–270), *c1* 260 (240–280), *c2* 280 (270–310), *d1* 215 (190–220), *d2* 235 (235–255), *e2* 135 (110–140), *f1* 25 (20–35), *f2* 40 (25–40), *h1* 45 (35–45), *ag1* 70 (70–100), *ag2* 25 (20–30), *ag3* 90 (90–100), *tc'III–IV* (50), *tc"III–IV* (60), *3b* 30 (25–40), *3c* 110 (100–135).

MALE (3 paratypes). Total body length 350–365. *Gnathosoma*. Hypostomal apex without protuberances (Fig. 2E). Distal end of movable cheliceral digit dentate. Each medial branch of peritremes with 6 chambers, each lateral branch with 6 chambers (Fig. 2F). Length of stylophore 100–105. *Idiosoma*. Propodonotal shield entire, rectangular in shape, punctate, bearing bases of setae *vi*, *ve*, *si*, *se* and *c1*. Length ratio of setae *vi*:*ve*:*si* 1:3.5–4.3:3.8–4. Hysteronotal shield entire, apunctate, bearing bases setae *e2* and *d1*. Setae *d2* 8 times longer than *e2*. Pygidial shield apunctate. Agenital plate apunctate, well sclerotised, its anterior margin reach setae *4b*. Setae *ag1* slightly (1.2 times) longer than *ag2*. Setae *3c* about 3 times longer than *3b.* Cuticular striations as in figs 3A, B. *Lengths of setae*: *vi* 30–40, *ve* 130–140, *si* 155–160, *se* 185–190, *c1* 130–145, *c2* 165–185, *d1* 20–30, *d2* 155–165, *e2* 15–20, *f2* 10–15, *h2* 230–240, *ag1* 80, *ag2* 65, *3b* 20, *3c* 60–65.

Type material. Female holotype, 8 female and 3 male paratypes from quill of body feathers of *Ptilinopus iozonus* Gray (Columbidae); **PAPUA NEW GUINEA:** April 1910, coll. Wiedenfeld.

Type material deposition. All specimens are deposited in the AMU (Reg. No. AMU-SYR.489), except 1 female paratype in the ZSM (Reg. No. ZSM-20112043) and 1 female paratype in the ZISP (ZISP-AVB 011-2908-023).

Additional material. Four females from *Ducula pistrinaria* Bonaparte (Columbidae), **PAPUA NEW GUINEA**: New Britain Island, 17 August 1912, coll. Basenbruch (deposited in the AMU (Reg. No. AMU-SYR.496) and 1 female in the ZSM (Reg. No. ZSM-20112044)). Two females and 3 males from *Ducula rosacea*

(Temminick) (Columbidae); **INDONESIA**: East Nusa Tenggara, Kupang, Semau Island, 21 April 1911, coll. Haniel (deposited in the AMU (Reg. No. AMU-SYR.497), except 1 female in the ZSM (Reg. No. ZSM20112051)). Three females from *Ducula rufigaster* (Quoy and Gaimard) (Columbidae), **PAPUA NEW GUINEA**: Astrolabe, 5 March 1894, coll. Hagen (deposited in AMU (Reg. No. AMU-SYR.498)). One female from *Ducula luctuosa* (Temminick) (Columbidae), **INDONESIA:** Sulawesi Island, coll. Rvedel (deposited in AMU (Reg. No. AMU-SYR.501)). Two females from *Ducula spilorrhoa* (Gray) (Columbidae), **PAPUA NEW GUINEA**: 17 March 1911, coll. Wiedenfeld (deposited in AMU (Reg. No. AMU-SYR.502)).

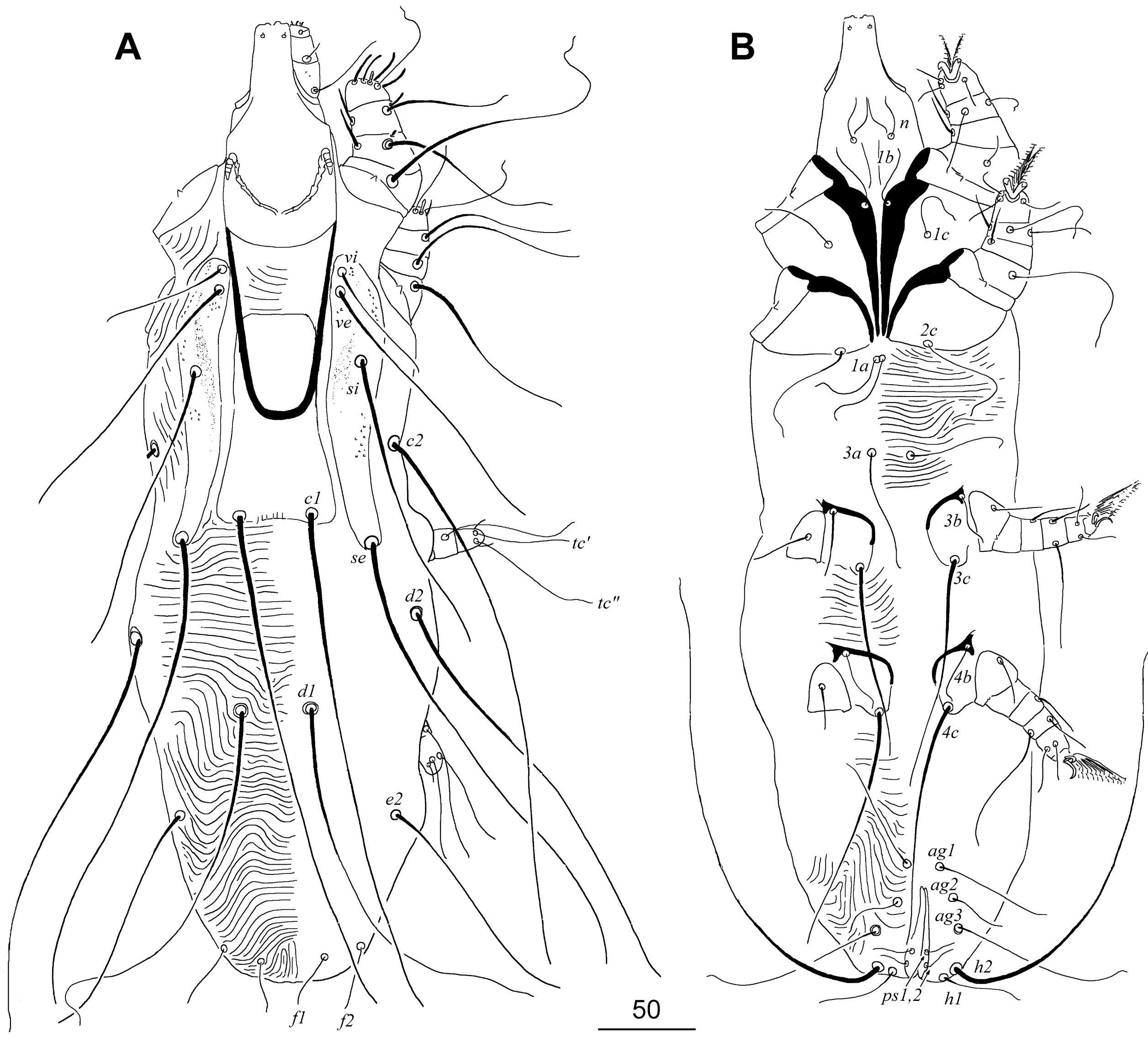

FIGURE 1A, B. *Gunabopicobia masalaje* **sp. nov.**, female. **A**, dorsal view; **B**, ventral view.

Differential diagnosis. This new species is distinguished from a single previously described species in this genus, *Gunabopicobia zumpti* (Lawrence, 1959), by the following features: in females of *G. masalaje* **sp. nov.**, each medial branch of the peritremes has 6–7 chambers, each lateral branch has 5–6 chambers; the propodonotal shield is densely punctate near bases of setae *vi* and *si*; the length ratios of setae *vi*:*ve*:*si* and *ag1*:*ag2*:*ag3* are 1:2.5–2.7:2.6–2.8 and 2.8–3.5:1:3.8–4, respectively. In females of *G. zumpti*, each medial branch of the peritremes has 2–3 chambers, each lateral branch of the peritremes has 10–11 chambers, the length ratios of setae *vi*:*ve*:*si* and *ag1*:*ag2*:*ag3* are 1:2–2.2:3.2–3.8 and 1:1:3, respectively.

Etymology. The specific epithet "*masalaje*" derives from the Papuan and New Guinean spirit which inhabit the forest—Masalaje.

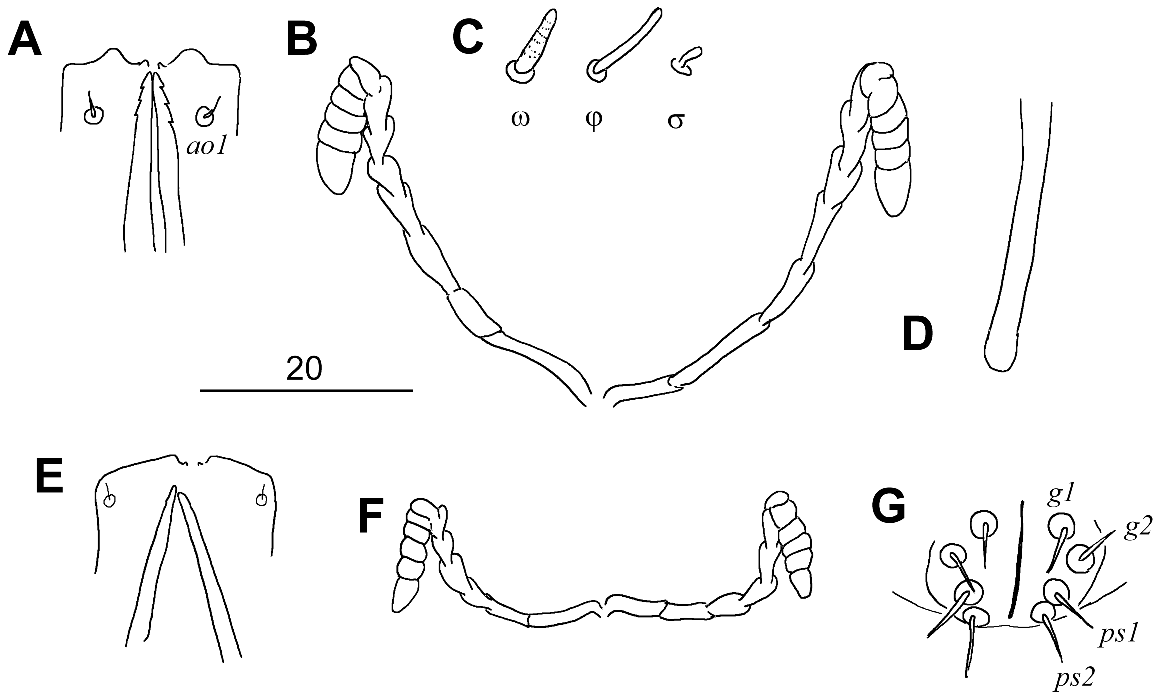

FIGURE 2A–G. *Gunabopicobia masalaje* **sp. nov.**, female (**A–D**). **A**, hypostomal apex with distal part of movable cheliceral digit; **B**, peritremes; **C**, solenidia of legs I; **D**, proximal part of movable cheliceral digit. Male (**E–G**). **E**, hypostomal apex with distal part of movable cheliceral digit; **F**, peritremes; **G**, genito-anal region.

Subfamily Syringophilinae Lavoipierre

Genus *Peristerophila* Kethley

Peristerophila lature sp. nov.
(Figs. 4–5)

Description. FEMALE, holotype. Total body length 615 (595–665 in 5 paratypes). *Gnathosoma.* Infracapitulum punctate. Each medial branch of peritremes with 1 chamber, each lateral branch with 5–6 chambers (Fig. 5A). Stylophore 135 (135–140) long. *Idiosoma.* Propodonotal shield divided into 3 narrow, sparsely punctate sclerites: pair of lateral, bearing bases of setae *ve* and *si*, and narrow central sclerite with anterior margin reaching level of setae *si*. Length ratio of setae *ve*:*si*:*se* 1:2.2–2.6:4.6–5.1. Hysteronotal shield well developed, fused with pygidial shield, punctate in posterior part. Setae *d1* and *e2* subequal in length, situated near hysteronotal shield. Length ratio of setae *f1*:*f2* 1:5.1–6. Setae *h1* and *f1* subequal in length. Length ratio of setae *ag1*:*ag2*:*ag3* 2.5–2.9:1:3–3.4. Coxal fields of legs I–IV densely punctate. Setae *3c* 3.3 times longer than *3b*. Cuticular striations as in figs. 4A, B. *Legs*. Setae *tc"* of legs III–IV twice as long as *tc'III–IV.* Fan-like setae of legs III and IV with 15–17 tines (Fig. 5B). Solenidia of legs I as in fig. 5C. *Lengths of setae: ve* 40 (35–45), *si* 90 (90–115), *se* 185 (185–205), *c1* 210 (195–225), *c2* (180–225), *d1* 185 (170–185), *d2* 195 (195–205), *e2* 150 (150–175), *f1* 25 (15–30), *f2* 150 (140–155), *h1* 25 (20–35), *h2* 280 *ag1* 100 (90–105), *ag2* 40 (40–50), *ag3* 130 (130–145), *3b* 25 (25–30), *3c* 75 (65–85).

MALE (2 paratypes).Total body length 430–445. *Gnathosoma*. Each medial branch of peritremes with 2 chambers, each lateral branch with 4–5 chambers (Fig. 5D). Stylophore 115 long. *Idiosoma*. Propodonotal shield well developed, punctate, bearing setae *vi*, *si* and *c1*. Length ratio of *ve*:*si*:*se* 1:1.2–1.6:2.8–3.6. Hysteronotal shield weakly sclerotised, divided longitudinally, apunctate. Setae *h2* 7 times longer than *f2*. Setae *ag1* 2.8–3.5 times longer than *ag2*. Coxal fields of legs I–IV apunctate. *Lengths of setae*: *ve* 30–40, *si* 50–60, *se* 100–110, *c1* 90–105, *c2* 80–100, *d1* 20, *d2* 50–70, *e2* 15–30, *f2* 25, *h2* 175, *ag1* 55–70, *ag2* 20–30.

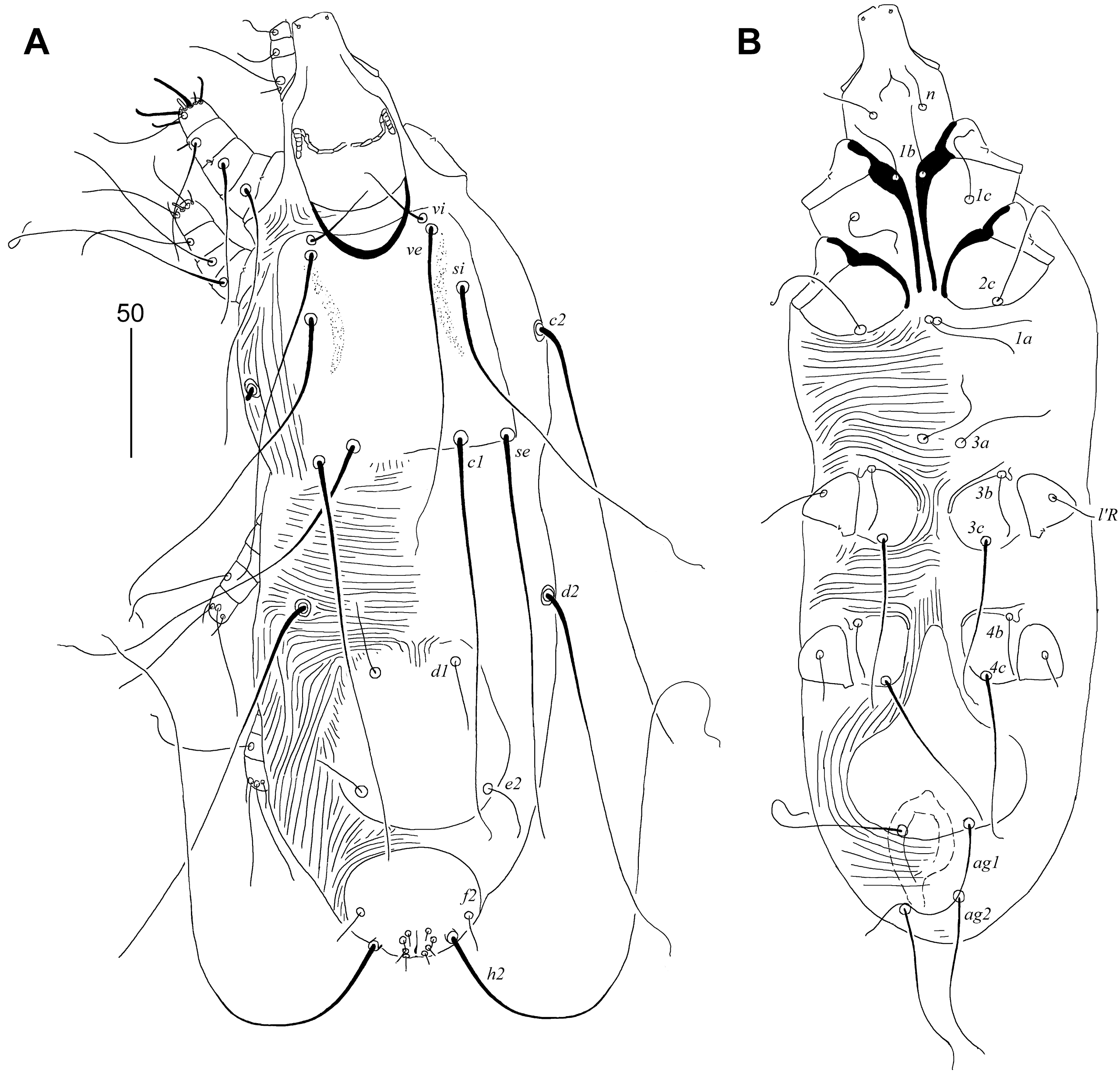

FIGURE 3A, B. *Gunabopicobia masalaje* **sp. nov.**, male. **A**, dorsal view; **B**, ventral view.

Type material. Female holotype, 6 female and 2 male paratypes from *Ducula luctuosa* (Temminick) (Columbidae); **INDONESIA:** Sulawesi Island, coll. Rvedel.

Type material deposition. All material is deposited in the AMU (Reg. No. AMU-SYR.503), except 1 female paratype in the ZSM (Reg. No. ZSM-20112052) and 1 female paratype in the ZISP (Reg. No. ZISP-AVB011-2908-025).

Additional material. Two females and 1 male from *Ducula spilorrhoa* (Gray) (Columbidae), **PAPUA NEW GUINEA:** 17 March 1911, coll. Wiedenfeld (deposited in the AMU (Reg. No. AMU-SYR.504)). Eight females from *Ptilinopus jambu* Gmelin (Columbidae), **INDONESIA:** Sumatra, Lampung Province, 1908, coll. Elbert (deposited in the AMU (Reg. No. AMU-SYR.505), except 1 female in the ZSM (Reg. No. ZSM-20112053) and 1 female in the ZISP (ZISP-AVB 011-2908-026). Five females from *Ptilinopus melanospilus* Salvadori (Columbidae), **INDONESIA**: West Java, Bogor, Cisaura, Tugu Selatan, Mount Gede Pangrango National Park, Gede Mt., 2 June 1909, coll. Primavesi (deposited in the AMU (Reg. No. AMU-SYR.506)). Six females from *Ptilinopus porphyreus* Temminck (Columbidae), **INDONESIA:** Java, no other data (deposited in the AMU (Reg. No. AMU-SYR.507), except 1 female in the ZSM (Reg. No. ZSM20112054) and 1 female in the ZISP (Reg. No. ZISP-AVB011-2908-027)). Three females from *Ptilinopus regina* Swainson (Columbidae), **INDONESIA:** Mariana Islands, no other data (deposited in the AMU (Reg. No. AMU-SYR.508)).

Differential diagnosis. *Peristerophila lature* is similar to *P. columbae* (Hirst) known from *Columba livia* Gmelin and *Zenaida auriculata* (De Murs) (Columbiformes: Culumbidae) (Kethley 1970; Skoracki 2011). In females of both species, the number of chambers in medial and lateral branches of the peritremes are similar; the hysteronotal shield is fused to the pygidial shield; setae *d2* and *e2* are unequal in length. This new species differs from *P. columbae* by the following features: in females of *P. lature*, the length ratio of setae *ve*:*si*:*se* is 1:2.2–2.6:4.6–5.1; the pygidial shield is punctate in the posterior part. In females of *P. columbae*, the length ratio of setae *ve:si:se* 1:1.5:9.5; the pygidial shield is apunctate in the posterior part.

Etymology. The specific ephitet "*lature*" is adapted from the name of the Indonesian god of the abyss—Lature.

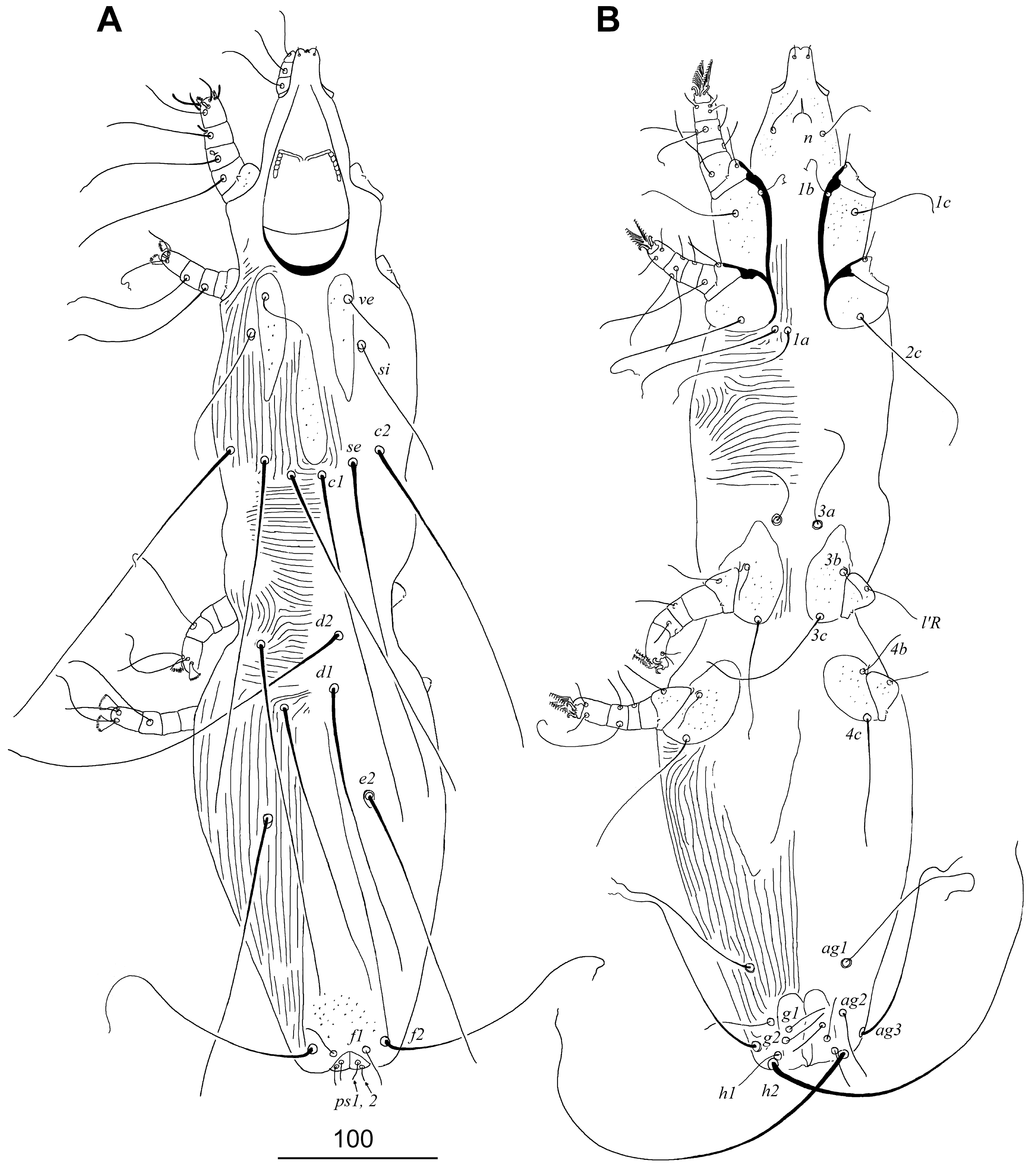

FIGURE 4A, B. *Peristerophila lature* **sp. nov.**, female. **A**, dorsal view; **B**, ventral view.

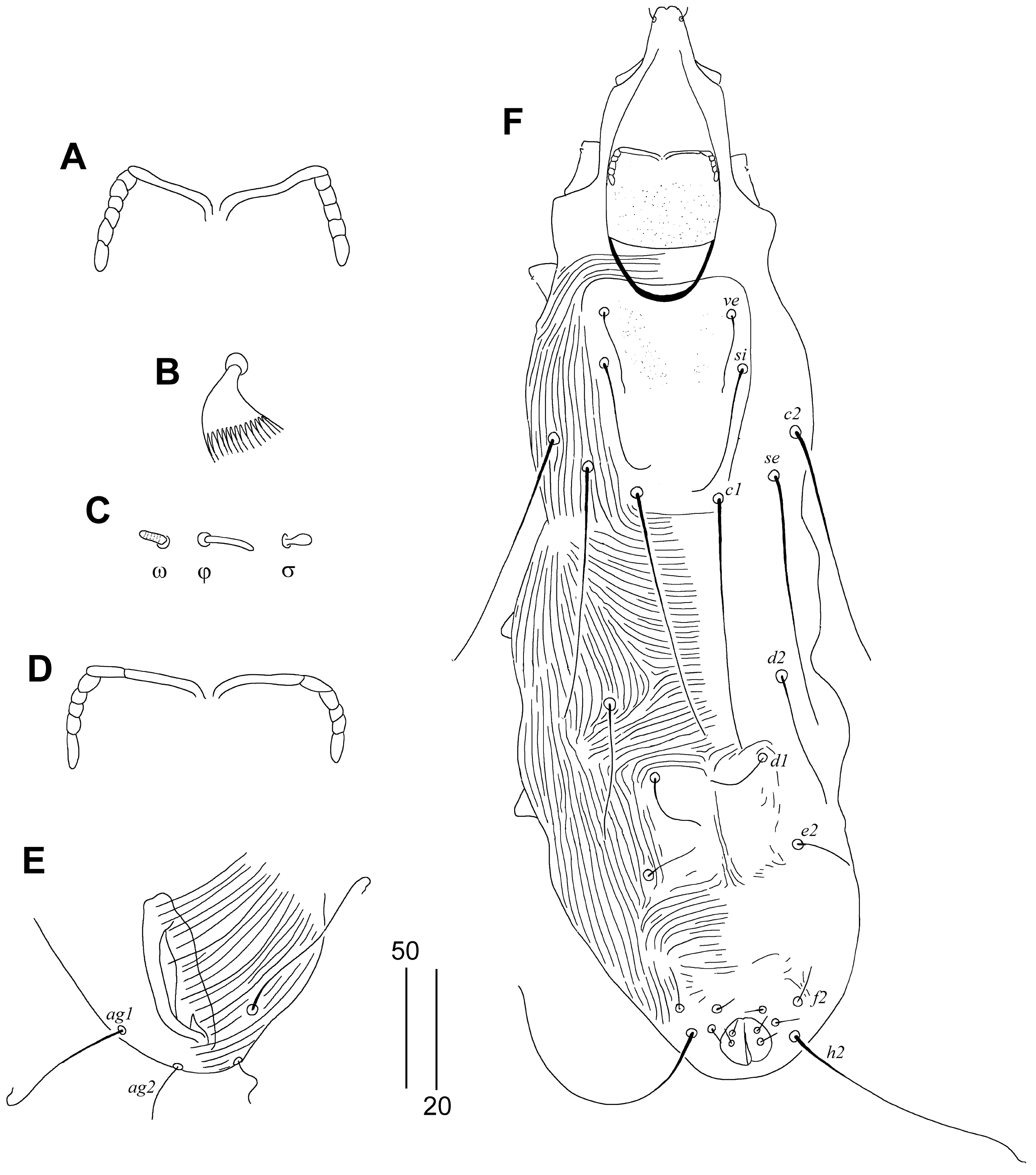

FIGURE 5A–F. *Peristerophila lature* **sp. nov.**, female (**A–C**). **A**, peritremes; **B**, fan-like seta *p'* of tarsi III; **C**, solenidia of legs I. Male (**D–F**). **D**, peritremes; **E**, opisthosoma in ventral view; **F**, dorsal view.

Genus *Meitingsunes* Glowska and Skoracki

Meitingsunes columbicus Skoracki, 2011

Until now, this species has been recorded from *Columba oenas* Linnaeus in Kazakhstan, *Columba livia* in Poland and *Columba palumbus* in Russia (Skoracki 2011). Below we give a new host record - *Treron waalia*.

Material examined. Eight females from *Treron waalia* (Meyer) (Columbidae), **CAMEROON**,:Adamawa, 20

November 1912, coll. Nack (deposited in the AMU (Reg. No. AMU-SYR.509), except 1 female in the ZSM (Reg. No. ZSM20112055) and 1 female in the ZISP (Reg. No. ZISP-AVB011-2908-028)).

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II

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Two new *Meitingsunes* species (Acari: Syringophilidae) from Indonesian doves (Columbiformes: Columbidae)

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Abstract

We describe two new quill mite species of the genus *Meitingsunes* Glowska and Skoracki, 2010 (Acari: Prostigmata: Syringophilidae) parasitizing columbiform birds (Columbiformes: Columbidae): *M. chalcophaps* **sp. nov.** collected from the Emerald Dove, *Chalcophaps indica* (Linnaeus) and *M. turacoenas* **sp. nov.** from the White-faced Cuckoo Dove, *Turacoena manadensis* (Quoy and Gaimard) (type host) and the Black Cuckoo-Dove, *Turacoena modesta* (Temminck). All host species were collected in Indonesia. These represent two new genus-level host records for *Meitingsunes*. In addition, we summarize the diversity of *Meitingsunes* and present a key to species in this genus.

Key words: Acari, Columbiformes, ectoparasites, *Meitingsunes*, quill mites, Syringophilidae

Introduction

The genus *Meitingsunes* Glowska and Skoracki, 2010 (Acari: Prostigmata: Syringophilidae) includes species mostly associated with birds of the order Columbiformes (Kaszewska *et al*. 2014; Glowska *et al*. 2015), with one species *M. caprimulgus* Skoracki *et al*., 2015 recorded on a bird from a different order—Caprimulgiformes, probably an example of host switching (Skoracki *et al*. 2015). The systematic diversity of this genus is still poorly known and currently only four species have been described from columbiform birds: *M. aldwelles* Glowska and Skoracki, 2010, *M. columbicus* Skoracki, 2011, *M. tympanistria* (Skoracki and Dabert, 2002), and *M. zenadourae* (Clark, 1964). They have been recorded from the five columbid genera (*Columba*, *Geotrygon*, *Treron*, *Turtur*, *Zenaida*) distributed in Afrotropical, Nearctic, Neotropical and Palaearctic regions (Clark 1964; Casto 1976; Bochkov & Mironov 1998; Skoracki & Dabert 2002; Skoracki & Sikora 2002, Glowska & Skoracki 2010; Skoracki 2011; Kaszewska *et al*. 2014; Skoracki *et al*. 2015) (see Table 1).

In this paper, we describe two new quill mites species of the genus *Meitingsunes* collected from three columbid host species from Indonesia.

Material and methods

The mite material used in this study was collected from dry bird skins housed in the ornithological collection of the Bavarian State Collection of Zoology, Munich, Germany according to the methodology presented in Skoracki (2011). Identification of mite specimens and the making of drawings were carried out with a ZEISS Axioscope™ light microscope with DIC optics and camera lucida. In the descriptions below, the idiosomal setation follows Grandjean (1939) as adapted for Prostigmata by Kethley (1990). The nomenclature of leg chaetotaxy follows that proposed by Grandjean (1944). The morphological terminology follows Skoracki (2011). All measurements are in micrometres (µm). Measurement ranges for paratypes are given in parentheses following the data for a holotype. Scientific names of the birds follow Clements *et al*. (2014).

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Specimen depositories are cited using the following abbreviations: AMU—A. Mickiewicz University, Department of Animal Morphology, Poznan, Poland; ZSM—Bavarian State Collection of Zoology, Munich, Germany.

TABLE 1. Quill mite species of the genus *Meitingsunes* Glowska and Skoracki with their hosts and geographical distribution; *—type host.

Mite species	Host species	Distribution	References
M. aldwelles Glowska and Skoracki, 2010	*Geotrygon frenata* (Tschudi)	Colombia	Glowska & Skoracki 2010
M. caprimulgus Skoracki *et al*., 2015	*Chordeiles minor* (Forster)	Colombia	Skoracki *et al*. 2015
M. chalcophaps **sp. nov.**	*Chalcophaps indica* (Linnaeus)	Indonesia	present paper
M. columbicus Skoracki, 2011	*Columba livia* Gmelin	Poland	Skoracki 2011
"	*Columba oenas* Linnaeus*	Kazakhstan	Skoracki 2011
"	*Columba palumbus* Linnaeus	Russia	Skoracki 2011
"	*Treron waalia* (Meyer)	Cameroon	Kaszewska *et al*. 2014
M. turacoenas **sp. nov.**	*Turacoena manadensis* (Quoy and Gaimard)*	Indonesia	present paper
"	*Turacoena modesta* (Temminck)	Indonesia	present paper
M. tympanistria (Skoracki and Dabert, 2002)	*Turtur tympanistra* (Temminck)	Togo	Skoracki & Dabert 2002
M. zenadourae (Clark, 1964)	*Columba liva* Gmelin	USA, N. Africa	Casto 1976; Bochkov & Mironov 1998
"	*Zenaida asiatica* (Linnaeus)	USA	Clark, 1964
"	*Zenaida auriculata* (De Murs)	Argentina	Skoracki & Sikora 2002
"	*Zenaida macroura* (Linnaeus)*	USA	Clark 1964

Systematics

Family Syringophilidae Lavoipierre

Subfamily Syringophilinae Lavoipierre

Genus *Meitingsunes* Glowska and Skoracki, 2010

Meitingsunes chalcophaps sp. nov.
(Figs. 1, 2, 3A–F)

Description. FEMALE, holotype. Total body length 715 (615–720 in 4 paratypes). *Gnathosoma*. Infracapitulum apunctate. Length of stylophore 190 (160–190) with visible striae. Each medial branch of peritremes with 3 chambers, each lateral branch with 6–7 chambers. *Idiosoma*. Propodonotal shield weakly sclerotized, reduced to 2 medial triangular shields with indiscernible margins. Length ratio of setae *ve*:*si*:*c1* 1:2.4–2.7:3.6–4.5. Bases of setae *se* situated slightly posterior to level of setae *c1*. Hysteronotal shield small, triangular, bearing bases of setae *d1*. Hysteronotal setae *d2*, *d1*, and *e2* subequal in length. Pygidial shield well sclerotized in posterior part, punctate between bases of setae *f1* and *f2*, anterior margin indiscernible. Setae *f2* 6.5–7.8 times longer than setae *f1*. Coxal fields I–IV well sclerotized, apunctate. Bases of setae *3a* situated out of coxal fields III. Setae *3c* 1.2–1.7 times longer than *3b*. Genital plate absent. Length ratio of setae *ag1*:*ag2*:*ag3* 3.1:1:2.5–3.4. Genital setae (*g1–2*) subequal in length and twice as long as pseudanal setae (*ps1–2*). *Legs*. Length ratio of setae *l'RII*:*l'RIII*:*l'RIV* 1:1.5:1.3–1.4. Podomeres of legs apunctate. Setae *tc"III–IV* 1.7–2.7 times longer than *tc'III–IV*. Fan-like setae *p'* and *p"* of legs III and IV multiserrate, each with ca. 20 tines. *Lengths of setae*: *ve* 65 (60–75), *si* 180 (165–180), *se* 215 (185–215), *c1* (275), *c2* (190–195), *d1* 180 (180–200), *d2* 215 (210–215), *e2* 180 (180–215), *f1* 30 (30), *f2* 195 (195–235), *h1* (35), *h2* 280 (270–290), *ag1* (155), *ag2* 50 (50), *ag3* (140–170), *g1* and *g2* 30 (30–35), *ps1* and *ps2* 15 (15), *tc'III–IV* 30 (20–35), *tc"III–IV* 55 (55–60), *l'RII* 35 (30–35), *l'RIII* 55 (45–55), *l'RIV* 50 (40–50), *3b* 65 (45–75), *3c* 95 (80–95).

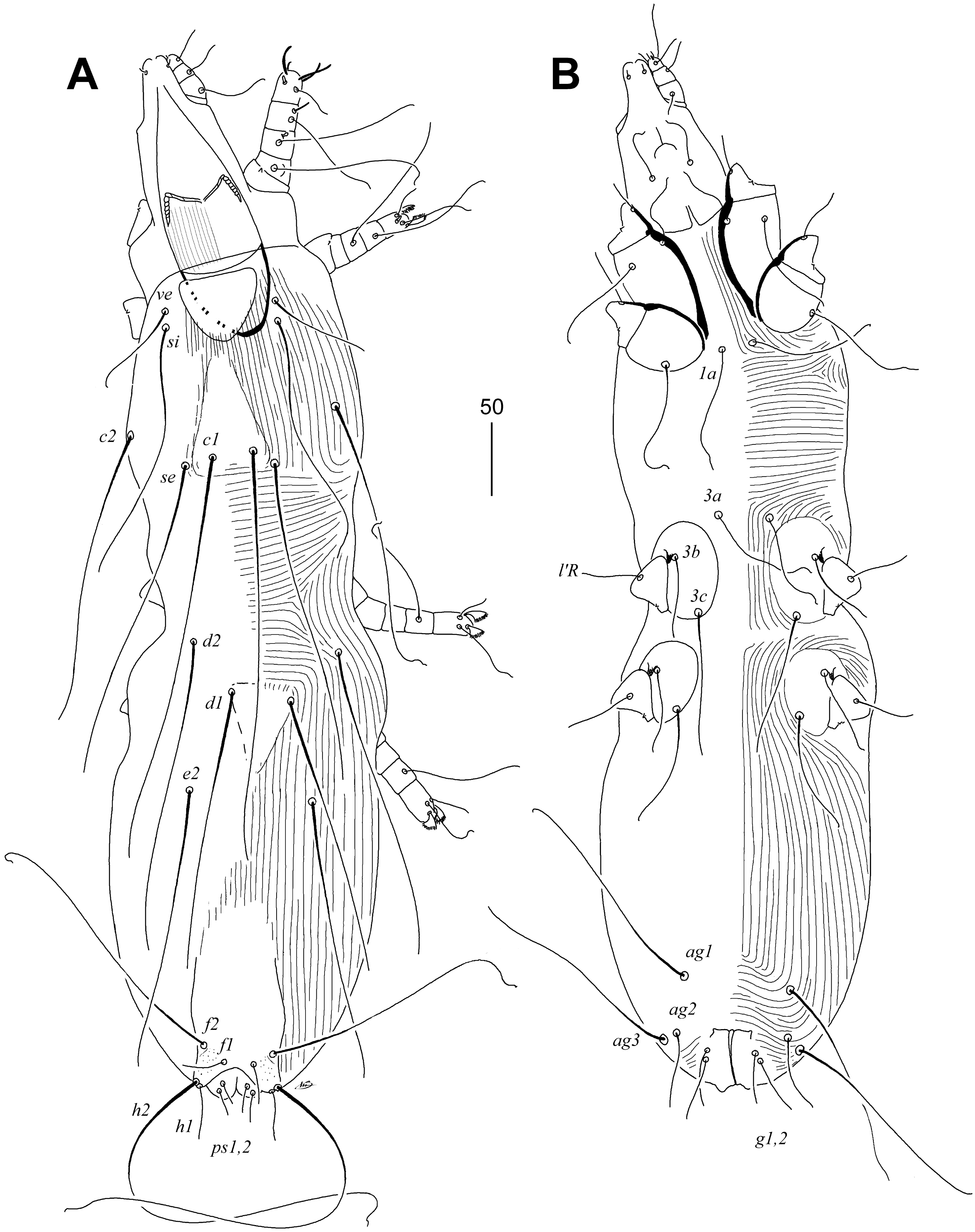

FIGURE 1. *Meitingsunes chalcophaps* **sp. nov.**, female. **A,** dorsal view; **B,** ventral view.

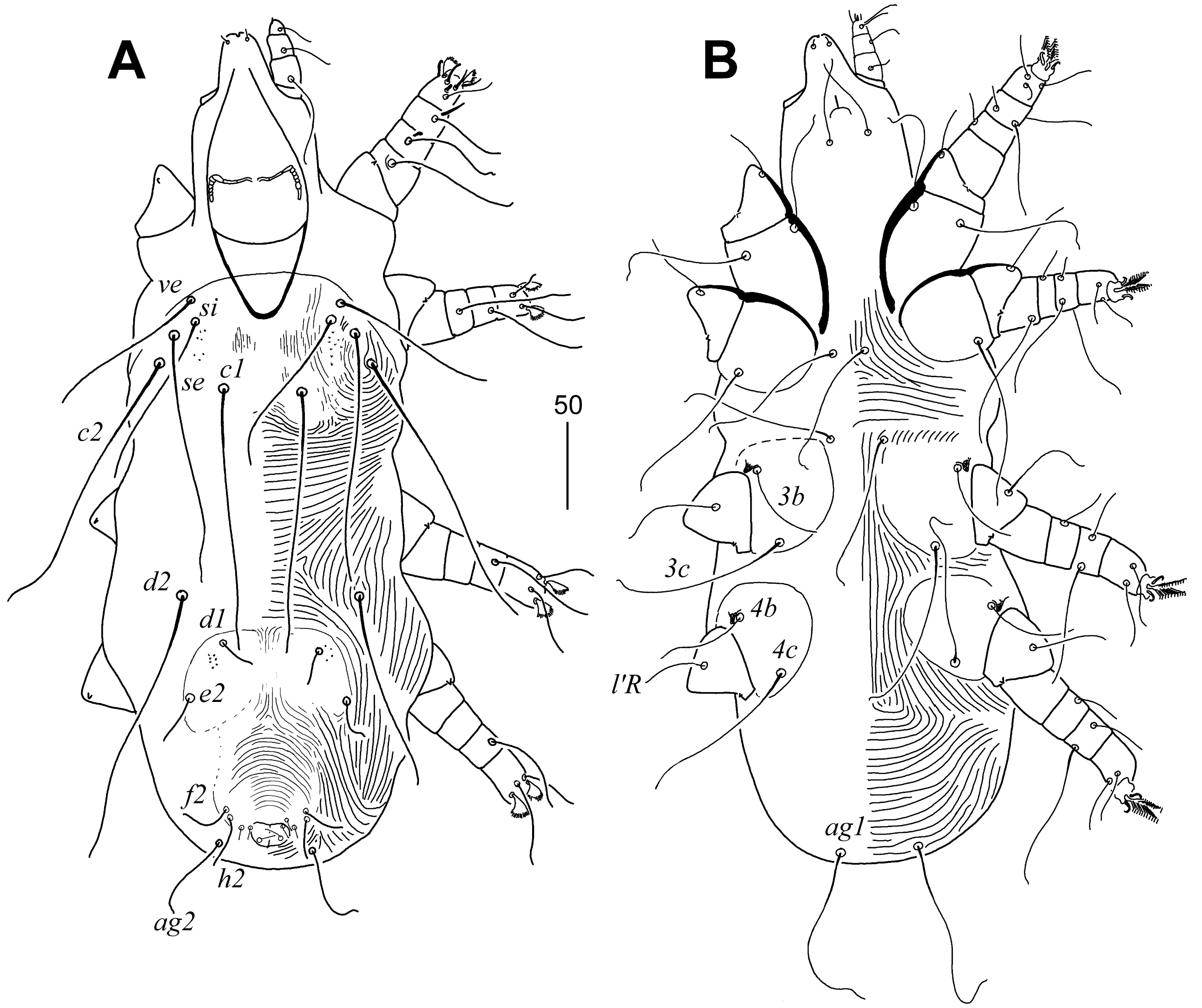

FIGURE 2. *Meitingsunes chalcophaps* **sp. nov.**, male. **A,** dorsal view; **B,** ventral view.

MALE. Total body length 465–500 in 2 paratypes. *Gnathosoma*. Each medial branch of peritremes with 3–4 chambers, each lateral branch with 5–6 chambers. Stylophore 160 long. *Idiosoma*. Propodonotal shield weakly sclerotized, all margins indiscernible, punctate below bases of setae *si*. Bases of setae *se* situated distinctly anterior to level of setae *c1*. Length ratio of setae *ve*:*si*:*c1* 1:1:1.2–1.5. Hysteronotal shield with indiscernible medial part, bearing bases of setae *d1* and *e2*, punctate near bases of setae *d1*. Length ratio of setae *d2*:*d1*:*e2* 4.8–6.4:1:1.2. Setae *f2* and *h2* subequal in length. Agenital setae *ag1* 2.1–2.3 times longer than *ag2*. Coxal fields of legs I–IV apunctate. Setae *3c* 1.2–1.6 times longer than *3b*. *Legs*. Podomeres of legs I–IV apunctate. Setae *l'RII–IV* subequal in length. Setae *tc"III–IV* 2–2.6 times longer than *tc'*III–IV. *Lengths of setae*: *ve* 90–120, *si* 100–120, *se* 120–150, *c1*140–150, *c2* 165 150–165, *d1* 25, *d2* 120–160, *e2* 30, *f2* 25–30, *h2* 30, *ag1* 105–115, *ag1* 50, *tc'III–IV* 15, *tc"III–IV* 30–40, *l'RII* 30–40, *l'RIII* 40, *l'RIV* 35–40, *3b* 70–80, *3c* 100–115.

Type material. Female holotype, 4 female and 2 male paratypes (Reg. No. AMU-SYR.526) from lesser covert quill of *Chalcophaps indica* (Linnaeus) (Columbiformes: Columbidae), **INDONESIA**: West Timor, 4 July 1911, coll. C. B. Haniel.

Types deposition. All type material is deposited in the AMU, except 1 female paratype in the ZSM.

Differential diagnosis. *Meitingsunes chalcophaps* **sp. nov.** is morphologically similar to *M. zenadourae* (Clark, 1964) described from *Zenaida macroura* (Columbidae) in the USA. In females of both species, each lateral branch has six chambers; all coxal fields are apunctate, and bases of setae *3a* are situated off coxal fields III. This new species differs from *M. zenadourae* by the following features: in females of *M. chalcophaps*, the propodonotal shield is divided into two triangular sclerites, bases of setae *ve*, *si*, and *se* are situated off the propodonotal shield;

the hysteronotal shield is reduced to a single, triangular sclerite, bearing bases of setae *d1*; the pygidial shield is punctate near bases of setae *f2* and *f1*. In females of *M. zenadourae*, the propodonotal shield is entire and rectangular in shape, bearing bases of setae *ve*, *si* and *se*; the hysteronotal shield is divided into three sclerites—two lateral, oval sclerites surrounding bases of setae *d2* and an unpaired rectangular sclerite situated between bases of setae *d1*; central part of the pygidial shield is punctate.

Etymology. The name "*chalcophaps*" is taken from the generic name of the host.

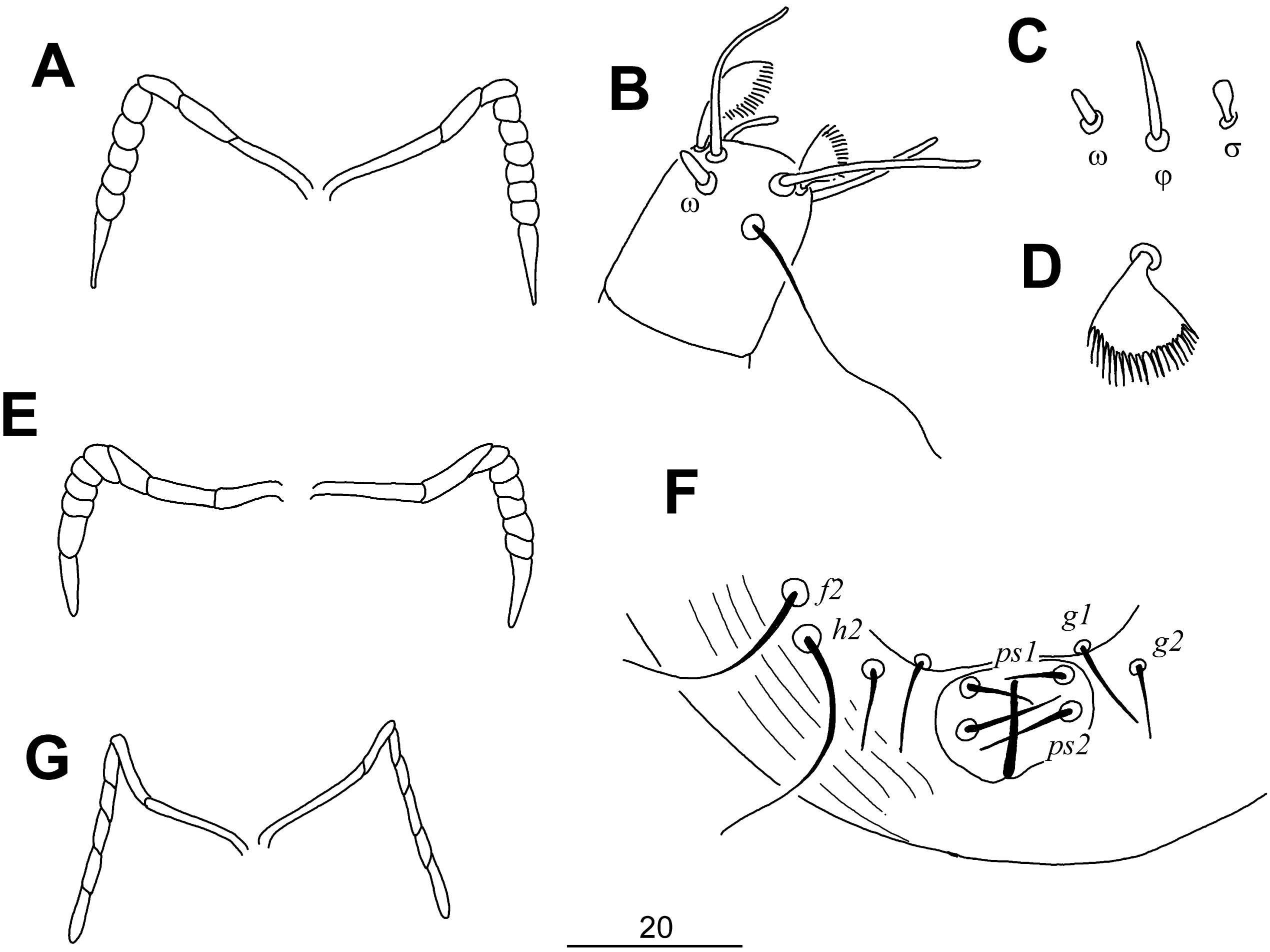

FIGURE 3. *Meitingsunes* spp. *M. chalcophaps* **sp. nov.**, female (**A–D**): **A,** peritremes; **B,** tarsus I in dorsal view; **C,** solenidia of leg I; **D,** fan-like seta *p'III*; male (**E, F**): **E,** peritremes; **F,** genito-anal region. *M. turacoenas* **sp. nov.**, female (**G**): **G,** peritremes.

Meitingsunes turacoenas sp. nov.

(Figs. 3G, 4)

Description. FEMALE, holotype. Total body length 560 (485–580 in 7 paratypes). *Gnathosoma*. Infracapitulum apunctate. Each medial branch of peritremes with 2–3 chambers, each lateral branch with 5–6 chambers. Length of stylophore 170 (170). *Idiosoma*. Propodonotal shield weakly sclerotized, divided into unpaired medial shield bearing bases of setae *c1* and 2 lateral sclerites bearing bases of setae *ve* and *si*. Length ratios of setae *ve*:*si*:*c1* and *d2*:*d1*:*e2* 1:2.4–3.1:4.5–5.4 and 1.2–1.3:1:1, respectively. Hysteronotal shield absent. Pygidial shield well sclerotized, punctate, with deeply concave anterior margin. Setae *f2* 8.4–9.6 times longer than setae *f1*. Coxal fields I–IV well sclerotized, sparsely punctate. Bases of setae *3a* situated off coxal fields III. Setae *3c* 1.4–2 times longer than *3b*. Genital plate absent. Length ratio of setae *ag1*:*ag2*:*ag3* 2.3–2.5:1:3–3.4. Genital setae *g1–2* subequal in length. Pseudanal setae *ps1–2* subequal in length. *Legs*. Setae *l'RII–l'RIV* subequal in length. Podomeres of legs III–IV punctate. Setae *tc"III–IV* 1.3–1.5 times longer than *tc'III–IV.* Fan-like setae *p'* and *p"* multiserrate, each with about 20 tines. *Lengths of setae*: *ve* 50 (50–55), *si* 130 (115–130), *se* 200 (200–225), *c1* 200 (195–225), *c2* 220

(220–240), *d1* 175 (170–195), *d2* 170 (150–210), *e2* 180 (165–180), *f1* 30 (25–30), *f2* 200 (190–225), *h1* 25 (25–30), *h2* 320 (290–320), *ag1* 105 (90–105), *ag2* 40 (40), *ag3* 150 (150–195), *g1* and *g2* 20 (20–25), *ps1* and *ps2* 15 (15) *tc'III–IV* 35 (30–40), *tc"III–IV* 55 (35–55), *l'RII* 30 (25–30), *l'RIII* 40 (30–40), *l'RIV* 40 (35–40), *3b* 40 (30–45), *3c* 90 (90–95).

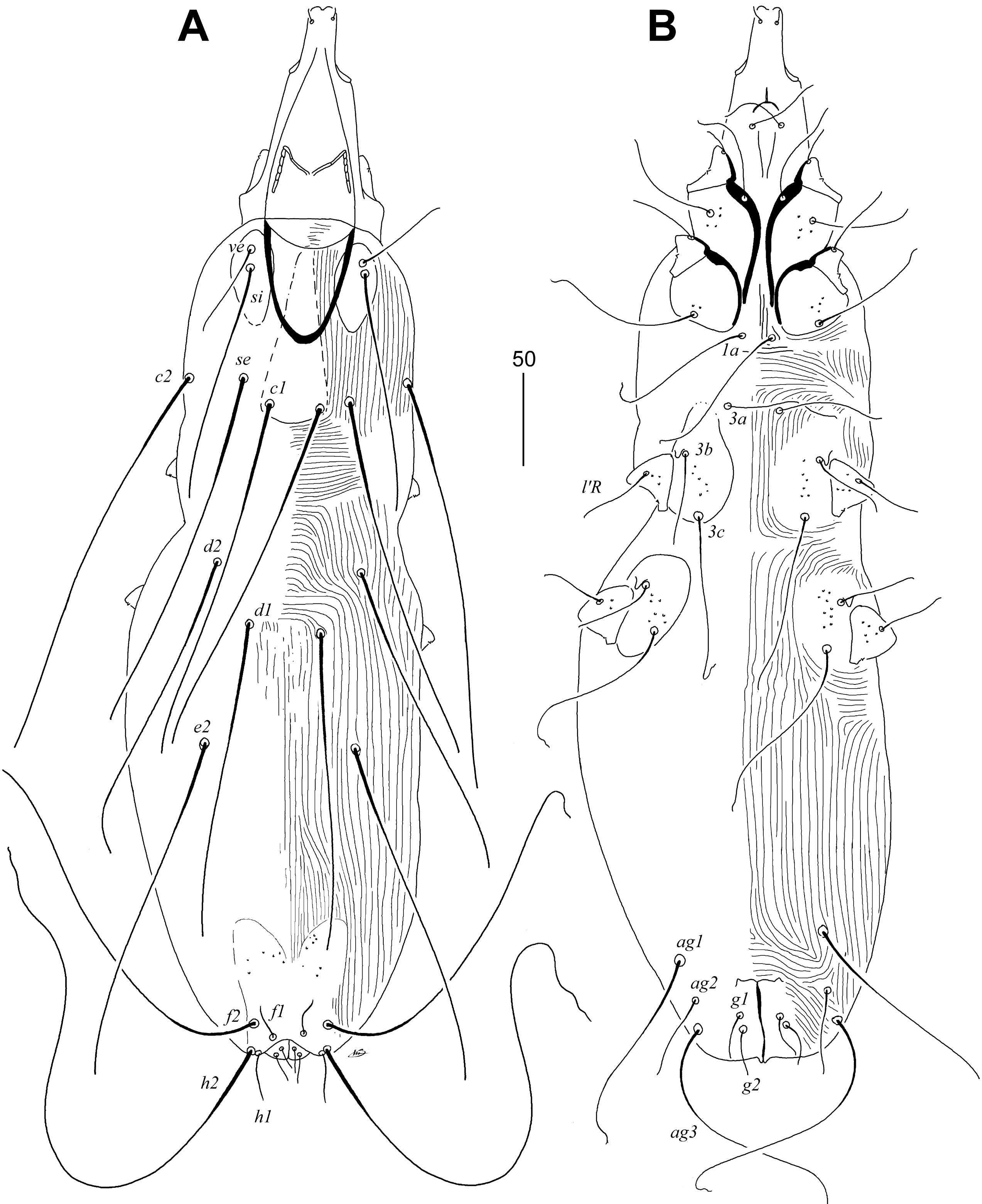

FIGURE 4. *Meitingsunes turacoenas* **sp. nov.**, female. **A,** dorsal view; **B,** ventral view.

MALE. Unknown.

Type material. Female holotype and 7 female paratypes (Reg. No. AMU-SYR.524) from lesser covert quill of *Turacoena manadensis* (Quoy and Gaimard) (Columbiformes: Columbidae), **INDONESIA**: Sulawesi Isl., Manado, coll. Frank.

Types deposition. All type material is deposited in the AMU, except 1 female paratype in the ZSM.

Additional material. Four females (Reg. No. AMU-SYR.525) from lesser covert quill of *Turacoena modesta* (Temminck) (Columbidae), **INDONESIA**: West Timor, 5 July 1911, coll. C. B. Haniel. All specimens deposited in the AMU, except 1 female in the ZSM.

Differential diagnosis. *Meitingsunes turacoenas* **sp. nov.** is morphologically similar to *M. columbicus* Skoracki, 2011 described from *Columba oenas* (Columbiformes: Columbidae) from Kazakhstan (Skoracki 2011). In females of both species, the peritremes have the same number of chambers in each of medial (three chambers) and lateral (4–5) branches. This new species differs from *M. columbicus* by the following features: in females of *M. turacoenas*, bases of setae *3a* are situated off coxal fields III; the hysteronotal shield is absent; the pygidial shield is sparsely punctate and with deeply concave anterior margin. In females of *M. columbicus*, bases of setae *3a* are situated on coxal fields III; the hysteronotal shield is represented by a long narrow shield that is fused with the apunctate pygidial shield.

Etymology. The name "*turacoenas*" is taken from the generic name of the host.

Key to species of the genus *Meitingsunes*

(Females)

1. Hysteronotal shield absent, coxal fields I–IV punctate. . . . . *M. turacoenas* **sp. nov.**
- Hysteronotal shield present, coxal fields I–IV apunctate 2
2. Setae *f1* twice as long as *h1*. . . . . *M. aldwelles* Glowska and Skoracki, 2010
- Setae *f1* and *h1* subequal in length or *f1* 1.7–2 times shorter than *h1* 3
3. Body length less than 600µm, length of setae *ve* 20–30, *si* 70–100, *se* 130–150 . . . . *M. caprimulgus* Skoracki e*t al*. 2015.
- Body length more than 600µm, length of setae *ve* 50–120, *si* 130–190, *se* 185–260. 4
4. Propodonotal shield entire and punctate; bases of setae *ve* and *si* situated on propodonotal shield. 5
- Propodonotal shield divided into 2 triangular sclerites, apunctate; bases of setae *ve* and *si* situated off propodonotal shield. . . . . *M. chalcophaps* **sp. nov.**
5. Bases of setae *3a* situated on coxal fields III . . . . *M. columbicus* Skoracki, 2011
- Bases of setae *3a* situated off coxal fields III 6
6. Hysteronotal shield represented by 3 sclerites, medial fused to punctate pygidial shield . . . . *M. zenadourae* (Clark, 1964)
- Hysteronotal shield represented by unpaired sclerites not fused to pygidial shield . . . . *M. tympanistria* (Skoracki and Dabert, 2002)

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III

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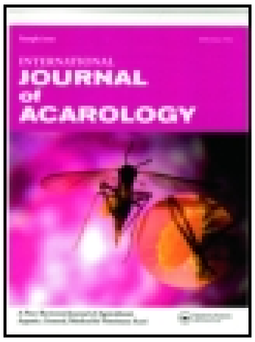

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A review of the quill mites of the genus *Gunabopicobia* Skoracki and Hromada (Acariformes: Prostigmata: Syringophilidae) associated with birds of the order Columbiformes

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ABSTRACT

Gunabopicobia Skoracki and Hromada, 2013, the only genus of the subfamily Picobiinae Johnston and Kethley, 1973, associated exclusively with birds of the order Columbiformes is reviewed. Five new species are described: *G. lathami* **sp. nov**. ex *Leucosarcia melanoleuca* (Latham) from Australia and ex *Caloenas nicobarica* (Linnaeus) from Papua New Guinea and Indonesia; *G. leptotila* **sp. nov**. ex *Leptotila verreauxi* Bonaparte from Argentina; *G. claravis* **sp. nov**. ex *Claravis pretiosa* (Ferrari-Pérez) from Colombia; *G. geotrygoni* **sp. nov**. ex *Geotrygon linearis* (Prévost) from Venezuela, ex *G. chrysie* Bonaparte from Martinique, ex *G. frenata* (Tschudi) from Colombia, and ex *G. montana* (Linnaeus) from Paraguay, and *G. metriopelia* **sp. nov**. ex *Metriopelia melanoptera* (Molina) from Argentina. Based on the shape of the propodonotal shield and the coalescence of the setal bases *1a*, we established two species groups in the genus *Gunabopicobia: zumpti* and *metriopelia*. Additionally, we constructed a key to all species of the genus and discussed the host–parasite relationships between *Gunabopicobia* species and columbiform birds.

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Acari; doves and pigeons; ectoparasites; Picobiinae; host specificity

Introduction

Syringophilid mites (Acariformes: Prostigmata: Cheyletoidea) are highly specialized ectoparasites of birds inhabiting quill feathers where they live and reproduce (Kethley 1970, 1971). These mites feed on the live tissue fluid of their hosts by piercing quill wall of the calamus with their long and flexible chelicerae (Kethley 1971; Skoracki 2011). Syringophilid mites are represented by two subfamilies: Syringophilinae Lavoipierre, 1953 with 292 species and Picobiinae Johnston and Kethley, 1973 with 85 species. Currently, representatives of these both subfamilies have been recorded on birds from 24 orders (Zmudzinski and Skoracki 2017).

Mites of the subfamily Picobiinae occupy exclusively quills of the contour feathers with one exception to this rule – *Calamincola lobatus* Casto, 1977 – a representative of the enigmatic and monotypic genus that is found in the quills of wing feathers (see Skoracki et al. 2016). Picobines are associated with neognathous birds (Aves: Neognathae) belonging to ten orders. The fauna of the subfamily Picobiinae associated with birds of the order Columbiformes is still poorly recognized. Until now, only two species of the genus *Gunabopicobia* Skoracki and Hromada, 2013 have been described: *G. zumpti* (Lawrence, 1959) from birds of the genera *Columba, Streptopelia, Zenaida*, and *G. masalaje* Kaszewska et al. 2014 from birds of the genera *Ducula* and *Ptilinopus* (Skoracki and Hromada 2013; Kaszewska et al. 2014; Skoracki et al. 2016).

In the present paper, we describe five new species of the genus *Gunabopicobia* inhabiting quills of contour feathers of columbiform birds: *G. lathami* **sp. nov**. from *Leucosarcia melanoleuca* (Latham) and *Caloenas nicobarica* (Linnaeus); *G. leptotila* **sp. nov**. from *Leptotila verreauxi* Bonaparte; *G. claravis* **sp. nov**. from *Claravis pretiosa* (Ferrari-Pérez); *G. geotrygoni* **sp. nov**. from *Geotrygon linearis* (Prévost), *G. chrysie* Bonaparte, *G. frenata* (Tschudi), and *G. montana* (Linnaeus), all of them placed in the newly established *zumpti*-species-group, and *G. metriopelia* **sp. nov**. from *Metriopelia melanoptera* (Molina) placed in the *metriopelia*-species-group. Additionally, we recorded the new hosts from the genera *Streptopelia* and *Patagioenas* for previously described species *G. zumpti* (Lawrence, 1959). A key to species is constructed and the host–parasite relationship in the system composed of *Gunabopicobia* mites and columbiform birds is discussed.

Material and methods

The new material used in the present study was collected from dry bird skins housed in the ornithological collections housed in the Bavarian State Collection of Zoology, Munich, Germany (ZSM) and National Museum of Kenya, Nairobi, Kenya (NMK). Quills of contour feathers were examined using a dissecting microscope, and opened with a fine scalpel. Before mounting, mites were softened and cleared in Nesbitt's solution at room temperature for three days (see Skoracki 2011). Then, mites were mounted on slides in Hoyer's medium. The remaining material was loaned from acarological collections (listed below).

Identifications and drawings of mite specimens were carried out with a light microscope an Olympus BH-2 (Olympus Corp., Japan), equipped with DIC optics and a camera lucida. All measurements are given in micrometres. Measurements (ranges) of paratypes are given in brackets following data for a holotype.

In the descriptions below, the idiosomal chaetotaxy follows Grandjean (1939) as adapted for Prostigmata by Kethley (1990). The nomenclature of leg setae follows that proposed by Grandjean (1944). Morphological terminology follows Skoracki (2011).

The abbreviations NPF and PF are for non-physogastric and physogastric form of females, respectively.

The scientific names of the birds follow Clements et al. (2017). Host specificity for particular mite species follows Caira et al. (2003) and Skoracki et al. (2016). Zoogeographic regions follow Holt et al. (2013).

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Specimen depositories are cited using the following abbreviations: AMU – A. Mickiewicz University, Department of Animal Morphology, Poznan, Poland; FMNH – Field Museum of Natural History, Chicago, USA; NMK – National Museum of Kenya, Nairobi, Kenya; NMSA – Natal Museum, Pietermaritzburg, South Africa; ZSM – Bavarian State Collection of Zoology, Munich, Germany; RMCA – Royal Museum of Central Africa, Tervuren, Belgium.

Bipartite networks and statistics

To visualize pattern in studied parasite–host ecological web, we used "bipartite" package for R (Dormann et al. 2008). A parasite prevalence was used as quantitative indices.

Descriptive statistics was computed using Quantitative Parasitology on the Web (Rózsa et al. 2000; Reiczigel et al. 2013).

Visualization of host phylogeny

To visualize host phylogeny, a tree of the columbiform species was constructed based on consensus avian phylogenetic tool available at http://birdtree.org/ (Jetz et al. 2012). As the source of our consensus tree we used 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 (Drummond and Rambaut 2007). The consensus tree was then graphically adjusted in FigTree v1.4.2 (Andrew Rambaut, University of Edinburgh, UK; http://tree.bio.ed.ac.uk/software/figtree/).

Results

Systematics

Family Syringophilidae Lavoipierre, 1953
Subfamily Picobiinae Johnston and Kethley, 1973

Genus *Gunabopicobia* Skoracki and Hromada, 2013
Gunabopicobia Skoracki and Hromada, 2013: 197.

Type species: *Picobia zumpti* Lawrence, 1959 by original designation.

Diagnosis

Female. Hypostomal apex hilly. Peritremes V- or U-shaped. Setae *vi* situated anterior to level of setae *ve*. Propodonotal shield entire (*metriopelia* species-group) or divided into two wide lateral shields bearing bases of setae *vi, ve, si*, and *se*, and large unpaired medial shield bearing bases of setae *c1* (*zumpti* species-group). Opisthonotal and genital lobes absent. Pseudanal setal series represented by two pairs. Genital setae absent. Apodemes I without thorn-like protuberances. Legs with full complement of solenidia. Physogastric form with distinctly enlarged idiosoma, worm-shaped in outline.

Male. Features as in females except: peritremes M-shaped; propodonotal shield entire, bearing bases of all propodonotal setae except *c2*; genital setal series represented by two pairs.

Species included. *G. geotrygoni* **sp. nov.**, *G. masalaje* Kaszewska, Kavetska and Skoracki, 2014; *G. metriopelia* **sp. nov.**, *G. lathami* **sp. nov.**, *G. claravis* **sp. nov.**, *G. leptotila* **sp. nov.**, and *G. zumpti* (Lawrence, 1959).

Host range. This genus is restricted to birds of the order Columbiformes and its representatives were recorded on the following host genera: *Caloenas, Claravis, Columba, Ducula, Geotrygon, Leptotila, Leucosarcia, Metriopelia, Patagioenas, Ptilinopus, Streptopelia*, and *Zenaida*.

Distribution. Afrotropical (Dem. Rep. Congo, Central Africa, Ethiopia, South Africa, Tanzania), Australian (Australia), Nearctic (USA, Martinique), Neotropical (Argentina, Colombia, Paraguay, Venezuela), Oceanian (Indonesia, Papua New Guinea), and Palaearctic (Poland, Macedonia) regions (see Table 1).

Habitat. Members of this genus occupy exclusively quills of contour feathers.

Remark. Based on the shape of the propodonotal shield and the coalescence of the setal bases *1a*, we established two species groups in this genus: *zumpti* and *metriopelia*.

zumpti species group

Diagnosis

Female. Propodonotal shield divided onto three sclerites. Bases of setae *1a* coalesced.

Gunabopicobia lathami **sp. nov.**

Description

Female (PF), holotype. (Figure 1(a–e)). Total body length 1440 µm (1415 in 1 paratype). *Gnathosoma*. Infracapitulum apunctate.

Table 1. Quill mite species of the genus *Gunabopicobia* Skoracki and Hromada, 2013 with their hosts and distribution.

Mite species	Hosts species	Distribution	References
G. claravis **sp. nov.**	*Claravis pretiosa* (Ferrari-Perez)	Colombia	This study
G. geotrygoni **sp. nov.**	*Geotrygon linearis* (Prevost)	Venezuela	This study
"	*Geotrygon chrysia* Bonaparte	Martinique	This study
"	*Geotrygon frenata* (Tschudi)	Colombia	This study
"	*Geotrygon montana* (Linnaeus)	Paraguay	This study
G. masalaje Kaszewska et al. 2014	*Ducula bicolor* (Scopoli)	Indonesia	This study
"	*Ducula rufigaster* (Quoy and Gaimard)	Papua New Guinea	Kaszewska et al. 2014
"	*Ducula rosacea* (Temminck)	Indonesia (Semau Isl.)	Kaszewska et al. 2014
"	*Ducula pistrinaria* Bonaparte	Papua New Guinea	Kaszewska et al. 2014
"	*Ducula spilorrhoa* (Gray)	Indonesia (Semau Isl.)	Kaszewska et al. 2014
"	*Ducula luctuosa* (Temminck)	Papua New Guinea	Kaszewska et al. 2014
"	*Ptilinopus iozonus* Gray	Papua New Guinea	Kaszewska et al. 2014
G. metriopelia **sp. nov.**	*Metriopelia melanoptera* (Molina)	Argentina	This study
G. lathami **sp. nov.**	*Leucosarcia melanoleuca* Gould	Australia	This study
"	*Caloenas nicobarica* (Linnaeus)	Indonesia, Papua New Guinea	This study
G. leptotila **sp. nov.**	*Leptotila verreauxi* (Bonaparte)	Argentina	This study
G. zumpti (Lawrence 1959)	*Columba livia* Gmelin	USA, Poland	Bochkov et al. 2005; Skoracki et al. 2016
"	*Columba speciosa* Gmelin	North Brazil	This study
"	*Columba delegorquei* Delegorgue	Tanzania	This study
"	*Patagioenas picazuro* (Temminck)	West Brazil	This study
"	*Streptopelia capicola* (Sundevall)	South Africa	Lawrence 1959
"	*Streptopelia senegalensis* (Linnaeus)	South Africa	Skoracki and Hromada 2013
	Streptopelia semitorquata (Ruppell)	Ethiopia	This study
"	*Zenaida macroura* (Linnaeus)	USA	Skoracki 2014

Each medial branch of peritremes with 5–6 chambers, each lateral branch with 7–8 chambers (Figure 1(c)). Stylophore 250 (260–265) long, punctate only in antero-lateral parts. *Idiosoma*. Each lateral shield of propodonotum punctate and with belt-like sclerotization; large medial shield apunctate. Bases of setae *c1* situated slightly anterior to level of setal bases *se*. Bases of setae *f2* situated anterior to level of setal bases *f1*. Coxal fields I sparsely punctate, II–IV apunctate. Posterior end of apodemes II distinctly extending beyond coxal fields II (Figure 1(b)). *Lengths of setae: vi* (65–85), *ve* 130 (130–140), *si* 130 (120–140), *se* 280 (280–310), *c1* 260 (240), *c2* 305 (280–340), *d1* 235 (210–225), *d2* 245 (235–240), *e2* 90 (90), *f1* 35, *f2* 30 (35), *h1* 50 (45), *ag1* 135, *ag2* 20 (25), *ag3* 140, *ps1* 20 (20), *ps2* 25 (25), *tc'III–IV* 55 (55–65), *tc"III–IV* 60 (55–60), *3b* 30 (30–35), *3c* 120 (110–130). *Length ratios of setae: vi:ve:si* 1:1.5–2.1:1.6–1.8, *f1:f2* 1:1, *f1:h1* 1:1.4, *ag1:ag2:ag3* 6.7:1:7.

Male. Not found.

Type material

Female holotype (PF) and two female paratypes (PF) from Wonga Pigeon *Leucosarcia melanoleuca* (Latham) (Columbiformes: Columbidae), AUSTRALIA: no other data. This bird species is distributed in the Coastal forests of the Australia (from central Queensland to S.E. Victoria (Clements et al. 2017).

Types deposition

The type material is deposited in the AMU (Reg. No. AMU-SYR.557), except 1 female paratype in the ZSM (Reg. No. ZSM 20112068).

Additional material

Ex Nicobar Pigeon *Caloenas nicobarica* (Linnaeus) (Columbidae), PAPUA NEW GUINEA: East New Britain Province, Gezelle, Kambaira, coll. Hall; two females (PF) deposited in the AMU (Reg. No. AMU-SYR.558A) and one female in ZSM (Reg. No. ZSM 20112069). Same host species, INDONESIA: Borneo, Pulau Pejantan, 10 April 1907, coll. Bruegel; 1 female (PF) in the AMU (Reg. No. AMU-SYR.558B).

Differential diagnosis

G. lathami **sp. nov**. is morphologically similar to *G. masalaje* Kaszewska, Kavetska and Skoracki, 2014. In females of both species, the infracapitulum and the medial shield of the propodonotum are apunctate, and each medial branch of the peritremes has five or six chambers. This new species differs from *G. masalaje* by the following features: in females of *G. lathami*, the stylophore is punctate in antero-lateral parts; each lateral branch of the peritremes has seven or eight chambers; posterior end of the apodemes II are extended beyond coxal field II; and coxal fields I are sparsely punctate. In females of *G. masalaje*, the stylophore is apunctate; each lateral branch of the peritremes has five or six

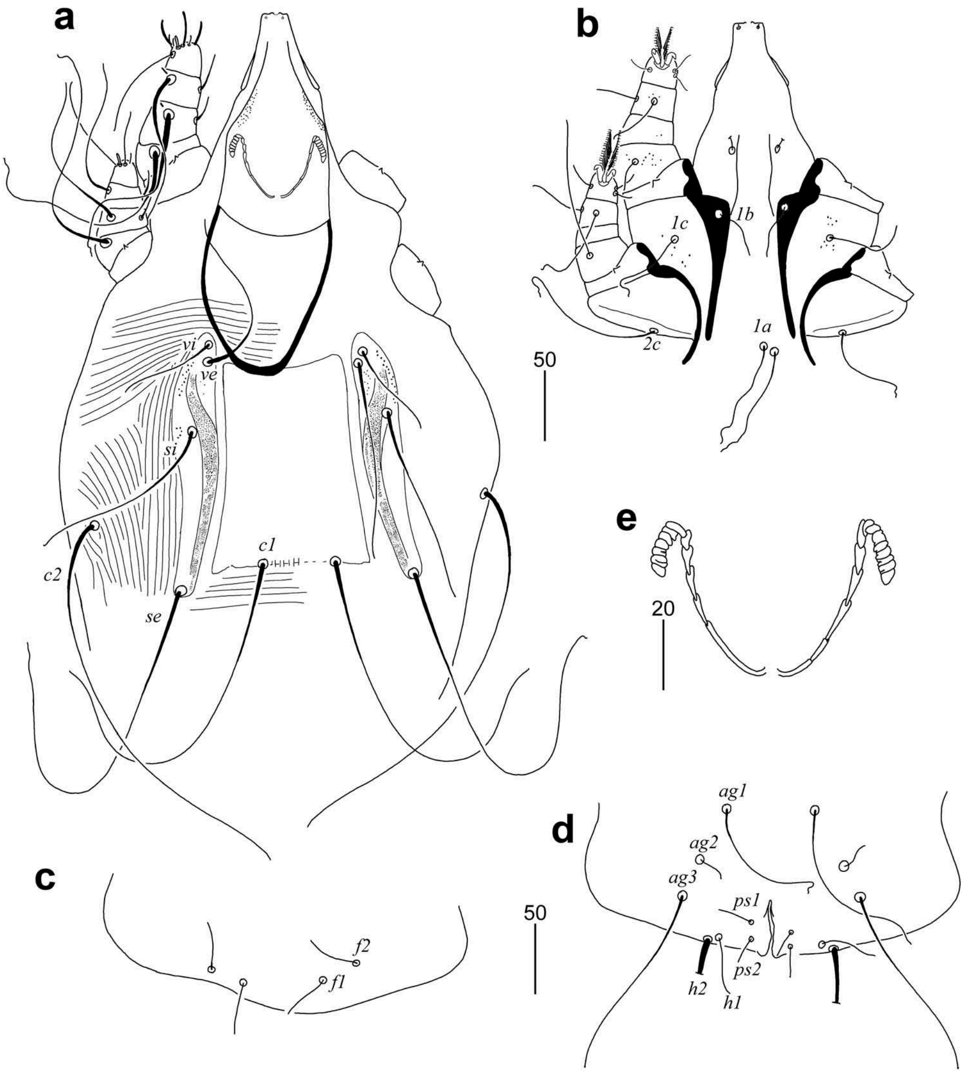

Figure 1. *Gunabopicobia lathami* **sp. nov**. female: (A) anterior part of the body in dorsal view; (B) anterior part of the body ventral view; (C) opisthosoma in dorsal view; (D) opisthosoma in ventral view; (E) peritremes.

chambers; posterior end of the apodemes II are not extended beyond coxal fields II; and coxal fields I are apunctate.

Etymology

This species is named in the honour of an English naturalist, called also as the "grandfather" of Australian ornithology – John Latham (1740–1837).

Gunabopicobia leptotila sp. nov.

Description

Female (NPF), holotype. (Figure 2(a–c)). Total body length 680 (750 in 1 paratype). *Gnathosoma*. Infracapitulum and stylophore densely punctate. Each medial branch of peritremes with 4–5 chambers, each lateral branch with 10–11 chambers (Figure 2(c)). Stylophore 200 long. *Idiosoma*. Each lateral shield of propodonotum punctate and with belt-like sclerotization; medial shield punctate. Bases of setae *c1* situated slightly anterior to level of setal bases *se*. Bases of setae *f2* situated anterior to level of setal bases *f1*. Coxal fields I–II punctate. Posterior end of apodemes II distinctly extending beyond coxal field II (Figure 2(b)). *Lengths of setae: vi* 70 (70), *ve* 150, *si* 240 (255), *se* 280 (295), *c1* 330, *c2* 290 (305), *d1* 225, *d2* 220 (225), *e2* 130 (135), *f1* 45 (45), *f2* 50 (50), *h1* 10 (10), *h2* 340, *ag1* 100 (115), *ag2* 65 (85), *ag3* 125 (110), *ps1* 10 (5), *ps2* 10 (10), *tc'III–IV* 45 (35–55), *tc"III–IV* 50 (35–55), *3b* 30, *3c* 100. *Length ratios of setae: vi:ve:si* 1:1.4:3.4–3.6, *e2:d1:d2* 1:1.7:1.6, *ag1:ag2:ag3* 1.3–1.5:1:1.2–1.9, *f1:h1* 4.5:1, *f1:f2* 1:1.

Female (PF). All characters as in female (NPF) except: total body length 1060–1080 in three paratypes.

Male. Not found.

Type material

Female holotype (NPF), paratypes: 1 female (NPF), 3 female (PF) from White-tipped Dove *Leptotila verreauxi* Bonaparte (Columbiformes: Columbidae), ARGENTINA: Formosa Province, Tapiciolé, 30 December 1925, coll. Kiefer.

Types deposition

All type material is deposited in the AMU (Reg. No. AMU-SYR.556), except 1 female (PF) paratype in the ZSM (Reg. No. ZSM 20112070).

Differential diagnosis

Gunabopicobia leptotila **sp. nov**. is morphologically similar to *G. zumpti* (Lawrence, 1959). In females of both species, the infracapitulum and the stylophore are densely punctate; each lateral branch of the peritremes has 10–11 chambers; coxal fields I–II are punctate.

This new species differs from *G. zumpti* by the following features: in females of *G. leptotila*, the medial shield of the propodonotum is punctate, the lengths of setae *vi, ve, f1*, and *f2* are 70, 290, 45, and 50, respectively; the length ratios of setae *f1:h1, f1:f2*, and *e2:d1:d2* are 4.5:1, 1:1, and 1:1.7:1.6, respectively; and coxal fields III–IV are apunctate. In females of *G. zumpti*, the medial shield of the propodonotum is apunctate, the lengths of setae *vi, ve, f1*, and *f2* are 50–55, 150–155, 10, and 20–30, respectively; the length ratios of setae *f1:h1, f1:f2*, and *e2:d1:d2* are 1:1, 1:2–3, and 1:1–1.2:1, respectively; and coxal fields III–IV are punctate.

Etymology

The name *leptotila* is taken from the generic name of the host.

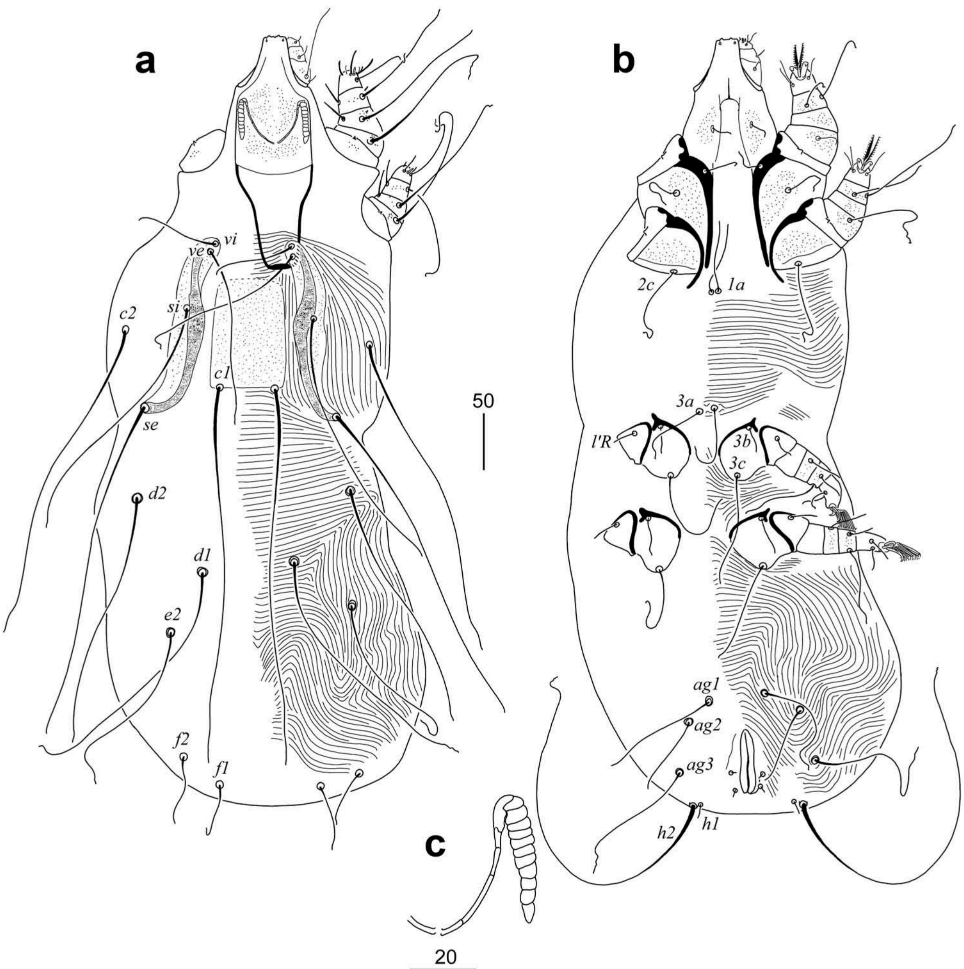

Figure 2. *Gunabopicobia leptotila* **sp. nov**. female: (A) dorsal view; (B) ventral view; (C) peritreme.

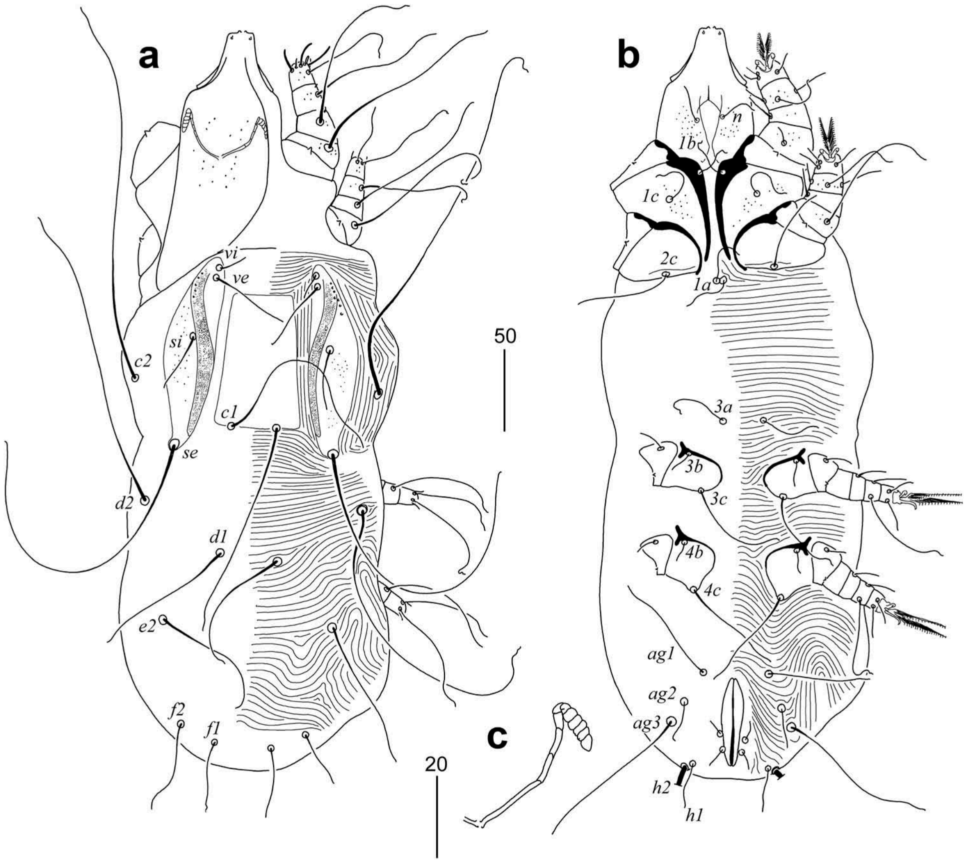

Figure 3. *Gunabopicobia claravis* **sp. nov**. female: (A) dorsal view; (B) ventral view; (C) peritreme.

Gunabopicobia claravis sp. nov.

Description

Female (NPF), holotype. (Figure 3(a–c)). Total body length 450 (445–440 in two paratypes). *Gnathosoma*. Infracapitulum punctate. Each medial branch of peritremes with 4–5 chambers, each lateral branch with 5–6 chambers (Figure 3(c)). Stylophore punctate, 160 long. *Idiosoma*. Each lateral shield of propodonotum punctate, with belt-like sclerotization; medial shield apunctate. Bases of setae *c1* situated anterior to level of setal bases *se*. Bases of setae *f2* situated slightly anterior to level of setae *f1*. Coxal fields I punctate, II–IV apunctate. Posterior end of apodemes II not extending beyond coxal field II (Figure 3(b)). *Lengths of setae: vi* 20 (20), *ve* 45 (35), *si* 35 (30), *se* 190 (195), *c1* 155 (130), *c2* 230 (210), *d1* 80 (95), *d2* 175 (195), *e2* 80 (95), *f1* 30 (20–30), *f2* 55 (30–40), *h1* 20 (30), *h2* 265 (270), *ag1* 75 (70–80), *ag2* 25 (15), *ag3* 105 (70), *ps1* and *ps2* 5 (5), *tc'III–IV* 40 (50), *tc"III–IV* 55 (60), *3b* 15 (20), *3c* 60 (70). *Length ratios of setae: vi:ve:si* 1:1.7–2.2:1.5–1.7, *c1:c2* 1:1.5, *e2:d1:d2* 1:1:2.1–2.3, *ag1:ag2:ag3* 3–4.6:1:4–5.3, *h1:f1* 1:1–1.2.

Female (PF). All characters as in female NPF except: total body length 1030–1080 in five paratypes.

Male. Not found.

Type material

Female holotype (NPF), paratypes: 2 female (NPF) and 5 females (PF) from Blue Ground-Dove *Claravis pretiosa* (Ferrari-Pérez) (Columbiformes: Columbidae), COLOMBIA: Cauca Prov., Mercaderes, 17 November 1965, coll. Haffer.

Types deposition

All type material is deposited in the AMU (Reg. No. AMU-SYR.531), except 1 female (PF) paratype in the ZSM (Reg. No. ZSM 20112071).

Additional material

Same host species, MEXICO: Sciama, 1896, coll. Dalmas; 2 females (PF) deposited in the AMU (Reg. No. AMU-SYR.563).

Differential diagnosis

Gunabopicobia claravis **sp. nov**. is morphologically similar to below described species *G. geotrygoni* **sp. nov**. In females of both species, the infracapitulum and the stylophore are punctate; each lateral branch of the peritremes has four chambers; posterior end of the apodemes II do not extend beyond coxal fields II; coxal fields I are punctate, and II–IV are apunctate. This new species differs from *G. geotrygoni* by the following features: in females of *G. claravis*, the medial shield of propodonotum is apunctate; the lengths of setae *si, c1*, and *d1* are 30–35, 130–155, and 80–95, respectively. In females of *G. geotrygoni*, the medial shield of propodonotum is punctate; the lengths of setae *si, c1*, and *d1* are 75–85, 240–250, and 200–205, respectively.

Etymology

The name *claravis* is taken from the generic name of the host.

Gunabopicobia geotrygoni sp. nov. (Figures 4–5)

Description

Female (PF) holotype. (Figure 4(a–e)). Total body length 1055 (1050–1055 in five paratypes). *Gnathosoma*. Infracapitulum sparsely punctate. Each medial branch of peritremes with 4 chambers, each lateral branch with 5–6 chambers (Figure 4(e)). Stylophore sparsely punctate, 190 long. *Idiosoma*. Each lateral shield of propodonotum punctate and with belt-like sclerotization; medial shield punctate. Bases of setae *c1* situated slightly anterior to level of setal bases *se*. Bases of setae *f2* situated anterior to level of setal bases *f1* (Figure 4(c)). Coxal fields I punctate, II–IV

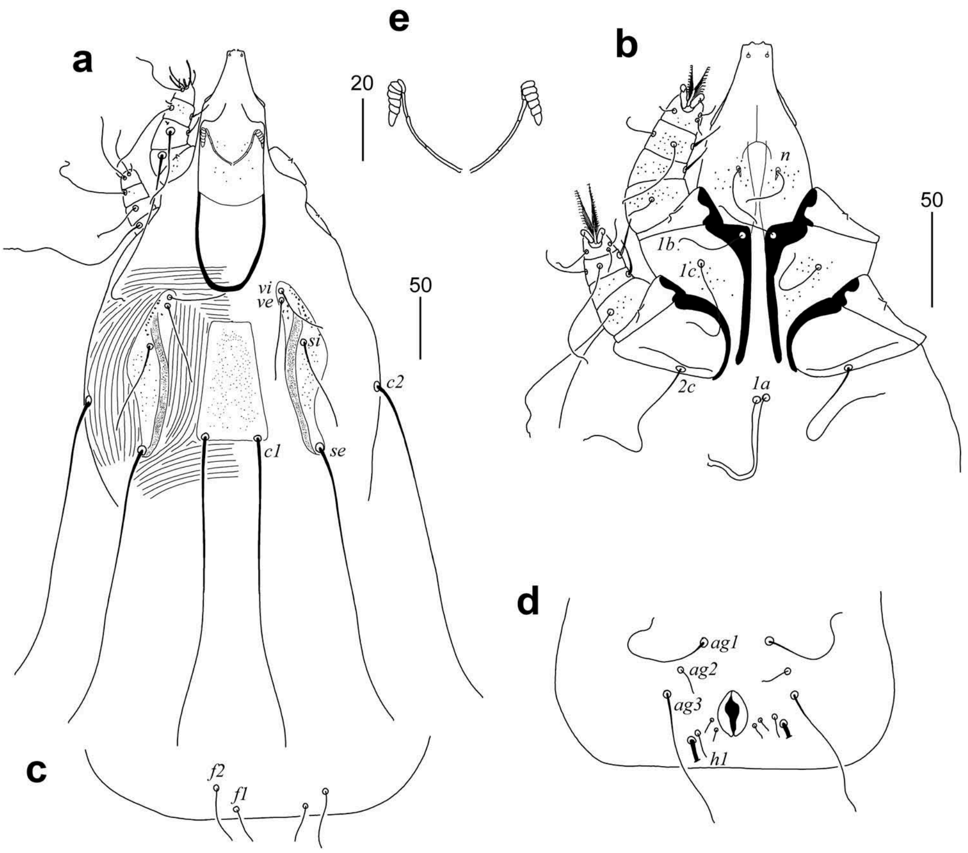

Figure 4. *Gunabopicobia geotrygoni* **sp. nov**. female: (A) anterior part of the body in dorsal view; (B) anterior part of the body in ventral view (C) opisthosoma in dorsal view; (D) opisthosoma in ventral view; (E) peritremes.

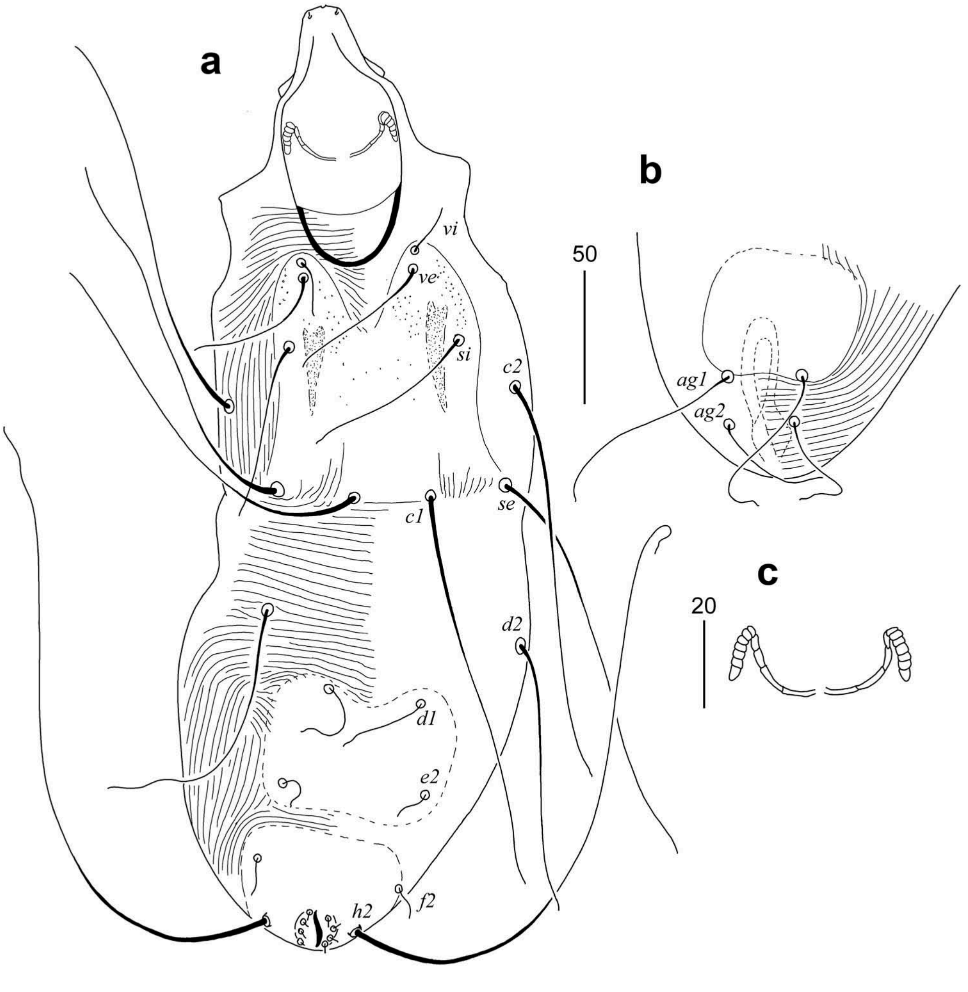

Figure 5. *Gunabopicobia geotrygoni* **sp. nov**. male: (A) dorsal view; (B) opisthosoma in ventral view; (C) peritremes.

apunctate. Posterior end of apodemes II not extend beyond coxal field II (Figure 4(b)). *Lengths of setae: vi* 55 (30–55), *ve* 60 (60), *si* 75 (75–85), *se* 235 (235–250), *c1* 250 (240–250), *c2* 290 (265–290), *d1* 205 (200–205), *d2* 155 (145–195), *e2* 115 (95–115), *f1* 25 (25–30), *f2* 30 (30–40), *h1* 25 (20–25), *h2* 330 (320–330), *ag1* 100 (100–105), *ag2* 15 (15–20), *ag3* 95 (95–105), *ps1* and *ps2* 5 (5), *tc'III–IV* 50 (50–65), *tc"III–IV* 60 (60), *3b* 15 (15–20), *3c* 65 (65–90). *Length ratios of setae: vi:ve:si* 1:1–2:2.5–2.8, *e2:d1:d2* 1:1.7–2.1:1.6, *f1:f2* 1:1.2–1.5, *h1:f1* 1:1, *ag1:ag2:ag3* 5.2–6.6:1:5.2–6.3.

Female (NPF). Not found.

Male. (Figure 5(a–c)). Total body length 285 in 1 paratype. *Gnathosoma*. Infracapitulum sparsely punctate. Each medial branch of peritremes with 4 chambers, each lateral branch with 6–7 chambers (Figure 5(c)). Stylophore 85 long. *Idiosoma*. Propodonotal shield entire, with concave anterior margin, punctate in anterior half. Hysteronotal shield well sclerotized, apunctate, bearing bases of setae *d1* and *e2*, not fused to pygidial shield. Pygidial shield apunctate. Coxal fields of legs I–II sparsely punctate, III–IV apunctate. *Lengths of setae: vi* 20, *ve* 50, *si* 65, *se* 130, *c1* 145, *c2* 150, *d1* 35, *d2* 90, *e2* 8, *f2* 8, *h2* 190, *ag1* 50, *ag2* 35, *3b* 10, *3c* 25. *Length ratios of setae: vi:ve:si* 1:2.5:3.2, *d2:d1:e2* 11.2:4.3:1, *ag1:ag2* 1:1.4, *3b:3c* 1:2.5, *f2:h2* 1:15.

Type material

Female holotype (PF), paratypes: 5 females (PF) and 1 male from Lined Quail-Dove *Geotrygon linearis* (Prévost) (Columbiformes: Columbidae), VENEZUELA: Silla de Caracas, 17 January 1914, coll. Klages.

Type deposition

All type material is deposited in the AMU (Reg. No. AMU-SYR.554), except 1 female (PF) paratype in the ZSM (Reg. No. ZSM20112072).

Additional material

Columbiformes (Columbidae): ex Key West Quail-Dove *Geotrygon chrysia* Bonaparte, MARTINIQUE: 16 September 1897, coll. Dofbin; 1 female (PF) in the AMU (Reg. No. AMU-SYR.552). Ex White-throated Quail-Dove *Geotrygon frenata* (Tschudi), COLOMBIA: Pueblo Rico Choco, San Juan Slopes of Colombia, 27 October 1909, coll. Palmer; 2 females (NPF), 1 female (PF) in the AMU (Reg. No. AMU-SYR.553), 1 female (NPF) in ZSM (Reg. No. ZSM 20112073). Ex Ruddy Quail-Dove *Geotrygon montana* (Linnaeus), PARAGUAY: 13 March 1932, coll. Schuhmacher; 2 females (PF) in the AMU (Reg. No. AMU-SYR.555), 1 female (PF) in ZSM (Reg. No. ZSM 20112074).

Differential diagnosis

See differential diagnosis for *G. claravis*.

Etymology

The name *geotrygoni* is taken from the generic name of the host.

Gunabopicobia masalaje Kaszewska, Kavetska and Skoracki, 2014

Gunabopicobia masalaje Kaszewska et al. 2014: 294, Figures 1–3. Holotype deposited in the AMU, examined.

Type host: *Ptilinopus iozonus* Gray (Columbidae) from Papua New Guinea.

Diagnosis

Female (NPF). Total body length 530–570. Infracapitulum and stylophore apunctate. Each medial branch of peritremes with 6–7 chambers, each lateral branch with 5–6 chambers. Each lateral shield of propodonotum punctate; medial shield apunctate. Bases of setae *f1* and *f2* situated at same transverse level. Coxal fields I–IV apunctate. Posterior end of apodemes II extend beyond coxal fields II. *Lengths of setae: vi* 50–65, *ve* 150–185, *si* 150–170, *d1* 190–200, *d2* 235–255, *f1* 20–35, *f2* 25–40, *h1* 35–45. *Length ratios of setae: vi:ve:si* 1:2.5–2.7:2.6–2.8, *f1:h1* 1:1.8, *f1:f2* 1:1.2–1.6, *ag1:ag2:ag3* 2.8–3.5:1:3.6–4.

Male. Total body length 350–365. Infracapitulum and stylophore apunctate. Each medial and lateral branch of peritremes with 6 chambers. Propodonotal shield entire, rectangular in shape, punctate. Coxal fields I–IV apunctate. Lengths of setae *vi* 30–40, *ve* 130–140, *si* 155–160, *se* 185–190, *d1* 20–30, *d2* 155–165, *e2* 15–20.

Type material (examined)

Female holotype, 8 female and 3 male paratypes from Orange-bellied Fruit-Dove *Ptilinopus iozonus* Gray (Columbidae), PAPUA NEW GUINEA: April 1910, coll. Wiedenfeld.

Additional material (examined)

Columbiformes (Columbidae): Ex Island Imperial-Pigeon *Ducula pistrinaria* Bonaparte, PAPUA NEW GUINEA: New Britain Island, 17 August 1912, coll. Basenbruch; 3 females in the AMU and 1 female in the ZSM. Ex Pink-headed Imperial-Dove *Ducula rosacea* (Temminck), INDONESIA: East Nusa Tenggara, Kupang, Semau Island, 21 April 1911, coll. Haniel; 1 female and 3 males in the AMU, 1 female in the ZSM. Ex Purple-tailed Imperial-Pigeon *Ducula rufigaster* (Quoy and Gaimard), PAPUA NEW GUINEA: Astrolabe, 5 March 1894, coll. Hagen; 3 females in the AMU. Ex White Imperial-Pigeon *Ducula luctuosa* (Temminck), INDONESIA: Sulawesi Island, coll. Riedel; 1 female in the AMU. Ex Torresian Imperial-Pigeon *Ducula spilorrhoa* (Gray), PAPUA NEW GUINEA: 17 March 1911, coll. Wiedenfeld; 2 females in the AMU.

New material (examined)

Ex Pied Imperial-Pigeon *Ducula bicolor* (Scopoli), INDONESIA: Celebes, 1907, coll. Riedel; 2 females (PF) in the AMU.

Hosts and distribution

Columbiformes (Columbidae): *Ducula bicolor* [**new host**] (present paper), *D. rosacea* and *D. luctuosa* from Indonesia, *D. pistrinaria, D. rufigaster, D. spilorrhoa*, and *Ptilinopus iozonus* (type host), all from Papua New Guinea (Kaszewska et al. 2014).

Gunabopicobia zumpti (Lawrence, 1959)

Syringophilus zumpti Lawrence, 1959: 425, Figure 5. Types deposited in NMSA, not examined.

Picobia zumpti, Kethley 1970: 65, figure 37; Skoracki and Dabert 2002: 144; Skoracki et al. 2004: 171; Bochkov et al. (2005): 122, Figures 1–3.

Neopicobia zumpti, Skoracki 2011: 384.

Gunabopicobia zumpti, Skoracki and Hromada 2013: 197, Figure 3.

Type host: *Streptopelia capicola* (Sundevall) (Columbiformes: Columbidae) from South Africa.

Diagnosis

Female (NPF). Total body length 510–550. Infracapitulum and stylophore densely punctate. Each medial branch of peritremes with 3–4 chambers, each lateral branch with 10–11 chambers. Each lateral shield of propodonotum punctate and with narrow belt-like sclerotization; medial shield apunctate. Bases of setae *f2* situated anterior to level of setae *f1*. Posterior end of apodemes II distinctly extending beyond coxal plate II. Coxal fields I–IV punctate. *Lengths of setae: vi* 50–55 *ve* 150–155, *si* 230–250, *d1* 255–295, *d2* 250–255, *e2* 220–230, *f1* 10, *f2* 20–30. *Length ratios of setae: vi:ve:si* 1:2.8–3:4.5–4.6, *e2:d1:d2* 1:1–1.2:1, *f1:h1* 1:1, *f1:f2* 1:2–3, *ag1:ag2:ag3* 2.2–4.3:1:3.2–4.

Type material (not examined)

Female holotype from the Ring-necked Dove *Streptopelia capicola* (Columbidae), SOUTH AFRICA: Cape Prov., Colesberg; holotype is deposited in the NMSA.

Additional material (examined)

Columbiformes (Columbidae): Ex Rock Pigeon *Columba livia* Gmelin, POLAND: Wielkopolskie, Poznan, 21 December 2010, coll. T. Tymcio; 1 female (PF) and 1 male deposited in the AMU. Same host species, USA: Illinois, Ford County, near Paxton, July 1999, coll. D. Clayton and B. Moyer; 2 females and 1 male in the ZISP. Same host species, USA: Massachusetts, Suffolk County, Boston, 1969, coll. N. S. Brown; 1 female (NPF) in the AMU. Ex Laughing Dove *Streptopelia senegalensis* (Linnaeus), SOUTH AFRICA: Brakkloof, October 1963, collector unknown; 4 females in the RMCA. Ex Mourning Dove *Zenaida macroura* (Linnaeus), USA: Georgia, Hall County, Gainesville, February 1970, coll. Kethley; 2 females (PF) and 1 male in the FMNH.

New material (examined)

Columbiformes (Columbidae): Ex Eastern Bronze-naped Pigeon *Columba delegorguei* Delegorgue, TANZANIA: Arusha region, Arusha, USA-river, 12 April 1960, coll. Nagy; 1 female (NPF) and 4 females (PF) in the AMU. Ex Picazuro Pigeon *Patagioenas picazuro* (Temminck), BRAZIL: Matto Grosso, Cuyaba, 23 September 1824, coll. Naltzoer; 1 female (NPF) and 4 females (PF) in the AMU. Ex Scaled Pigeon *Patagioenas speciosa* (Gmelin), BRAZIL: Para, Jpitinga, Rio Acard, 3 July 1910, coll. Mueller; 1 female (PF) and 1 male in the AMU. Ex Red-eyed Dove *Streptopelia semitorquata* Rueppell ETHIOPIA: El Carre, 17 January 1945; 2 females (NPF) and 1 female (PF) in the AMU.

Hosts and distribution

Columbiformes (Columbidae): *Columba livia* from USA (Bochkov et al. 2005; Skoracki et al. 2016) and Poland (Skoracki et al. 2014), *C. delegorguei* [**new host**] from Tanzania, *Patagioenas picazuro* [**new host**] and *Patagioenas speciosa* [**new host**] both from Brazil (present paper), *Streptopelia capicola*, from South Africa (Lawrence 1959), *S. semitorquata* from Ethiopia [**new host**] and *S. senegalensis* also South Africa (Skoracki and Hromada 2013), and *Zenaida macroura* from USA (Skoracki et al. 2014).

Metriopelia species group

Diagnosis

Female. Propodonotal shield entire. Bases of setae *1a* not coalesced.

Gunabopicobia metriopelia sp. nov.

Description

Female (NPF), holotype. (Figure 6(a–c)). Total body length 370 (470 in 1 paratype). *Gnathosoma*. Infracapitulum punctate. Each medial branch of peritremes with 4–5 chambers, each lateral branch with 5–6 chambers (Figure 6(c)). Stylophore densely punctate, 170 long. *Idiosoma*. Propodonotal shield entire, densely punctate, with narrow belt-like sclerotizations. Bases of setae *c1* situated anterior to level of setal bases *se*. Bases of setae *f2* situated in close proximity and slightly anterior to level of setae *f1* (Figure 6(b)). Coxal fields I punctate, II–IV apunctate. *Lengths of setae: vi* 10 (10), *ve* 10 (15), *si* 20 (20), *se* 110 (130), *c1* 165 (145), *c2* (95), *d1* 170 (150), *d2* 135 (130), *e2* 140 (140), *f1* 90 (80), *f2* 115 (105), *h1* 60 (50), *h2* 300 (290), *ag1* 55 (40), *ag2* 80 (80), *ag3* 90 (100), *ps1* and *ps2* 20 (20), *tc'III–IV* 50 (45), *tc"III–IV* 35 (40), *3b* 15 (15), *3c* 55 (50). *Length ratios of setae: vi:ve:si* 1:1–1.5:1.3–2, *e2:d1:d2* 1:1.1–1.2:1, *ag1:ag2:ag3* 1:1.5–2:1.6–2.5, *h1:f1* 1:1.3–1.5, *f1:f2* 1:1.2–1.3.

Female (PF). All characters as in female NPF, except: total body length 560–800 in three paratypes.

Male. Not found.

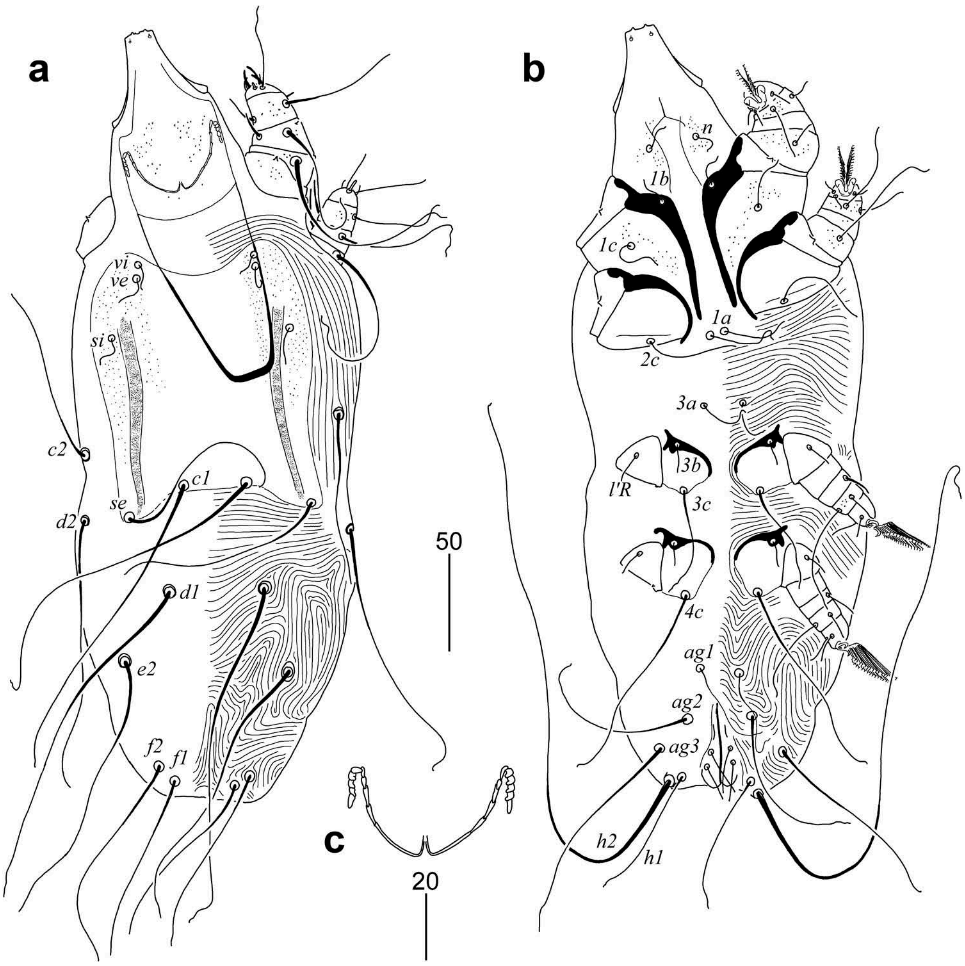

Figure 6. *Gunabopicobia metriopelia* **sp. nov**. female: (A) dorsal view; (B) ventral view; (C) peritremes.

Table 2. Representatives of the Columbiformes (Columbidae) examined in this study and their quill mite parasites.

Host species	All	Infected	Prev. (CI (Sterne))	QM species
Caloenas nicobarica	4	2	50 (9.8–90.2)	*G. lathami* sp. nov.
Chalcophaps indica	23	0	–	–
Chalcophaps stephani	2	0	–	–
Claravis montedoura	2	0	–	–
Claravis pretiosa	10	2	20 (3.7–55.3)	*G. claravis* sp. nov.
Columba araucana	12	0	–	–
Columba arquatrix	4	0	–	–
Columba cayenensis	18	0	–	–
Columba delegorquei	7	1	14.3 (0.7–55.4)	*G. zumpti*
Columba guinea	36	0	–	–
Columba livia	20	0	–	–
Columba oenas	9	0	–	–
Columba palumbea	11	0	–	–
Columba palumbus	4	0	–	–
Columba rupestris	11	0	–	–
Columba subvinacea	3	0	–	–
Columbina cruziana	2	0	–	–
Columbina minuta	4	0	–	–
Columbina passerina	15	0	–	–
Columbina talpacoti	32	0	–	–
Ducula aena	4	0	–	–
Ducula bicolor	2	2	100 (22.4–100)	*G. masalaje*
Ducula carola	2	0	–	–
Ducula concinna	1	0	–	–
Ducula finschi	2	0	–	–
Ducula luctuosa	1	0	–	–
Ducula perspicillata	1	0	–	–
Ducula pristinaria	2	0	–	–
Ducula rosacea	1	0	–	–
Ducula rufigaster	1	0	–	–
Ducula zoeae	7	0	–	–
Gallicolumba luzonica	2	0	–	–
Gallicolumba rufigula	1	0	–	–
Geopelia cuneata	2	0	–	–
Geopelia placida	2	0	–	–
Geopelia striata	13	0	–	–
Geotrygon chiriquensis	1	0	–	–
Geotrygon chrysia	1	1	100 (22.4–100)	*G. geotrygoni* sp. nov.
Geotrygon frenata	3	1	33 (1.7–86.5)	*G. geotrygoni* sp. nov.
Geotrygon linearis	8	1	12.5 (0.6–50)	*G. geotrygoni* sp. nov.
Geotrygon martinica	3	0	–	–
Geotrygon montana	8	2	25 (4.6–63.5)	*G. geotrygoni* sp. nov.
Geotrygon veraguensis	1	0	–	–
Geotrygon violacea	1	0	–	–
Gymnophaps albertisii	2	0	–	–
Henicophaps albifrons	1	0	–	–
Henicophaps foersteri	1	0	–	–
Leptoptila cassini	1	0	–	–
Leptoptila verreauxi	24	1	4.2 (0.2–20.4)	*G. leptotila* sp. nov.
Leptoptilla rufaxilla	10	0	–	–
Leucosarcia melanoleuca	1	1	100 (5–100)	*G. lathami* sp. nov.
Leucotreron cincta	6	0	–	–
Leucotreron porphyrea	3	0	–	–
Lophophaps feruginea	1	0	–	–
Macropygia amboinensis	6	0	–	–
Macropygia magna	3	0	–	–
Macropygia phasianella	14	0	–	–
Macropygia ruficeps	4	0	–	–
Macropygia unchall	3	0	–	–
Megaloprepia formosa	1	0	–	–
Megaloprepia magnifica	17	0	–	–
Metropelia ceciliae	2	0	–	–
Metropelia melanoptera	8	1	12.5 (0.6–50.0)	*G. metriopelia* sp. nov.
Nesopelia galapagoensis	8	0	–	–
Ocyphaps lophotes	1	0	–	–
Oena capensis	17	0	–	–
Otidiphaps nobilis	1	0	–	–
Patagioenas oenops	4	0	–	–
Patagioenas picazuro	16	1	6.2 (0.3–30.5)	*G. zumpti*
Patagioenas speciosa	8	1	12.5 (0.6–50)	*G. zumpti*
Ptilinopus coronulatus	4	0	–	–
Ptilinopus jambu	5	0	–	–
Ptilinopus milanospila	3	0	–	–
Ptilinopus ornatus	1	0	–	–
Ptilinopus pulchellus	5	0	–	–
Ptilinopus pustulatus	3	0	–	–
Ptilinopus regina	4	0	–	–
Ptilinopus solomonensis	1	0	–	–
Ptilinopus superbus	6	0	–	–
Ptilonopus rivoli	1	0	–	–

(*Continued*)

Table 2. (Continued).

Host species	All	Infected	Prev. (CI (Sterne))	QM species
Reinwardtoena reinwardtsi	2	0	–	–
Scardafelle squammata	11	0	–	–
Streptopelia decaocto	12	0	–	–
Streptopelia orientalis	22	0	–	–
Streptopelia picturata	1	0	–	–
Streptopelia roseogrisea	3	0	–	–
Streptopelia semitorquata	21	1	4.8 (0.2–23.3)	*G. zumpti*
Streptopelia senegalensis	26	0	–	–
Streptopelia tranquebarica	5	0	–	–
Streptopelia turtur	30	0	–	–
Toracoena manadensis	4	0	–	–
Treron australis	12	0	–	–
Treron calva	7	0	–	–
Turacoena modesta	5	0	–	–
Turtur chalcospilos	13	0	–	–
Turtur tympanistria	13	0	–	–
Zenaida auriculata	10	0	–	–
Zenaida macroura	1	0	–	–

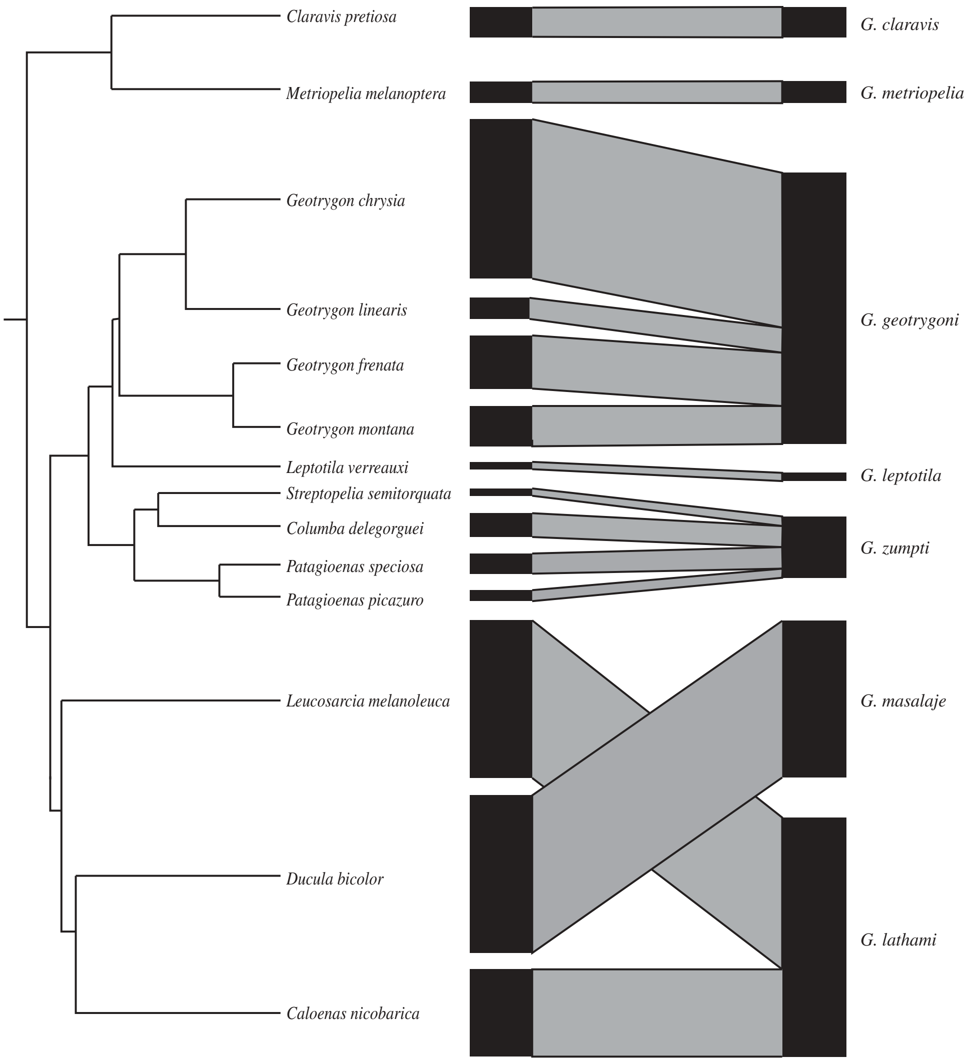

Figure 7. Bipartite network of interactions between quill mites permanent ectoparasites of birds (right) and their hosts (left). Strength of each interaction is represented by number of interactions (prevalence). Host phylogeny based on Jetz et al. (2012) .

Type material

Female holotype (NPF), paratypes: 1 female (NPF) and 3 females (PF) from Black-winged Ground-Dove *Metriopelia melanoptera* (Molina) (Columbiformes: Columbidae), ARGENTINA: Neuquén Prov., Patagonia, 8 December 1907; coll. Lendl.

Types deposition

All type material is deposited in the AMU (Reg. No. AMU-SYR.532), except 1 female (PF) paratype in the ZSM (Reg. No. ZSM 20112075).

Differential diagnosis

Gunabopicobia metriopelia **sp. nov**. is morphologically distinguished from all other species of this genus by the presence of the entire propodonotal shield (*vs*. divided in other species), long setae *f1, f2, h1, ag2* long which are 4–6 times longer than pseudanal setae (*vs*. less than 2 times), and not coalesced bases of setae *1a* (*vs*. coalesced).

Etymology

The name *metriopelia* is taken from the generic name of the host.

Key to *Gunabopicobia* species (females)

1. Propodonotal shield entire. Bases of setae 1a not coalesced.. .... metriopelia-species-group............... *G. metriopelia* **sp. nov.**
– Propodonotal shield divided into 3 sclerites. Bases of setae *1a* coalesced................................... *zumpti*-species-group................. 2
2. Posterior end of apodemes II not extending beyond coxal fields II... 3
– Posterior end of apodemes II distinctly extending beyond coxal fields II 4
3. Length ratio of setae f1:f2 1:1.2–1.5, length of setae vi, ve, and si 30–55, 60, and 75–85, respectively.. *G. geotrygoni* **sp. nov.**
– Length ratio of setae *f1:f2* 1–1.2:1, length of setae *vi, ve, si* 20, 35–45, 30–55, respectively............................ *G. claravis* **sp. nov.**
4. Infracapitulum apunctate... .... G. masalaje Kaszewska, Kavetska and Skoracki, 2014
– Infracapitulum distinctly and densely punctate 5
5. Length ratio of setae h1:f1 1:4.5................. *G. leptotila* **sp.nov.**
– Length ratio of setae *h1:f1* 1–1.2:1.. 6
6. Each lateral branch with 10–11 chambers. Setae si 3.2–3.8 times longer than vi. Coxal fields of legs I–IV punctate............ .... *G. zumpti* (Lawrence, 1959)
– Each lateral branch with 7–8 chambers. Setae *si* 1.7 times longer than *vi*. Coxal fields of legs I punctate, II–IV apunctate .... *G. lathami* **sp. nov.**

Discussion

Columbiform birds and their quill mite parasites of the genus gunabopicobia

The Columbidae, the only extant family in the order Columbiformes, is represented by about 310 species distributed in all zoogeographical regions, except Arctic and Antarctic (Pereira et al. 2007; Clements et al. 2017).

In the current study, total of 659 individuals of 98 species (32% of the World fauna) of the 30 genera (70%) columbid hosts have been investigated. The picobine fauna associated with pigeons and doves comprises seven quill mite species of the genus *Gunabopicobia* (incl. five species new for science) found on 24 columbid species belonging to 12 genera (Table 1).

The presence of representatives of *Gunabopicobia* on pigeons and doves belonging to all subfamilies, i.e. Columbinae, Claravinae, and Raphinae (Pereira et al. 2007; Johnson and Weckstein 2011; Fulton et al. 2012; Banks et al. 2013), suggests that mites of this genus could start to parasitize the common ancestor of these bird clades. Pereira et al. (2007) revealed a temporal gap of about 41 to 46 Mya between the origin of Columbiformes in the Late Cretaceous and diversification of genera within the order in the Eocene. Considering the estimated Cretaceous age for modern Columbiformes lineages and their Gondwanaland origin (Cooper and Penny 1997; Pereira and Baker 2006), we suggest that representatives of *Gunabopicobia* invade columbiform birds before their generic and subfamiliar divergence.

Taking into consideration the zoogeography of pigeons and doves, the subfamily Columbinae includes genera from South and North America (e.g. *Geotrygon, Leptotila, Zenaida*) and from Old World (e.g. *Columba, Streptopelia*); subfamily Claravinae includes genera distributed in Neotropical region (e.g. *Metriopelia, Claravis*), and subfamily Raphinae includes doves distributed in Afrotropical, Sino-Jappanese, Australian, Oriental, and Oceanian regions (e.g. *Ducula, Ptilinopus, Chalcophaps*) (Pereira et al. 2007). Based on the host distribution, we distinguished three zoogeographic groups of *Gunabopicobia*: (1) Afro-Eurasian group with *G. zumpti*, (2) New World group with *G. claravis, G. geotrygoni, G. metriopelia, G. leptotila*, and (3) Australo-Indonesian group with *G. lathami* and *G. masalaje*.

Prevalence and host specificity of Gunabopicobia

The prevalence for *Gunabopicobia* species was relatively high which ranged from 20% to 100% with the exception of a few cases where the prevalence was less than 20% (Table 2). The quite high prevalence corresponds with social life of their hosts. On the other hand, our results can be attached with the low size of samples (2–24 examined individuals). The confidence interval was wide for each of the examined sample. Future research need to focus on examination of more individuals for greater accuracy of estimation.

Gunabopicobia, similar to other syringophilid genera, includes highly host-specific mites. Among our mite material, the monoxenous parasites (restricted to one host species) are represented by three species, *G. claravis, G. metriopelia*, and *G. leptotila* parasitizing *Claravis pretiosa, Metriopelia melanoptera, Leucosarcia melanoleuca*, respectively. Oligoxenous parasite (more than one host, but restricted to one genus) is represented by *G. geotrygoni* associated with four species of the genus *Geotrygon*. Mesostenoxenous group (inhabiting more than one genus of host, but restricted to one family) comprise three quill mites species: *G. masalaje, G. lathami*, and *G. zumpti* recorded on 2–5 genera of columbids (Figure 7).

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Disclosure statement

No potential conflict of interest was reported by the authors.

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IV

Kaszewska K., Skoracki M. 2018.

Two new quill mite species of the genus Psittaciphilus Fain, Bochkov & Mironov, 2000 (Acariformes: Syringophilidae) associated with pigeons and doves (Columbiformes: Columbidae).

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Two new quill mite species of the genus *Psittaciphilus* Fain, Bochkov & Mironov, 2000 (Acariformes: Syringophilidae) associated with pigeons and doves (Columbiformes: Columbidae)

Katarzyna Kaszewska · Maciej Skoracki

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Abstract Two new quill mite species of the genus *Psittaciphilus* Fain, Bochkov & Mironov, 2000 (Acariformes: Prostigmata: Syringophilidae) collected from columbiform birds (Columbiformes) are described: *Psittaciphilus montanus* n. sp. form the ruddy quail-dove *Geotrygon montana* Gosse from Trinidad and Tobago, Brazil and Panama, and *Psittaciphilus patagioenas* n. sp. from the band-tailed pigeon *Patagioenas fasciata* (Say) from Colombia and the scaled pigeon *Patagioenas speciosa* (Gmelin) from Surinam. A key to the species of the genus *Psittaciphilus* is provided. Our finding is the first record of the representatives of this genus on columbiform birds.

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Introduction

The quill mites of the family Syringophilidae Lavoipierre, 1953 (Acariformes: Prostigmata) are permanent and highly specialised ectoparasites, infesting quills of different types of feathers in the plumage of their avian hosts (Kethley, 1970). These mites show a high degree of host specificity, where most of species are mono- or stenoxenous parasites (Skoracki, 2011; Skoracki et al., 2016). Currently, the family includes 377 described species grouped in 62 genera and two subfamilies and recorded from about 500 host species belonging to 95 families and 24 orders (Zmudzinski & Skoracki, 2017).

The *Psittaciphilus* Fain, Bochkov & Mironov, 2000 is one of less known genera in the family Syringophilidae. Until now, only two species have been described, *P. amazonae* Fain, Bochkov & Mironov, 2000 and *P. fritschi* Fain, Bochkov & Mironov, 2000, both associated with parrots (Fain et al., 2000). Mites of this genus predominantly live inside the quills of the wing coverts, under-tail coverts and contour feathers (pers. obs.) and together with five other genera belong to the *Psittaciphilus*-generic-group established by Bochkov & Perez (2002).

In this paper we describe two new species of the genus *Psittaciphilus* associated with the South American pigeons and doves: *P. montanus* n. sp. from *Geotrygon montana* (Linnaeus) and *P. patagioenas* n.

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sp. from *Patagioenas fasciata* (Say) and *Patagioenas speciosa* (Gmelin).

Materials and methods

The mite material used in the present study was collected from dry bird skins housed in the ornithological collection of the Bavarian State Collection of Zoology, Munich, Germany (ZSM). Feathers were examined using a dissecting microscope and opened with a fine scalpel. Before mounting, mites were softened and cleared in Nesbitt's solution at room temperature for three days. Then, mites were mounted on slides in Hoyer's medium. Taxonomic analysis of mite specimens was carried out with an Olympus BH-2 light microscope (Olympus Corp., Japan), equipped with DIC optics and a camera lucida. All measurements are given in micrometres. Measurements (ranges) of paratypes are given in parentheses following data for the holotype. In the descriptions below, the idiosomal chaetotaxy follows Grandjean (1939) as adapted for Prostigmata by Kethley (1990). The nomenclature of leg setae follows that proposed by Grandjean (1944). Morphological terminology follows Skoracki (2011). The scientific names of the birds follow Clements et al. (2017).

Specimen depositories are cited using the following abbreviations: AMU, A. Mickiewicz University, Department of Animal Morphology, Poznan, Poland; ZSM, Bavarian State Collection of Zoology, Munich, Germany.

Family Syringophilidae Lavoipierre, 1953
Subfamily Syringophilinae Lavoipierre, 1953
Genus *Psittaciphilus* Fain, Bochkov & Mironov, 2000

Psittaciphilus montanus n. sp.

Type-host: *Geotrygon montana* (Linnaeus) (Columbiformes: Columbidae), ruddy quail-dove.
Type-locality: Trinidad Island, Aripo Berge, Trinidad and Tobago.
Type-material: Female holotype and 19 female paratypes from quills of under-tail coverts, 25.viii.1912, coll. Klages. The holotype and 17 paratypes were deposited in the AMU (Reg. no. AMU-SYR.571A); 2 female paratypes were deposited in the ZSM (Reg. no. ZSM20112080).
Additional material examined: Six females from quills of tail coverts of the same host species; Brazil, Para and Rio Negro, 1844, collector unknown; all mite specimens deposited in the AMU (Reg. no. AMU-SYR.571B). Eleven females from quills of tail coverts of the same host species; Panama, Chiriqui, 1895, coll. Dalmas; all mite specimens deposited in the AMU (Reg. no. AMU-SYR.571C), except 2 females in the ZSM (Reg. no. ZSM20112081).
ZooBank registration: To comply with the regulations set out in article 8.5 of the amended 2012 version of the *International Code of Zoological Nomenclature* (ICZN, 2012), details of the new species have been submitted to ZooBank. The Life Science Identifier (LSID) for *Psittaciphilus montanus* n. sp. is urn:lsid:zoobank.org:act:7E5C92C2-911D-474F-9BB0-B69DDCEBF06C.
Etymology: The name *montanus* is taken from the specific name of the host.

Description (Fig. 1)

Female. Total body length of the holotype 600 (615–750 in 18 paratypes). *Gnathosoma*. Infracapitulum apunctate. Stylophore apunctate, 190 (160–190) long. Each medial branch of peritremes with 2 chambers, each lateral branch with 4 or 5 chambers (Fig. 1C). *Idiosoma*. Propodonotal shield sparsely punctate with 3 oval patches. Hysteronotal shield divided onto pair of oval sclerites surrounding bases of setae *d2*, and unpaired shield with bases of setae *d1* and fused to apunctate pygidial shield. Coxal fields I-IV apunctate. Setae *3a* situated out of coxal fields III. *Legs*. Solenidia of legs I as in Fig. 1D. Fan-like setae p' and p'' of legs III and IV with 22–24 tines (Fig. 1E). Setae $tc''III–IV$ 1.8–2.3 times longer than $tc'III–IV$. Setae $l'RIII$ 1.2–1.3 times longer than $l'RIV$. *Lengths of setae*: *ve* 75 (60–85); *si* 60 (40–60); *se* 205 (210–245); *c1* 215 (220–230); *c2* 195 (180–205); *d1* 180 (170–190); *d2* 220 (230–255); *e2* 170 (170–195); *f1* 25 (30–35); *f2* 150 (150–180); *h1* 25 (25–30); *h2* 330 (310–315); *ag1* 125 (120–145); *ag2* 40 (35–55); *ag3* 165 (160–185); *g1* and *g2* 45 (30–45); *ps1* and *ps2* 10 (10); $tc'III–IV$ 20 (15–30); $tc''III–IV$ 40 (35–55); $l'RIII$ 55 (55–60); $l'RIV$ 45 (45); *3b* 60 (65–75); *3c* 75 (90–100). *Length ratios of setae*: *ve*:*si*:*se* 1.2–1.6:1:4–5.3; *d2*:*d1*:*e2* 1.3–1.4:1:1; *ag1*:*ag2*:*ag3*

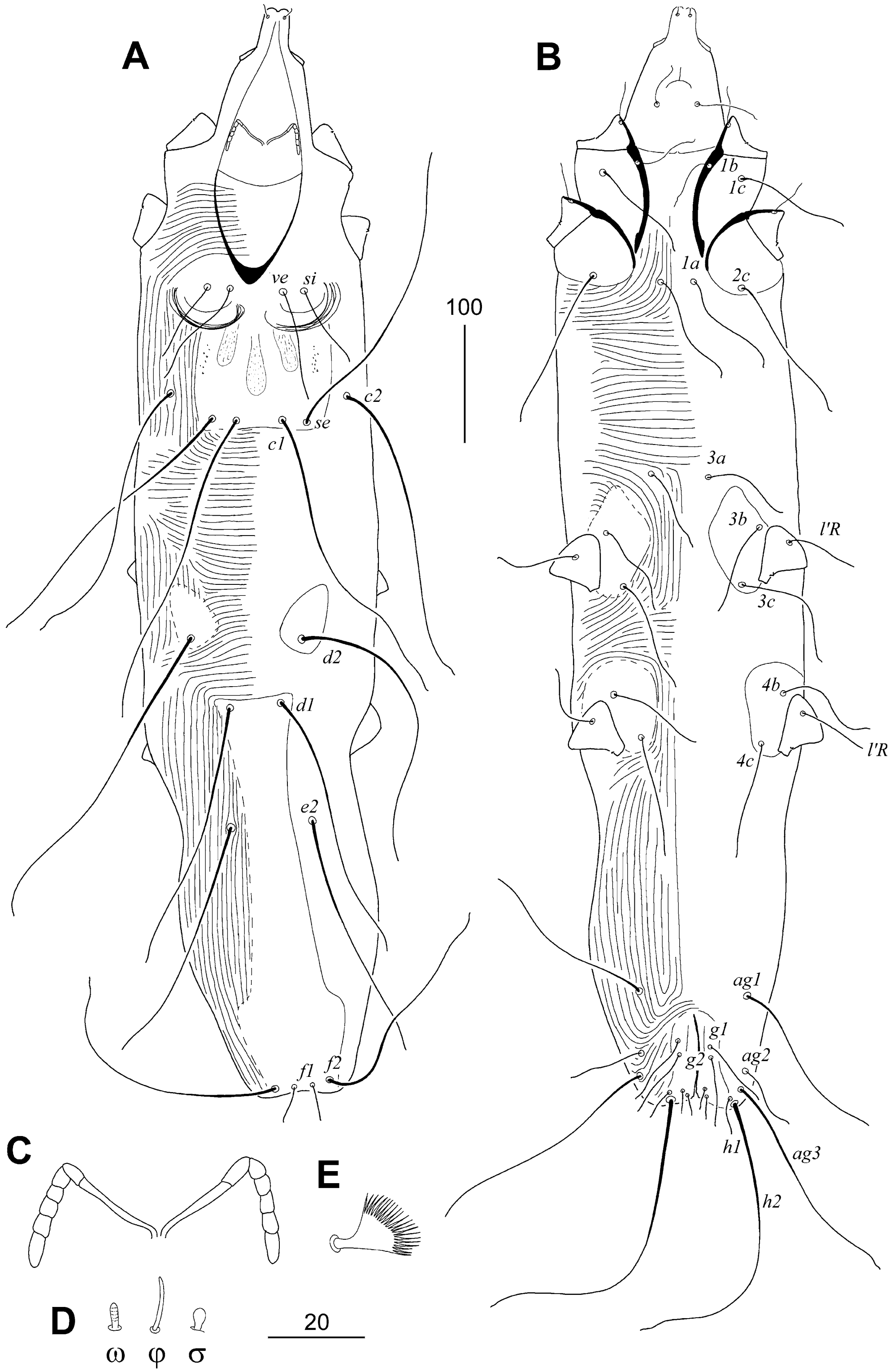

Fig. 1 *Psittaciphilus montanus* n. sp., female. A, Dorsal view; B, Ventral view; peritremes; D, Solenidia of legs I; E, Fan-like seta *p′* of tarsi III

2.4–3.1:1:3.2–4.1; *f1*:*f2* 1:5–6; *h1*:*f1* 1:1–1.2; *3b*:*3c* 1:1.2–1.3; *ps*:*g* 1:3–4.5.

Differential diagnosis

Psittaciphilus montanus n. sp. is morphologically similar to *P. fritschi*, collected from unidentified parrot from Zoo of Anverp (Belgium) (Fain et al., 2000). In females of both species, the stylophore, the infracapitulum and the pygidial shield are apunctate, and the medial branch of the peritremes has two chambers. This new species differs from *P. fritschi* by the following features: in females of *P. montanus* n. sp., each lateral branch of the peritremes has four or five chambers, the propodonotal shield is punctate and with three oval patches, and a pair of hysteronotal sclerites surrounding bases of setae *d2* is present. In females of *P. fritschi*, each lateral branch of the peritremes has six chambers, the propodonotal shield is apunctate and without oval shape patches, the hysteronotal shields surrounding bases of setae *d2* are absent.

***Psittaciphilus patagioenas* n. sp.**

Type-host: *Patagioenas fasciata* (Say) (Columbiformes: Columbidae), band-tailed pigeon.
Type-locality: Near San Juan River, Chocó Department Lama Hermosa, Colombia.
Type-material: Female holotype, 14 female paratypes from quill of under-tail coverts, 19.ix.1909, coll. Palmer. The holotype and 12 paratypes were deposited in the AMU (Reg. no. AMU-SYR.572); 2 female paratypes were deposited in the ZSM (Reg. no. ZSM20112082).
Additional material examined: Twenty-seven females from quills of wing coverts of the scaled pigeon *Patagioenas speciosa* (Gmelin) (Columbiformes: Columbidae); Surinam, Kraka, 23.ii.1963, coll. Haverschmidt; all mite specimens deposited in the AMU (Reg. no. AMU-SYR.573), except 2 females in the ZSM (Reg. no. ZSM20112083).
ZooBank registration: To comply with the regulations set out in article 8.5 of the amended 2012 version of the *International Code of Zoological Nomenclature* (ICZN, 2012), details of the new species have been submitted to ZooBank. The Life Science Identifier (LSID) for *Psittaciphilus patagioenas* n. sp. is urn:lsid:zoobank.org:act:4411F4FE-6BBF-45DE-8C62-5B82ED65A214.
Etymology: The name *patagioenas* is taken from the generic name of the host.

Description (Fig. 2)

Female. Total body length of the holotype 735 (690–720 in 14 paratypes). *Gnathosoma*. Infracapitulum apunctate. Stylophore apunctate, 230 (220–230) long. Each medial branch of peritremes with 2 chambers, each lateral branch with 5 or 6 chambers (Fig. 2C). Propodonotal shield apunctate, without patches. Hysteronotal shield divided onto pair of oval sclerites surrounding bases of setae *d2*, and unpaired shield with bases of setae *d1* and fused to apunctate pygidial shield. Coxal fields weakly sclerotised and apunctate. Setae *3a* situated out of coxal fields III. *Legs*. Solenidia of legs I as in Fig. 2D. Fan-like setae p' and p'' of legs III and IV with 19–20 tines (Fig. 2E). Setae tc''*III–IV* 2–2.3 times longer than tc'*III–IV*. Setae l'*RIII* and l'*RIV* subequal in length. *Lengths of setae*: *ve* 130 (120–125); *si* 40 (30–35); *se* 245 (245–260); *c1* 260 (260–285); *c2* 245 (235–250); *d1* 250 (240–250); *d2* 255 (260–280); *e2* (230–260); *f1* 45 (30–40); *f2* 280 (250–260); *h1* 30 (30–35); *h2* 360 (370–405); *ag1* 195 (190–210); *ag2* 70 (50–60); *ag3* 275 (280–295); *g1* and *g2* 45 (35–45); *ps1* and *ps2* 20 (10–15); tc'*III–IV* 35 (30–35); tc''*III–IV* 70 (70–80); l'*RIII* 55 (55–60); l'*RIV* 50 (50–70); *3b* 100 (70–95); *3c* 160 (130–145). *Length ratios of setae*: *ve*:*si*:*se* 3.4–4.3:1:6–8.5; *d2*:*d1*:*e2* 1:1:1; *ag1*:*ag2*:*ag3* 2.7–4.2:1:3.9–5.6; *f1*:*f2* 1:5.7–8.3; *h1*:*f1* 1:1; *3b*:*3c* 1:1.6–1.8; *ps*:*g* 1:2.2–3.5.

Differential diagnosis

Psittaciphilus patagioenas n. sp. is morphological similar to *P. amazonae*, collected from *Amazona amazonica* (Linnaeus) (Psittaciformes: Psittacidae) from Colombia (Fain et al., 2000). In females of both species, the stylophore and the infracapitulum are apunctate, the lengths of setae *ve* and *si* are 110–120 and 30–47 μm, respectively, and coxal fields I-IV are apunctate. This new species differs from *P. amazonae* by the following features: in females of *P. patagioenas* n. sp., the propodonotal and the pygidial shields are apunctate, the hysteronotal shields surrounding bases of setae *d2* are present, the lengths of hysteronotal

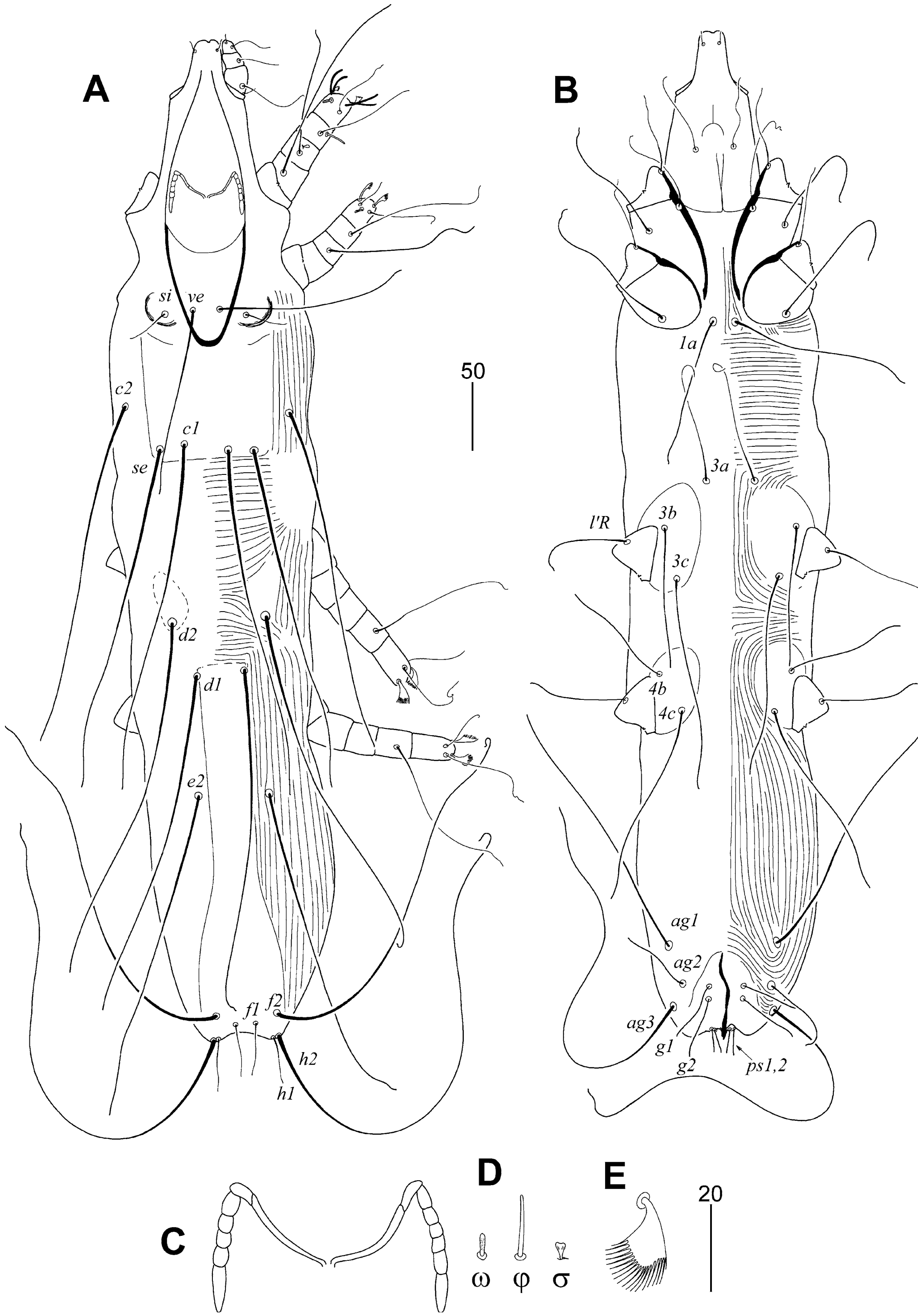

Fig. 2 *Psittaciphilus patagioenas* n. sp., female. A, Dorsal view; B, Ventral view; peritremes; D, Solenidia of legs I; E, Fan-like seta *p*′ of tarsi III

setae *d1*, *d2*, and *e2* are 240–250, 255–280 and 230–260 µm, respectively. In females of *P. amazonae*, the propodonotal and the pygidial shields are punctate, the hysteronotal shields surrounding bases of setae *d2* are absent, and the lengths of hysteronotal setae *d1*, *d2*, and *e2* are 144–155, 179–192 and 179–184 µm, respectively.

Key to the species of *Psittaciphilus*

1a Propodonotal shield punctate with three patches, setae *ve* 1.2–1.6 times longer than *si* ……………………………. *P. montanus* n. sp.

1b Propodonotal shield apunctate without patches, setae *ve* at least 2.4 times longer than *si* …… 2

2a Lengths of setae *ve* and *si* 83–101 and 18–22 µm, respectively ……………………………… …... *P. fritschi* Fain, Bochkov & Mironov, 2000

2b Lengths of setae *ve* and *si* 110–123 and 30–47 µm, respectively …………………………… 3

3a Propodonotal and pygidial shields punctate. Length of setae *d1*, *d2*, and *e2* 144–155, 179–192, and 179–184 µm, respectively. Hysteronotal shields surrounding bases of setae *d2* absent …………………………………… *P. amazonae* Fain, Bochkov & Mironov, 2000

3b Propodonotal and pygidial shields apunctate. Length of setae *d1*, *d2*, and *e2* 240–250, 260–280, and 230–260 µm, respectively. Hysteronotal shields surrounding bases of setae *d2* present ………………….. *P. patagioenas* n. sp.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable institutional, national and international guidelines for the care and use of animals were followed.

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The mites of the genus Meitingsunes Glowska and Skoracki (Acariformes: Syringophilidae) associated with pigeons and doves (Aves: Columbiformes): taxonomic studies with description of two new species.

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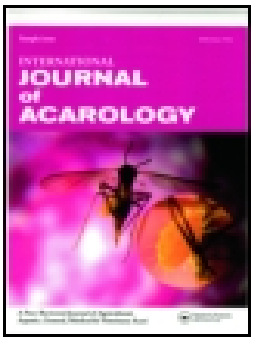

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The mites of the genus *Meitingsunes* Glowska and Skoracki (Acariformes: Syringophilidae) associated with pigeons and doves (Aves: Columbiformes): taxonomic studies with description of two new species

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ABSTRACT

Quill mite fauna of the genus *Meitingsunes* Glowska and Skoracki, 2010 associated with birds of the order Columbiformes is revised. Two new species are described: *Meitingsunes ptilinopus* **sp. nov**. from *Ptilinopus magnificus* (Temminck) in Australia and Papua New Guinea and from *P. rivoli* (Prévost) in Papua New Guinea, and *M. lengai* **sp. nov**. from *Columba delegorguei* Delegorgue in Tanzania, *Streptopelia semitorquata* (Rüppell) in Tanzania, and *Streptopelia orientalis* (Latham) in Kazakhstan and Kyrgyzstan. Additionally, we report several new hosts for previously known species of the genus and provide a key to all species of the genus.

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Introduction

The quill mites belonging to the family Syringophilidae (Acariformes: Prostigmata) are highly specialized parasites of birds living inside the feather quills. These obligatory ectoparasites have the ability to pierce the quill wall with long and flexible mobile digits of the chelicerae and feed on live tissue fluids of their hosts (Kethley 1970). Currently, the fauna of Syringophilidae comprises about 400 species belonging to 63 genera, and is associated with representatives of 27 birds orders (Zmudzinski et al. 2020). Based on potential hosts richness, Johnston and Kethley (1973) suggested that the number of quill mites species can be about 5000 species. Most syringophilid species are associated with one host species (monoxenous parasites) or with closely related hosts (oligoxenous parasites) (Skoracki 2011; Skoracki et al. 2016).

The genus *Meitingsunes* Glowska and Skoracki, 2010 presents a good example of the hosts-parasites interaction where a supraspecific taxon of parasites is primarily associated with one hosts order, Columbiformes, except one species, *M. caprimulgus* Skoracki et al., 2015, associated with the nightjars (Caprimulgiformes) (Skoracki et al. 2015). To this day, six species of *Meitingsunes* were found on 12 columbiform hosts species from the Neotropical, Nearctic, Palearctic, Oriental, and Afrotropical regions (Table 1) (Clark 1964; Skoracki and Dabert 2002; Skoracki and Sikora 2002; Glowska and Skoracki 2010; Skoracki 2011; Kaszewska et al. 2016).

Our paper provides descriptions of two new species the genus *Meitingsunes* associated with birds of the order Columbiformes and a key to all presently known species of this genus.

Material and methods

We examined all previously described species of the genus *Meitingsunes* based on the material deposited in the Department of the Animal Morphology, A, Mickiewicz University, Poland (AMU), Field Museum of Natural History, Chicago, IL, USA (FMNH), Royal Museum for Central Africa, Tervuren, Belgium (RMCA). The new mite material used in the present study was collected from dry bird skins housed in the ornithological collections of the Bavarian State Collection of Zoology, Munich, Germany (ZSM). Quills were examined using a dissecting microscope, and opened with a fine scalpel. We examined 739 dove individuals belonging to 109 species. In our attempt we found 30 host individuals infested by quill mites belonging to genus *Meitingsunes*. Infested doves represented 20 species from various genera and localities. We identified eight quill mites species, including two new for science (Table 1). Before mounting, mites were softened and cleared in Nesbitt's solution at room temperature for three days (Skoracki 2011). Mites were mounted on slides in Hoyer's medium. Identifications and drawings of mite specimens were carried out with a light microscope an Olympus BH-2 (Olympus Corp., Japan), equipped with DIC optics and a camera lucida. In the descriptions, all measurements are given in micrometres and measurements (ranges) of paratypes are given in brackets following data for a holotype. The idiosomal chaetotaxy follows Grandjean (1939) as adapted for Prostigmata by Kethley (1990). The nomenclature of leg setae follows that proposed by Grandjean (1944). Morphological terminology follows Skoracki (2011). The common and scientific names of the birds follow Clements et al. (2019). Zoogeographic regions follow Holt et al. (2013).

Results

Family Syringophilidae Lavoipierre, 1953
Subfamily Syringophilinae Lavoipierre, 1953
Genus ***Meitingsunes*** Glowska and Skoracki, 2010

Meitingsunes Glowska and Skoracki, 2010: 62.

Type species: *Syringophilus zenadourae* Clark, 1964, by the original designation.

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Table 1. Host associations and distribution of the quill mites genus *Meitingsunes* Glowska and Skoracki, 2010 with birds of the order Columbiformes. "*" – type host species.

Mite species	Hosts species	Distribution	References
M. aldwelles Glowska and Skoracki 2010	*Geotrygon frenata*	Colombia	Glowska and Skoracki 2010
M. columbicus Skoracki 2011	*Columba oenas**	Kazakhstan	Skoracki 2011
"	*Columba livia*	Poland, Slovakia	Skoracki 2011; this study
"	*Columba palumbus*	Russia, Germany	Skoracki 2011; this study
"	*Treron waalia*	Cameroon	Kaszewska et al. 2014
M. chalcophas Kaszewska, Skoracki and Kavetska, 2016	*Chalcophas indica*	Indonesia (Timor), Australia	Kaszewska et al. 2016; this study
M. ptilinopus **sp. nov.**	*Ptilinopus magnificus**	Australia, Papua New Guinea	This study
"	*Ptilinopus rivoli*	Papua New Guinea	This study
M. lengai **sp.nov.**	*Columba delegorguei**	Tanzania	This study
"	*Streptopelia semitorquata*	Tanzania	This study
"	*Streptopelia orientalis*	Kazakhstan, Kyrgyzstan	This study
M. turacoenas Kaszewska, Skoracki and Kavetska, 2016	*Gallicolumba luzonica*	Philippines	This study
"	*Macropygia aboinensis*	Papua New Guinea	This study
"	*Macropygia phasianella*	Philippines, Indonesia (Java)	This study
"	*Macropygia unchall*	Indonesia (Java), Nepal	This study
"	*Turacoena manadensis**	Indonesia (Sulawesi)	Kaszewska et al. 2016
"	*Turacoena modesta*	Indonesia (Timor)	Kaszewska et al. 2016
M. tympanistria (Skoracki and Dabert, 2002)	*Turtur chalcospilos*	Tanzania	This study
"	*Turtur tympanistria**	Togo, Tanzania	Skoracki and Dabert 2002; this study
M. zenadourae (Clark, 1964)	*Columba livia*	USA (Texas), N. Africa, Djibouti	Casto 1976; Bochkov and Mironov 1998; this study
"	*Geotrygon frenata*	Colombia	This study
"	*Leptotila rufaxilla*	Suriname, Argentina	This study
"	*Leptotila verreauxi*	Colombia	This study
"	*Patagioenas picazuro*	Paraguay	This study
"	*Zenaida asiatica*	USA (Texas)	Casto 1976
"	*Zenaida auriculata*	Argentina	Skoracki and Sikora 2002
"	*Zanaida macroura**	USA (Arizona, Maryland, San Francisco)	Clark 1964; Glowska and Skoracki 2010; this study

Diagnosis

Female. Medium-sized syringophilids, total body length 530–775. Hypostomal apex without median protuberances. Stylophore rounded to slightly constricted posteriorly. Setae *ve* situated anterior to *si*. Apodemes I slightly divergent, not fused to apodemes II. Leg setae *vsII* and *dFII–IV* absent.

Male. Characters as in female, except: total body length 380–555; stylophore constricted posteriorly; apodemes I distinctly divergent, not fused to apodemes II.

Species included

This genus includes eight species associated with birds of the order Columbiformes (Columbidae): *M. aldwelles* Glowska and Skoracki, 2010, *M. columbicus* Skoracki, 2011, *M. chalcophaps* Kaszewska, Skoracki and Kavetska, 2016, *M. ptilinopus* **sp. nov**., *M. lengai* **sp. nov**., *M. turacoenas*, Kaszewska, Skoracki and Kavetska, 2016, *M. tympanistria* (Skoracki and Dabert, 2012), and *M. zenadourae* (Clark, 1964).

Host range

Currently, members of this genus are associated with 25 columbiform host species belonging to following genera: *Columba, Chalcophas, Gallicolumba, Geotrygon, Leptotila, Macropygia, Patagioens, Ptilinopus, Streptopelia, Treron, Turacoena, Turtur*, and *Zenaida*.

Distribution

Palearctic (Germany, Poland, Slovakia, Russia, Kazakhstan, Kyrgyzstan, Nepal), Nearctic (USA), Neotropical (Bolivia, Argentina, Colombia, Paraguay, Suriname), Afrotropical, (Cameroon, Togo, Tanzania), Oriental (Indonesia, Philippines), Oceanian (Papua New Guinea), and Australian (Australia).

Habitat

Under and upper tail-coverts and wing coverts.

Meitingsunes ptilinopus sp. nov.
(Figure 1)

Description

Female, holotype. Total body length 640 (455–530 in 6 paratypes). *Gnathosoma*. Infracapitulum sparsely punctate. Length of stylophore 135 (130–140). Each medial branch of peritremes with 2 chambers, each lateral branch with 3 chambers. *Idiosoma*. Propodonotal shield divided into 3 sclerites – pair of oval, lateral sclerites with bases of setae *ve* and *si*, and unpaired triangular shield with bases of setae *c1*. Length ratio of setae *ve:si:se* 1:2–2.8:3.6–4.9. Hysteronotal shied reduced to small and triangular sclerite, situated between setal bases *d1*. Pygidial shield with concave anterior margin, densely punctate. Length ratio of hysteronotal setae *d2:d1:e2* 1.4:1:1–1.2. Setae *f2* 7.8–11.5 times longer than setae *f1*. Setae *h1* and *f1* subequal in length. Coxal fields I–IV densely punctate. Bases of setae *3a* situated out of coxal fields III. Setae *3 c* 1.6–2.8 times longer than *3b*. Length ratio of setae *ag1:ag2: ag3* 2.5–3.4:1:3.5–4.6. Genital setae (*g1–2*) subequal in length and 1.5–2 times longer than pseudanal setae (*ps1–2*). *Legs*. Length ratio of setae *l'RII:l'RIII:l'RIV* 1:1.3–1.5:1–1.3. Setae *tc"III–IV* 2–2.2 times longer than *tc'III–IV*.

Lengths of setae: *ve* 50 (50–60), *si* 150 (155–160), *se* 245 (220–245), *c1* 215 (215–230), *c2* 210 (205–215), *d1* (170–205), *d2* 240 (210–250), *e2* (185), *f1* 30 (20–30), *f2* 240 (220–240), *h1* 35 (20–30), *h2* 325 (325–350), *ag1* 155 (130–155), *ag2* 60 (45–60), *ag3* 215 (180–210), *g1* and *g2* 35 (30–40), *ps1* and ps2 20 (20), *tc'III–IV* 20 (20–30), *tc"III–IV* 60 (45–60), *l'RII* 45 (45), *l'RIII* 60 (45–70), *l'RIV* 45 (45–60), *3b* 45 (35–55), *3 c* (80–105).

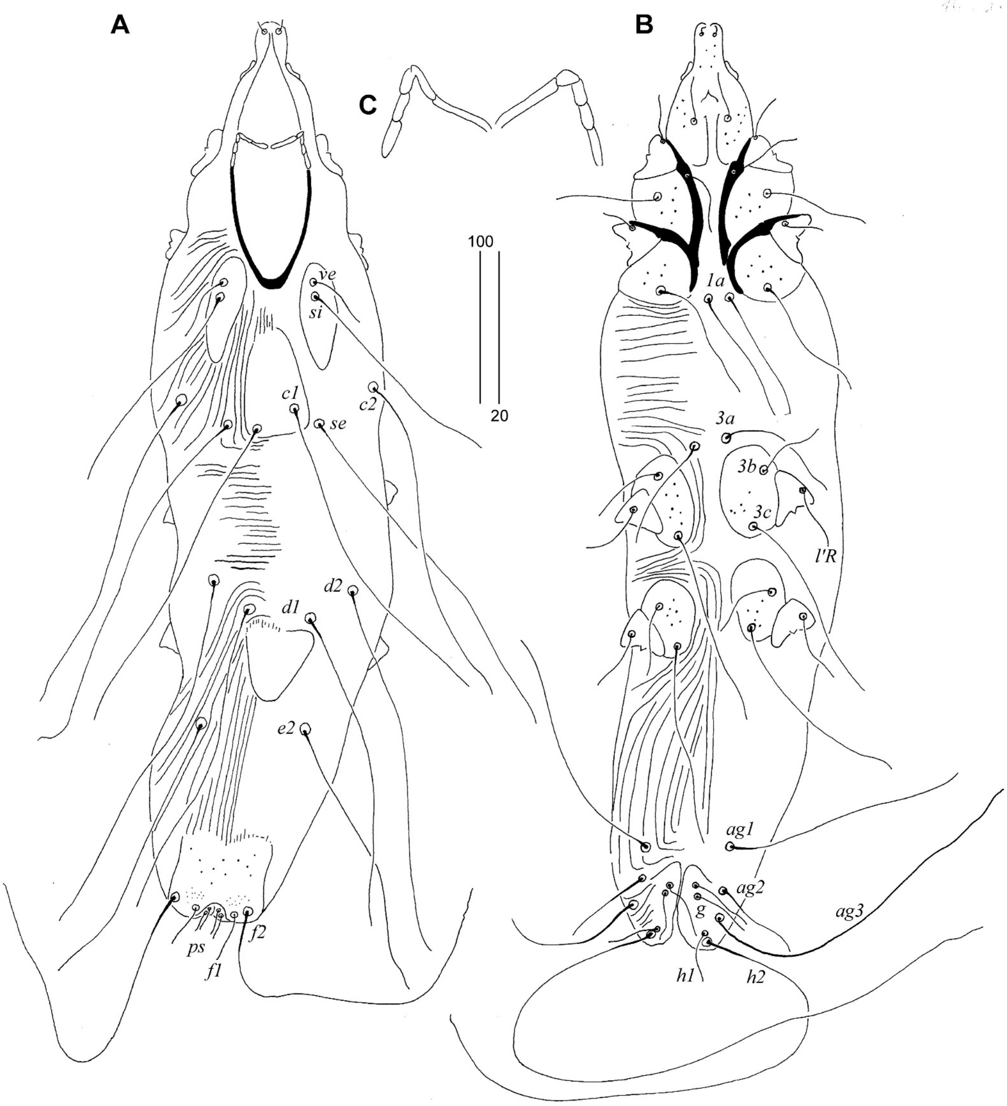

Figure 1. *Meitingsunes ptilinopus* sp. nov., female: (a) dorsal view; (b) ventral view; (c) peritremes. Scale bars: (a, b) = 100 µm; (c) = 20 µm.

Male. Not found.

Type material

Female holotype and 10 female paratypes from quills of under-tail coverts of Wompoo Fruit Dove *Ptilinopus magnificus* (Temminck) (Columbiformes: Columbidae); AUSTRALIA: 1923, no other data [host reg. no. ZSM 26.207].

Type material deposition

All type specimens are deposited in the AMU (reg. no. AMU-SYR. 848), except 2 female paratypes in the ZSM (reg. no. ZSMA20190398).

Additional material

Columbiformes (Columbidae). Ex Wompoo Fruit Dove *Ptilinopus magnificus* (Temminck); PAPUA NEW GUINEA: Aurie, 1910, coll. Hahl [host in the ZSM, uncatalogued]: 3 females deposited in the AMU (reg. no. AMU-SYR.849) and 1 female in the ZSM (reg. no. ZSMA20190399). Ex. White-bibbed Fruit-Dove *Ptilinopus rivoli* (Prévost); PAPUA NEW GUINEA: Morobe Prov., Sattelberg, 1913, coll. Hahl [host reg. no. ZSM 13.99]: 4 females deposited in the AMU (reg. no. AMU-SYR.850) and 1 female in the ZSM (reg. no. ZSMA20190400).

Differential diagnosis

Meitingsunes ptilinopus **sp. nov.** is morphologically most similar to *M. turacoenas* Kaszewska, Skoracki and Kavetska, 2016 described from White-faced Cuckoo Dove *Turacoena manadensis* (Quoy and Gaimard) (Columbidae) from Indonesia (Kaszewska et al. 2016). In females of both species, the propodonotal shield is divided into three apunctate sclerites; bases of setae *ve, si*, and *c1* are situated on the propodonotal shield; the pygidial shield is punctate and with concave anterior margin; and coxal fields I–IV are punctate. This new species differs from *M. turacoenas* by the following features: in females of *M. ptilinopus*, the infracapitulum is punctate; each lateral branch of the peritremes has three chambers; the hysteronotal shield is present; and the length of setae *ag1* is 130–155. In female of *M. turacoenas*, the infracapitulum is apunctate; each lateral branch of the peritremes has 5–6 chambers; the hysteronotal shield is absent; and the length of setae *ag1* is 90–105.

Etymology

The specific epithet "*ptilinopus*" taken from the generic name of the host.

***Meitingsunes lengai* sp. nov.**

(Figure 2)

Description

Female, holotype. Total body length 695 (645–705 in 11 paratypes). *Gnathosoma*. Infracapitulum apunctate. Length of stylophore 150 (145–155). Each medial branch of peritremes with 2

Figure 2. *Meitingsunes lengai* sp. nov., female: (a) dorsal view; (b) ventral view; (c) peritremes. Scale bars: (a, b) = 100 µm; (c) = 20 µm.

chambers, each lateral branch with 5–6 chambers. *Idiosoma.* Propodonotal shield reduced to single oval in shape sclerite with bases of setae *c1* and visible pocket-like structures situated near bases of setae *ve* and *si*. Length ratio of setae *ve:si:se* 1:1.6–2.6:2.9–3.5. Hysteronotal shield variable, weakly sclerotized or absent. Pygidial shield apunctate with concave anterior margin. Length ratio of setae *d2:d1:e2* 1.3–1.5:1:1–1.5. Setae *f2* 6.2–8.2 times longer than setae *f1*. Setae *h1* and *f1* subequal in length. Coxal fields I–IV well sclerotized and apunctate. Bases of setae *3a* situated out of coxal fields III. Setae *3 c* 1.3–1.8 times longer than *3b*. Length ratio of setae *ag1:ag2:ag3* 2–2.2:1:2.7–3.4. Genital setae (*g1–2*) subequal in length and twice as long as pseudanal setae (*ps1–2*). *Legs.* Length ratio of setae *l'RII:l'RIII:l'RIV* 1.2–1.3:1:1–1.2. Setae *tc"III–IV* 1.7–2.3 times longer than *tc'III–IV*.

Lengths of setae: *ve* 75 (80–95), *si* 195 (155–195), *se* 265 (255270), *c1* (240–270), *c2* (255–270), *d1* 165 (170–190), *d2* 260 (250260), *e2* 230 (210–230), *f1* 30 (25–35), *f2* 210 (205–220), *h1* (30–35), *h2* 380 (335–380), *ag1* 140 (135–165), *ag2* 70 (55–85), *ag3* 240 (225–240), *g1* and *g2* 40 (30–40), *ps1* and ps2 20 (15–20), *tc'III–IV* 30 (35–40), *tc"III–IV* 55 (60–70), *l'RII* 50 (35–-45), *l'RIII* 60 (35–55), *l'RIV* 55 (60–70), *3b* 85 (60–80), *3 c* 100 (85–105).

Male. Not found.

Type material

Female holotype and 18 female paratypes from quill of under-tail coverts of Estern Bronze-naped Pigeon *Columba delegorguei* Delegorgue (Columbiformes: Columbidae); TANZANIA: Arusha, USA-river, 12 April 1960, coll. Nagy [host reg. no. ZSM 60.2015].

Types deposition

All type specimens are deposited in the AMU (reg. no. AMU-SYR. 851), except 4 female paratypes in the ZSM (reg. no. ZSMA20190401).

Additional material

Columbiformes (Columbidae). Ex Red-eyed Dove *Streptopelia semitorquata* (Rüppell); TANZANIA: Pwani, Soga, 9 February 1962, coll. Th. Andersen [host reg. no. ZSM 62.41]: 12 females deposited in the AMU (reg. no. AMU-SYR 852) and 4 females in the ZSM (reg. no. ZSMA20190402). Ex Oriental Turtle-Dove *Streptopelia orientalis* (Latham); KAZAKHSTAN: Semipalatinsk, 10 June 1921, coll. Kriestofik [host reg. no. ZSM 27.147]; 2 females deposited in the AMU (reg. no. AMU-SYR.853) and 2 females in the ZSM (reg. no. ZSMA20190403). Ex same host species; KYRGYZSTAN: Tian-Schan, Naryn Distr., 15 May 1909, coll. Datschenko and Laurenty [host reg. no. ZSM 12.362]; 2 females deposited in the AMU (reg. no. AMU-SYR 854) and 2 females in the ZSM (reg. no. ZSMA20190404).

Differential diagnosis

Meitingsunes lengai **sp. nov**. is morphologically most similar to *M. chalcophas* Kaszewska, Skoracki and Kavetska, 2016 described from Common Emerald Dove *Chalcophas indica* (Linnaeus) (Columbidae) from Indonesia (Kaszewska et al. 2016). In females of both species, the infracapitulum is apunctate; each lateral branch of the peritremes has six chambers; coxal fields I–IV are apunctate; and setae *3a* are situated out of coxal fields III. Females of *Meitingsunes lengai* differ from *M. chalcophas* by the following features: the propodonotal shield is reduced to a pair pocket-like structures situated near the bases of setae *ve* and *si*; the pygidial shield is apunctate and with distinctly concave anterior margin; the lengths of setae *se, c2*, and *d2* are 255–270, 255–270, and 250–260 respectively. In *M. chalcophas*, the propodonotal shield is divided into a pair of triangular apunctate sclerites; the pocket-like structures are absent, the pygidial shield is punctate near the bases of setae *f1* and *f2*; the lengths of setae *se, c2*, and *d2* are 185–215, 190–195, and 210–215, respectively.

Etymology

The name "*lengai*" is taken from active volcano Ol Doinyo Lengai located in the Gregory Rift within the Arusha Region of Tanzania where the type host species has been collected.

Meitingsunes aldwelles Glowska and Skoracki, 2010

Meitingsunes aldwelles Glowska and Skoracki, 2010: 65, figs 11–13. Holotype deposited in the AMU, examined.
Type host: *Geotrygon frenata* (Tschudi) (Columbiformes: Columbidae). Type locality: Colombia.

Diagnosis

Female. Total body length 530–570. Infracapitulum apunctate. Each medial branch of peritremes with 1–2 chambers, each lateral branch with 4–6 chambers. Propodonotal shield entire and rectangular in shape, laterally punctate, pocket-like structures absent. Hysteronotal shield entire and fused to apunctate pygidial shield. Coxal fields apunctate, setae *3a* situated out of coxal fields III. Setae *f1* two times longer than *h1*. Lengths of setae: *ve* 105–110, *si* 180–190, *se* 245, *f1* 30–35, *h1* 15.

Male. Unknown.

Host and distribution

Columbiformes (Columbidae) – White-throated Quail-Dove *Geotrygon frenata* (Tschudi) from Colombia (Glowska and Skoracki 2011).

Meitingsunes columbicus Skoracki, 2011

Meitingsunes columbicus, Skoracki, 2011: 302, figs 222–224. Holotype deposited in the AMU, examined.
Type host: *Columba oenas* Linnaeus (Columbiformes: Columbidae). Type locality: Kazakhstan.

Diagnosis

Female. Total body length 720–880. Infracapitulum apunctate. Each medial branch of peritremes with 2–3 chambers, each lateral branch with 5–6 chambers. Propodonotal shield entire and rectangular in shape, punctate, pocket-like structures absent. Hysteronotal shield entire and fused to apunctate pygidial shield. Coxal fields apunctate, setae *3a* situated on coxal fields III. Setae *f1* and *h1* subequal in length. Lengths of setae: *ve* 105–110, *si* 180–185, *se* 225–260, *f1* 30–40, *h1* 30–40.

Male. Total body length 515–555. Each medial branch of peritremes with 3–4 chambers, each lateral branch with 4 chambers. Propodonotal shield punctate, pocket-like structure absent. Hysteronotal shield apunctate. Setae *f2* and *h2* subequal in length. Coxal fields I–IV apunctate, setae *3a* situated on coxal fields III. Lengths of setae: *d2* 165–195, *d1* 25–30, *e2* 30–40.

Hosts and distribution

Columbiformes (Columbidae) – Stock Dove *Columba oenas* Linnaeus (Columbidae) from Kazakhstan (Skoracki 2011), Feral Pigeon *Columba livia f. urbana* from Poland (Skoracki 2011) and Slovakia **[new locality]** (this study), Common Wood-Pigeon *Columba palumbus* Linnaeus from Russia (Novogrod Prov.) (Skoracki 2011), and Germany **[new locality]** (this study), and Green-Pigeon *Treron waalia* (Meyer) from Cameroon (Kaszewska et al. 2014).

New material examined

Ex. *Columba livia f. urbana*; SLOVAKIA: Tulčík, 28 September 1998, coll. Oboňa: 8 females deposited in the AMU (reg. no. AMU-SYR. 855). Ex. *Columba palumbus*; GERMANY: Regensburg, 2 August 1910, coll. J. Gengler [host reg. no. ZSM 28.2939]: 6 females deposited in the AMU (reg. no. AMU-SYR.856.), 2 females in the ZSM (reg. no. ZSMA20190405).

Meitingsunes chalcophaps Kaszewska, Skoracki and Kavetska, 2016

Meitingsunes chalcophaps Kaszewska et al., 2016: 2, figs 1, 2, 3A–F. Holotype deposited in the AMU, examined.
Type host: *Chalcophaps indica* (Linnaeus) (Columbiformes: Columbidae). Type locality: Indonesia (W. Timor).

Diagnosis

Female. Total body length 615–720. Infracapitulum apunctate. Each medial branch of peritremes with 3 chambers, each lateral branch with 6–7 chambers. Propodonotal shield divided into 2 triangular apunctate sclerites, pocket-like structure absent. Hysteronotal shield reduced to single triangular sclerite, bearing bases of setae *d1*. Pygidial shield densely punctate between bases of setae *f1* and *f2*. Coxal fields I–IV apunctate. Setae *3a* situated out of coxal fields III. Setae *f1* and *h1* subequal in length. Length of setae: *ve* 60–70, *si* 165–180, *se* 185–215, *f1* 30, *h1* 35.

Male. Total body length 465–500. Each medial branch of peritremes with 3–4 chambers, each lateral branch with 5–6 chambers. Propodonotal shield punctate, pocket-like structure absent. Hysteronotal shield punctate near bases of setae *d1*, medial part indiscernible. Setae *f2* and *h2* subequal in length. Coxal fields I–IV apunctate, setae *3a* situated out of coxal field III. Length of setae *d2* 120–160, *d1* 25, *e2* 30.

Host and distribution

Columbiformes (Columbidae) – Emerald Dove *Chalcophaps indica* (Linnaeus) from Indonesia (Timor) (Kaszewska et al. 2016) and Australia [**new locality**] (this study).

New material examined

Ex Emerald Dove *Chalcophaps indica*; AUSTRALIA: Queensland, Cooktown, 10 October 1896, coll. R. Suess [host in the ZSM, uncatalogued]: 5 females deposited in the AMU (reg. no. AMU-SYR.875).

Meitingsunes turacoenas Kaszewska, Skoracki and Kavetska, 2016

Meitingsunes turacoenas Kaszewska et al., 2016: 5, figs 3 G, 4. Holotype deposited in the AMU, examined.
Type host: *Turacoena manadensis* (Quoy and Gaimard) (Columbiformes: Columbidae). Type locality: Indonesia (Sulawesi Isl.).

Diagnosis

Female. Total body length 485–580. Infracapitulum apunctate. Each medial branch of peritremes with 2–3 chambers, each lateral branch with 5–6 chambers. Propodonotal shield divided into pair of lateral and apunctate shields, bearing bases of setae *ve* and *si* and unpaired medial sclerite, bearing bases of setae *c1*, pocket-like structure absent. Hysteronotal shield absent. Pygidial shield sparsely punctate, with deeply concave anterior margin. Coxal fields sparsely punctate, bases of setae *3a* situated out of coxal fields III. Setae *f1* and *h1* subequal in length. Length of setae: *ve* 60–70, *si* 165–180, *se* 185–215, *f1* 30, *h1* 35.

Male. Unknown.

Hosts and distribution

Columbiformes (Columbidae) – Luzon Bleeding-heart *Gallicolumba luzonica* (Scopoli) **[new host]** from Philippines, Amboyna Cuckoo-Dove *Macropygia amboinensis* (Linnaeus) **[new host]** from Papua New Guinea, Brown Cuckoo-Dove *Macropygia phasianella* (Temminck) **[new host]** from Papua New Guinea and Philippines, Barred Cuckoo-Dove *Macropygia unchall* (Wagler) **[new host]** from Papua New Guinea and Nepal (this study), White-faced Cuckoo-Dove *Turacoena manadensis* (Quoy and Gaimard) and Black Cuckoo-Dove *Turacoena modesta* (Temminck) both from Indonesia (Kaszewska et al. 2016).

New material examined

Ex. *Gallicolumba luzonica* (Scopoli); PHILIPPINES: Luzon, Manila, 1930, coll. I. Marschall [host reg. no. ZSM 30.216]: 5 females deposited in the AMU (reg. no. AMU-SYR.857) and 2 females in the ZSM (reg. no. ZSMA20190406). Ex. *Macropygia aboinensis*; PAPUA NEW GUINEA: 1 March 1910, coll. Wiedenfeld [host in the ZSM, uncatalogued]: 2 females deposited in the AMU (reg. no. AMU-SYR.858). Ex. *Macropygia phasianella*; PHILIPPINES: Luzon, Manila, 1930, coll. I. Marschall [host reg. no. ZSM 30.209]: 3 females deposited in the AMU (reg. no. AMU-SYR.859). Ex. same host species; PHILIPPINES: Luzon, Manila, 1896, coll. Dalmas [host reg. no. ZSM 09.4358]: 4 females deposited in the AMU (reg. no. AMU-SYR.860) and 2 females in the ZSM (reg. no. ZSMA20190407). Ex. same host species; INDONESIA: Java, Gede, Djampang, 1 July 1909, coll. A. Primavesi [host in the ZSM, uncatalogued]: 2 females deposited in the AMU (reg. no. AMU-SYR.861). Ex. same host species; INDONESIA: Java, Trinil, 1908, coll. Elbert [host reg. no. ZSM 08.859]: 4 females deposited in the AMU (reg. no. AMU-SYR.862). Ex. *Macropygia unchall*; INDONESIA: Java, Gede, Soekaboemi, 1910, coll. A. Primavesi [host in ZSM, uncatalogued]: 3 females deposited in the AMU (reg. no. AMU-SYR.863) and 2 females in the ZSM (reg. no. ZSMA20190408). Ex. same host species; NEPAL: 16 March 1961, coll. R.L. Fleming [host reg. no. ZSM 62.1879]: 8 females deposited in the AMU (reg. no. AMU-SYR.863B).

Meitingsunes tympanistria (Skoracki and Dabert, 2002)

Peristerophila tympanistria Skoracki and Dabert, 2002: 141, figs 8–15. Holotype deposited in the RMCA, examined.
Meitingsunes tympanistria, Glowska and Skoracki 2010: 65.
Type host: *Turtur tympanistria* (Temminck) (Columbiformes: Columbide). Type locality: Togo.

Diagnosis

Female. Total body length 530–570. Infracapitulum apunctate. Each medial branch of peritremes with 3 chambers, each lateral branch with 5–6 chambers. Propodonotal shield entire, pocket-like structures absent. Hysteronotal shield reduced to triangular and punctate sclerite, bearing bases of setae *d1*, not fused to pygidial shield. Coxal fields apunctate, setae *3a* situated out of coxal fields III. Setae *f1* and *h1* subequal in length. Length of setae: *ve* 85–95, *si* 160–175, *se* 250, *f1* 30–35, *h1* 30.

Male. Total body length 510. Each medial branch of peritremes with 3 chambers, each lateral branch with 5–6 chambers. Propodonotal shield punctate, pocket-like structures absent. Hysteronotal shield punctate. Coxal fields I–IV apunctate, setae *3a* situated out of coxal fields III. Lengths of setae: *d2* 225, *d1* 30, *e2* 35–45.

Hosts and distribution

Columbiformes (Columbidae) – Emerald-spotted Wood-Dove *Turtur chalcospilos* (Wagler) [**new host**] from Tanzania (this study), Tambourine Dove *Turtur tympanistria* (Temminck) from Togo (Skoracki and Dabert 2002) and Tanzania [**new locality**] (this study).

New material examined

Ex. *Turtur chalcospilos*; TANZANIA: Soga, February 1962, coll. Th. Andersen (host in the ZSM, uncatalogued): 2 females deposited in the AMU (reg. no. AMU-SYR.865) and 2 females in the ZSM (reg. no. ZSMA20190409). Ex. *Turtur tympanistria*; TANZANIA: Arusha Region, Meru Mt., 2 February 1959, coll. Nagy [host reg. no. ZSM 60.1373]: 8 females deposited in the AMU (reg. no. AMU-SYR.866) and 2 females in the ZSM (reg. no. ZSMA20190410).

Meitingsunes zenadourae (Clark, 1964)

Syringophilus zenadourae Clark, 1964: 83, figs 22 and 23. Paratypes deposited in FMNH, examined.
Peristerophila zenadourae, Kethley 1970: 56.
Meitingsunes zenadourae, Glowska and Skoracki 2010: 62, figs. 1–8.
Type host: *Zenaida macroura* (Linnaeus) (Columbiformes: Columbidae). Type locality: USA (Maryland).

Diagnosis

Female. Total body length 620–645. Infracapitulum apunctate. Each medial branch of peritremes with 2 chambers, each lateral branch with 5–6 chambers. Propodonotal shield entire, rectangular in shape, bearing bases of setae *ve, si, se*, and *c1*, distinctive punctate. Hysteronotal shield divided into pair of small sclerites surrounding bases of setae *d2* and unpaired sclerite fused to punctate pygidial shield. Coxal fields sparsely punctate, setae *3a* situated out of coxal field III. Setae *f1* and *h1* subequal in length. *Length of setae: ve* 70–85, *si* 140–170, *se* 235, *f1* 35–45, *h1* 35–45.

Male. Unknown.

Hosts and distribution

Columbiformes (Columbidae) – Rock Pigeon *Columba livia* Gmelin from USA (Texas) (Casto 1976), North Africa (Bochkov and Mironov 1998), Djibouti **[new locality]** (this study), White-throated Quail-Dove *Geotrygon frenata* (Tschudi) **[new host]** from Colombia, Picazuro Pigeon *Patagioenas picazuro* (Temminck) **[new host]** from Paraguay, Grey-Fronted Dove *Leptotila rufaxilla* (Richard and Bernard) **[new host]** from Suriname and Argentina, White-Tipped Dove *Leptotila verreauxi* (Bonaparte) **[new host]** from Colombia (this study), White-winged Dove *Zenaida asiatica* (Linnaeus) from USA (Texas) (Casto 1976), Eared Dove *Zenaida auriculata* (Des Murs) from Argentina (Skoracki and Sikora 2002), Mourning Dove *Zenaida macroura* (Linnaeus) from USA (Arizona **[new locality]**, Maryland, San Francisco) (Clark 1964; Glowska and Skoracki 2010; this study).

New material examined

Ex. *Columba livia*; DJIBOUTI: November 1980, coll. Gaud: 14 female paratypes deposited in AMU (reg. no. AMU-SYR.867). Ex. *Geotrygon frenata*; COLOMBIA: Pueblo Rico, 27 October 1972, coll. Palmer: 6 females deposited in the AMU (reg. no. AMU-SYR.868). Ex. *Patagioenas picazuro*; PARAGUAY: Alto Parana, 15 May 1938, coll. Neunteufel [host in the ZSM, uncatalogued]: 9 females deposited in the AMU (reg. no. AMU-SYR.869) and 2 females in the ZSM (reg. no. ZSMA20190411). Ex. same host species; PARAGUAY:

Cambyreta, 7 August 1935, coll. Neunteufel [host. reg. no. ZSM 36.240]; 18 females deposited in the AMU (reg. no. AMU-SYR. 870). Ex. *Leptotila rufaxilla*; SURINAME: Paramaribo, 22 January 1961, coll. F. Haverschmidt [host reg. no. ZSM 61.407]: 5 females deposited in the AMU (reg. no. AMU-SYR. 871). Ex. same host species; ARGENTINA: Salta, August 1898, coll. F. Silvestri [host reg. no. ZSM 21.120]: 6 females deposited in the AMU (reg. no. AMU-SYR.872). Ex. *Leptotila verreauxi*; COLOMBIA: 2 km west of El Bardo, Dep. Cauca, 11 November 1965, coll. J. Haffer [host reg. no. ZSM 67.412]: 4 females deposited in the AMU (reg. no. AMU-SYR.873) and 2 females in the ZSM (reg. no. ZSMA20190412). Ex. *Zenaida macroura*; USA: Arizona, Mahave Co., 25 October 2006, coll. unknown: 4 female deposited in AMU (reg. no. AMU-SYR.874).

Key to Meitingsunes species

(Females)

(1) Pocket-like structures near bases of setae *ve* and *si* present … *M. lengai* **sp. nov**.
– Pocket-like structures near bases of setae *ve* and *si* absent … 2

(2) Length ratio of setae *f1:h1* 2:1 … *M. aldwelles* Glowska and Skoracki, 2010
– Length ratio of setae *f1:h1* 1:1 … 3

(3) Setae *3a* situated on coxal fields III … *M. columbicus* Skoracki, 2011
– Setae *3a* situated off coxal fields III … 4

(4) Propodonotal shield entire … 5
–Propodonotal shield divided into two or three sclerites … 6

(5) Hysteronotal shield represented by 3 separate sclerites … *M. zenadourae* (Clark, 1964)
– Hysteronotal shield represented by single and punctate shield … *M. tympanistria* (Skoracki and Dabert, 2002)

(6) Hysteronotal shield absent … *M. turacoenas* Kaszewska, Skoracki and Kavetska, 2016
– Hysteronotal shield present … 7

(7) Setae *ve* and *si* situated on propodonotal shield, infracapitulum and coxal fields III–IV punctate … *M. ptilinopus* **sp. nov.**
– Setae *ve* and *si* situated out of the propodonotal shield, infracapitulum and coxal fields III–IV apunctate … *M. chalcophas* Kaszewska, Skoracki and Kavetska, 2016

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No potential conflict of interest was reported by the authors.

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New species and records of the quill mites of the genus Peristerophila Kethley, 1970 (Acariformes: Syringophilidae) associated with pigeons and doves (Aves: Columbiformes).

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New species and records of the quill mites of the genus *Peristerophila* Kethley, 1970 (Acariformes: Syringophilidae) associated with pigeons and doves (Aves: Columbiformes)

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Abstract

The fauna of the quill mite genus *Peristerophila* Kethley, 1970 (Acariformes: Prostigmata: Syringophilidae) associated with pigeons and doves (Aves: Columbiformes) is reviewed. In our study, we examined 109 species of columbiform hosts of which 28 species belonging to nine genera were infested by *Peristerophila* mites. In the analyzed mite material, six species of this genus were found including two new species described herein: *P. geopelis* **sp. nov.** from *Geopelia cuneata*, *G. placida*, *G. striata*, as well as *Ocyphaps lophotes* and *P. leucomela* **sp. nov.** from *Columba leucomela.* Additionally, eighteen new host species and many new locality records for the previously described taxa are reported.

Key words: Acari, birds, ectoparasites, Columbiformes, systematics

Introduction

Quill mites of the family Syringophilidae Lavoipierre (Acariformes: Prostigmata) are highly specialized mono- or stenoxenous ectoparasites of birds. These mites feed and reproduce inside quills of feathers (Kethley 1970). Currently, syringophilid mites are represented by 400 species grouped in 62 genera and recorded from about 670 bird species belonging to 27 orders (Zmudzinski *et al*. 2020).

The Columbiformes is one of the most diverse and cosmopolitan orders of birds. This order comprises 321 species grouped in one family, the Columbidae (Clements *et al*. 2019), and is distributed in all zoogeographical regions, except the Arctic and Antarctic (Gibbs *et al*. 2001).

The quill mite fauna associated with columbiforms was extensively studied and currently includes 14 species belonging to four genera of the subfamily Syringophilinae Lavoipierre, i.e. *Peristerophila* Kethley, 1970, *Meitingsunes* Glowska and Skoracki, 2010, *Psittaciphilus* Fain, Bochkov and Mironov, 2000, and *Terratosyringophilus* Bochkov and Perez, 2002, and seven species of the genus *Gunabopicobia* Skoracki and Hromada, 2013 of the subfamily Picobiinae Johnston and Kethley (Skoracki & Glowska 2008; Skoracki 2011; Kaszewska *et al*. 2014, 2016, 2018; Kaszewska & Skoracki 2018).

Peristerophila is one of many syringophilid genera associated with non-passeriform birds and, currently, 12 species of this genus have been described from hosts of six avian orders: Accipitriformes, Bucerotiformes, Columbiformes, Coraciiformes, Falconiformes, and Psittaciformes (Zmudzinski *et al*. 2020). Most *Peristerophila* species are restricted to a particular host order, except *P. mucuya* Casto, 1980, which is known from hosts of the orders Columbiformes and Psittaciformes. Moreover the genus *Peristerophila* is characterized by presence of two forms of the females—homeomorphic and heteromorphic (Skoracki *et al*. 2020)—similar to the genera *Stibarokris* Kethley, 1970 and *Chenophila* Kethley, 1970.

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Currently, there are four known *Peristerophila* species associated with columbiform hosts: *P. columbae* (Hirst, 1920), *P. claravis* (Skoracki and Glowska, 2008), *P. mucuya* Casto, 1980, and *P. lature* Kaszewska, Kavetska and Skoracki, 2014 (Table 1). In this paper, we review all above-mentioned species and describe two new species: *P. geopelis* **sp. nov.** and *P. leucomela* **sp. nov.** Additionally, we report 18 new host species, and many new locality records for the previously described taxa.

TABLE 1. Quill mite species of the genus *Peristerophila* Kethley 1970 associated with birds of the order Columbiformes; *—type host species; pp—present paper.

Mites species	Hosts species	Distribution	References
P. columbae (Hirst, 1920)	*Columba arguatrix* (Temminck)	Kenya	**pp**
	Columba guinea Linnaeus	South Africa	**pp**
		Tanzania	**pp**
	Columba leuconota (Vigors)	Nepal	**pp**
	Columba livia Gmelin*	Canada	**pp**
		England	Nattres & Skoracki 2009
		India	Bochkov & Mironov 1998
		Iran	Bochkov & Mironov 1998
		Macedonia	**pp**
		Poland	Skoracki 2011
		Turkey	Bochkov & Mironov 1998
		USA	Hirst 1920
	Columba oenas Linnaeus	Germany	**pp**
	Columba palumbus Linnaeus	England	**pp**
		Germany	**pp**
	Columba trocaz Heineken	Portugal	**pp**
	Geotrygon chiriquensis Sclater	Panama	**pp**
	Patagioenas speciosa (Gmelin)	Surinam	**pp**
	Streptopelia capicola (Sundevall)	Angola	**pp**
	Streptopelia decaocto (Frivaldszky)	Jordan	Skoracki 2011
	Streptopelia decipiens (Hartlaub and Finsch)	Macedonia	**pp**
		Tanzania	**pp**
	Streptopelia orientalis (Latham)	Japan	**pp**
	Streptopelia semitorquata (Rueppell)	Angola	**pp**
		Tanzania	pp
		D. R. Congo	**pp**
	Streptopelia tranquebarica (Hermann)	China	**pp**
	Streptopelia turtur (Linnaeus)	Germany	**pp**
		Greece	**pp**
		Hungary	**pp**
		Macedonia	**pp**
P. claravis (Skoracki and Glowska, 2008)	*Claravis pretiosa* Ferrari-Pérez*	Bolivia	Skoracki & Glowska 2008
		Colombia	**pp**
		Panama	**pp**

......*continued on the next page*

TABLE 1. (Continued)

Mites species	Hosts species	Distribution	References
		Paraguay	**pp**
	Oena capensis (Linnaeus)	Ethiopia	**pp**
		Sudan	**pp**
		Tanzania	**pp**
P. geopelis **sp. nov.**	*Geopelia cuneata* (Latham)	Australia	**pp**
	Geopelia placida Gould	Australia	**pp**
	Geopelia striata (Linnaeus)*	Indonesia (Celebos)	**pp**
		Indonesia (Java)	pp
		Indonesia (Sumatra)	**pp**
	Ocyphaps lophotes (Temminck)	Australia	**pp**
P. lature Kaszewska, Kavetska and Skoracki, 2014	*Ducula luctuosa** (Temminck)	Indonesia (Sulawesi Isl.)	Kaszewska *et al*. 2014
	Ducula spilorrhoa (Gray)	Papua New Guinea	Kaszewska *et al*. 2014
	Ptilinopus jambu (Gmelin)	Indonesia (Sumatra)	Kaszewska *et al*. 2014
	Ptilinopus melanospilus (Salvadori)	Indonesia (Mount Gade)	Kaszewska *et al*. 2014
	Ptilinopus porphyreus (Temminck)	Indonesia (Java)	Kaszewska *et al*. 2014
	Ptilinopus regina (Swainson)	Mariana Isl.	Kaszewska *et al*. 2014
P. leucomela **sp.nov.**	*Columba leucomela* Temminck*	Australia	**pp**
P. mucuya (Casto, 1980)	*Columbina minuta* Linnaeus	Paraguay	**pp**
	Columbina passerina (Linnaeus)*	Colombia	**pp**
		Surinam	**pp**
		USA	Casto 1980
	Columbina squammata (Lesson)	Brazil	Bochkov & Fain, 2003
		Paraguay	**pp**
	Columbina talpacoti (Temminck)	Brazil	Skoracki & Glowska 2008; **pp**
		Monaco	**pp**
		Surinam	**pp**
		Trinidad and Tobago	**pp**
	Geophaps plumifera Gould	Australia	Bochkov & Fain, 2003
	Metriopelia ceciliae (Lesson)	Peru	**pp**
	Metriopelia melanoptera (Molina)	Argentina	Skoracki & Glowska

Materials and methods

The new material used in the present study was collected from dry bird skins housed in the ornithological collection of the Bavarian State Collection of Zoology, Munich, Germany (ZSM) according to the technique described by Skoracki (2011). Before mounting, mites were softened and cleared in Nesbitt's solution at room temperature for three days (Skoracki 2011). Mites were mounted on slides in Hoyer's medium. Identifications and drawings of mite specimens were carried out with an Olympus BH-2 light microscope (Olympus Corp., Japan), equipped with DIC optics and a camera lucida. All measurements are in micrometers. In the descriptions below, the idiosomal chaetotaxy follows Grandjean (1939) as adapted for Prostigmata by Kethley (1990). The nomenclature of leg setae follows that proposed by Grandjean (1944). Morphological terminology follows Skoracki (2011). Measurements (ranges) of paratypes are given in brackets following data for a holotype. The length of legs is measured from the proximal margin of trochanter to the distal tip of tarsus. The scientific names of the birds follow Clements *et al*. (2019). Zoogeographic regions follow Holt *et al*. (2013). Specimen depositories are cited using the following abbreviations: AMU—A. Mickiewicz University, Department of Animal Morphology, Poznan, Poland; ZSM—Bavarian State Collection of Zoology, Munich, Germany.

Results

Family Syringophilidae Lavoipierre, 1953

Subfamily Syringophilinae Lavoipierre, 1953

Genus *Peristerophila* Kethley, 1970

Peristerophila Kethley, 1970: 53.
Type species. *Syringophilus columbae* Hirst, 1920, by the original designation.

Diagnosis. FEMALE, HOMEOMORPHIC FORM. Medium-size syringophilids: total body length 535–750. Hypostomal apex with two pairs of medial sausage-like protuberances. Stylophore rounded posteriorly. Gnathosoma 1.2–1.5 times longer than apodemes I. Propodonotal shield entire (Fig. 1D) or divided into 3 sclerites (Fig. 1A–C). Five pairs of propodonotal setae present (*vi* absent). Bases of setae *ve*, *si*, and *c1* situated on propodonotal shield or out off this shield. Hysteronotal shield variable, if present fused (Fig. 1E) or not to pygidial shield (Fig. 1F–H). Apodemes I parallel and fused to apodemes II. Length ratio of legs I:II 1–1.2:1. Leg setae *vsII* and *dFII–IV* absent.

FEMALE, HETEROMORPHIC FORM. Characters as in homeomorphic female, except: total body length 800–1000; apodemes I and gnathosoma equal in length; legs I 1.3–1.6 times longer than legs II.

MALE. Characters as in female, except: total body length 335–455; hypostomal apex smooth; propodonotal shield entire; apodemes I divergent posteriorly, not fused to apodemes II.

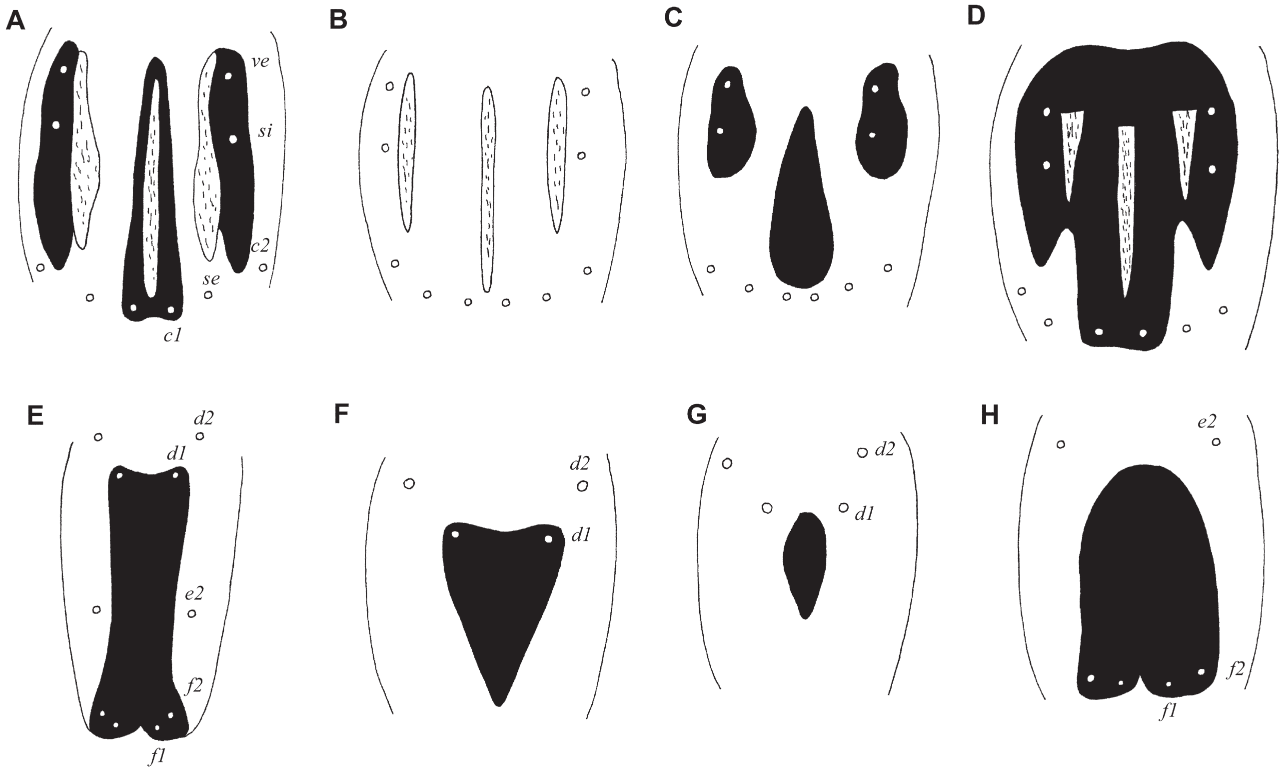

FIGURE 1. Scheme of details of *Peristerophila* idiosomal sclerotizations (females). **A–D,** propodonotal shield; **E–G,** hysteronotal shield; **H,** pygidial shield.

Species included. This genus includes five species associated exclusively with columbiform birds: *P. claravis*

(Skoracki and Glowska, 2008), *P. columbae* (Hirst, 1920), *P. geopelis* **sp. nov**., *P. lature* Kaszewska, Kavetska and Skoracki, 2014, *P. leucomela* **sp nov**., one species associated with columbiform and psittaciform birds: *P. mucuya* (Casto, 1980), and six species associated with non-columbiform birds: *P. accipitridicus* Skoracki, Lontkowski and Stawarczyk, 2010 (Accipitiformes), *P. meropis* (Skoracki, Hromada and Sikora, 2017) (Coraciiformes), *P. falcophila* Skoracki and Hromada, 2018 (Falconiformes), *P. forpi* (Bochkov and Perez, 2002) (Psittaciformes), *P. nestoriae* Marciniak, Skoracki and Hromada, 2019 (Psittaciformes), and *P. upupi* Klimovicova, Mikula, Kahure and Hromada, 2014 (Bucerotiformes).

Columbiform hosts. Members of this genus are associated with 46 species belonging to the following genera: *Columba*, *Columbina*, *Claravis*, *Ducula*, *Geopelia*, *Geophaps*, *Geotrygon*, *Metriopelia*, *Ocyphaps*, *Oena*, *Patagioenas*, *Ptilinopus*, and *Streptopelia*.

Habitats. Quills of primaries, secondaries, wing coverts, under- and upper tail coverts, and contour feathers.

Review of the Peristerophila species associated with Columbiformes

Peristerophila geopelis sp. nov.

(Figure 2, 4C–D)

Description. FEMALE, HOMEOMORPHIC FORM (HOM), holotype. Total body length 685 (560–680 in 9 paratypes). *Gnathosoma*. Gnathosoma 90 (85–95) long. Infracapitulum densely punctate. Stylophore 130 (130–145) long. Each medial branch of peritremes with 2 chambers, each lateral branch with 4–5 chambers. *Idiosoma*. Propodonotal shield entire, T-shaped, with punctate belt-like ornament, bases of setae *ve* and *si* situated on this shield. Length ratio of setae *ve:si:se* 1:1.5–2:7.5–11. Hysteronotal shield reduced to narrow and oval sclerite. Pygidial shield punctate in posterior part. Length ratio of setae *d2:d1:e2* 1.2–1.3:1:1. Setae *f2* 6–7.8 times longer than setae *f1*. Setae *h1* and *f1* subequal in length. Coxal fields I–IV punctate. Bases of setae *3a* situated out of coxal fields III. Setae *3c* 2.6–3.1 times longer than *3b*. Length ratio of setae *ag1:ag2:ag3* 2–2.3:1:1.6. Genital setae (*g1–2*) and pseudanal setae (*ps1–2*) subequal in length. *Legs*. Length ratio of legs I:II 1–1.2:1. Setae *tc"III–IV* 1.3–1.8 times longer than *tc'III–IV.* Lengths of setae: *ve* 15 (15–20), *si* 30 (30–35), *se* 225 (205–220), *c1* 260 (230–240), *c2* 220 (185–230), *d1* 185 (170–185), *d2* 245 (230–235), *e2* 190 (170–180), *f1* (30), *f2* (180–190), *h1* (30), *h2* (280–310), *ag1* 95 (85–90), *ag2* 40 (40–45), *ag3* 145 (145–150), *g1* and *g2* 20 (15–20), *ps1* and *ps2* 15 (15–20), *tc'III–IV* 30 (25–30), *tc"III–IV* 35 (40–45), *3b* 30 (30), *3c* (80–95). Length of apodemes I 70 (60–75), length of legs I 65 (65–70), legs II 55 (55–70).

FEMALE HETEROMORPHIC FORM. Characters as in homeomorphic female, except: total body length 730–795; length of gnathosoma 85; apodemes I and gnathosoma subequal in length; legs I 1.3 times longer than II; length of apodemes I 85, length of legs I 80, legs II 60.

MALE. Not found.

Type material. Female (HOM) holotype and paratypes: 2 females (HOM), 1 female (HET), 1 tritonymph, 1 larva (reg. no. AMU-SYR.901) from Zebra Dove *Geopelia striata* (Linnaeus) (Columbiformes: Columbidae), **INDONESIA:** Java, Trinil, coll. W. Elbert [host reg. no. ZSM 08.862]; 4 females (HOM) (reg. no. AMU-SYR.904) from same host species, **INDONESIA:** Java, 21 May 1909, coll. A. Primavesi [host reg. no. ZSM 10.1015]; 3 females (HOM) (reg. no. AMU-SYR.905) from same host species, **INDONESIA:** Sumatra, Martin, 1895, coll. unknown [host in the ZSM, uncatalogued]; 1 female (HET) (reg. no. AMU-SYR.906) from same host species, **INDONESIA**: Celebes, Makassar, coll. M. Weber [host reg. no. ZSM 09.4342].

Type material deposition. All type specimens are deposited in the AMU.

Additional material. Columbiformes (Columbidae): 6 females (HOM) (reg. no. AMU-SYR.902) from Diamond Dove *Geopelia cuneata* (Latham), **AUSTRALIA:** no other data [host reg. no. ZSM 21.1951]. 5 females (HOM), 1 protonymph (reg. no. AMU-SYR.903) from Peaceful Dove *Geopelia placida* Gould, **AUSTRALIA:** Melbourne, 1890, coll. unknown [host in the ZSM, uncatalogued]. 8 females (HOM) (reg. no. AMU-SYR.907) from Creasted Pigeon *Ocyphaps lophotes* (Temminck), **AUSTRALIA:** Adelaide, coll. Beyer [host in the ZSM, uncatalogued]. Whole mite material is deposited in the AMU and ZSM.

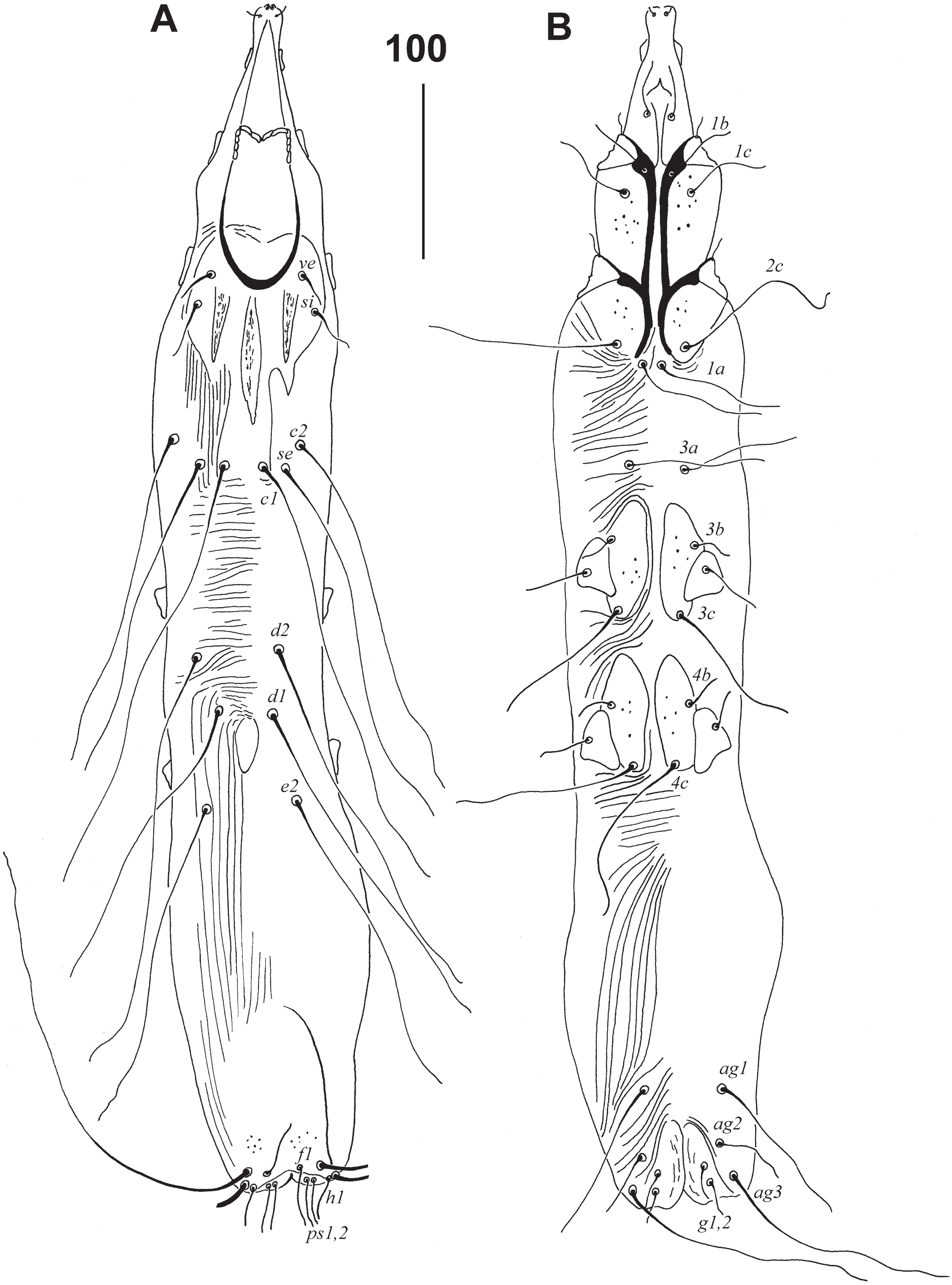

FIGURE 2. *Peristerophila geopelis* **sp. nov.**, female. **A,** dorsal view; **B,** ventral view.

Differential diagnosis. *Peristerophila geopelis* **sp. nov.** is morphologically most similar to *P. mucuya* (Casto, 1980) described from *Columbina passerina* (Columbidae) from USA (Texas) (Casto 1980). In females of both species, the infracapitulum is punctate; lateral and medial branch of the peritremes has 5 and 2 chambers, respectively; and the hysteronotal shield is reduced to the single sclerite which is not fused with the pygidial shield. This new species differs from *P. mucuya* by the following features: in females of *P. geopelis*, the propodonotal shield is entire and T-shaped; bases of setae *c1* are situated on the propodonotal shield. In females of *P. mucuya*, the propodonotal shield is divided onto three oval-shaped sclerites; bases of setae *c1* are situated out of propodonotal shield.

Etymology. The name *geopelis* is taken from the generic name of the host.

Peristerophila leucomela sp. nov.

(Figures 3, 4E–F)

Description. FEMALE, HOMEOMORPHIC FORM (HOM), holotype. Total body length 555 (535– 555 in 2 paratypes). *Gnathosoma*. Length of gnathosoma 80 (75–80). Infracapitulum densely punctate. Length of stylophore 120 (115–120). Length ratio of apodemes I: gnathosoma 1:1.2–1.3. Each medial branch of peritremes with 2 chambers, each lateral branch with 4 chambers. *Idiosoma*. Propodonotal shield divided onto two ovate lateral and one median pear-like sclerites; bases of setae *ve* and *si* situated on lateral shields. Length ratio of setae *ve:si:se* 1:4.5–4.7:4.6–5.2. Hysteronotal shield absent. Pygidial shield punctate, with concave anterior margin. Length ratio of setae *d2:d1:e2* 1.2–1.3:1:1. Setae *f2* 4.4–5.6 times longer than setae *f1*. Setae *h1* and *f1* subequal in length. Coxal fields I, III, and IV punctate, II apunctate. Bases of setae *3a* situated out of coxal fields III. Setae *3c* twice as long as *3b.* Length ratio of setae *ag1:ag2:ag3* 1.7–2.1:1:2.6–2.7. Genital setae (*g1–2*) subequal in length and 3 times longer than pseudanal setae (*ps1–2*). *Legs*. Setae *tc"III–IV* 1.8–2.3 times longer than *tc'III–IV*. Length ratio of legs I:II 1–1.2:1. Lengths of setae: *ve* 35 (40–45), *si* 165 (180), *se* 185 (185–205), *c1* 220 (185), *c2* 205 (185–205), *d1* 165 (140), *d2* 195 (175–215), *e2* 150 (160–175), *f1* 30 (30–35), *f2* 150 (155–170), *h1* 30 (25–30), *h2* 310 (280–300), *ag1* 80 (85–95), *ag2* 45 (40–45), *ag3* 120 (110–120), *g1* and *g2* 30 (30), *ps1* and *ps2* 10 (10), *tc'III–IV* 20 (15–20), *tc"III–IV* 40 (35–45), *3b* (30–35)*, 3c* (70–85). Length of apodemes I 60 (60–65). Length of legs I 60 (60–75), legs II 55 (50–70).

FEMALE, HETEROMORPHIC FORM and MALE. Not found.

Type material. Female (HOM) holotype, 2 female (HOM) paratypes (reg. no. AMU-SYR.900) from White-headed pigeon *Columba leucomela* Temminck (Columbiformes: Columbidae), **AUSTRALIA:** no other data [host in ZSM uncatalogued].

Type material deposition. All type specimens are deposited in the AMU.

Differential diagnosis. *Peristerophila leucomela* **sp. nov.** is morphologically similar to *P. claravis* Glowska and Skoracki, 2008 described from *Claravis pretiosa* Ferrari-Pérez (Columbidae) from Bolivia (Glowska & Skoracki 2008). In females of both species, the infracapitulum is punctate, the propodonotal shield is divided onto three sclerites and the hysteronotal shield is absent. This new species differs from *P. claravis* by the following features: in females of *P. leucomela*, bases of setae *ve* and *si* are situated on the lateral propodonotal shields; the lengths of setae *si*, *d1*, and *f2* are 165–180, 140–165, and 150–170 respectively; and the pygidial shield is punctate. In females of *P. claravis*, bases of setae *ve* and *si* are situated off the lateral propodonotal shields, the lengths of setae *si*, *d1*, and *f2* are 25–35, 205–255, and 230–260 respectively; and the pygidial shield is apunctate.

Etymology. The name *leucomela* is taken from the specific name of the host.

Peristerophila columbae (Hirst, 1920)

Syringophilus columbae Hirst, 1920: 121.
Peristerophila columbae, Kethley1970: 56, figs. 32.
Type host: *Columba livia* Gmelin (Columbiformes: Columbidae) from USA.

Diagnosis. FEMALE HOMEOMORPHIC FORM. Total body length 635–680. Infracapitulum punctate. Length of gnathosoma 85–110. Length ratio of apodemes I : gnathosoma 1:1.3–1.5. Each medial branch of peritremes with 2 chambers, each lateral branch with 4–5 chambers. Propodonotal shield punctate, weakly sclerotized, rectangular in shape or reduced to 3 sabre-like, vertical sclerites. Hysteronotal shield fused to pygidial shield. and punctate in posterior part; bases of setae *d1* situated on anterior margin of this shield. Coxal fields I densely punctate, II–IV sparsely punctate. Bases of setae *3a* situated out of coxal fields III. *Lengths of setae*: *ve* 20–25, *si* 20–25, *se* 190–220, *c1* 200–230, *c2* 180–195. Length of apodemes I 65–70. Length of legs I 60–75, legs II 50–70. Length ratios of setae: *ve*:*si*:*se* 1:1.2–1.5:7.8–9.5, *e2*:*d2* 1:1.4–1.6.

FEMALE, HETEROMORPHIC FORM. Unknown.

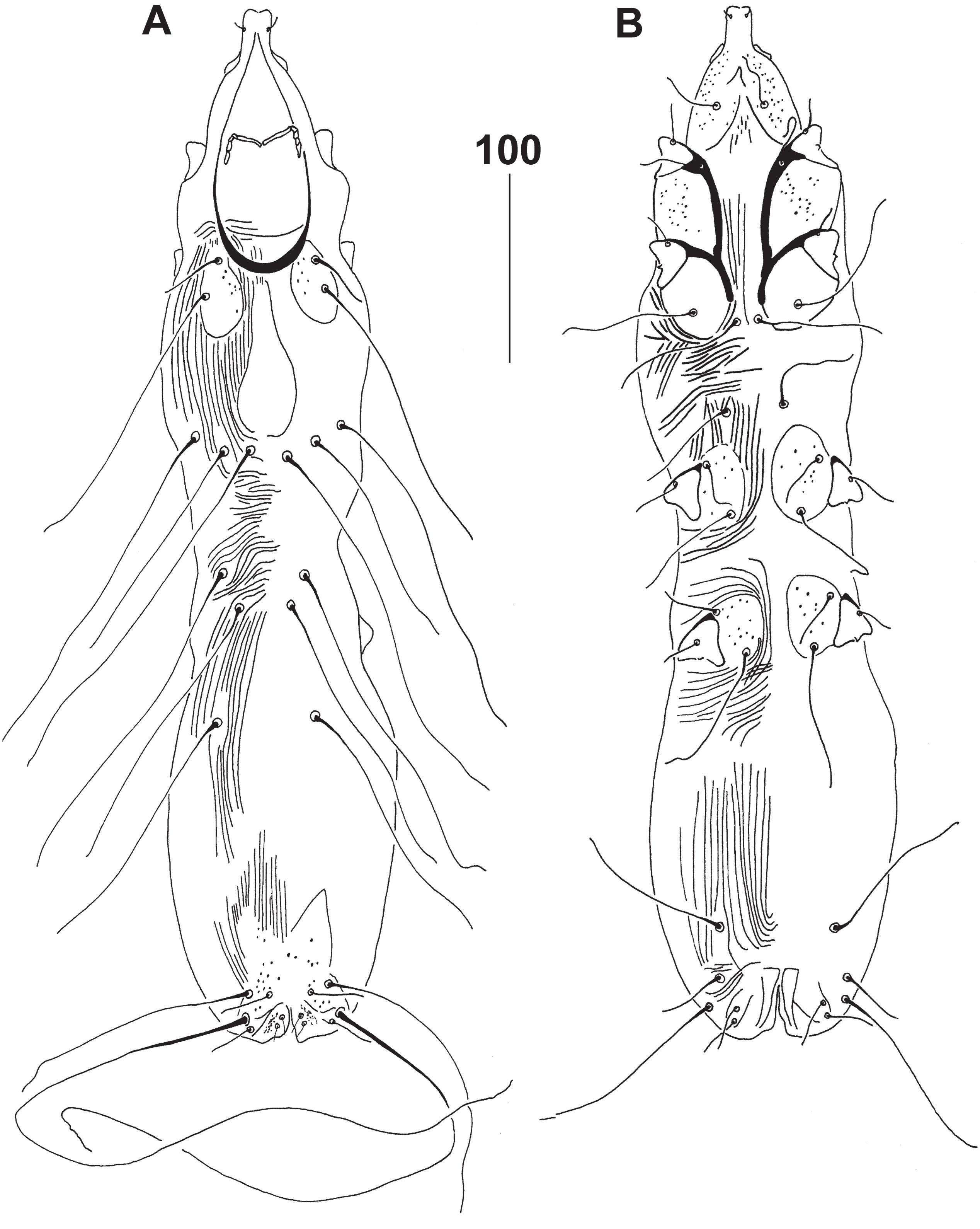

FIGURE 3. *Peristerophila leucomela* **sp. nov.**, female. **A,** dorsal view; **B,** ventral view.

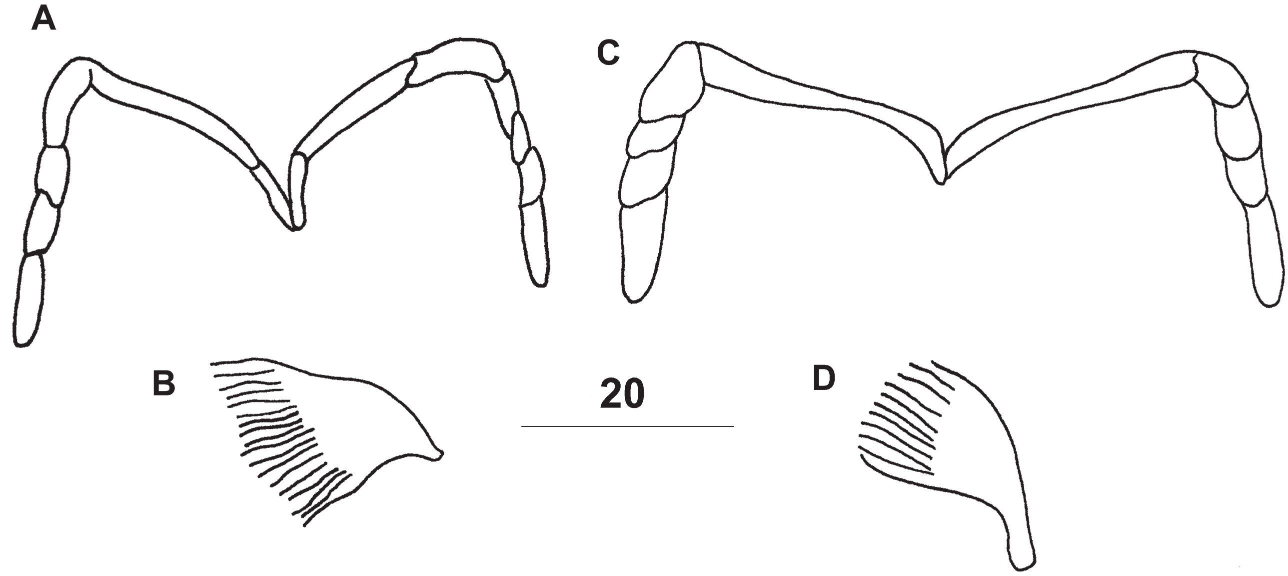

FIGURE 4. *Peristerophila geopelis* **sp. nov.**, female. **A,** peritremes, **B,** fan-like seta *p'III*, *Peristerophila leucomela* **sp. nov.**, female. **C,** peritremes; **D,** fan-like seta *p'III.*

MALE. Total body length 335–370. Infracapitulum apunctate. Each medial branch of peritremes with 2 chambers, each lateral branch with 4 chambers. Propodonotal shield entire, apunctate. Setae *se* and *c2* situated at same transverse level. Hysteronotal shield not fused to pygidial shield. Pygidial shield apunctate. Coxal fields I–IV apunctate. Length of setae: *ve* 20–25, *si* 20–25, *se* 70, *d1* 20, *d2* 55, *e2* 20. Length ratios of setae *ve*:*si*:*se* 1:1.2–1.5:2.8–3.5; *e2*:*d2* 1:2.7.

Hosts and distribution. Columbiformes (Columbidae)—African Olive-pigeon *Columba arquatrix* (Temminck) (**new host**) from Kenya, Speckled Pigeon *Columba guinea* Linnaeus (**new host**) from Tanzania and South Africa, Snow Pigeon *Columba leuconota* (Vigors) (**new host**) from Nepal (this study), Rock Pigeon *Columba livia* Gmelin from Poland (Skoracki 2011), England (Nattress & Skoracki 2009), Turkey, Iran, India (Bochkov & Mironov 1998), Macedonia (**new locality**), and Canada (**new locality**) (this study), Stock Pigeon *Columba oenas* Linnaeus (**new host**) from Germany, Common Wood-Pigeon *Columba palumbus* Linnaeus (**new host**) from Germany and England, Madeira laurel Pigeon *Columba trocaz* Heineken (**new host**) from Portugal, Chiriqui Quail-Dove *Geotrygon chiriquensis* Sclater (**new host**) from Panama, Scaled Pigeon *Patagioenas speciosa* (Gmelin) from Surinam (**new host**) (this study), Eurasian Collared-Dove *Streptopelia decaocto* (Frivaldszky) from Jordan (Skoracki 2011), Mourning Collared-Dove *Streptopelia decipiens* (Hartlaub and Finsch) (**new host**) from Tanzania, Ring-necked Dove *Streptopelia capicola* (Sundevall) (**new host**) from Angola, Oriental Turtle Dove *Streptopelia orientalis* (Latham) (**new host**) from Japan , Red-eyed Dove *Streptopelia semitorquata* (Rueppell) (**new host**) from Tanzania, Angola, and D.R. Congo, Red Collared-Dove *Streptopelia tranquebarica* (Hermann) (**new host**) from China, European Turtle-Dove *Streptopelia turtur* (Linnaeus) (**new host**) from Macedonia, Hungary, Germany, and Greece (this study).

New material examined herein. Columbiformes (Columbidae)—10 females (HOM) (reg. no. AMU-SYR.908) from *Columba arguatrix*, **KENYA:** Central Province, Kikuyu, December 1894, coll. Neumann [host in the ZSM, uncatalogued]. 4 females (HOM) (reg. no. AMU-SYR.909) from *Columba guinea* Linnaeus, **SOUTH AFRICA:** February 1911, coll. Kattwinkel [host reg. no. ZSM 11.2614]. 7 females (HOM) (reg. no. AMU-SYR.910) from same host species, **TANZANIA:** 8 June 1961, coll. Th. Andersen [host reg. no. ZSM 62.40]. 6 females (HOM) deposited in the AMU (reg. no. AMU-SYR.912) from same host species, **TANZANIA:** Dodoma Distr., 12 March 1953, coll. Th. Andersen [host reg. no. ZSM 1428]. 9 females (HOM) (reg. no. AMU-SYR.912) from *Columba leuconota*, **NEPAL:** Himalayas, 30 June 1962, coll. unknown [host in the ZSM, uncatalogued]. 2 females (HOM) (reg. no. AMU-SYR.913) from *Columba livia*, **MACEDONIA:** 20 February 1918, coll. L. Mueller [host reg. no. ZSM 18.1764]. 1 female (HOM) (reg. no. AMU-SYR.914) from same host species, **CANADA:** March 2005, coll. Edmonton. 9 females (HOM) (reg. no. AMU-SYR.915) from *Columba oenas*, **GERMANY:** Westheim Pfalz, 18 May 1909, coll. Laubmann [host in the ZSM, uncatalogued]. 10 females (HOM) (reg. no. AMU-SYR.916) from

Columba palumbus, **GERMANY:** no other data [host in the ZSM, uncatalogued]. 7 females (HOM) (reg. no. AMU-SYR.917) from same host species, **ENGLAND:** no other data [host in the ZSM uncatalogued]. 3 females (HOM) (reg. no. AMU-SYR.918) from *Columba trocaz*, **PORTUGAL:** Madeira Isl., no other data [host in the ZSM, uncatalogued]. 8 females (HOM) (reg. no. AMU-SYR.919) from *Geotrygon chiriquensis*, **PANAMA:** Chiriqui, 1895, coll. Dalmas [host reg. no. ZSM 09.3564]. 4 females (HOM), 1 tritonymph (reg. no. AMU-SYR.920) from *Patagioenas speciosa*, **SURINAM:** Paramaribo,1843, no other data [host in the ZSM, uncatalogued]. 5 females (HOM) deposited in the AMU (reg. no. AMU-SYR.921) from *Streptopelia capicola*, **ANGOLA:** Entre Rios, 27 June 1953, coll. W. Hellmid [host reg. no. ZSM 55.43]. 9 females (HOM) (reg. no. AMU-SYR.922) from *Streptopelia decaocto*, **MACEDONIA**: Veles, 7 March 1918, coll. L. Mueller [host reg. no. ZSM 18.1863]. 7 females (HOM), 1 protonymph, 1 tritonymph (reg. no. AMU-SYR.923) from *Streptopelia tranquebarica*, **CHINA:** Yangtze, 29 July 1899, coll. Haberer [host in the ZSM uncatalogued]. 2 females (HOM) (reg. no. AMU-SYR.924) from *Streptopelia decipiens*, **TANZANIA:** Maasailand, December 1893, coll. O. Neumann host in the ZSM, uncatalogued]. 2 females (HOM) (reg. no. AMU-SYR.925) from *Streptopelia orientalis*, **JAPAN:** Nara, 7 December 1904, coll. Doflein [host in the ZSM, uncatalogued]. 6 females (HOM) (reg. no. AMU-SYR.927) from *Streptopelia semitorquata*, **TANZANIA:** Mtwara Distr. Mikindami, 19 September 1962, coll. Th. Andersen [host reg. no. ZSM 63.276]. 3 females (HOM) (reg. no. AMU-SYR.928) from same host species, **ANGOLA:** 26 June 1953, coll. W. Hellmid [host reg. no. ZSM 55.41]. 3 females (HOM) (reg. no. AMU-SYR.929) from same host species, **D. R. CONGO:** Katanga, coll. Michell, no other data [host in the ZSM, uncatalogued]. 5 females (HOM) (reg. no. AMU-SYR.930) from *Streptopelia turtur*, **MACEDONIA:** Veles, 26 May 1918, coll. Mueller [host reg. no. ZSM 18.2663]. 5 females (HOM) (reg. no. AMU-SYR.930a) from same host species, **GREECE:** Thessaloniki, 10 May 1931, coll. Kattinger [host reg. no. ZSM 33.403]. 4 females (HOM) (reg. no. AMU-SYR.931) from same host species, **HUNGARY:** Dabas, Tatarszentgyorgy, 11 July 1924, coll. M. Kiefer [host reg. no. ZSM 24.373]. 2 females (HOM), 1 protonymph and 1 larva (reg. no. AMU-SYR.932), **GERMANY:** Bayern, 9 June 1925, coll. unknown [host reg. no. ZSM 24.373].

Peristerophila lature Kaszewska, Kavetska and Skoracki, 2014

Peristerophila lature Kaszewska *et al*., 2014: 296, figs. 4–5.
Type host: *Ducula luctuosa* (Temminck) (Columbiformes: Columbidae) from Indonesia (Sulawesi Isl.).

Diagnosis. FEMALE, HOMEOMORPHIC FORM. Total body length 595–695. Infracapitulum punctate. Length of gnathosoma 85–95. Length ratio of apodemes I : gnathosoma 1:1.2–1.3. Each medial branch of peritremes with 1 chamber, each lateral branch with 5–6 chambers. Propodonotal shield divided into 2 lateral and 1 medial punctate sclerites; bases of setae *ve* situated on lateral sclerites. Hysteronotal shield fused with punctate pygidial shield. Coxal fields I–IV punctate. Bases of setae *3a* situated out of coxal fields III. Length of setae: *ve* 35–45, *si* 90–115, *se* 185–205, *c1* 195–225, *c2* 180–225. Length of apodemes I 70. Length of legs I 55–70, legs II 45–60. Length ratios of setae: *ve*:*si*:*se* 1:1.2–1.5:7.8–9.5, *e2*:*d2* 1:1.4–1.6.

FEMALE, HETEROMORPHIC FORM. Unknown.

MALE. Total body length 430–445. Each medial branch of peritremes with 2 chambers, each lateral branch with 4–5 chambers. Propodonotal shield rectangular in shape and punctate, bearing bases of setae *ve*, *si*, *c1*. Bases of setae *se* situated slightly anterior to level of setae *c2*. Hysteronotal shield not fused with pygidial shield. Coxal field I–IV apunctate. Lengths of setae: *ve* 30–40, *si* 50–60, *d1* 20, *d2* 50–70, *e2* 15–30. Length ratios of setae: *ve*:*si*:*se* 1:1.2–1.6:2.8–3.6, *e2*:*d2* 1:2.3–3.3.

Hosts and distribution. Columbiformes (Columbidae)—Silver-tipped Imperial-Pigeon *Ducula luctuosa* (Temminck) from Indonesia, Torresian Imperial-pigeon *Ducula spilorrhoa* (Gray) from Papua New Guinea, Jambu Fruit-Dove *Ptilinopus jambu* (Gmelin) form Indonesia, Black-naped Fruit-Dove *Ptilinopus melanospilus* (Salvadori) from Indonesia, Pink-headed Fruit-Dove *Ptilinopus porphyreus* (Temminck) from Indonesia (Kaszewska *et al*. 2014). Rose-crowned Fruit Dove *Ptilinopus regina* (Swainson) from Mariana Isl. (Kaszewska *et al*. 2014).

Peristerophila claravis (Skoracki and Glowska, 2008)

Castosyringophilus claravis Skoracki and Glowska, 2008: 155, figs 9–15.

Peristerophila claravis, Skoracki *et al*. 2020.
Type host: *Claravis pretiosa* (Ferrari-Perez, 1886) (Columbiformes: Columbidae) from Bolivia.

Diagnosis. FEMALE, HETEROMORPHIC FORM. Total body length 730–805. Infracapitulum punctate. Length of gnathosoma 90–100. Length ratio of apodemes I : gnathosoma 1:1. Each medial branch of peritremes with 1 chamber, each lateral branch with 4 chambers. Propodonotal shield divided into 3 narrow sclerites; bases of setae *ve* and *si* situated out of lateral sclerites. Hysteronotal shield absent. Pygidial shield apunctate. Coxal fields I–IV sparsely punctate. Bases of setae *3a* situated out of coxal fields III. Lengths of setae: *ve* 25–30, *si* 25–30, *se* 200–255, *c1* 230–285, *c2* 170–220. Length of apodemes I 85–100. Length of legs I 65–80, legs II 45–70. Length ratios of setae: *ve*:*si*:*se* 1:1:7.5–8, *e2*:*d2* 1:1–1.2.

FEMALE, HOMEOMORPHIC FORM and MALE. Unknown.

Hosts and distribution. Columbiformes (Columbidae)—Blue Ground-Dove *Claravis pretiosa* Ferrari-Pérez from Bolivia (Glowska & Skoracki 2008), Colombia (**new locality**), Paraguay (**new locality**), Panama (**new locality**) (this study), Namaqua Dove *Oena capensis* (Linnaeus) (**new host**) from Tanzania, Sudan, and Ethiopia (this study).

New material examined herein. Columbiformes (Columbidae)—2 females (HET) (reg. no. AMU-SYR.935) from *Claravis pretiosa*, **PARAGUAY:** Apa-Bergland, 1 November 1931, coll. E. Schuhmacher [host reg. no. ZSM 32.183]. 6 females (HET) (reg. no. AMU-SYR.936) from same host species, **PANAMA:** Chiriqui, 1895, coll. Dalmas [host reg. no. ZSM 09.3554]. 3 females (HET) (reg. no. AMU-SYR.937) from same host species, **COLOMBIA:** Patia valley, Mercaderes, 17 November 1965, coll. Haffer [host reg. no. ZSM 67.413]. 3 females (HET) (reg. no. AMU-SYR.938) from *Oena capensis*, **TANZANIA:** Tanganyika, North Gaze, 7 February 1958, coll. Th. Andersen [host reg. no. ZSM 3277]. 2 females (HET) (reg. no. AMU-SYR.939) from same host species, **SUDAN:** 30 January1912, coll. Hesselberger [host reg. no. ZSM 12.2261]. 7 females (HET), 1 tritonymph, 3 protonymphs (reg. no. AMU-SYR.939a) from same host species, **ETHIOPIA:** Langano, 24–27 November 1965, coll. Linsenmair [host reg. no. ZSM 66.219].

Peristerophila mucuya Casto, 1980

Peristerophila mucuya Casto, 1980: 1, figs 1 and 2. Skoracki *et al*. 2020.
Castosyringophilus mucuya, Bochkov and Perez 2002: 152.
Type host: *Columbina passerina* (Linnaeus) (Columbiformes: Columbidae) from USA.

Diagnosis. FEMALE, HETEROMORPHIC FORM. Total body length 940–1020. Infracapitulum punctate. Length of gnathosoma 90–95. Length ratio of apodemes I : gnathosoma 1:1. Each medial branch of peritremes with 2 chambers, each lateral branch with 4–5 chambers. Propodonotal shield divided into 3 ovate sclerites with narrow belt-like ornament; bases of setae *ve* and *si* situated on lateral sclerites. Hysteronotal shield reduced to single and triangular sclerite; bases of setae *d1* situated out of this shield. Pygidial shield apunctate with deep concave anterior margin. Coxal fields I–II sparsely punctate, III–IV apunctate. Bases of setae *3a* situated out of coxal fields III. Length of setae: *ve* 20–25, *si* 25–30, *se* 250–270, *c1* 230–250, *c2* 210–220. Length of apodemes I 80–100. Length of legs I 65–70, legs II 45–55. Length ratios of setae *ve*:*si*:*se* 1:1–1.2:10–10.8, *e2*:*d2* 1:1.

MALE. Unknown.

Hosts and distribution. Columbiformes (Columbidae)—Common Ground-Dove *Columbina passerina* (Linnaeus) from USA (Texas) (Casto 1980), Colombia and Surinam (**new localities**) (this study), Scaled Dove *Columbina squammata* (Lesson) from Brazil (Bochkov & Fain 2003) and Paraguay (**new locality**) (this study), Ruddy Ground-Dove *Columbina talpacoti* (Temminck) from Brazil (Skoracki & Glowska 2008; this study), Trinidad and Tobago, Monaco, Surinam (**new localities**) (this study), Plain-breasted Ground-Dove *Columbina minuta* Linnaeus (**new host**) from Paraguay, Bare-faced Ground-Dove *Metriopelia ceciliae* (Lesson) (**new host**) from Peru (this study), Black-winged Ground-Dove *Metriopelia melanoptera* (Molina) from Argentina (Skoracki & Glowska 2008), *Geophaps plumifera* Gould from Australia (Bochkov & Fain 2003).

New material examined herein. Columbiformes (Columbidae)—4 females (HET) (reg. no. AMU-SYR. 940) from *Columbina passerina*, **COLOMBIA:** Mojarras, Dept. Cauca, alt 600m, 15 November 1965, coll. J. Haffer [host reg. no. ZSM 67.415]. 2 females (HET) (reg. no. AMU-SYR. 941) from same host species, **SURINAM:** 27

July 1958, coll. F. Haverschmidt [host reg. no. ZSM 59.36]. 1 female (HET) (reg. no. AMU-SYR. 942) from *Columbina talpacoti*, **BRAZIL:** Rio Machados, Rio Madeira, 25 July 1908, Hoffmann [host reg. no. ZSM 09.590]. 2 females (HOM) (reg. no. AMU-SYR. 943) from same host species, **BRAZIL:** Para, coll. E. Lohse [host reg. no. ZSM 19.457]. 3 females (HOM) (reg. no. AMU-SYR. 944) from same host species, **SURINAM:** Peperpof, 24 September 1961, coll. F. Haverschmidt [host reg. no. ZSM 61.432]. 2 females (HOM) and 4 females (HET), 2 tritonymphs, 2 protonymphs (reg. no. AMU-SYR. 944a) from same host species, **SURINAM:** Paramaribo, 14 January 1961, coll. F. Haverschmidt [host reg. no. ZSM 61.502]. 3 females (HET) (reg. no. AMU-SYR. 945) from same host species, **TRINIDAD AND TOBAGO:** Caparo, 14 June 1912, coll. unknown [host reg. no. ZSM 13.189]. 1 female (HET) (reg. no. AMU-SYR. 946) from same host species, **MONACO:** Monte Carlo, 9 April 1938, coll. unknown [host reg. no. ZSM 317]. 10 females (HET) (reg. no. AMU-SYR. 947) from *Columbina minuta*, **PARAGUAY:** Apa-Bergland, 6 December 1931, coll. Kiefer and Schuhmacher [host reg. no. ZSM 32.189]. 5 females (HET) (reg. no. AMU-SYR.948) from *Columbina squammata*, **PARAGUAY:** Apa-Bergland, 7 November 1931, coll. E. Schuhmacher [host reg. no. ZSM 32.183]. 1 female (HET) (reg. no. AMU-SYR. 949) from *Metriopelia ceciliae*, **PERU:** Marcapata, 1900, coll. G. Ockenden [host reg. no. ZSM 03.694].

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Tabela 1. Roztocze dutkowe z rodziny Syringophilidae związane z ptakami z rzędu Columbiformes

Table 1 Quill mites from family Syringophilidae associated with birds from order Columbiformes

Gatunki Syringophilidae opisane w ramach rozprawy doktorskiej / New Syringophilidae species described under the dissertation.

Nowe gatunki żywicielskie wykazane w ramach rozprawy doktorskiej / New host species shown under the dissertation.

Nowe lokalizacje wykazane w ramach rozprawy doktorskiej / New locations shown under the dissertation.

T Gatunek typowy (Type species)

Afro.—Afrotropical, Aust.—Australian, Near.—Nearctic, Neot.—Neotropical, Ocea.—Oceanian, Orie.—Oriental, Pala.—Palaearctic, Pana.—Panamanian, Sa-Arab.—Saharo-Arabian, Si-Jap.—Sino-Jappanese (Holt et al. 2013).

Gatunki roztoczy dutkowych **Quill mite species**	**Gatunki żywicielskie** **Host species**	**Lokalizacja** **Distribution**	**Cytacje** **References**
Meitingsunes Glowska and Skoracki, 2010			
M. aldwelles Glowska and Skoracki 2010	*Geotrygon frenata*^{T} (Tschudi)	Neot. (Colombia)	Glowska and Skoracki, 2010
M. columbicus Skoracki 2011	*Columba oenas*^{T} Linnaeus	Pala.(Kazakhstan)	Skoracki, 2011
"	*Columba livia* Gmelin	Pala. (Poland, **Slovakia**)	Skoracki, 2011; Kaszewska et al., 2020a
"	*Columba palumbus* Linnaeus	Pala. (**Germany**, Russia)	Skoracki, 2011; Kaszewska et al., 2020a
"	***Treron waalia*** (Meyer)	Afro. (**Cameroon**)	Kaszewska et al., 2014

M. chalcophas Kaszewska, Skoracki and Kavetska, 2016	***Chalcophas indica***^{T} (Linnaeus)	Orie. (Indonesia: **Timor**) Aust. (**Australia**)	Kaszewska et al., 2016; Kaszewska et al., 2020a
M. ptilinopus Kaszewska, Skoracki and Hromada, 2020	***Ptilinopus magnificus***^{T} Temminck	Aust. (**Australia**)	Kaszewska et al., 2020a
"	***Ptilinopus rivoli*** (Prevost)	Ocea. (**Papua New Guinea**)	Kaszewska et al., 2020a
M. lengai Kaszewska, Skoracki and Hromada, 2020	***Columba delegorguei***^{T} Delegorgue	Afro. (Tanzania)	Kaszewska et al., 2020a
"	*Streptopelia orientalis* (Latham)	Afro. (Tanzania)	Kaszewska et al., 2020a
"	*Streptopelia semitorquata* Ruppell	Pala. (**Kazakhstan, Kyrgyzstan**)	Kaszewska et al., 2020a
M. turacoenas Kaszewska, Skoracki and Kavetska, 2016	***Gallicolumba luzonica*** Scopoli	Orie. (**Philippines**)	Kaszewska et al., 2020
"	***Macropygia amboinensis*** (Linnaeus)	Ocea. (**Papua New Guinea**)	Kaszewska et al., 2020
"	***Macropygia phasianella*** (Temminck)	Orie. (**Philippines**, **Indonesia**: **Java**)	Kaszewska et al., 2020
"	***Macropygia unchall*** (Wagler)	Ocea. (**Papua New Guinea**)	Kaszewska et al., 2020
"	***Turacoena manadensis***^{T} (Quoy &Gaimard)	Orie. (Indonesia: **Sulavesi**, **Nepal**)	Kaszewska et al., 2016
"	***Turacoena modesta*** (Temminck)	Orie. (**Indonesia**)	Kaszewska et al., 2016
M. tympanistria (Skoracki and Dabert, 2012)	***Turtur chalcospilos*** (Wagler)	Afro. (Tanzania)	Kaszewska et al., 2020

"	*Turtur tympanistria*[T] (Temminck)	Afro. (Togo, **Tanzania**)	Skoracki and Dabert, 2012; Kaszewska et al., 2020
M. zenadourae (Clark, 1964)	*Columba livia* Gmelin	Near. (USA: Texas); Afro. (N. Africa, **Djibouti**)	Casto, 1980; Bochkov and Mironov, 1998; Kaszewska et al., 2020
"	***Geotrygon frenata*** (Tschudi)	Neot. (**Colombia**)	Kaszewska et al., 2020a
"	***Leptotila rufaxilla*** (Richard, Bernard)	Neot. (Surinam, Argentina)	Kaszewska et al., 2020a
"	***Leptotila verreauxi*** (Bonaparte)	Neot. (Colombia)	Kaszewska et al., 2020a
"	***Patagioenas picazuro*** Temminck	Neot. (Paraguay)	Kaszewska et al., 2020a
"	*Zenaida asiatica* (Linnaeus)	Near. (USA: Texas)	Casto, 1976
"	*Zenaida auriculata* (Murs)	Neot. (Argentina)	Skoracki and Sikora, 2002
"	*Zenaida macroura*[T] (Linnaeus)	Near. (USA: Maryland, Arizona, **San Francisko****)	Clark, 1964; Glowska and Skoracki, 2010; Kaszewska et al., 2020a
Peristerophila Kethley 1970			
P. columbae (Hirst, 1920)	***Columba arguatrix*** (Temminck)	Afro. (Kenya)	Kaszewska et al., 2020b
"	***Columba guinea*** Linnaeus	Afro. (S Africa, Tanzania)	Kaszewska et al., 2020b
"	***Columba leuconota*** (Vigors)	Orie. (Nepal)	Kaszewska et al., 2020b

"	*Columba livia*^{T} Gmelin	Pala. (England, **Macedonia,** Poland, Turkey); Near. (**Canada**, USA); Orie. (India); Sa-Arab. (Iran)	Nattres and Skoracki 2009; Bochkov and Mironov 1998; Skoracki 2011; Hirst 1920; Kaszewska et al., 2020b
"	***Columba oenas*** Linnaeus	Pala. (Germany)	Kaszewska et al., 2020b
"	***Columba palumbus*** Linnaeus	Pala. (Germany, England)	Kaszewska et al., 2020b
"	***Columba trocaz*** Heineken	Pala. (Portugal)	Kaszewska et al., 2020b
"	***Geotrygon chiriquensis*** Sclater	Pana. (Panama)	Kaszewska et al., 2020b
"	***Patagioenas speciosa*** (Gmelin)	Neot. (Surinam)	Kaszewska et al., 2020b
"	***Streptopelia capicola*** (Sundevall)	Afro. (Angola)	Kaszewska et al., 2020b
"	*Streptopelia decaocto* (Frivaldszky)	Sa-Arab. (Jordan)	Skoracki, 2011
"	***Streptopelia decipiens*** *(*Hartlaub & Finsch.)	Pala. (**Macedonia**), Afro. (Tanzania)	Kaszewska et al., 2020b
"	***Streptopelia orientalis*** (Latham)	Si-Jap. (**Japan**)	Kaszewska et al., 2020b
"	***Streptopelia semitorquata*** (Ruppell)	Afro. (Angola, Tanzania, **D. R. Congo**)	Kaszewska et al., 2020b
"	***Streptopelia tranquebarica*** (Hermann)	Orie. (China)	Kaszewska et al., 2020b
"	***Streptopelia turtur*** (Linnaeus)	Pala. (Germany, **Greece, Hungary, Macedonia**)	Kaszewska et al., 2020b

P. claravis (Skoracki and Glowska, 2008)	*Claravis pretiosa*[T] Ferrari-Pérez	Neot. (Bolivia, **Colombia**, **Paraguay**, Pana. **Panama**	(Skoracki and Glowska, 2008); Kaszewska et al., 2020b
"	***Oena capensis*** (Linnaeus)	Afro. (**Ethiopia, Sudan, Tanzania**)	Kaszewska et al., 2020b
P. geopelis Kaszewska, Skoracki, Kosicki, Hromada, 2020	***Geopelia cuneata*** (Latham)	Austr. (Australia)	Kaszewska et al., 2020b
"	***Geopelia placida*** Gould	Austr. (Australia)	Kaszewska et al., 2020b
"	***Geopelia striata***[T] (Linnaeus)	Orie. (Indonesia: **Celebes**, **Java, Sumatra**)	Kaszewska et al., 2020b
"	***Ocyphaps lophotes*** (Temminck)	Austr. (Australia)	Kaszewska et al., 2020b
P. lature Kaszewska, Kavetska and Skoracki, 2014	***Ducula luctuosa***[T] (Temminck)	Austr. (Australia)	Kaszewska et al., 2014
"	***Ducula spilorrhoa*** (Gray)	Austr. (**Papua New Guinea**)	Kaszewska et al., 2014
"	***Ptilinopus jambu*** (Gmelin)	Orie. (Indonesia: **Sumatra**)	Kaszewska et al., 2014
"	***Ptilinopus melanospilus*** (Salvadori)	Orie. (Indonesia: **Mount Gade**)	Kaszewska et al., 2014
"	***Ptilinopus porphyreus*** (Temminck)	Orie. (Indonesia: **Java**)	Kaszewska et al., 2014
"	***Ptilinopus regina*** (Swainson)	Orie. (Indonesia: **Marina** Isl.)	Kaszewska et al., 2014
P. leucomela Kaszewska, Skoracki, Kosicki, Hromada, 2020	***Columba leucomela***[T] Temminck	Austr. (**Australia**)	Kaszewska et al., 2020b

P. mucuya Casto, 1980	***Columbina minuta*** Linnaeus	Neot. (Paraguay)	Kaszewska et al., 2020b
"	*Columbina passerina** (Linnaeus)	Neot. (**Colombia**, **Surinam**); Near. (USA)	Casto, 1980; Kaszewska et al., 2020b
"	*Columbina squammata* (Lesson)	Neot. (Brazil, **Paraguay****)	Bochkov and Fain, 2003; Kaszewska et al., 2020b
"	*Columbina talpacoti* (Temminck)	Neot. (Brazil, **Surinam**, **Trinidad and Tobago**); Pala. (**Monaco**)	Skoracki and Glowska 2008; Kaszewska et al., 2020b
"	*Geophaps plumifera* Gould	Aust. (Australia)	Bochkov and Fain, 2003
"	***Metriopelia ceciliae*** (Lesson)	Neot. (**Peru**)	Kaszewska et al., 2020b
"	*Metriopelia melanoptera* (Molina)	Neot. (Argentina)	Skoracki and Glowska 2008
"	*Brotogeris versicolurus* Muller	Neot. (Brazil)	Bochkov and Fain, 2003
"	*Psilopsiagon aymara*** d'Orbigny	Neot. (S. America)	Bochkov and Fain, 2003
"	*Trichoglossus haematodus*** (Linnaeus)	Ori. (Indonesia)	Bochkov and Fain, 2003
Psittaciphilus Fain, Bochkov, and Mironov			
P. montanus Kaszewska and Skoracki, 2018	***Geotrygon montana***[T] (Linnaeus)	Neot. (**Brazil**, **Trinidad and Tobago**); Pana. (**Panama**)	Kaszewska and Skoracki, 2018

P. patagioenas Kaszewska and Skoracki, 2018	***Patagioenas fasciata***[T] (Say)	Neot. (**Colombia**)	Kaszewska and Skoracki, 2018
"	***Patagioenas speciosa*** (Gmelin)	Neot. (**Surinam**)	Kaszewska and Skoracki, 2018
Terratosyringophilus Bochkov and Perez, 2002			
T. geotrygonus Skoracki and Glowska 2008	*Geotrygon linearis*[T] (Prévost)	Neot. (Venezuela)	Skoracki and Glowska 2008
T. longisoma (Casto 1979)	*Zenaida asiatica*[T] (Linnaeus)	Near. (USA)	Casto 1979
"	*Zenaida macroura* (Linnaeus)	Near. (USA)	Skoracki and Glowska 2008
Gunabopiocobia Skoracki and Hromada, 2013			
G. claravis Kaszewska, Skoracki and Hromada, 2018	*Claravis pretiosa*[T] (Ferrari-Perez)	Neot. (**Colombia**)	Kaszewska et al., 2018
G. geotrygoni Kaszewska, Skoracki and Hromada, 2018	***Geotrygon linearis***[T] (Prevost)	Neot. (**Venezuela**)	Kaszewska et al., 2018
"	***Geotrygon chrysia*** Bonaparte	Ocea. (**Martinique**)	Kaszewska et al., 2018
"	*Geotrygon frenata* (Tschudi)	Neot. (**Colombia**)	Kaszewska et al., 2018
"	***Geotrygon montana*** (Linnaeus)	Neot. (**Paraguay**)	Kaszewska et al., 2018
G. masalaje Kaszewska, Kavetska and Skoracki, 2014	***Ducula bicolor*** (Scopoli)	Orie. (**Indonesia**)	Kaszewska et al., 2014
"	***Ducula rufigaster*** (Quoy and Gaimard)	Ocea. **(Papua New Guinea**)	Kaszewska et al., 2014

"	***Ducula rosacea*** (Temminck)	Orie. (Indonesia: **Semau Isl.**)	Kaszewska et al., 2014
"	***Ducula pistrinaria*** Bonaparte	Ocea. (**Papua New Guinea**)	Kaszewska et al., 2014
"	***Ducula spilorrhoa*** (*Gray*)	Orie. (Indonesia: **Semau Isl.**)	Kaszewska et al., 2014
"	***Ducula luctuosa*** (Temminck)	Ocea. (**Papua New Guinea**)	Kaszewska et al., 2014
"	***Ptilinopus iozonus***[T] Gray	Ocea. (**Papua New Guinea**)	Kaszewska et al., 2014
G. metriopelia Kaszewska, Skoracki and Hromada, 2018	***Metriopelia melanoptera***[T] (Molina)	Neot. (**Argentina**)	Kaszewska et al., 2018
G. lathami Kaszewska, Skoracki and Hromada, 2018	***Leucosarcia melanoleuca***[T] Gould	Orie. (Indonesia); Ocea. (Papua New Guinea)	Kaszewska et al., 2018
"	***Caloenas nicobarica*** (Linnaeus)	Orie. (Indonesia); Ocea. (**Papua New Guinea**)	Kaszewska et al., 2018
G. leptotila Kaszewska, Skoracki and Hromada, 2018	***Leptotila verreauxi***[T] (Bonaparte)	Neot. (**Argentina**)	Kaszewska et al., 2018
G. zumpti (Lawrence, 1959)	*Columba livia* Gmelin	Near. (USA); Pala. (Poland)	Bochkov et al., 2005; Skoracki et al., 2016
"	***Columba delegorquei*** Delegorgue	Afro. (**Tanzania**)	Kaszewska et al., 2018
"	***Patagioenas picazuro*** (Temminck)	Neot. (**West Brazil**)	Kaszewska et al., 2018
"	***Patagioenas speciosa*** Gmelin	Neot. (**North Brazil**)	Kaszewska et al., 2018
"	*Streptopelia capicola*[T] (Sundevall)	Afro. (South Africa)	Lawrence 1959
"	***Streptopelia semitorquata***	Afro. **(Ethiopia**)	Kaszewska et al., 2018

	(Ruppell)		
"	*Streptopelia senegalensis* (Linnaeus)	Afro.(South Africa)	Skoracki and Hromada 2013
"	*Zenaida macroura* (Linnaeus)	Near. (USA)	Skoracki 2014

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Global Studies of the Host-Parasite Relationships between Ectoparasitic Mites of the Family Syringophilidae and Birds of the Order Columbiformes

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Simple Summary: Mites of the family Syringophilidae (Acariformes: Cheyletoidea)—also called quill mites—are permanent and highly specialized ectoparasites of birds living inside the calamus of the various types of the feathers. In the present paper, we conducted a study focused on prevalence, host specificity, networks, and phylogeny of the syringophilid mites parasitizing on pigeon and doves (Columbiformes). We postulate that the Syringophilidae mites and Columbiformes bird system represent a model which can be used in a broader study of the relationship between hosts and parasites.

Abstract: The quill mites belonging to the family Syringophilidae (Acari: Prostigmata: Cheyletoidea) are obligate ectoparasites of birds. They inhabit different types of the quills, where they spend their whole life cycle. In this paper, we conducted a global study of syringophilid mites associated with columbiform birds. We examined 772 pigeon and dove individuals belonging to 112 species (35% world fauna) from all zoogeographical regions (except Madagascan) where Columbiformes occur. We measured the prevalence (IP) and the confidence interval (CI) for all infested host species. IP ranges between 4.2 and 66.7 (CI 0.2–100). We applied a bipartite analysis to determine host–parasite interaction, network indices, and host specificity on species and whole network levels. The Syringophilidae–Columbiformes network was composed of 25 mite species and 65 host species. The bipartite network was characterized by a high network level specialization $H2' = 0.93$, high nestedness $N = 0.908$, connectance $C = 0.90$, and high modularity $Q = 0.83$, with 20 modules. Moreover, we reconstructed the phylogeny of the quill mites associated with columbiform birds on the generic level. Analysis shows two distinct clades: *Meitingsunes* + *Psittaciphilus*, and *Peristerophila* + *Terratosyringophilus*.

Keywords: Acari; biodiversity; quill mites; pigeons and doves; network

1. Introduction

Knowing how many species inhabit Earth is among the most fundamental questions in science [1]. Despite often being neglected [2], one of the major components of biodiversity are parasites [3], comprising at least half of all species [4–6]; up to 75% of all interactions in food webs involve a parasitic species [3]. Many estimates of global species diversity of parasites are based on extrapolations of patterns of host specificity [2]; however, a contrast between the proportion that parasites comprise in local and global faunas suggests that parasites are most probably less host specific and more widespread than local scale studies suggest [6]. To get over such difficulties, it has been increasingly recognized that biotic interactions matter not only at local but also at regional, continental, or global spatial scales [7]. Thus, in determining the host specificity of parasites, more precise data on different parasitic taxa on different scales, from local to global, are crucially needed.

The networks can be useful to illustrate and analyze relationships and ecological interaction between any type of community [8]. Such analyses not only give a visual graph links between two trophic levels, but they also offer an opportunity to quantify indices such as parasite–host specificity and species richness in hosts, and they give a topological description of connectance, nestedness, or modularity [8,9].

The monophyletic Columbiformes are one of the oldest and the most diverse non-passerine clade of Neoaves, comprising more than 320 species grouped in one family Columbidae [10]. Pigeons and doves can be found in all zoogeographical regions except the high Arctic and Antarctic and adjacent islands [11]. Despite some studies suggesting as old as Cretaceous origin of Columbiformes [12], there is a major consensus that they diverged from other basal land bird clades in Eocene [13,14]; radiation of major extant lineages continued until the Miocene [15]. Thus, this group can serve as a good model for global studies of their ectoparasite richness, interactions, and specificity.

The quill mites belonging to the family Syringophilidae (Acariformes: Prostigmata) are highly specialized parasites of birds [16] that live inside the quills of feathers. These obligatory ectoparasites pierce the quill wall with extremely long stylet-like movable digits of chelicerae. Each stylet can be extended independently from the other, this movement occurs in the course of piercing the wall of quill and thus feed on live tissue fluids of their avian hosts [16–19].

Currently, the fauna of Syringophilidae comprises about 400 species belonging to 63 genera and associated with 27 bird orders [20]. However, Johnson and Kethley suggested that, considering their potential host richness, the number of quill mite species can reach as much as 5000 [21]. Most of the quill mites are either restricted to only one host species (monoxenous parasites) or adjusted to live in closely related hosts (oligoxenous parasites) [22,23]. However, the host specificity of syringophilids is still insufficiently investigated.

Until now, trophic interaction analyses and bipartite networks have been used for the description of quill mite associations with the following host groups: sunbirds (Passeriformes: Nectariniidae) [24] estrildids (Estrildidae) [25], and doves and pigeons (Columbiformes: Columbidae) [26]. However, more detailed studies of network indices such as connectance, modularity, nestedness and nest specificity of the quill mites from family Syringophilidae are still needed. The analysis of bipartite network metrics obtained for global quill mite–columbiform trophic interactions can shed more light on the architecture and relation between host and parasites.

Quill mite fauna associated with the members of Columbiformes comprises 25 quill mite species belonging to the following genera: *Meitingsunes* Glowska & Skoracki 2010, (8 species), *Peristerophila* Kethley, 1970 (6 species), *Psittaciphilus* Fain, Bochkov & Mironov 2000 (2 species), *Terratosyrinophilus* Bochkov & Pérez 2002, (2 species), and *Gunabopicobia* Skoracki & Hromada, 2013 (7 species), recorded from 65 bird species belonging to 22 pigeons and doves genera. The quill mites–columbiform fauna was studied by Hirst [27], Clark [28], Kethley [16], Lawrence [29], Casto [30,31], Bochkov and Mironov [32], Fain et al. [33], Bochkov and Perez [34], Bochkov and Fain [35], Bochkov et al. [36], Skoracki and Glowska [37], Nattres and Skoracki [38], Glowska and Skoracki [39], Skoracki [22], Skoracki and Dabert [40], Skoracki and Hromada [41], Kaszewska and Skoracki [42], and Kaszewska et al. [43–46].

Historical Review of Quill Mite Genera Associated with Doves and Pigeons

Among five genera of the quill mites infested birds of the order Columbiformes, only one—*Gunabopicobia*—belongs to the subfamily Picobiinae. The first species of this subfamily—*Syringophilus zumpti*—was described by Lawrence in 1959 based on the material collected from *Streptopelia capicola* (type host) [29]. In 1970, Kethley moved this species to the genus *Picobia* in the subfamily Picobiinae. In 2011, Skoracki established a new genus *Neopicobia* and placed *P. zumpti* in its species content [22]. However, two years later, considering morphological details (hypostomal apex bumpy and apodemes I without thorn-like protuberances), it was moved by Skoracki and Hromada [41] a new monotypic genus *Gunabopicobia*. New host records as well as numerous new *Gunabopicobia* species were described by Kaszewska et al. [42] and Skoracki et al. [47].

Members of the subfamily Syringophilinae associated with columbiform birds belong to four genera. The revision of Syringophilidae conducted by Kethley in 1970 resulted in a description of a new genus *Peristerophila*. In 2002, Bochkov and Pérez [34] erected a new genus—*Castosyringophilus*—closely related to *Peristerophila*. They also moved *P. mucuya* Casto, 1980 to *Castosyringophilus*. Subsequently, new quill mites species (12 species) from both genera with new hosts records belonging to the orders Columbiformes, Accipitriformes, and Falconiformes were given in the following papers: Bochkov and Fain [35], Skoracki et al. [48]; Skoracki [22], Skoracki and Glowska [37]; Kaszewska et al. [43,46]. In 2020, Skoracki et.al. [49] carried out a comparative study of the ontogeny and morphological structures of the quill mites belonging to genus *Peristerophila*. The results of this study indicated that the females of this genus, which are characterized by the presence of the two morphotypes: homeomorph forms belong to the genus *Peristerophila* while the heteromorphy ones formerly referred to the genus *Castosyringophilus*. Therefore, considering the ontogeny, the genus *Castosyringophilus* was synonymized with the genus *Peristerophila*. In 2003, Bochkov and Fain [35] published the results of their taxonomic studies on syringophilid mites associated with parrots, and established the genus *Terratosyringophilus*. They moved the previously described species *Peristerophila longisoma* Casto, 1979 recorded from *Zenaida asiatica* to the genus *Terratosyringophilus*. To date, *Terratosyringophilus* is comprised of five quill mites species infesting both doves and parrots. The other genus known from doves and parrots is *Psittaciphilus*, described by Fain et al. in 2000 [33]. Originally, Fain and co-authors recorded it only from parrots, but later, Kaszewska and Skoracki [42] found two new quill mites species of this genus, *P. montanus* and *P. patagioenas*, on columbiform birds. The results of this study allowed to addition of another genus to Columbiformes–Psittaciformes hosts group. The last genus associated with columbiforms closely related to *Psittaciphilus* is *Meitingsunes* described by Glowska and Skoracki in 2010 [39]. Type species of this genus—*M. zenadourae*—was originally described as *Syringophilus zenadourae* by Clark 1964 [28]. In taxonomic revision of syringophilids, Kethley [16], moved this species to the *Peristerophila* genus. Finally, Glowska and Skoracki 2010 [39] based on morphological difference (apodemes I divergent, not fused to apodemes II) established a new genus—*Meitingsunes*—for this species. In 2011–2020, numerous taxonomic studies added five new quill mite species associated with birds from order Columbiformes. Currently, only one species of the letter genus, *M. caprimulgus*, has been recorded from another bird order, such as Caprimulgiformes [50].

Recent examples of studies on multispecies interactions at macroscales can be broadly grouped into two analytical approaches: analyses of species richness and ecological networks. The ecological network approach usually relies on observed interactions among multiple species at fine spatial resolutions [7].

Therefore, in this study, we focus on describing the richness, interactions, and measuring the specialization of syringophilid ectoparasites and their columbiform hosts in a global scale. Moreover, we reconstruct the syringophilid phylogeny at the generic level. Additionally, based on an earlier study, we summarize all taxonomic and locality records to create a worldwide distribution of the quill mites associated with birds from the order Columbiformes. We also discuss the host–parasite relationships between syringophilid species and columbiform birds.

2. Materials and Methods

In the present study, we re-examined the ornithological collections of the columbiform specimens housed in the Bavarian State Collection of Zoology, Munich, Germany

(ZSM) and Museum of Natural History, Nairobi, Kenya (NMK). These bird collections have been previously used as donors of mite species described or recorded in the several published papers (see Skoracki and Dabert [40]; Skoracki and Glowska [37]; Glowska and Skoracki [39], Skoracki [22]; Skoracki and Hromada [41]; Skoracki et al. [47]; Kaszewska and Skoracki [42]; Kaszewska et al. [42–46]). We also analyzed the host specimens collected from frozen collections housed in several veterinary centers. Bird specimen was examined using a dissecting microscope and the infested quills were opened with a fine scalpel. From each bird specimen, we removed one wing covert, about 5 under-tail coverts, and about 10 contour feathers. Before mounting, mites were softened and cleared in Nesbitt's solution at room temperature for three days [22], and then mites were mounted on slides in Hoyer's medium.

2.1. Bipartite Networks and Statistics

The bipartite graph consists of rectangles representing compartment species and the width is proportion to the sum of interaction involving this species. Interacting species are linked by lines whose width is proportional to the number of interactions [51]. To visualize patterns in the studied host–parasite–ecological web, we used the 'bipartite' package available for R software [51]. To visualize bipartite networks we used functions plotweb (Figure 1) and visweb (Figure S1). For all host species recorded in earlier papers without information about prevalence, we gave score 1. Indices were calculated by using network-level and network-species functions available in bipartite packages.

We calculated the following bipartite index: network specialization (H2′) nestedness (N), connectance (C), and modularity (Q), to measured interaction on species-level we used species specialization metrics (d′). For this purpose, we prepared the matrices where quill mites species are in the rows (parasites) and the bird species (host) in the columns. 'H2′ network-level measure of specialization, based on the deviation of a species' realized number of interactions and that expected from each species' total number of interactions [52]. Values of H2′ range from 0 to 1, where 0 indicates low specialization, while 1 suggests high specialization [53]. We also calculated the connectance, defined as the proportion of possible links observed in the network [54], ranged from 0 (low connectance in the network) to 1 to imply more connectance in the network. Nestedness measures how many interactions realized by specialists are a subset of those realized by generalists. The base metric of nestedness is the nestedness temperature T (0°–100°), which measures the departure from a perfectly nested interaction matrix [55]. For this study, we used a binary system, where metrics define as $N = (100 - T)/100$, with values ranging from 0 to 1 (maximum nestedness) [56–58].To calculate network modularity we calculate 'likelihood' implemented in computeModules in the bipartite library for R; this index is the same value as Q (or M), the modularity as given by Newman [59] or Guimerà & Amaral [60] and well known from QuanBiMo (Q) library [61], currently not supported. According to network permutation, we obtained 100 Q values (observed likelihood) [62] and compared them with 100 Q values coming from permutations for null models (null likelihood). To test a significant difference between the Q observed and Qnull values, we calculated the null.t.test ($p < 0.05$). For each quill mites species associated with doves and pigeons in the network, we calculated d′ index measured specialization at species level [52].

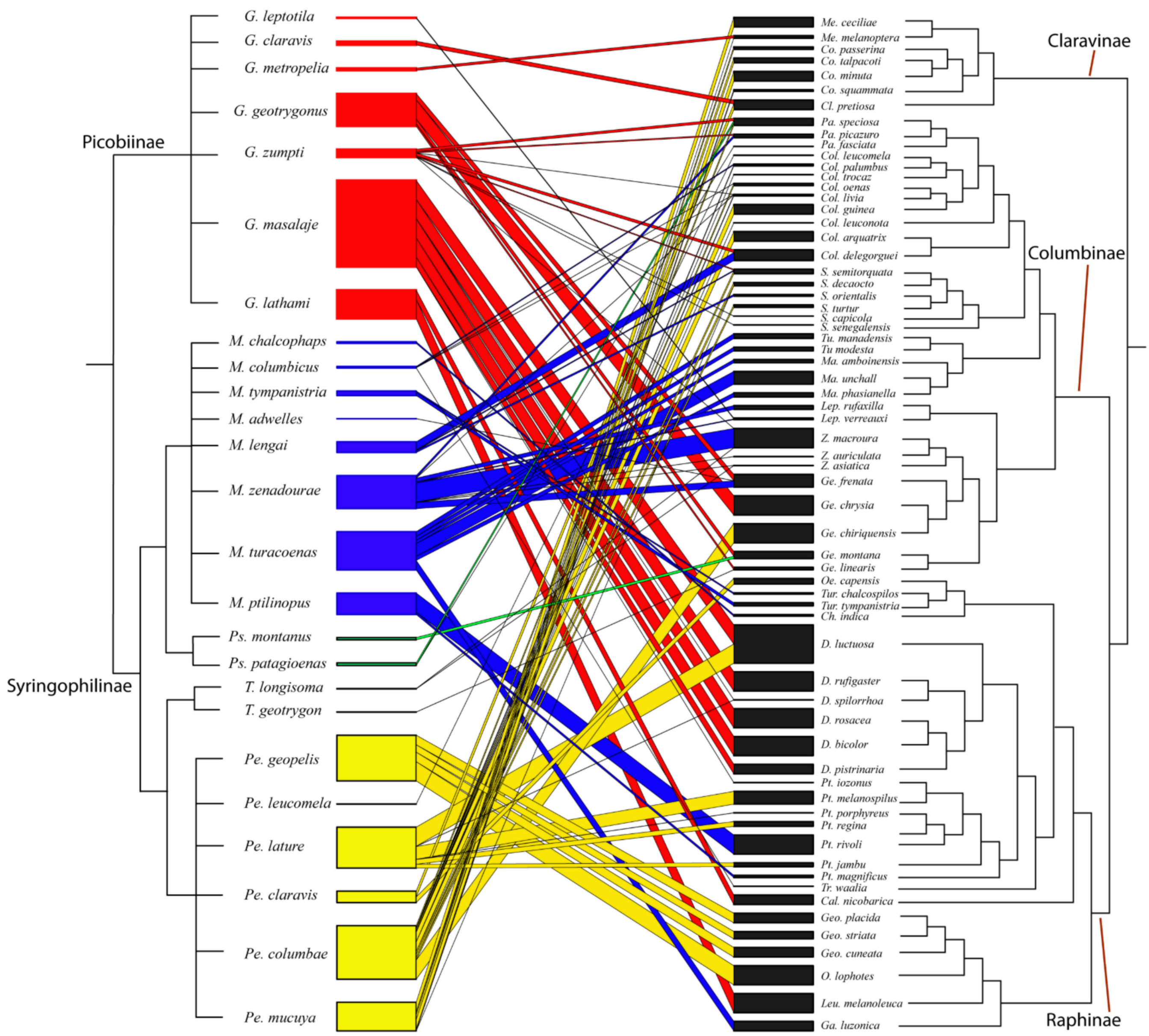

Figure 1. Bipartite network graph of interactions between quill mite species (**left**) and their doves and pigeons hosts (**right**).

2.2. Prevalence

Descriptive statistics were computed using Quantitative Parasitology on the Web [63], with 95% confidence intervals (Sterne method).

2.3. Mite Phylogeny

In the cladistic analysis, we examined relationships at the generic level. All operational taxonomic units (OTUs) were represented by taxonomic species, i.e., type species for each genus. A free-living predator *Cheyletus eruditus* (Schrank) and quill-inhabiting predator *Metacheletoides numidae* Fain both belonging to the sister family Cheyletidae, were used as outgroups in the analyses. Because each particular syringophilid genus is represented by a single species in the present analysis, the character states appearing as autapomorphies represent true synapomorphies for genera.

A total of five OTUs representing all genera associated with columbiform birds, two taxa as the outgroup, and 26 non-additive and unordered morphological characters were included in our data matrix (data matrix and morphological characters are supplemented (Figures S2 and S3)). A detailed discussion of the morphological characters used in the present study is provided by Skoracki [22]; Skoracki et al. [47]. The matrix was done using NEXUS Data Editor 0.5.0 [64]. Analyses of character distribution on the tree were performed in WINCLADA [65]. Only unordered, qualitative, and unweighted characters were used in analyses. We applied a multistate contingent coding strategy [66], which is considered as the most useful among available approaches [67]. Following this strategy, characters with multiple states were interpreted as unordered and not modified into binary characters. Reconstruction of phylogenetic relationships was performed with PAUP 4.0 beta version for IBM [68] in conjunction with PRAP2 [69] to conduct a ratchet analysis (1000 iterations; 10 random cycles, collapsed zero-branches in effect; options are the default). Nodal support was evaluated by Bremer indices calculated with PRAP2. Analysis of character distributions, drawing, and editing of the trees was performed in TreeView 1.5.2. [70].

2.4. Visualization of Host Phylogeny

To visualize host phylogeny, a tree of the columbiform species was constructed based on a consensus avian phylogenetic tool available at http://birdtree.org/ (accessed on 5 March 2019) [71]. As the source of our consensus tree, we used the 'Hackett All Species tree' with 1000 randomly generated trees. The most credible tree was then determined using the tool TreeAnnotatorv1.8.2 in the software BEAST v1.8.2 [72]. The consensus tree was then graphically adjusted in FigTree v1.4.2 (Andrew Rambaut, University of Edinburgh, UK; http://tree.bio.ed.ac.uk/software/figtree/ (accessed on 5 March 2019)).

2.5. Host Specificity

Host specificity for particular mite species follows Caira et al. [73] and Skoracki et al. [47]. The division stands out monoxenous species (parasite infest single host species), oligoxenous (more than one host, but restricted to one genus), mesostenoxenous (more than one genus of hosts, but restricted to one subfamily), metastenoxenous (more than one subfamily of hosts but restricted to one order), and polyxenous species (more than one order). The common and scientific names of the birds follow Clements et al. [10]. Zoogeographic regions follow Holt et al. [74].

3. Results

A total of 772 individuals of pigeons and doves and belonging to 29 genera and 112 species were examined for the presence of quill mites belonging to the family Syringophilidae. Among them, 117 individuals representing 65 species had been infested by the quill mites belonging to the following genera *Meitingsunes* Glowska & Skoracki, 2010 (7 species), *Peristerophila* Kethley 1970 (6), *Psittaciphilus* Bochkov & Mironov, 2000 (2), (subfamily *Syringophilinae*), and *Gunabopicobia* Bochkov & Perez, 2002 (7) (subfamily Picobiinae) (Tables 1 and S1).

In total, 22 out of 25 known quill mites species associated with Columbiformes birds were identified (*Terratosyringophilus geotrygonus*, *T. longisoma*, and *M. adwelles* were not found). Among non-infested columbid specimens, some taxa were examined for the presence of quill mites for the first time, for example: *Reinwardtoena reinwardtsi*, *Gymnophaps albertisii*, *Henicophaps albifrons*, and *Henicophaps foersteri*.

Table 1. Quill mite species of the family Syringophilidae parasitizing birds of the order Columbiformes with their distribution.

Quill Mite Species	Host Species	Host Subfamily	Distribution	References
Subfamily Syringophilinae Lavoipierre, 1953				
Genus *Meitingsunes* Glowska & Skoracki, 2010				
M. aldwelles Glowska & Skoracki, 2010	*Geotrygon frenata* * (Tschudi)	Columbinae	Neot. (Colombia)	[39]
M. columbicus Skoracki, 2011	*Columba oenas* * Linnaeus	Columbinae	Pala. (Kazakhstan)	[22]
"	*Columba livia* Gmelin	Columbinae	Pala. (Poland, Slovakia)	[22,45]
"	*Columba palumbus* Linnaeus	Columbinae	Pala. (Germany, Russia)	[22,45]
"	*Treron waalia* (Meyer)	Raphinae	Afro. (Cameroon)	[43]
M. chalcophas Kaszewska, Skoracki & Kavetska, 2016	*Chalcophas indica* * (Linnaeus)	Raphinae	Orie. (Indonesia: Timor) Aust. (Australia)	[44,45]
M. ptilinopus Kaszewska, Skoracki & Hromada, 2020	*Ptilinopus magnificus* * Temminck	Raphinae	Aust. (Australia)	[45]
"	*Ptilinopus rivoli* (Prevost)	Raphinae	Ocea. (Papua New Guinea)	[45]
M. lengai Kaszewska, Skoracki & Hromada, 2020	*Columba delegorguei* * Delegorgue	Columbinae	Afro. (Tanzania)	[45]
"	*Streptopelia orientalis* (Latham)	Columbinae	Afro. (Tanzania)	[45]
"	*Streptopelia semitorquata* Ruppell	Columbinae	Pala. (Kazakhstan, Kyrgyzstan)	[45]
M. turacoenas Kaszewska, Skoracki & Kavetska, 2016	*Gallicolumba luzonica* Scopoli	Raphinae	Orie. (Philippines)	[45]
"	*Macropygia amboinensis* (Linnaeus)	Columbinae	Ocea. (Papua New Guinea)	[45]
"	*Macropygia phasianella* (Temminck)	Columbinae	Orie. (Philippines, Indonesia: Java)	[45]
"	*Macropygia unchall* (Wagler)	Columbinae	Ocea. (Papua New Guinea)	[45]
"	*Turacoena manadensis* * (Quoy &Gaimard)	Columbinae	Orie. (Indonesia: Sulavesi, Nepal)	[44]
"	*Turacoena modesta* (Temminck)	Columbinae	Orie. (Indonesia)	[44]
M. tympanistria (Skoracki & Dabert, 2012)	*Turtur chalcospilos* (Wagler)	Raphinae	Afro. (Tanzania)	[40]
"	*Turtur tympanistria* * (Temminck)	Raphinae	Afro. (Togo, Tanzania)	[40,45]
M. zenadourae (Clark, 1964)	*Columba livia* Gmelin	Columbinae	Near. (USA: Texas); Afro. (N. Africa, Djibouti)	[30,39,45]
"	*Geotrygon frenata* (Tschudi)	Columbinae	Neot. (Colombia)	[45]
"	*Leptotila rufaxilla* (Richard, Bernard)	Columbinae	Neot. (Surinam, Argentina)	[45]
"	*Leptotila verreauxi* (Bonaparte)	Columbinae	Neot. (Colombia)	[45]
"	*Patagioenas picazuro* Temminck	Columbinae	Neot. (Paraguay)	[45]
"	*Zenaida asiatica* (Linnaeus)	Columbinae	Near. (USA: Texas)	[75]
"	*Zenaida auriculata* (Murs)	Columbinae	Neot. (Argentina)	[76]
"	*Zenaida macroura* * (Linnaeus)	Columbinae	Near. (USA: Maryland, Arizona, San Francisco)	[28,39,45]

Table 1. *Cont.*

Quill Mite Species	Host Species	Host Subfamily	Distribution	References
		Genus *Peristerophila* Kethley, 1970		
P. columbae (Hirst, 1920)	*Columba arguatrix* (Temminck)	Columbinae	Afro. (Kenya)	[46]
"	*Columba guinea* Linnaeus	Columbinae	Afro. (S Africa, Tanzania)	[46]
"	*Columba leuconota* (Vigors)	Columbinae	Orie. (Nepal)	[46]
"	*Columba livia* * Gmelin	Columbinae	Pala. (England, Macedonia, Poland, Turkey); Near. (Canada, USA); Orie. (India); Sa-Arab. (Iran)	[22,27,32,38,46]
"	*Columba oenas* Linnaeus	Columbinae	Pala. (Germany)	[46]
"	*Columba palumbus* Linnaeus	Columbinae	Pala. (Germany, England)	[46]
"	*Columba trocaz* Heineken	Columbinae	Pala. (Portugal)	[46]
"	*Geotrygon chiriquensis* Sclater	Columbinae	Pana. (Panama)	[46]
"	*Patagioenas speciosa* (Gmelin)	Columbinae	Neot. (Surinam)	[46]
"	*Streptopelia capicola* (Sundevall)	Columbinae	Afro. (Angola)	[46]
"	*Streptopelia decaocto* (Frivaldszky)	Columbinae	Sa-Arab. (Jordan)	[22]
"	*Streptopelia decipiens* (Hartlaub & Finsch.)	Columbinae	Pala. (Macedonia), Afro. (Tanzania)	[46]
"	*Streptopelia orientalis* (Latham)	Columbinae	Orie. (Japan)	[46]
"	*Streptopelia semitorquata* (Ruppell)	Columbinae	Afro. (Angola, Tanzania, D. R. Congo)	[46]
"	*Streptopelia tranquebarica* (Hermann)	Columbinae	Orie. (China)	[46]
"	*Streptopelia turtur* (Linnaeus)	Columbinae	Pala. (Germany, Greece, Hungary, Macedonia)	[46]
P. claravis (Skoracki & Glowska, 2008)	*Claravis pretiosa* * Ferrari-Pérez	Claravinae	Neot. (Bolivia, Colombia, Paraguay), Pana. (Panama)	[37,46]
"	*Oena capensis* (Linnaeus)	Raphinae	Afro. (Ethiopia, Sudan, Tanzania)	[46]
P. geopelis Kaszewska, Skoracki, Kosicki & Hromada, 2020	*Geopelia cuneata* (Latham)	Raphinae	Austr. (Australia)	[46]
"	*Geopelia placida* Gould	Raphinae	Austr. (Australia)	[46]
"	*Geopelia striata* * (Linnaeus)	Raphinae	Orie. (Indonesia: Celebes, Java, Sumatra)	[46]
"	*Ocyphaps lophotes* (Temminck)	Raphinae	Austr. (Australia)	[46]
P. lature Kaszewska, Kavetska & Skoracki, 2014	*Ducula luctuosa* * (Temminck)	Raphinae	Austr. (Australia)	[43]
"	*Ducula spilorrhoa* (Gray)	Raphinae	Austr. (Papua New Guinea)	[43]
"	*Ptilinopus jambu* (Gmelin)	Raphinae	Orie. (Indonesia: Sumatra)	[43]
"	*Ptilinopus melanospilus* (Salvadori)	Raphinae	Orie. (Indonesia: Mount Gade)	[43]
"	*Ptilinopus porphyreus* (Temminck)	Raphinae	Orie. (Indonesia: Java)	[43]
"	*Ptilinopus regina* (Swainson)	Raphinae	Orie. (Indonesia: Marina Isl.)	[43]
P. leucomela Kaszewska, Skoracki, Kosicki & Hromada, 2020	*Columba leucomela* * Temminck	Columbinae	Austr. (Australia)	[46]
P. mucuya Casto, 1980	*Columbina minuta* Linnaeus	Claravinae	Neot. (Paraguay)	[46]

Table 1. *Cont.*

Quill Mite Species	Host Species	Host Subfamily	Distribution	References
"	*Columbina passerina* * (Linnaeus)	Claravinae	Neot. (Colombia, Surinam); Near. (USA)	[30,46]
"	*Columbina squammata* (Lesson)	Claravinae	Neot. (Brazil, Paraguay)	[35,46]
"	*Columbina talpacoti* (Temminck)	Claravinae	Neot. (Brazil, Surinam, Trinidad and Tobago); Pala. (Monaco)	[37,46]
"	*Geophaps plumifera* Gould	Columbinae	Aust. (Australia)	[35]
"	*Metriopelia ceciliae* (Lesson)	Claravinae	Neot. (Peru)	[46]
"	*Metriopelia melanoptera* (Molina)	Claravinae	Neot. (Argentina)	[37]
"	*Brotogeris versicolurus* ** Muller	Psittacidae	Neot. (Brazil)	[35]
"	*Psilopsiagon aymara* ** d'Orbigny	Psittacidae	Neot. (S. America)	[35]
"	*Trichoglossus haematodus* ** (Linnaeus)	Psittaculidae	Ori. (Indonesia)	[35]
		Genus *Psittaciphilus*, Bochkov & Mironov, 2000		
P. montanus Kaszewska & Skoracki, 2018	*Geotrygon montana* * (Linnaeus)	Columbinae	Neot. (Brazil, Trinidad and Tobago); Pana. (Panama)	[42]
P. patagioenas Kaszewska & Skoracki, 2018	*Patagioenas fasciata* * (Say)	Columbinae	Neot. (Colombia)	[42]
"	*Patagioenas speciosa* (Gmelin)	Columbinae	Neot. (Surinam)	[42]
		Genus *Terratosyringophilus* Bochkov and Perez, 2002		
T. geotrygonus Skoracki & Glowska, 2008	*Geotrygon linearis* * (Prévost)	Columbinae	Neot. (Venezuela)	[37]
T. longisoma (Casto, 1979)	*Zenaida asiatica* * (Linnaeus)	Columbinae	Near. (USA)	[31]
"	*Zenaida macroura* (Linnaeus)	Columbinae	Near. (USA)	[37]
		Subfamily Picobiinae Johnson & Kethley, 1973		
		Genus *Gunabopicobia* Skoracki & Hromada, 2013		
G. claravis Kaszewska, Skoracki & Hromada, 2018	*Claravis pretiosa* * (Ferrari-Perez)	Claravinae	Neot. (Colombia)	[26]
G. geotrygoni Kaszewska, Skoracki & Hromada, 2018	*Geotrygon linearis* * (Prevost)	Columbinae	Neot. (Venezuela)	[26]
"	*Geotrygon chrysia* Bonaparte	Columbinae	Ocea. (Martinique)	[26]
"	*Geotrygon frenata* (Tschudi)	Columbinae	Neot. (Colombia)	[26]
"	*Geotrygon montana* (Linnaeus)	Columbinae	Neot. (Paraguay)	[26]
G. masalaje Kaszewska, Kavetska & Skoracki, 2014	*Ducula bicolor* (Scopoli)	Raphinae	Orie. (Indonesia)	[43]
"	*Ducula rufigaster* (Quoy and Gaimard)	Raphinae	Ocea. (Papua New Guinea)	[43]
"	*Ducula rosacea* (Temminck)	Raphinae	Orie. (Indonesia: Semau Isl.)	[43]
"	*Ducula pistrinaria* Bonaparte	Raphinae	Ocea. (Papua New Guinea)	[43]
"	*Ducula spilorrhoa (Gray)*	Raphinae	Orie. (Indonesia: Semau Isl.)	[43]
"	*Ducula luctuosa* (Temminck)	Raphinae	Ocea. (Papua New Guinea)	[43]

Table 1. *Cont.*

Quill Mite Species	Host Species	Host Subfamily	Distribution	References
"	*Ptilinopus iozonus* * Gray	Raphinae	Ocea. (Papua New Guinea)	[43]
G. metriopelia Kaszewska, Skoracki and Hromada, 2018	*Metriopelia melanoptera* * (Molina)	Claravinae	Neot. (Argentina)	[26]
G. lathami Kaszewska, Skoracki and Hromada, 2018	*Leucosarcia melanoleuca* * Gould	Raphinae	Orie. (Indonesia); Ocea. (Papua New Guinea)	[26]
"	*Caloenas nicobarica* (Linnaeus)	Raphinae	Orie. (Indonesia); Ocea. (Papua New Guinea)	[26]
G. leptotila Kaszewska, Skoracki & Hromada, 2018	*Leptotila verreauxi* * (Bonaparte)	Columbinae	Neot. (Argentina)	[26]
G. zumpti (Lawrence, 1959)	*Columba livia* Gmelin	Columbinae	Near. (USA); Pala. (Poland)	[36,47]
"	*Columba delegorquei* Delegorgue	Columbinae	Afro. (Tanzania)	[26]
"	*Patagioenas picazuro* (Temminck)	Columbinae	Neot. (West Brazil)	[26]
"	*Patagioenas speciosa* Gmelin	Columbinae	Neot. (North Brazil)	[26]
"	*Streptopelia capicola* * (Sundevall)	Columbinae	Afro. (South Africa)	[29]
"	*Streptopelia semitorquata* (Ruppell)	Columbinae	Afro. (Ethiopia)	[26]
"	*Streptopelia senegalensis* (Linnaeus)	Columbinae	Afro.(South Africa)	[41]
"	*Zenaida macroura* (Linnaeus)	Columbinae	Near. (USA)	[28]

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-Jappanese (according to Holt et al. [71]). *—type host; **—host from order Psittaciformes; "— previous species name. Locality established based on the host distribution.

3.1. Prevalence Index Birds from Order Columbiformes

The index of prevalence (IP) of host species from Columbiformes order ranges from 4.2% to 100% (IP = 100 in 17 cases); however, the confidence intervals were wide and ranged from 0.2 to 100 (Table 2). In our material, 49 host species (239 individuals) were not infested by the syringophilid mites.

(1) IP 1–10% *Chalcophaps indica* (8.7%), *Columba livia* (8.7%), *Columba palumbus* (5%), *Columbina squammata* (6.7%), *Leptotila verreauxi* (4.2%), *Patagioenas picazuro* (6.2%), *Streptopelia orientalis* (9.1%), *Streptopelia semitorquata* (4.8%), *Turtur chalcospilos* (7%).

(2) IP 11–20% *Claravis pretiosa* (20%), *Columba delegorguei* (14.3%), *Columba oenas* (11.1%), *Columbina raucana* (13.3%), *Geotrygon linearis* (12.5%), *Geotrygon montana* (12.5%), *Leptotila rufaxilla* (20%), *Macropygia amboinensis* (16.7%), *Metriopelia melanoptera* (12.5%), *Patagioenas picazuro* (12.5%), *Patagioenas speciosa* (12.5%), *Patagioenas speciosa* (12.5%), *Ptilinopus magnificus* (11.8%), *Streptopelia semitorquata* (14.3%), *Streptopelia turtur* (13.3%), *Turacoena modesta* (20), *Turtur tympanistria* (16.7%).

(3) IP 21–30% *Columbina talpacoti* (25%), *Geotrygon montana* (25%), *Macropygia phasianella* (21.4%), *Oena capensis* (29.4%), *Turacoena manadensis* (25%).

(4) IP 31–40% *Geotrygon frenata* (33%), *Geopelia striata* (38.5%).

(5) IP 41–50% *Caloenas nicobarica* (50%), *Columba arquatrix* (50%), *Columba delegorguei* (42%), *Columba guinea* (50%), *Columbina minuta* (50%), *Gallicolumba luzonica* (50%), *Geopelia cuneata* (50%), *Geopelia placida* (50%), *Metriopelia ceciliae* (50%).

(6) IP 61–70 *Macropygia unchall* (66.7%), *Ptilinopus melanospilus* (66.7%).

(7) IP 100% *Ducula bicolor*, *Geotrygon chrysie*, *Geotrygon chiriquensis*, *Leucosarcia melanoleuca*, *Ocyphaps lophotes*, *Ptilonopus rauca*, *Zenaida macroura*.

In Table 2. We excluded the following examined but non-infested bird species: *Chalcophaps stephani* [N = 2], *Claravis mondetoura* [N = 2], *Columba rupestris* [N = 11], *Columbina cruziana* [N = 2], *Ducula aenea* [N = 4], *Ducula carola* [N = 2], *Ducula concinna* [N = 1], *Ducula finschii* [N = 2], *Ducula perspicillata* [N = 1], *Ducula zoeae* [N = 7], *Gallicolumba rufigula* [N = 1], *Geotrygon violacea* [N = 1], *Gymnophaps albertisii* [N = 2], *Henicophaps albifrons* [N = 1], *Henicophaps foersteri* [N = 1], *Leptotila cassini* [N = 1], *Leptotrygon veraguensis* [N = 1], *Macropygia magna* [N = 3], *Macropygia ruficeps* [N = 4], *Otidiphaps nobilis* [N = 1], *Patagioenas raucana* [N = 12], *Patagioenas cayennensis* [N = 18], *Patagioenas oenops* [N = 4], *Patagioenas subvinacea* [N = 3], *Ptilinopus bernsteinii* [N = 1], *Ptilinopus cinctus* [N = 6], *Ptilinopus coronulatus* [N = 4], *Ptilinopus ornatus* [N = 1], *Ptilinopus porphyreus* [N = 3], *Ptilinopus pulchellus* [N = 5], *Ptilinopus solomonensis* [N = 1], *Ptilinopus superbus* [N = 6], *Reinwardtoena reinwardtii* [N = 2], *Streptopelia picturata* [N = 1], *Streptopelia roseogrisea* [N = 3], *Streptopelia senegalensis* [N = 26], *Streptopelia tranquebarica* [N = 5], *Treron bicinctus* [N = 3], *Treron calva* [N = 7], *Treron capellei* [N = 3], *Treron curvirostra* [N = 8], *Treron delalandii* [N = 20], *Treron fulvicollis* [N = 4], *Treron olax* [N = 2], *Treron pompadora* [N = 7], *Treron sieboldii* [N = 5], *Treron sphenurus* [N = 3], *Treron vernanus* [N = 18], *Zenaida galapagoensis* [N = 8].

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

Host Species		Exa.	Inf.	IP; CI	Mite Species	Habitat
Caloenas nicobarica *	Nicobar pigeon	4	2	50 (9.8–90.2)	*G. lathami*	contour
Chalcophaps indica	Grey-capped Emerald Dove	23	2	8.7 (1.6–27.8)	*M. chalcophas*	coverts
Claravis pretiosa	Blue Ground-dove	10	3	30 (8.7–61.9)	*P. claravis*	coverts
" *			2	20 (3.7–55.3)	*G. claravis*	contour
Columba arquatrix	African Olive-pigeon	4	2	50 (9.8–90.2)	*P. columbae*	under-wings cov.
Columba delegorguei	Delegorgue's Pigeon	7	2	42 (14.9–77.5)	*M. lengai*	under-tail cov.
" *			1	14.3 (0.7–55.4)	*G. zumpti*	contour
Columba guinea	Speckled Pigeon	4	2	50 (9.8–90.2)	*P. columbae*	under-wings cov.
Columba leucomela	White-headed Pigeon	1	1	100 (5.0–100)	*P. leucomela*	-
Columba leuconota	Snow Pigeon	1	1	100 (5.0–100)	*P. columbae*	-
Columba livia	Rock Pigeon	20	1	5 (0.3–24.4)	*P. columbae*	contour
"		NA	NA	-	*G. zumpti*	contour
"		1	1	100 (5.0–100)	*M.zenadourae*	covert
"		NA	NA	-	*M. columbicus*	secondaries
Columba oenas	Stock Dove	NA	NA	-	*M. columbicus*	secondaries
"		9	1	11.1 (0.6–44.4)	*P. columbae*	under-wings cov.
Columba palumbus	Common Wood-Pigeon	20	1	5 (0.3–24.4)	*M. columbicus*	tail cov.
"		20	1	5 (0.3–24.4)	*P. columbae*	covert
Columba trocaz	Madeira laurel Pigeon	1	1	100 (5.0–100)	*P. columbae*	under wing cov.
Columbina minuta	Plain-breasted Ground-Dove	4	2	50 (9.8–90.2)	*P.mucuya*	contour
Columbina passerina	Common Ground-Dove	15	2	13.3 (2.4–39.7)	*P.mucuya*	secondaries
Columbina talpacoti	Ruddy Ground-Dove	32	8	25 (12.2–42.3)	*P.mucuya*	under-wings cov
Columbina squammata	Scaled Dove	11	1	9.1 (0.5–40.5)	*P.mucuya*	tertials
Ducula bicolor *	Pied Imperial-Pigeon	2	2	100 (22.4–100)	*G. masalaje*	contour
Ducula luctuosa *	Silver-tipped Imperial-Pigeon	1	1	100 (22.4–100)	*G. masalaje*	contour
"		1	1	100 (22.4–100)	*P.lature*	covert
Ducula pistrinaria *	Island Imperial-Pigeon	2	1	50 (2.5–97.5)	*G. masalaje*	contour
Ducula rosacea *	Pink-headed Imperial-Pigeon	1	1	100 (22.4–100)	*G. masalaje*	contour
Ducula rufigaster *	Purple-tailed Imperial-Pigeon	1	1	100 (22.4–100)	*G. masalaje*	contour
Ducula spilorrhoa *	Torresian Imperial-Pigeon	1	1	100 (5.0–100)	*G. masalaje*	contour
"		1	1	100 (5.0–100)	*P.lature*	-
Gallicolumba luzonica	Luzon Bleeding-heart	2	1	50 (2.5–97.5)	*M. turacoenas*	contour
Geopelia cuneata	Diamond Dove	2	1	50 (2.5–97.5)	*P. geopelis*	covert
Geopelia placida	Peaceful Dove	2	1	50 (2.5–97.5)	*P. geopelis*	contour
Geopelia striata	Zebra Dove	13	5	38.5 (16.6–65.8)	*P. geopelis*	covert
Geotrygon chrysie *	Key West Quail-Dove	1	1	100 (22.4–100)	*G. geotrygoni*	contour

Table 2. *Cont.*

Host Species		Exa.	Inf.	IP; CI	Mite Species	Habitat
Geotrygon chiriquensis	Chiriqui Quail-Dove	1	1	100 (5–100)	*P. columbae*	under-tail cov.
Geotrygon frenata	White-throated Quail-Dove	3	1	33 (1.7–86.5)	*M. zenadourae*	-
" *			1	33 (1.7–86.5)	*G. geotrygoni*	contour
Geotrygon linearis *	Lined Quail-Dove	8	1	12.5 (0.6–50)	*G. geotrygoni*	contour
			1	12.5 (0.6–50)	*T. geotrygonus*	primaries
Geotrygon montana *	Ruddy Quail-Dove	8	2	25 (4.6–63.5)	*G. geotrygoni*	contour
"			1	12.5 (0.6–50)	*P. montanus*	under tail cov.
Leptotila verreauxi	White-tipped dove	24	1	4.2 (0.2–20.4)	*M. zenadourae*	under-tail cov.
" *			1	4.2 (0.2–20.4)	*G. leptotila*	contour
Leptotila rufaxilla	Gray-fronted Dove	10	2	20 (3.7–55.3)	*M. zenadourae*	under-tail cov.
Leucosarcia melanoleuca *	Wonga Pigeon	1	1	100 (5–100)	*G. lathami*	contour
Macropygia amboinensis	Amboyna Cuckoo-Dove	6	1	16.7 (0.9–58.9)	*M. turacoenas*	-
Macropygia phasianella	Brown Cuckoo-Dove	14	3	21.4 (6.1–50)	*M. turacoenas*	under and upper-tail cov.
Macropygia unchall	Barred Cuckoo-Dove	3	2	66.7 (13.5–98.3)	*M. turacoenas*	under-tail cov.
Metriopelia ceciliae	Bare-faced Ground-Dove	2	1	50 (2.5–97.5)	*P. mucuya*	secondaries, covert
Metriopelia melanoptera *	Black-winged Ground-Dove	8	1	12.5 (0.6–50)	*G. metriopelia*	contour
Ocyphaps lophotes	Crested Pigeon	1	1	100 (5–100)	*P. geopelis*	small covert under-tail cov.
Oena capensis	Namaqua Dove	17	5	29.4 (12.4–54.4)	*P. claravis*	under-tail cov.
Patagioenas fasciata	Band-tailed pigeon	1	1	100 (5.0–100)	*P. patagioenas*	upper-tail cov.
Patagioenas picazuro	Picazuro Pigeon	16	2	12.5 (2.3–37.2)	*M. zenadourae*	under-wing cov.
" *			1	6.2 (0.3–30.5)	*G. zumpti*	contour
Patagioenas speciosa	Scaled Pigeon	8	1	12.5 (0.6–50)	*P. columbae*	-
" *			1	12.5 (0.6–50)	*G. zumpti*	contour
"			1	12.5 (0.6–50)	*P. patagioenas*	coverts
Ptilinopus iozonus *	Orange-Bellied Fruit Dove	4	1	25 (1.3–75.1)	*G. masalaje*	contour
Ptilinopus jambu	Jambu Fruit-Dove	5	1	20 (1–65,7)	*P. lature*	coverts
Ptilinopus magnificus	Wompoo Fruit-Dove	17	2	11.8 (2.1–35)	*M. ptilinopus*	under-tail cov.
Ptilinopus melanospilus	Black-naped Fruit-Dove	3	2	66.7 (13.5–98.3)	*P. lature*	coverts
Ptilinopus regina	Rose-crowned Fruit-Dove	4	1	25 (1.3–75.1)	*P. lature*	coverts
Ptilonopus rivoli	White-bibbed Fruit-Dove	1	1	100 (5–100)	*M. ptilinopus*	under-tail cov.
Streptopelia decaocto	Eurasian Collared-Dove	12	2	16.7 (3–45.7)	*P. columbae*	secondaries
Streptopelia capicola	Ring-Necked Dove	NA	NA	-	*G. zumpti*	contour
Streptopelia orientalis	Oriental Turtle-Dove	22	2	9.1 (1.6–29.1)	*M. lengai*	under-tail cov.
Streptopelia semitorquata	Red-eyed Dove	21	1	4.8 (0.2–23.3)	*M. lengai*	rectrices
" *			1	4.8 (0.2–23.3)	*G. zumpti*	contour
"			3	14.3 (4–35.4)	*P. columbae*	coverts
Streptopelia turtur	European Turtle-Dove	30	4	13.3 (4.7–29.8)	*P. columbae*	contour under-tail cov.
Treron waalia	Bruce's Green-Pigeon	1	1	100 (5.0–100)	*M. columbicus*	covert
Turacoena manadensis	White-faced Cuckoo-Dove	4	1	25 (1.3–75.1)	*M. turacoenas*	under tail cov
Turacoena modesta	Black Cuckoo-Dove	5	1	20 (1–65.7)	*M. turacoenas*	under tail cov
Turtur chalcospilos	Emerald-spotted Wood-Dove	13	1	7 (0.4–34.2)	*M. tympanistria*	coverts
Turtur tympanistria	Tambourine Dove	12	2	16.7 (3–45.7)	*M. tympanistria*	rectrices
Zenaida asiatica	White-winged Dove	NA	NA	-	*M. zenadourae*	-
"		NA	NA	-	*T. longisoma*	-
Zenaida auriculata	Eared Dove	NA	NA	-	*M. zenadourae*	-
Zenaida macroura	Mourning Dove	1	1	100 (5–100)	*M. zenadourae*	coverts
"		NA	NA	-	*T. longisoma*	primaries

Exa.—number of individual host species examined during study; Inf.—number of individual host species, infected by quill mites; IP—prevalence index given in (%); CI—confidence interval (Sterne method); NA—infected hosts species, but prevalence index was unknown. *—type host; "— previous species name.

3.2. Host Specificity of the Quill Mites

Based on previously recorded host species, we classified all syringophilids associated with columbiform birds into the following host specificity groups (Tables 3 and 4):

(1) Monoxenous parasites, including 8 species: *Gunabopicobia claravis*, *G. leptotila*, *G. metriopelia*, *Meitingsunes adewlles*, *M. chalcophas*, *Peristerophila leucomela*, *Psittaciphilus montanus*, *Terratosyringophilus geotrygonus*.

(2) Oligoxenous parasites, including 5 species: *Gunabopicobia geotrygoni*, *Meitingsunes ptilinopus*, *M. tympanistria*, *Psittaciphilus patagioenas*, *Terratosyringophilus longisoma*.

(3) Mesostenoxenous parasites, including 8 species: *Gunabopicobia lathami*, *G. masalaje*, *G. zumpti*, *Meitingsunes lengai*, *M. zenadourae*, *Peristerophila columbae*, *P. geopelis*, *P. lature*.

(4) Metastenoxenous parasites, including 3 species: *Meitingsunes turacoenas*, *Peristerophila claravis*, *Meitingsunes columbicus*.

(5) Polyxenous parasites, including only one species: *Peristerophila mucuya*.

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	0.2	*Meitingsunes adwelles*	*Geotrygon frenata*
	1	*Meitingsunes chalcophas*	*Chalcophaps indica*
	1	*Peristerophila leucomela*	*Columba leucomela*
	0.75	*Psittaciphilus montanus*	*Geotrygon montana*
	0.5	*Terratosyringophilus geotrygonus*	*Geotrygon linearis*
Oligoxenous	1	*Meitingsunes tympanistria*	*Turtur chalcospilos* *Turtur tympanistria*
	0.77	*Psittaciphilus patagioenas*	*Patagioenas fasciata* *Patagioenas speciosa*
	0.46	*Terratosyringophilus longisoma*	*Zenaida asiatica* *Zenaida macroura*
	1	*Meitingsunes ptilinopus*	*Ptilinopus magnificus* *Ptilinopus rivoli*
Mesostenoxenous	0.9	*Meitingsunes lengai*	*Columba delegorguei* *Streptopelia orientalis* *Streptopelia semitorquata*
	0.92	*Meitingsunes zenadourae*	*Columba livia* *Geotrygon frenata* *Leptotila verreauxi* *Leptotila rufaxilla* *Patagioenas picazuro* *Zenaida asiatica* *Zenaida auriculata* *Zenaida macroura*
	0.95	*Peristerophila columbae*	*Columba arquatrix* *Columba guinea* *Columba livia* *Columba oenas* *Columba palumbus* *Columba leuconota* *Columba trocaz* *Geotrygon chiriquensis* *Patagioenas speciosa* *Streptopelia capicola* *Streptopelia decaocto* *Streptopelia orientalis* *Streptopelia semitorquata* *Streptopelia tranquebarica* *Streptopelia turtur*
	1	*Peristerophila geopelis*	*Geopelia cuneata* *Geopelia placida* *Geopelia striata* *Ocyphaps lophotes*
	0.86	*Peristerophila lature*	*Ducula luctuosa* *Ducula spilorrhoa* *Ptilinopus melanospilus* *Ptilinopus porphyreus* *Ptilinopus regina*

Table 3. *Cont.*

Specificity	d′	Quill Mites	Hosts Spectrum
Metastenoxenous	1	*Meitingsunes turacoenas*	*Gallicolumba luzonica*
			Macropygia amboinensis
			Macropygia phasianella
			Macropygia unchall
			Turacoena manadensis
			Turacoena modesta
	0.92	*Peristerophila claravis*	*Claravis pretiosa*
			Oena capensis
	0.78	*Meitingsunes columbicus*	*Columba livia*
			Columba oenas
			Columba palumbus
			Treron waalia
Polixenous	0.98	*Peristerophila mucuya*	*Columbina minuta*
			Columbina passerina
			Columbina squammata
			Columbina talpacoti
			Metriopelia ceciliae
			Metriopelia melanoptera
			Streptopelia decaocto
			Brotogeris versicolurus *
			Psilopsiagon aymara *
			Trichoglossus haematodus *

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

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

Specificity	d′	Quill Mites	Hosts Spectrum
Monoxenous	0.78	*Gunabopicobia claravis*	*Claravis pretiosa*
	0.85	*Gunabopicobia leptotila*	*Leptotila verreauxi*
	0.98	*Gunabopicobia metriopelia*	*Metriopelia melanoptera*
Oligoxenous	0.92	*Gunabopicobia geotrygoni*	*Geotrygon chrysia*
			Geotrygon frenata
			Geotrygon linearis
			Geotrygon montana
Mesostenoxenous	1	*Gunabopicobia lathami*	*Caloenas nicobarica*
			Leucosarcia melanoleuca
	0.9	*Gunabopicobia masalaje*	*Ducula bicolor*
			Ducula luctuosa
			Ducula pistrinaria
			Ducula rosacea
			Ducula rufigaster
			Ducula spilorrhoa
			Ptilinopus iozonus
	0.66	*Gunabopicobia zumpti*	*Columba delegorguei*
			Columba livia
			Patagioenas picazuro
			Patagioenas speciosa
			Streptopelia capicola
			Streptopelia semitorquata
			Streptopelia senegalensis
			Zenaida macroura

d′—index measured specialization on species level.

3.3. Co-Infestation of the Quill Mites

The analysis of the host spectrum showed several various patterns of co-infestation with niche factor (quill mites occupying a different habitats) (Table 5):

(1) "*Syr-Pic*" (quill mite species belonging to the differential subfamily Syringophilinae or Picobiinae and inhabiting the same host species but different habitats.

- (i) Inhabiting niches: contour feathers (representatives of Picobiinae) and covert (representatives of Syringophilidae): *Guanabopicobia claravis* + *Peristerophila claravis* from *Claravis pretiosa*; *G. masalaje* + *P. lature* from *Ducula luctuosa* and *D. spilorrhoa*; *G. metriopelia* + *P. mucuya* from *Metriopelia melanoptera*, *G. zumpti* + *P. columbae* from *Streptopelia semitorquata* and *Patagioenas speciosa*.
- (ii) Inhabiting niche: contour feathers (Picobiinae) and under wing coverts (Syringophilidae): *G. geotrygoni* + *M. zenadourae* from *Geotrygon frenata*, *G. zumpti* + *M. zenadourae* from *Patagioenas picazuro*.
- (iii) Inhabiting niches: contour feathers (Picobiinae) and under tail coverts (Syringophilidae): *G. geotrygoni* + *Psittaciphilus montanus* from *Geotrygon, montana*, *G. leptotila* + *M. zenadourae* from *Leptotila verreauxi*.
- (iv) Inhabiting niches: contour feathers (Picobiinae) and rectrictres (Syringophilidae): *G. zumpti* + *M. lengai*.

(2) "*Syr-Syr*" (different quill mites species belonging to the same subfamily-Syringophilinae and occupying the same host species.

- (i) Inhabiting niches: secondaries and covert: Meitingsunes columbicus + Peristerophila columbae from Columba palumbus.

Table 5. Host species infested by two or more syringophilid species with notation of the habitat preference; P—Picobiinae; S—Syringophilinae.

Hosts	Quill Mites	Subfamily	Niche
Claravis pretiosa	*Gunabopicobia claravis*	P	contour
	Peristerophila claravis	S	covert
Columba palumbus	*Meitingsunes columbicus*	S	secondaries
	Peristerophila columbae	S	covert
Ducula spilorrhoa	*Gunabopicobia masalaje*	P	contour
	Peristerophila lature	S	covert
Ducula luctuosa	*Gunabopiconia masalaje*	P	contour
	Peristerophila lature	S	covert
Geotrygon frenata	*Gunabopicobia geotrygoni*	P	contour
	Meitingsnes zenadourae	S	under-wing covert
Geotrygon montana	*Gunabopicobia geotrygoni*	P	contour
	Psittaciphilus montanus	S	under-tail covert
Leptotila verreauxi	*Gunabopicobia leptotila*	P	contour
	Meitingsunes zenadoure	S	under tail-covert
Metriopelia melanoptera	*Gunapopicobia metriopelia*	P	contour
	Peristerophila mucuya	S	covert

Table 5. *Cont.*

Hosts	Quill Mites	Subfamily	Niche
Patagioenas picazuro	*Gunabopicobia zumpti*	P	contour
	Meitingsunes zenadourae	S	under-wing covert
Patagioenas speciosa	*Gunabopicobia zumpti*	P	contour
	Peristerophila columbae	S	covert
	Psittaciphilus patagioenas	S	covert
Streptopelia semitorquata	*Gunabopicobia zumpti*	P	contour
	Meitingsunes lengai	S	rectrices
	Peristerophila columbae	S	covert

Subfamily of the family Syringophilidae: (P)—Picobiinae, (S)—Syringophilidae.

Moreover, in one sample, we observed quill mite species belonging to the same subfamily and inhabiting the same host species, and moreover occupying the same type of feathers. This pattern was found in *Peristerophila columbae* + *Psittaciphilus patagioenas* where both species occupied covert feathers of *Patagioenas speciosa* (Table 4).

3.4. Bipartite Network Analysis

The Columbiformes–Syringophilidae bipartite network (Figure 1) had high connectance (C = 0.90) and high specialization (H2′ = 0.93) with a high degree of nestedness (0.908). The comparison between H2′ and null model values, showed significant differences (mean for null model = 0.56; p = 0.0009271).

We also measured specialization on the species-level (d′). Quill mites specialization ranged between 0.20 and 1 (see Tables 3 and 4).

(1) d′ 0.1–0.59: *M. adwelles* (0.2), *T. longisoma* (0.46), *T. geotrygonus* (0.5).
(2) d′ 0.6–0.99: *G. zumpti* (0.66), *P. montanus* (0.75), *P. patagioenas* (0.77), *M. columbicus* (0.78), *G. claravis* (0.78), *G. leptotila* (0.85), *P. lature* (0.86), *M. lengai* (0.9), *G. masalaje* (0.9), *M. zenadourae* (0.92), *G. geotrygoni* (0.92), *P. claravis* (0.92), *P. columbae* (0.95), *G. metriopelia* (0.98), *P. mucuya* (0.98).
(3) d′ = 1: *G. lathami*, *M. chalophaps*, *M. tympanistria*, *M. turacoenas*, *M. ptilinopus*, *P. geopelis*, *P. leucomela*.

The strength (thickness of connecting bar between parasites and hosts) of each interaction is representative of the number of interactions (prevalence). Each link corresponds to species interaction and represent quill mites genera: red—*Gunabopicobia*, blue—*Meitingsunes*, black—*Terratosyringophilus*, green—*Psittaciphilus*, yellow—*Peristerophila*. Host phylogeny based on Jetz et al. [68].

We registered a high modularity (likelihood = 0.83) with 20 modules. Modules were split to (A) single-host (quill mites associated with one host species), (B) multi-host (quill mites associated with more the one host species), and (C) multi-parasites (modules encompasses more than one quill mite species) modules (Figure 2).

A. Single-host module: (1) *Gunabopicobia leptotila*—*Leptotila verrauxi*, (2) *Gunabopicobia metriopelia*—*Metriopelia melanoptera*, (6) *Peristerophila leucomela*—*Columba leucomela*, (14) *Terratosyringophilus longisoma*—*Zenaida asiatica*, (16) *Meitingsunes chalcophas*—*Chalcophaps indica*.
B. Multi-host module: (4) *Gunabopicobia masalaje*—(*Ducula bicolor*, *Ducula rufigaster*, *Ducula rosacea*, *Ducula pistrinaria*, *Ptilinopus iozonus*); (5) *Gunabopicobia lathami*—(*Leucosarcia melanoleuca*, *Caloenas nicobarica*); (7) *Meitingunes columbicus*—(*Columba palumbus*, *Treron waalia*); (8) *Meitingsunes tympanistria*—(*Turtur chalcospilos*, *Turtur tympanistria*); (10) *Meitingsunes zenadourae*—(*Leptotila rufaxilla*, *Patagioenas picazuro*, *Zenaida auriculata*, *Zenaida macroura*); (11) *Meitingsunes turacoenas* (*Gallicolumba luzonica*, *Macropygia amboinensis*, *Macropygia phasianella*, *Macropygia unchall*, *Turacoena manadensis*, *Turacoena modesta*); (12) *Meitingsunes psittaciphilus*

(*Ptilinopus magnificus*, *Ptilinopus rivoli*); (13) *Psittaciphilus patagioenas*—(*Patagioenas fasciata*, *Patagioenas speciosa*); (15) *Peristerophila geopelis* (*Geopelia cuneata*, *Geopelia placida*, *Geopelia striata*, *Ocyphaps lophotes*); (17) *Peristerophila lature* (*Ducula luctuosa*, *Ducula spilorrhoa*, *Ptilinopus jambu*, *Ptilinopus melanospilus*, *Ptilinopus porphyreus*, *Ptilinopus regina*); (19) *Peristerophila columbicus* (*Columba arguatrix*, *Columba guinea*, *Columba livia*, *Columba oenas*, *Columba trocaz*, *Columba leuconota*, *Geotrygon chiriquensis*, *Streptopelia decaocto*, *Streptopelia semitorquata*, *Streptopelia turtur*); (20) *Peristerophila mucuya* (*Columbina minuta*, *Columbina passerina*, *Columbina squammata*, *Columbina talpacoti*, *Metriopelia ceciliae*).

C. Multi-parasite module: (18) *Peristerophila claravis*—*Gunabopicobia claravis Gunabopicobia geotrygoni*—*Meitingsunes zenadourae*—*Psittaciphilus montanus*—*Meitingsunes columbicus*; (9) *Gunabopicobia zumpti*—*Meitingsunes lenagi*.

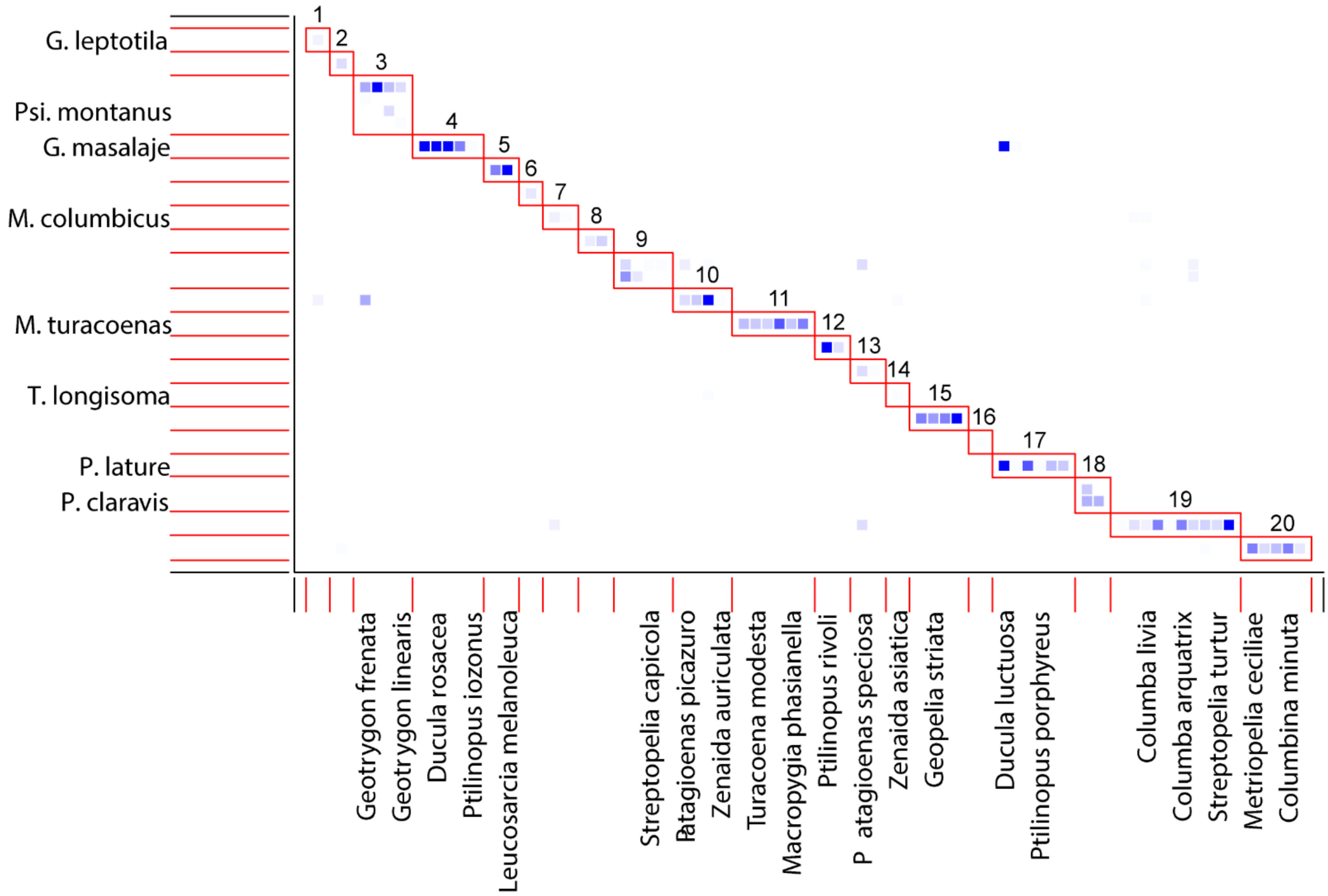

Figure 2. Modules of the quill mites–doves communities. Modules 1–20, generated for quill mites species and doves and pigeons. The intensity of the colors of the squares indicates the strength of the interaction, between particularly parasites species (vertical axis) and their hosts species (horizontal axis).

3.5. Zoogeographical Distribution of Quill Mite Species Associated with Pigeons and Doves

Based on previous reports (see Table 1), we summarized the distribution of the Syringophilidae associated with birds from order Columbiformes. Quill mite species were recorded in hosts inhabiting the following zoogeographical regions: Neotropical, Nearctic, Panamanian, Palaearctic, Saharo-Arabian, Afrotropical, Oriental, Australasian, and Oceanian (Table 6, Figure 3). In particular regions, we noted the following genera with number of quill mites species:

- Neotropical: *Gunabopicobia* (5), *Meitingsunes* (2), *Peristerophila* (3), *Psittaciphilus* (2), *Terratosyringophilus* (1);
- Nearctic: *Meitingsunes* (1), *Peristerophila* (2), *Terratosyringophilus* (1), *Gunabopicobia* (1);
- Panamanian: *Psittaciphilus* (1), *Peristerophila* (2), *Gunabopicobia* (1);
- Palaearctic: *Meitingsunes* (8), *Peristerophila* (2), *Gunabopicobia* (1);
- Saharo-Arabian: *Peristerophila* (1);
- Afrotropical: *Meitingsunes* (4), *Peristerophila* (2), *Gunabopicobia* (1);
- Oriental: *Meitingsunes* (2), *Peristerophila* (4), *Gunabopicobia* (2);
- Oceanian: *Meitingsunes* (2), *Peristerophila* (1), *Gunabopicobia* (2);
- Australasian: *Meitingsunes* (2), *Peristerophila* (4).

Table 6. Distribution of syringophilid associated with birds from order Columbiformes in zoogeographical regions.

	Zoogeographic Regions								
Quill Mites Species	**Neot.**	**Near.**	**Pana.**	**Pala.**	**Sa-Ara.**	**Afro.**	**Orie.**	**Ocean.**	**Austr.**
M. aldwelles	■								
M. columbicus				■		■			
M. chalcophas							■		■
M. ptilinopus								■	■
M. lengai				■		■			
M. turacoenas							■	■	
M. tympanistria						■			
M. zenadourae	■	■				■			
P. columbae	■	■	■	■	■	■	■		
P. claravis	■		■			■			
P. geopelis							■		■
P. lature							■	■	■
P. leucomela									■
P. mucuya	■	■		■					■
P. montanus	■		■						
P. patagioenas	■								
T. geotrygonus	■								
T. longisoma		■							
G. claravis	■								
G. geotrygoni	■		■					■	
G. masalaje							■	■	
G. metriopelia	■								
G. lathami							■	■	
G. leptotila	■								
G. zumpti	■	■		■		■			

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. [71]).

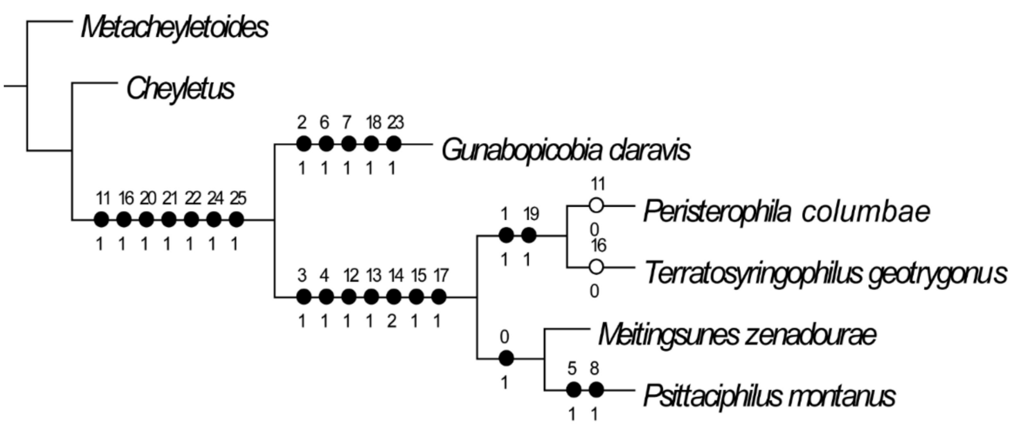

Figure 3. Phylogenetic tree of selected genera of Syringophilidae mites associated with Columbiformes birds.

Among all quill mites species, eight of them were only noted from one region: Neotropical—*Gunabopicobia metriopelia*, *G. claravis*, *G. leptotila*, *Meitingsunes adwelles*, *Psittaciphilus patagioenas Terratosyringophilus geotrygonus*; Afrotropical—*Meitingsunes tympanistria*; Australian—*Peristerophila leucomela*. Others quill mites species were recorded from more than one zoogeographical region:

- Neotropical + Nearctic + Palaearctic + Afrotropical: *Gunabopicobia zumpti*; *Meitingsunes zenadourae*; *Peristerophila claravis*;
- Neotropical + Nearctic: *Psittaciphilus patagioenas*;
- Palaearctic + Afrotropical: *Meitingsunes columbicus*, *Meitingsunes lengai*;
- Oriental + Oceanian: *Meitingsunes turacones*;
- Oriental + Australasian: *Meitingsunes chalcophas*;
- Oceanian + Oriental + Australasian: *Peristerophila lature*;
- Neotropical + Nearctic + Palaearctic + Afrotropical + Saharo-Arabian + Oriental: *Peristerophila columbae*.

3.6. Phylogenetic Analysis

The analysis under equal weights resulted in one most parsimonious tree (MPT) shown in Figure 4. Number of characters—26 (Figures S2 and S3), number of parsimony-informative characters—19, tree length (L) = 30, consistency index (CI) = 0.9, retention index (RI) = 0.9, rescaled consistency index (RC) = 0.8, homoplasy index (HI)—0.1, Goloboff-fits (G-fit) = −18.25.

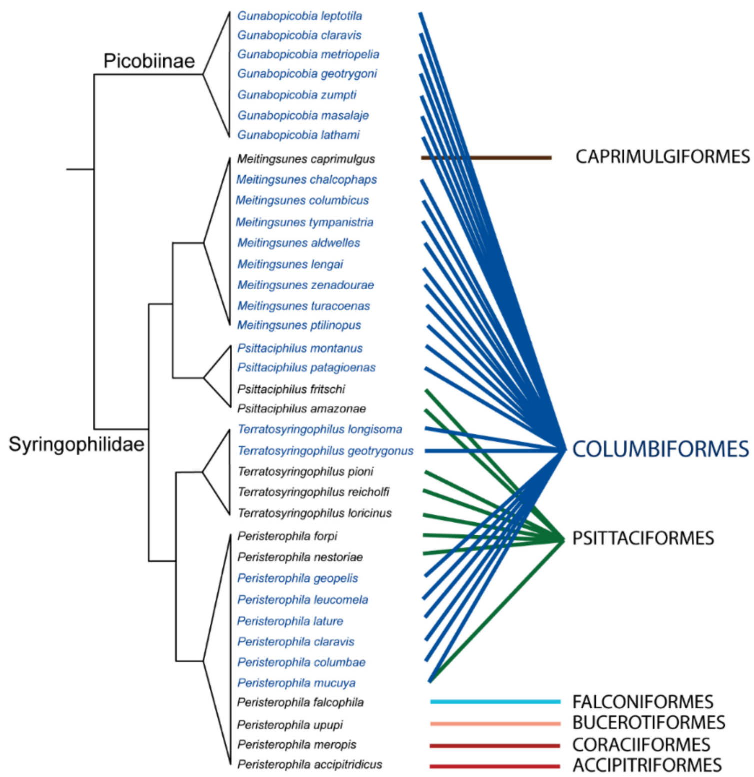

Figure 4. Phylogenetic tree of selected genera of Syringophilidae associated with differential hosts order.

The analysis shows that except the genus *Gunabopicobia* which represents subfamily Picobiinae, other syringophilinae genera form two distinct clades: *Peristerophila* + *Terratosyringophilus* (supported by synapomorphies: the presence of large finger-like protuberances on the hypostomal apex, presence of parallel apodemes I, and presence of dimorphic females) and *Meitingsunes* + *Psittaciphilus* (supported by synapomorphy: the presence of the constricted posterior end of the stylophore.

4. Discussion

The parasitological studies on quill mites of the family Syringophilidae and their hosts have a long history spanning over 140 years [16,22]. However, the extensive studies on this group of parasites started about 40 years ago, and investigation of a small fraction of the about 10,000 extant bird species recognized to date recording of more than 400 species of syringophilid mites arranged in 63 genera and two families [20].

The studies on the host–parasite relationship in the system composed of quill mites and the particular taxonomical groups of their hosts are still rare in the literature. Moreover, comprehensive research of the quill mite fauna on the host representatives of the whole bird order and considering mite species richness, host and habitat specificities, prevalence, and phylogenetic relationships have not been provided so far. Most of the previously published papers have focused on describing syringophilid fauna of the particular zoogeographical regions e.g., [22,23,77], or on taxonomical reviewing the different taxa (genus or subfamily) of quill mites e.g., [23,26,41,78]. Recently, however, there have been published a few studies examining the syringophilid fauna on the particular taxonomical host groups (e.g., passeriform genus *Estrilda* [25], sub-Saharan Nectariniidae [24], cuckoos [79]), with primary analyses of host–parasite relationships.

This paper focuses on analyses of the species richness and measuring specialization and interaction between syringophilid mites parasitizing columbiform birds in their natural host–parasite system.

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

The fauna of quill mites associated with doves and pigeons encompasses 25 species belonging to the following five genera: *Meitingsunes*, *Peristerophila*, *Psittaciphilus*, *Terratosyringophilus* (subfamily Syringophilinae), and *Gunabopicobia* (subfamily Picobiinae) (see Table 1). Among them, only one—*Gunabopicobia*—is exclusively associated with columbiform birds and represented by monoxenous (3 species), oligoxenous (1), and mesostenoxenous (3) parasites. Thus, this genus is a perfect example of the host–parasite interaction where a supraspecific taxon of parasites is associated with one host order. This genus is known from hosts representing all columbiform subfamilies, i.e., Claravinae, Columbinae, and Raphinae. It was suggested by Kaszewska et al. [26] that mites of this genus could have started to parasitize the common ancestor in the Late Cretaceous (about 41 to 46 MYA) before their split on the particular subfamilies. Moreover, the Columbiformes are one of the oldest lineages of extant birds. A recent molecular study based on the complete mitochondrial genome suggests that the earliest radiation of the Columbidae occurred during the late Oligocene and continued diversification of the major clade in the Miocene [15]. However, older data suggest that the Columbiformes radiated from Eocene to Oligocene [13,14] or even from Early Eocene to middle Miocene [12].

Four genera of the syringophilines associated with columbiform birds have been previously assigned to the *Psittaciphilus*-generic-group [80]. In this study, we identified phylogenetically closely related clades *Meitingsunes* + *Psittaciphilus* and *Peristerophila* + *Terratosyringophilus*.

The genus *Meitingsunes* comprises nine described species where eight of them are exclusively associated with pigeons and doves infesting birds belonging to two subfamilies Columbinae and Raphinae (28 infested species in total) [45]. However, only one species of this genus, *M. caprimulgus,* has been noted from the phylogenetically distant clade of nightjars (Caprimulgiformes) [50]. Because birds belonging to the order Caprimulgiformes are extremely poorly examined (with only one host record), the status of *Meitingsunes* on nightjars is still unclear. The nightjars can represent real hosts for quill mites of this genus, or the single findings of *M. caprimulgus* can be an example of host-switching (e.g., from the columbiform host).

The genus *Psittaciphilus* includes four species found on representatives of Columbiformes (2 species) and Psittaciformes (2) [33,42]. On pigeons and doves, this genus infests birds of the genera *Geotrygon* and *Patagioenas*, which are also parasitized by members of the genus *Meitingsunes* mentioned above (e.g., *M. zenadourae* and *M. adwelles*).

The genus *Terratosyringophilus* includes three quill mites species found on parrots and two species noted from doves belonging to the subfamily Columbinae [31,34,35,37,81].

The *Terratosyringophilus* quill mites along with *Psittaciphilus* and partially *Peristerophila* (see below) have been found in birds from orders Columbiformes and Psittaciformes. The cases where both host orders are infested by mites belonging to the same genera can indicate the phylogenetically close relationship between these two bird orders. However, recent phylogenetic analysis does not confirm this hypothesis. It is commonly accepted that the lineage of doves and pigeons is a sister clade to sandgrouse (Pteroclidiformes) and mesites (Mesitornithiformes) [15,82–84]. At this moment, we cannot explain this multi-order infestation of the same genera of syringophilid mites. To resolve this problem, the molecular analyses of the quill mites phylogeny are needed as well as the studies on the host spectrum of the other symbionts parasitizing birds of these both orders.

The genus *Peristerophila* comprises 14 quill mites species and is the only genus that inhabits not only doves and parrots but also hosts belonging to hawks (Accipitriformes), falcons (Falconiformes), hoopoes (Bucerotiformes), rollers and bee-eaters (Coraciiformes) [43,46,48,75,85,86]. The *Peristerophila* mites associated with columbiform birds are recorded on hosts from all subfamilies, i.e., Columbinae, Raphinae, and Claravinae. Moreover, among all 30 species of syringophilines recorded on pigeons and doves, there is only one species—*Peristerophila mucuya*, representing polyxenous parasite—which is found on hosts belonging to the order Columbiformes and Psittaciformes (Figure 4).

4.2. Columbiform Hosts and Quill Mite Fauna

Our study of the quill mites associated with columbid birds was conducted on doves and pigeons representing all subfamilies, i.e., Columbinae, Claraviinae, and Raphinae. Based on material used for our research and records from previous publications, we estimated that the degree of species testing of Columbiformes ranged from 25% to 100% (for individual genera). In the subfamily Columbinae, regarding investigation degree of host species, more than 50% is in the following host genera: *Streptopelia* (52%), *Turacoena* (66%), *Zenaida* (85%), *Leptotrygon* (100%). In the subfamily Claravinae, we examined all currently recognized genera except monotypic genus *Uropelia*, *Claravis* (100%), *Columbina* (55%), *Metriopelia* (50%), *Paraclaravis* (50%). In the subfamily Raphinae, investigation degree more than 50% is in the following host genera: *Caloenas* (50%), *Chalcophas* (66%), *Geopelia* (60%), *Henicophaps* (100%), *Leptotrygon* (100%), *Leucosarcia* (100%), *Ocyphaps* (100%), *Oena* (100%), *Otidiphaps* (100%).

Considering high-level examination of columbiform birds under the presence of the quill mites, we suppose that the Syringophilidae fauna on the generic level has been fully explored. In the future, it would be worth intensifying research on the syringophilids inhabiting a single bird order. It will allow comparing our results with these ones conducted for other host orders. This approach allows for a better understanding of the parasite–host relationship as a whole. It would also be interesting to provide comprehensive studies on quill mite fauna associated with pacific island doves and pigeons. The future collection of the material from these regions will allow testing MacArthur and Wilson's "the island theory" for quill mites. Additionally, future molecular studies on co-phylogeny also give important information about the relationships and evolutionary events between particular columbid and quill mite species.

4.3. Prevalence

The prevalence index provided details of the strength of the relationship between a particular host and parasites species. Our study has shown that the prevalence of infested birds by the quill mites ranges between 4.2% and 66.7%. However, for 17 hosts species, IP was equal to 100%, the confidence interval (CI) was wide, and this result can be the effect of the small sample size of studied host specimens.

The highest prevalences were detected in the previous studies for birds kept on the farms, e.g., domestic hen *Gallus gallus domesticus* infested by *Syringophilu bipectinatus* Heller, where IP was 75% (N = 1.500) [87] or for social species, e.g., house sparrow *Passer domesticus* infested by *Syringophiloidus minor* where IP was 82% (N = 492) [88]. For non-social birds, the prevalence index is much lower. It usually does not reach 50% (see works on prevalence among various passerine species (IP varies between 3.5% and 42.9%) [24,25,89–93]; phasianids (IP = 5.5–7.3%) [94–96]; parrots (IP = 7.7–20%) [97].

Both factors, the number of examined bird individuals and the number of examined feathers, play a crucial role in determining the real prevalence of infested hosts in the environment. In current and previous studies on prevalence, the used bird material was from various sources. The first source includes birds deposited in the museum collections (mostly dry bird skins and frozen or alcohol preserved specimens) e.g., [24,25]. The second source are birds examined during fieldworks (e.g, [18,48,88,90,92,93,95,98–101]) or kept in the zoological gardens [97] and farms [94,96,102].

It is obvious that syringophilid mites infest not all host specimens in nature and not all feathers, and to present the real IP, we should examine as many as possible bird individuals (taking into consideration their age, season, locality, etc.) and as many as possible feathers; see also [93,95,103]. However, samples collected from ornithological collections and from live birds are limited and allow sampling only a few feathers. Therefore, to minimize this limiting factor, we should continue studies on habitat specificity (see below).

4.4. Habitat Specificity and Multi-Infestation of Syringophilid Mites

The feather environment gives opportunities to inhabit various niches by ectoparasites and commensal species. However, the phenomenon of co-infestation remains poorly documented, especially for ectoparasites belonging to the family Syringophilidae. The first remark about multi-infestation was pointed out by Kethley [16]. He indicated that one host species or even one host individual may be infected by several syringophilid species inhabiting different types of feathers. Later on, Schmäschke et al. [104] presented the observation of co-infestation of two species, *Syringophilopsis turdi* and *Syringophiloidus* sp. on one the fieldfare *Turdus pilaris* (Passeriformes: Turdidae), and *Syringophilopsis kirgizorum* and *Syringophiloidus* sp. found on the greenfinch *Carduelis chloris* (Passeriformes: Fringillidae). Other examples of multi-infestations were described by Skoracki et al. [91]. In this paper, the authors recorded the following patterns of infestation with the notation of infested niches, e.g., *Torotrogla rubeculi* (habitat: secondaries) + *Picobia* sp. (habitat: contour feathers) on the European robin *Erithacus rubecula* (Muscicapidae); *Syringophilipsis kirgizorum* (primaries) + *Torotrogla gaudi* (secondaries) on the chaffinch *Fringilla coelebs* (Fringillidae); *Syringophiloidus presentlis* (secondaries) + *Picobia sturni* and *Aulonastus buczekae* (habitat: contour feathers) on the common starling *Sturnus vulgaris* (Sturnidae).

Until now, the multi-infestations by quill mites have been observed only in passeriform birds. However, our study described other cases of syringophilid multi-infestation on columbiform birds and showed that the phenomenon of co-infestation can occur more frequently. In total, we found 13 examples of co-infestation in different configurations. The most frequent cases of co-infestation were recorded for quill mites that inhabited the same host species but occupied differential niche—"factor niche". For these cases, we observed two co-infestation patterns: (1) "*Syr-Pic pattern*"—quill mites belonging to two subfamilies Syringophilinae and Picobiinae occupying the same host individual or species; and (2) "*Syr-Syr pattern*"—quill mites belonging to the same subfamily, Syringophilinae. Currently, the pattern "*Pic-Pic*", i.e., two species of picobiine mites on the same host species, was not observed. In members of the "*Syr-Pic pattern*", representing two subfamilies, differences in morphology, life strategies, and niche preferences are clearly visible. For example, Picobiinae inhabit exclusively contour feathers while the members of Syringophilinae occur mainly inside the quills of secondaries, wing or tail coverts, rectrices; however, they are also occasionally found in contour feathers (Tables 2 and 5). For the "*Syr-Syr pattern*", we observed a similar strategy of avoiding competition by occupying different feathers.

However, for this group, we found two species, *Peristerophila columbae* and *Psittaciphilus patagioenas*, that infested the same host species and occupied the same niche—quills of wing coverts. Probably, this event could be an example of the horizontal transfer.

Niche separation among quill mites is a result of avoiding competition for the same microhabitat. According to the niche conception, the differential species cannot occupy the same niche (and use the same resources) because the advantage for one competitor will eventually drive others to extinction [105–107]. Finally, niche separation is the process of natural selection which drives competing species into using different hosts or different microhabitats [108].

Examples of niche separation are common and well documented for other ectoparasitic mites, e.g., mites from genus *Schizocarpus* infested *Castor fiber* [109] or feathers mites such as *Microspalax brevipes* and *Zachvatkinia ovata* associated with *Calonectris borealis* [110]. However, knowledge about competition and niche overlap phenomena for ectoparasites of the Syringophilidae is still unsuccessfully documented. The following examples of co-infestation in syringophilid groups provided in our study confirm the previous reports on the high degree of specificity of the quill mites to occupying niche. The observed preferences of syringophilids to colonize various types of feathers can result from the preferences to the specific parameters of the quills, such as the thickness of the quill wall and its volume. This hypothesis was proposed by Kethley [17], Casto [18], and Glowska et al. [111]. Moreover, recent studies by Grossi and Proctor [93] confirmed a strong correlation between quill volume and the average number of quill mites.

4.5. Bipartite Network of the Quill Mites–Doves Communities

The ecological network approach provides a lot of information about biological systems. Networks can be useful to illustrate and analyze the relationships and ecological interactions inside various types of communities [8]. Recently, an extensive study of an ecological network aimed to describe the character of mutualistic plant–animal interactions (pollination, seed dispersal, etc.) [5,56,112,113]. However, the network-thinking approach may also be useful in the study of the parasite ecology. Those analyses give a visual graph that illustrates links between two trophic levels, but above all, quantify indices such as host specificity in parasites and provide the topological description [5,9].

Network analyses were conducted for host–parasite systems, e.g., herbivorous insects–parasitoid food web [114] or tropical bats and their ectoparasitic bloodsucking flies [113]. Until now, bipartite analyses have been used for quill mites associated with the following host groups: sunbirds (Passeriformes: Nectariniidae) [24], estrildids (Estrildidae) [25], and doves (Columbiformes: Columbidae) [26].

In the present study, to describe the bipartite network, we used the following indices: connectance (C), nestedness (N), modularity (Q), and H2′. The values of these metrics provided information about: the number of interactions, the level of sharing partners, the degree of compartmentalization of the networks, and network-level specialization [52,115,116]. Our results confirm the hypothesis about the high specialization of syringophilid mites associated with pigeons and doves. We found strong specialization on both the network- and the species-level. The architecture of the quill mites-doves network was characterized by a high: connectance (C = 90), nestedness (N = 0.908), H2′ (H2′ = 0.93), and also with simultaneously high value of modularity (Q = 0.83) with 20 modules.

Recent studies of ecological networks have shown that the metrics such as nestedness, modularity, and connectance are correlated and depend on one another [57,58,117], which can be useful to understand the interaction between particular species in the network. One of the most important indices used to describe the quill mites-doves network was nestedness. We noted a high value of (N) = 0.908, close to 1. According to Bascompte et al. [56], the results close to 1 indicate a non-random community structure with a high level of diversity and complexity. Moreover, quill mites–doves communities were shown to have a highly modular structure. Modularity measures the tendency of a network to divide into modules (also called groups, clusters, or communities) [57]. It promotes stability by containing perturbations within a module, thereby constraining their spreading to the rest of the community [118]. In our networks, we found 20 modules, each of them had a strong interaction between species inside the modules. Some recognized modules (Figure 2) have more than one quill mite species, e.g., module number "3" had the highest number of quill mites species: *G. geotrygoni*, *M. zenadourae*, *P. montanus*, and *M. columbicus*. These multi-parasite communities interact with numerous hosts and probably can result from the phylogenetic relationship between particular quill mites and their hosts. The genera *Psittaciphilus* and *Meitingsunes* are sister clades (Figure 3) within subfamily Syringophilinae and share the same close relation to host species, while the genus *Gunabopicobia* is a separately evolutionary line. Moreover, those results suggest the structure of communities where competition for hosts can be expected. We observed another situation for modules where only one quill mite species has infested one host species. Those communities are represented, for example, by *Gunabopicobia metriopelia* associated with one host species, *Metriopelia melanoptera*. In this case, strong interaction with hosts species was observed.

The next indicator of complexity—connectance—was used in this study. The strong link between parasitic species and individual hosts (C = 0.90) observed in our research may be the result of non-random infestation.

The similar architecture of the bipartite network was presented in a study of ectoparasitic flies of the family Streblidae (Hippoboscoidea) and bat hosts from the tropical dry forest [113]. The authors of this study obtained structures similar to ours, such as high specialization (H2′ = 0.67), high modularity (Q = 0.7), but, contrary to the quill mites–doves nest, the authors found a low value of connectance (C = 0.30). The differential between C index can be related to sampled and network size. This relation was observed in the following networks: food webs (marine, estuarine, terrestrial), plant–pollinator, plant–herbivores–parasitoids in the forest [119–121]. However, some authors suggest that the connectance decreases when specialists are lost or generalists are gained [122,123]. In the quill mites–doves network, the proportion of specialized species is higher compared with the bat–fly network. Additionally, some analyses focusing on the conservation and protection of biodiversity suggest that the high C-value characterizes more stable communities, while low C-value can be an indicator of an ecological threat [122]. We hypothesize that the high C-value is observed in the stable and old hosts-parasites systems.

The Columbiformes and syringophilid mites have a long, common history. Quill mites have probably been associated with birds hosts for a very long time. Some studies based on the phylogeny of Syringophilidae and birds indicate that the quill mites of the family Syringophilidae could be associated with Neornithes birds around 66 million years ago or earlier [124]. Currently, the family Syringophilidae comprises about 400 species associated with birds from 27 orders. Most infested bird species belong to the clade Neoaves. However, quill mites species have also been found in Paleognathae (2 quill mite species), as well as Galloanserae (23 quill mite species) [20]. Considering the richness of parasites that inhabit modern birds, [124] suggested that their origins are not later than the Late Jurassic. Phylogeny analysis conducted by Skoracki et al. [78] showed that the mites on the earliest derivate branches are associated with birds of the advanced clade Neoaves. In contrast, genera associated with the earliest clades of extant birds, such as Tinamiformes (Palaeognathae) and Galloanserae (Anseriformes and Galliformes), are mosaically distributed in the core of the tree. On the other hand, ancestors of the quill mites could be associated with bird-like creatures before the K-Pg extinction event. Phylogeny analysis of parasitic mites from the superfamily Cheyletoidea (Acariformes: Prostigmata) showed that the Syringophilidae probably originated from a common ancestor with Cheyletidae, a predatory ancestor and inhabiting the litter of bird nests [124,125].

However, comparing the presented results with another host–parasites network is still unsatisfactory. The network-thinking approach used for the study of ectoparasites–hosts systems is limited. The most available research on bipartite networks was conducted on the mutualistic plant–pollinator food web. Moreover, we suggest that co-evolutionary analysis will be important to understand better the nature of the relationship between quill mites and doves.

5. Conclusions

The relation and interactions between host and parasites are still not well understood. We believe that this study focused on host specificity, prevalence, networks and evolutionary aspect has a particular role to identify the relation between host and parasites. The results of the presented study show that the quill mites belonging to family Syringophlidae and associated with pigeons and doves (Columbiformes) form stable and non-random communities.

The quill mites–doves bipartite has been characterized by a high value of nestedness, connectance, modularity, and H2'. We suggest that the observed network architecture in this study as well as high specificity and worldwide distribution of syringophlid mites is characteristic for: high host specificity systems with a long and common history.

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/ani11123392/s1, Table S1. The degree of Syringophilidae examination for each Columbiformes subfamily; Figure S1. A network matrix; Figure S2. Characters; Figure S3. Data matrix.

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Table S1. The degree of Syringophilidae examination for each Columbiformes subfamily

Host subfamily	Host genus	Species	Examined	Quill mites genus assocoaited with Columbiformes species				
				Meitingsunes	*Psittaciphilus*	*Peristerophila*	*Terratosyringophilus*	*Gunabopicobia*
Columbinae	*Columba*	36	(10) 27%			**8**		**2**
	Ectopistes	1	-					
	Geotrygon	17	(6) 35%	**1**	**1**	**1**	**1**	**3**
	Leptotila	10	(3) 30%	**2**				**1**
	Leptotrygon	1	(1) 100%					
	Macropygia	15	(5) 33%	**3**				
	Patagioenas	17	(7) 41%	**1**	**2**	**1**		
	Reinwardtoena	3	-					
	Streptopelia	17	(9) 52%	**2**		**3**		**2**
	Turacoena	3	(2) 66%	**2**				
	Zenaida	7	(6) 85%	**5**			**2**	
Claraviinae	*Claravis*	1	(1) 100%			**1**		**1**
	Columbina	9	(5) 55%			**4**		
	Metriopelia	4	(2) 50%			**1**		**1**
	Paraclaravis	2	(1) 50%					
	Uropelia	1	-					
Raphinae	*Alectroenas*	5	-					
	Alopecoenas	13	-					
	Caloenas	2	(1) 50%					**1**
	Chalcophas	3	(2) 66%	**1**				
	Cryptophaps	1	-					
	Didunculus	1	-					
	Drepanoptila	1	-					
	Ducula	39	(11) 28%			**2**		**6**
	Gallicolumba	7	(2) 28%	**1**				
	Geopelia	5	(3) 60%			**3**		
	Geophaps	3	-					

Goura	4	-					
Gymnophaps	4	(1) 25%					
Hemiphaga	2	-					
Henicophaps	2	(2) 100%					
Leptotrygon	1	(1) 100%					
Leucosarcia	1	(1) 100%					**1**
Lopholaimus	1	-					
Microgoura	1	-					
Nesoenas	4	-					
Ocyphaps	1	(1) 100%			**1**		
Oena	1	(1) 100%			**1**		
Otidiphaps	1	(1) 100%					
Petrophassa	2	-					
Pezophaps	1	-					
Phapitreron	4	-					
Phaps	3	-					
Ptilinopus	55	(14) 25%	**2**		**3**		**1**
Raphus	1	-					
Starnoenas	1	-					
Treron	29	(12) 41%	**1**				
Trugon	1	-					
Turtur	5	(2) 40%	**2**				

Figure S1. A network matrix

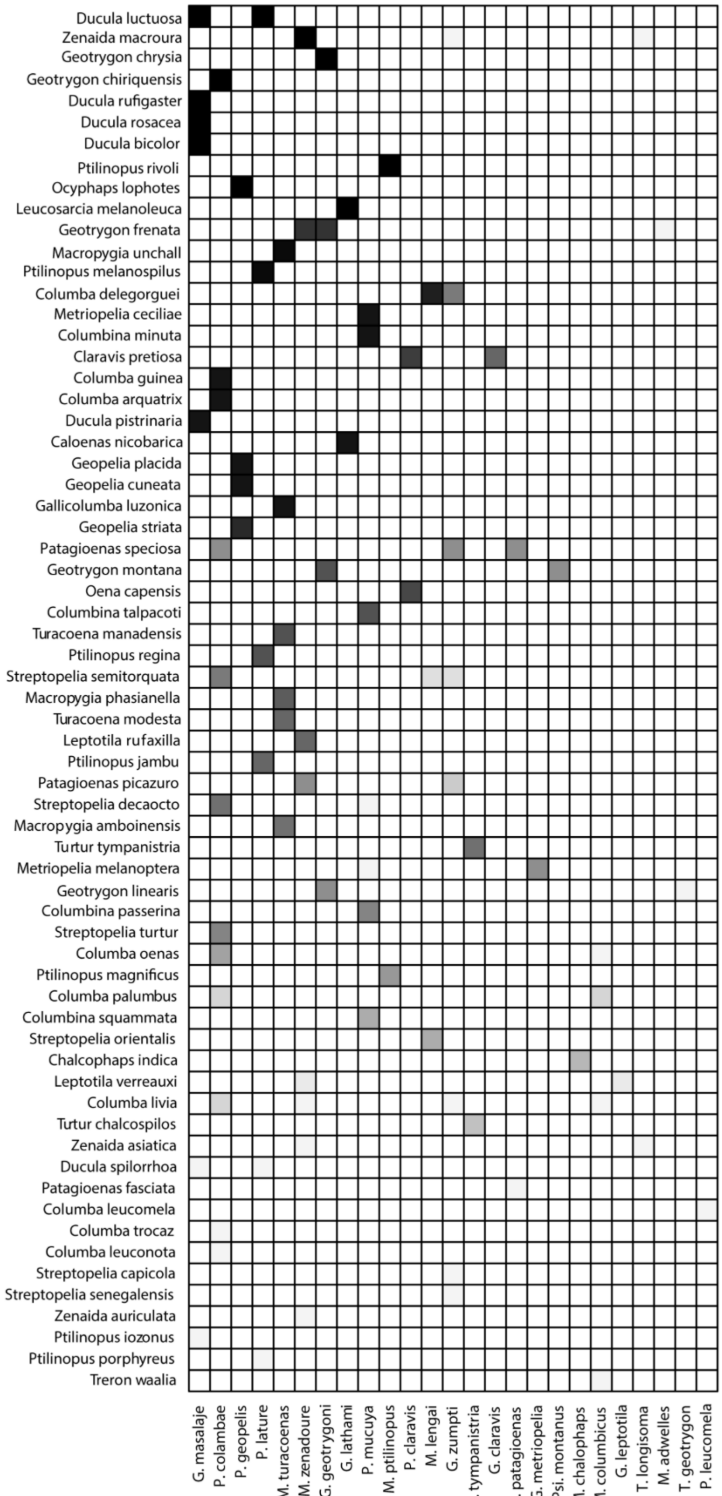

Figure S2. Characters

1. Posterior part of stylophore: 0. rounded; 1. strongly constricted.
2. Large sausage-like hypostomal structures: 0. absent; 1. present.
3. Peritremes - shape: 0. M-shaped; 1. U-shaped.
4. Distal tip of chelicerae: 0. edentate; 1. small teeth; 2. large teeth.
5. vi setae: 0. present; 1. absent.
6. Position of setae ve and si: 0. ve situated anterior to si; 1. ve and si situated at same transverse level.
7. Setae g1: 0. present; 1. absent.
8. Ornamentation of dorsal setae: 0. absent; 1. present.
9. Pocket-like structures: 0. absent; 1. present.
10. Leg thickness : 0. I thicker than II-IV; 1. I and II thicker than III and IV; 2. subequal.
11. Apodemes I: 0. divergent; 1. parallel.
12. Apodemes I and II fusion: 0. fused; 1. not fused; 2. fusion indistinct (adjoining).
13. Apodemes III-IV: 0. present; 1. absent.
14. Setae vs on tarsus II: 0. present; 1. absent.
15. Prorals setae p' and p": 0. rod-like, with rounded or serrate apex; 1. fan-like; 2. multiserrate.
16. Setae dF on femora II: 0. present; 1. absent.
17. Setae vF on femora III: 0. present; 1. absent.
18. Setae dF on femora III: 0. present; 1. absent.
19. Setae l'R on trochanters I: 0. present; 1. absent.
20. Bimorphism: 0. absent**;** 1. present.
21. Basal part of gnathosomanot: 0. not submerged; 1. deeply submerged.
22. Palpal tibia and tarsus: 0. separated; 1. fused.
23. Claw-like seta of palp: 0. present; 1. absent.
24. Palpal apex: 0. rounded; 1. truncated.
25. Setae e1 presence: 0. present; 1. absent.
26. Setae ps3 presentce: 0. present; 1. absent.

Figure S3. Data matrix.

Meitingsunes_zenadourae 1001100000111211100111011
Psittaciphilus_montanus 1001110010111211100111011
Peristerophila_nestoriae 0101100001011211101111011
Terratosyringophilus_geotrygonus
0101100001111210101111011
Gunabopicobia_claravis 0010001101100001010111111
Cheyletus 0000000000000000000000000
Metacheyletoides 0000000000000000000000000

Oświadczenia określające wkład poszczególnych autorów w powstanie artykułów

Authorship statements

Oświadczenie doktoranta o wkładzie w powstanie artykułu

Authorship statements of the PhD candidate

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Two new species of quill mites of the family Syringophilidae (Acariformes: Cheyletoidea) associated with Treroninae doves. Zootaxa, 293-300.

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Two new *Meitingsunes* species (Acari: Syringophilidae) from Indonesian doves Columbiforms: Columbidae. Zootaxa, 4109 (4): 479 – 486.

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Kaszewska K., Skoracki M., Hromada M. 2018.

A review of the quill mites of the genus *Gunabopicobia* Skoracki and Hromada (Acariformes: Prostigmata: Syringophilidae) associated with birds of the order Columbiformes. International Journal of Acarology, 1945 (3892):1 – 12.

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Mój całkowity wkład w pracę wynosi 60%

Oświadczenie doktoranta o wkładzie w powstanie artykułu

Authorship statements of the PhD candidate

Kaszewska K., Skoracki M. 2018.

Two new quill mite species of the genus *Psittaciphilus* Fain, Bochkov & Mironov, 2000 (Acariformes: Syringophilidae) associated with pigeons and doves (Columbiformes: Columbidae).
Syst. Parasitol, 95:953 – 958.

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Mój całkowity wkład w pracę wynosi 80%

K Gilas

Oświadczenie doktoranta o wkładzie w powstanie artykułu

Authorship statements of the PhD candidate

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Mój całkowity wkład w pracę wynosi 85%

KGilas

Oświadczenie doktoranta o wkładzie w powstanie artykułu

Authorship statements of the PhD candidate

Kaszewska K., Skoracki M., Kosicki Z.K., Hromada M. 2020.

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Mój całkowity wkład w pracę wynosi 80%

K Gilas

Oświadczenie doktoranta o wkładzie w powstanie artykułu

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Mój całkowity wkład w pracę wynosi 60%

Oświadczenia współautorów o wkładzie w powstanie artykułu

Authorship statements of co-authors of the article

Kaszewska K, Kavetska K, Skoracki M. 2014. Two new species of quill mites of the family Syringophilidae (Acariformes: Cheyletoidea) associated with treroninae doves. Zootaxa, 293-300.

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Mój całkowity wkład w pracę wynosi 5%

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Mój całkowity wkład w pracę wynosi 25%

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Mój całkowity wkład w pracę wynosi 5%

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Mój całkowity wkład w pracę wynosi 15%

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Mój całkowity wkład w pracę wynosi 20%

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Mój całkowity wkład w pracę wynosi 10%

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Mój całkowity wkład w pracę wynosi 5%

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Mój całkowity wkład w pracę wynosi 10%

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Mój całkowity wkład w pracę wynosi 5%

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Mój całkowity wkład w pracę wynosi 15%

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Mój całkowity wkład w pracę wynosi 20%

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Oświadczenie określające wkład w powstanie artykułu

Niniejszym oświadczam, że mój wkład w powstanie poniższego artykułu Kaszewska K., Kosicki Z.J, Hromada M., Skoracki M., 2021. Global studies on the host-parasite relationship between ectoparasitic mites of the family Syringophilidae and birds of the order Columbiformes. Animals 11, 3392: 1 – 32, polegał na: udziale w napisaniu manuskryptu oraz poprawie manuskryptu po recenzjach.

Mój całkowity wkład w pracę wynosi 5%