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Myrsidea quadrifasciata (Phthiraptera: Amblycera) – a unique host generalist among highly host-specific chewing lice

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http://zoobank.org/947916E5-BD42-4A0A-8B34-4CBA416F14B6

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Citation: Sychra O, Kolencik S, Papousek I, Bilbija B, Literak I (2021) *Myrsidea quadrifasciata* (Phthiraptera: Amblycera) – a unique host generalist among highly host-specific chewing lice). Arthropod Systematics & Phylogeny 79: 379–400. https://doi.org/10.3897/asp.79.e63975

Abstract

Ten species of the louse genus *Myrsidea* belonging to the "*serini*-species-group" have been reviewed. A redescription of *Myrsidea quadrifasciata* (Piaget, 1880), the earliest described and valid species of this species complex, is given and a neotype for this species is designated. Nine new junior synonymies of *M. quadrifasciata* are proposed and discussed. The new synonyms and their respective type hosts are: *Myrsidea anoxanthi* Price and Dalgleish, 2007 from *Loxipasser anoxanthus* (Gosse, 1847), *Myrsidea argentina* (Kellogg, 1906) from *Spinus magellanicus* (Vieillot, 1805), *Myrsidea balati* Macháček, 1977 from *Passer montanus* (Linnaeus, 1758), *Myrsidea darwini* Palma and Price, 2010 from *Geospiza fuliginosa* Gould, 1837, *Myrsidea major* (Piaget, 1880) from *Plectrophenax nivalis* (Linnaeus, 1758), *Myrsidea serini* (Séguy, 1944) from *Serinus serinus* (Linnaeus, 1766), *Myrsidea queleae* Tendeiro, 1964 from *Quelea quelea lathami* (Smith, A., 1836), *Myrsidea textoris* Klockenhoff, 1984 from *Ploceus cucullatus cucullatus* (Müller, 1776), and *Myrsidea viduae* Tendeiro, 1993 from *Vidua macroura* (Pallas, 1764). Intraspecific morphometric variability, relative genetic divergence (based on a 379 bp portion of the mitochondrial *COI* gene and a 347 bp portion of the nuclear *EF-1α* gene), geographical distribution, and host associations, including 8 new host records for these lice, are discussed. Taking into consideration these parameters we suggest that the only way to deal with these taxa is to follow concept of subspecies with the following taxa and their geographic distributon: Palearctic Region: *M. q. quadrifasciata* and *M. q. serini*, Neotropical Region: *M. q. anoxanthi*, *M. q. argentina*, *M. q. darwini*, Paleotropic Region: *M. q. queleae*, *M. q. textoris* and *M. q. viduae*.

Keywords

1. Introduction

Chewing lice are traditionally considered as highly host-specific ectoparasites. Lice infesting multiple unrelated hosts were long thought to constitute cryptic species, which resulted in the erection of new species, and even genera, based primarily on host relationships (Clay 1968). Fahrenholz's Rule has been used to describe the

expectation that louse phylogeny should mirror host phylogeny (Price et al. 2003). Recently, studies on chewing lice at the lower taxonomic level have revealed that multi-host, generalist louse species may be more common than we expected, and even more, that one genus of lice can contain strict monoxenous host specialists and polyxenous generalists side by side (Martinu et al. 2015). Also the fact that host switching certainly happens naturally and more often than we expected (Weckstein 2004; Martinu et al. 2015) is against the Fahrenholz's Rule, meaning, against the common practice of identification and description of lice solely on their host association. Moreover, differences between species were in the past often based only on different dimensions (Carriker 1960). The argument against these practices is the so called Harrison's Rule which implies that the size of the parasite is roughly proportional to the size of the hosts (Johnson et al. 2005; Harnos et al. 2016). Here we present revision of a species group of chewing lice to show that complex approach is necessary for evaluation host specificity of parasites.

Myrsidea is the most speciose genus of chewing lice with more than 380 species. It is also a good example of highly host-specific lice, with 80% of species being monoxenous – restricted to one avian host species (Price et al. 2003; Kolencik et al. 2018). The remaining 20% are oligoxenous or pleioxenous – infesting two or more congeneric or confamilial host species, respectively. There is only a single instance of polyxenous species *Myrsidea serini* (Séguy, 1944), that was recorded from eight passerine species from the families Emberizidae, Fringillidae and Icteridae occurring over three geographic regions (Cicchino and Valim 2015). Since it is very unique we wanted to check the host-specificity of this louse species by morphological and partial genetic analysis of all related species belonging to "*serini* species group" (see below).

Recently we collected *Myrsidea* lice from *Spinus magellanicus* (Vieillot, 1805) from the family Fringillidae. This avian speices is documented as the type host of *M. argentina* (Kellogg, 1906), in Peru. *Myrsidea argentina* was described by Kellogg (1906) on the basis of a single specimen, supposedly a female, from Argentina. Unfortunately, the slide with this holotype is lost (Roberta L. Brett, Essig Museum of Entomology, Berkeley, CA. pers. comm. 2016). On the basis of Kellogg's figure and description, Cicchino and Valim (2015) discussed morphological relationships between *M. argentina* and *M. serini*, because they found the latter species on a closely related host, *Spinus barbatus* (Molina, 1782) in Chile. Cicchino and Valim (2015) agree with note by Clay (1968: 238) that Kellogg's specimen was most likely a third instar nymph, not a female (Cicchino and Valim 2015). After comparison of morphometric characteristics of our specimens with the description of *M. serini* by Cicchino and Valim (2015) we could confirm not only that *S. magellanicus* would be a natural host of *M. argentina*, but also that this species is most likely conspecific with *M. serini*.

Our opinion was supported by our preliminary molecular data. A portion of the mitochondrial cytochrome oxi-dase I (*COI*) gene of *Myrsidea* from *Spinus magellanicus* from Peru and *M. serini* from *Agelaoides badius badius* (Vieillot, 1819) from the family Icteridae from Paraguay was sequenced and the divergence among these samples was only 6.6%. In comparison with other species of Neotropical *Myrsidea* with known sequences, these *Myrsidea* were highly differentiated from all others, with uncorrected p-distance exceeding 18.2% that is well over a limit of interspecific genetic diversity of amblyceran lice proposed at level of 12% by Kolencik et al. (2017).

Curiously, the closest to our sequence of *Myrsidea* from *S. magellanicus* was that of *Myrsidea textoris* Klockenhoff, 1984 ex *Ploceus intermedius cabanisii* (W.K.H. Peters, 1868) and *Ploceus velatus tahatali* Smith A., 1836 from the family Ploceidae from South Africa, with a p-distance of only 5.3%. The next closest sequence is of *Myrsidea* sp. ex *Vidua macroura* (Pallas, 1764) from the family Viduidae from Cameroon, with p-distance 7.7% (Kolencik et al. 2017). This relatively small genetic divergence led us to check morphometric characteristics of these species, and evaluate the hypothesis that these geographically distant taxa may also be conspecific with *M. argentina/serini* too. Since all aforementioned species of *Myrsidea* belong to the "*serini* species group" we decided to revise the taxonomy of all 10 species from this species group.

On the basis of morphology of male genitalia within *Myrsidea* species, Klockenhoff (1984b) and consequently Price and Dalgleish (2007) distinguished the "*serini* species group". This group is identical with "group B" described by Clay (1970). It includes *Myrsidea* parasitizing passerine birds from the families Emberizidae, Fringillidae, Icteridae, Passeridae, Ploceidae and Thraupidae: 1) *Myrsidea anoxanthi* Price and Dalgleish, 2007; 2) *M. argentina*; 3) *Myrsidea balati* Macháček, 1977; 4) *Myrsidea darwini* Palma and Price, 2010; 5) *Myrsidea major* (Piaget, 1880); 6) *Myrsidea quadrifasciata* (Piaget, 1880); 7) *Myrsidea queleae* Tendeiro, 1964; 8) *M. serini*; 9) *M. textoris*; and 10) *Myrsidea viduae* Tendeiro, 1993 (Clay 1970; Klockenhoff 1984b; Price and Dalgleish 2007; Palma and Price 2010). We have studied original descriptions of these species and also their available representatives (see Material examined), and have concluded that all taxa are conspecific. This result led us to a reconsideration of the first-described species from this group, i.e. *M. quadrifasciata* (Piaget, 1880) as its nominate species and we propose to rename this species group as the "*M. quadrifasciata* complex".

The aims of this paper are to: 1) re-describe *M. quadrifasciata*; 2) designate a neotype for this species; 3) analyze the validity of all other louse species currently placed in the "*serini* species group"; 4) synonymize all other 9 species from this species group with *M. quadrifasciata* and designate 8 subspecies; 5) present new host records for *M. quadrifasciata*; and 6) summarize its geographical distribution.

2. Material and methods

2.1. Morphology

We used the setal counting system for metanotal and tergal setae as recommended by Valim and Weckstein (2013) and Kolencik et al. (2016), as follows: (1) the number of metanotal setae does not include the most posterolateral setae; (2) the number of tergal setae on tergite I does not include the postspiracular setae; and (3) the numbers of tergal setae on tergites II–VIII neither include the postspiracular setae nor the short associated setae.

Since previous authors (Klockenhoff 1984a, b; Tendeiro 1993; Price and Dalgleish 2007; Palma and Price 2010; Cicchino and Valim 2015) used different setal counting system in their descriptions or redescriptions of species within the "*serini* species group", we modified their data according to the aforementioned system. Therefore, to avoid misunderstandings, we urge authors to make careful comparison of *Myrsidea* descriptions based on the different systems that include the metanotal and tergal setae. In the following descriptions, all measurements are in millimetres. Abbreviations for dimensions are: *dhs*, dorsal head seta; *ls5*, labial setae 5; TW, temple width; POW, preocular width; HL, head length at midline; PW, prothorax width; MW, metathorax width; AWIV, abdomen width at level of segment IV; TL, total length; ANW, female anus width; GW, male genitalia width; GL, male genitalia length; ParL, paramere length; GSL, genital sac sclerite length. Additionally, measurements were made for the setae which compose the aster of sternite II; these are presented from the inner seta to the outer most seta (*s1*, *s2*, *s3*, etc). The taxonomy and nomenclature of the birds follow those in Clements et al. (2019).

We were able to examine specimens of *M. balati*, *M. quadrifasciata*, *M. queleae*, *M. serini*, *M. textoris*, and *M. viduae*. For comparison to other species (*M. anoxanthi*, *M. darwini*, *M. major*), we used precise descriptions or redescriptions of these species by Price and Dalgleish (2007), and Palma and Price (2010). The specimens examined are deposited in the following institutions: K.C. Emerson Entomology Museum, Oklahoma State University, Stillwater, Oklahoma, USA (KCEM); Moravian Museum, Brno, Czech Republic (MMBC); Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand (MONZ); Museu Bocage, Museo Zoologico da Universidade de Lisboa, Lisboa, Portugal (MZUL); Natural History Museum, London, U.K. (NHML); Slovak National Museum, Bratislava, Slovakia (SNMB); National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA (USNM); and Zoological Research Museum Alexander Koenig, Bonn, Germany (ZFMK). As we propose synonymy of nine species from the "*serini* species group" with *M. quadrifasciata*, we rename this species group as the "*M. quadrifasciata* complex" and refer to *Myrsidea* from particular hosts under their previous names in quotation marks, for example, "*M. serini*", "*M. textoris*", etc. for better orientation and to avoid repetition of lists of hosts of these taxa in the following text (for specification see supplement Table S1).

2.2. Statistics

For statistical analysis, we used the most variable data mentioned by Klockenhoff (1984b) – the number of setae on the metanotum, tergites I–VIII, sternites III–VII and selected measurements – and compared them with our data by t-test (Tables S13–16). Correlation between host body size and louse body size was calculated according to Harnos et al. (2016). Avian body size in centimetres or body mass in grams was expressed as log-transformed body size or body mass obtained from del Hoyo et al. (2018). We use only two measures of louse body size: log-transformed total body length and temple width of adult females. By our experience, temple width is a measurement with the lowest intraspecific variability that is usually not affected by slide mounting.

Principal Component Analyses (PCAs) were run to additionally examine morphological characteristics of male and female lice. The R package ggplot2 (Wickham 2016) for R 4.0.3 (R Core Team, 2016) was used to visualise data. Obtained plots were adapted in INKSCAPE 0.91 (https://inkscape.org/de).

2.3. Molecular genetic and sequence analysis

Sequences of a 379 base pair (bp) fragment of the mitochondrial cytochrome c oxidase I gene (*COI*) were obtained from *Myrsidea* sp. ex *Spinus magellanicus* from Peru (A/N KY113129), *M. serini* ex *Agelaioides badius* from Paraguay (A/N KY113130), *Myrsidea* sp. ex *Microspingus melanoleucus* (A/N MT526017), *M. textoris* ex *Ploceus intermedius* and *Ploceus velatus* from South Africa (A/N KF768813–KF768815), using methods described by Johnson et al. (2002). Purified PCR products were sequenced using both respective primers (L6625 and H7005) by Macrogen Europe (The Netherlands).

Sequences of a 347 bp fragment of the nuclear elongation factor 1-alpha (*EF-1α*) gene were obtained from *Myrsidea* sp. ex *Spinus magellanicus* from Peru (A/N MT515729), *M. serini* ex *Agelaioides badius* from Paraguay (A/N MT515731), *Myrsidea* sp. ex *Microspingus melanoleucus* (A/N MT515735), and *Myrsidea* sp. ex *Sporophila nigricollis* (A/N MT968994) using methods described by Johnson et al. (2002). Purified PCR products were sequenced using both respective primers (EF1-For3 and Cho10) by Macrogen Europe (The Netherlands).

In order to assess the genetic divergence within the *M. quadrifasciata* complex, uncorrected p-distances from each specimen was obtained for *COI* and *EF-1α* sequences, sequences of five species with lowest p-distances of *COI* obtained by BLASTing our sequences against GenBank (*M.* cf. *bubalornithis* Klockenhoff, 1984, *M. seminuda* Eichler, 1951, *M.* cf. *textoris*, *Myrsidea* sp. ex *Vidua macroura*, and *Myrsidea* sp. ex *Linurgus oli-*

vaceus) and sequences of three species from Ploceidae (*M. eisentrauti* Klockenhoff, 1982, *M. ledgeri* Klockenhoff, 1984, and *Myrsidea* sp. ex *Ploceus nigricollis*) (see Table 2). Uncorrected p-distances were calculated in Geneious 9.1.8 (Kearse et al. 2012).

In order to evaluate the position of *M. quadrifasciata* complex within *Myrsidea*, two phylogenetic analyses were performed: 1) analysis based on the *COI* gene fragment, and 2) analysis based on concatenated sequences of the *COI* gene fragment and the *EF-1α* gene fragment. To build the *COI* gene tree, we first downloaded all available *Myrsidea* sequences from the GenBank and subsequently utilized all the full-length sequences (379 bp), which were unique (except for *M. nesomimi* where only single representatives of each of the subspecies *M. nesomimi borealis* Palma and Price, 2010 and *M. nesomimi nesomimi* Palma and Price, 2010 were selected in order to keep the analysis presentable). The final alignment consisted of 186 sequences (including *Dennyus hirundinis* as an outgroup taxon for rooting) and 387 bp. For a list of utilized sequences, see Table S2 in the Supplementary material.

For the concatenated tree, we downloaded all available *Myrsidea* sequences from the GenBank database and subsequently included all available samples with both *COI* and *EF-1α* sequences. Pairs of sequences for each sample were concatenated and all unique concatenates were subsequently used to build the phylogenetic tree. The final alignment consisted of 64 sequences (including *Dennyus hirundinis* as an outgroup taxon for rooting) and 675 bp. For a list of utilized sequences, see Table S2 in the supplementary material.

For both phylogenetic analyses, we first used the Akaike information criterion (AIC) computed in MEGA 7.0.14 (Kumar et al. 2016) to identify the most appropriate models of nucleotide substitution for each gene. Both trees were built using the maximum likelihood (ML) method conducted by PhyML 2.2.0 plugin in Geneious 9.1.8 (Guindon and Gascuel 2003; Kearse et al. 2012) with the GTR+G+I model and parameters estimated from the data; nodal supports were generated with 1,000 bootstrap replicates. The resulting trees with the best likelihood scores were chosen. The trees were visualised using TreeGraph 2.12.0 (Stöver and Müller 2010).

3. Results

3.1. Systematics and morphology

Psocodea Hennig, 1966: 187

Phthiraptera Haeckel, 1896: 703

Amblycera Kellogg, 1896a: 68

Menoponidae Mjöberg, 1910: 26

Myrsidea **Waterston, 1915: 12**

Myrsidea quadrifasciata (Piaget, 1880)

Figs 1–20

Menopon quadrifasciatum Piaget, 1880: 440, pl. XXXV, fig. 6. Type host: *Passer domesticus* (Linnaeus, 1758).

Myrsidea quadrifasciata (Piaget, 1880): Thompson (1937), Clay (1949b), Thompson (1957), Touleshkov (1962, 1974), Macháček (1977a), Lakshminarayana (1979), Gadzhiev and Mustafaeva (1981), Price et al. (2003: 131), Mey (2004), Manilla (2000), Saxena et al. (2007), Naz et al. (2021).

Menopon quadrifasciatum var. *major* Piaget, 1880: 441. Type host: *Plectrophenax nivalis* (Linnaeus, 1758). **New synonymy.**

Myrsidea major (Piaget, 1880): Thompson (1937), Clay (1949a), Emerson (1972), Price et al. (2003: 130), Price and Dalgleish (2007: 14).

Menopon argentinus Kellogg, 1906: 49, pl. II, fig. 7. Type host: *Spinus magellanicus* (Vieillot, 1805). **New synonymy.**

Myrsidea argentina (Kellogg, 1906): Price et al. (2003: 128), Cicchino and Valim (2015: 241, fig. 34).

Menopon serini Séguy, 1944: 80, fig. 84. Type host: *Serinus serinus* (Linnaeus, 1766). **New synonymy.**

Myrsidea serini (Séguy, 1944): Hopkins and Clay (1952: 233), Negru (1963: 11), Negru (1965: 499, fig. 1e), Klockenhoff (1984a: 18, figs 1–4, tables 1–2, 1984b: 283), Price et al. (2003: 131), Price and Dalgleish (2007: 12, fig. 39), Cicchino and Valim (2015: 232, figs 1–33), Kolencik et al. (2016: 245).

Liquidea serini (Séguy, 1944): Złotorzycka (1964: 169, 176).

Myrsidea queleae Tendeiro, 1964: 182, photos 11–16. Type host: *Quelea quelea lathami* (Smith A., 1836). **New synonymy.**

Myrsidea queleae Tendeiro, 1964: Klockenhoff (1984b: 281), Price et al. (2003: 131), Sychra et al. (2010), Halajian et al. (2014).

Myrsidea balati Macháček, 1977a: 1, figs 1a, b, 4, 7–8. Type host: *Passer montanus* (Linnaeus, 1758). **New synonymy.**

Myrsidea balati Macháček, 1977: Price et al. (2003: 128), Adam (2007), Adam et al. (2009).

Myrsidea textoris Klockenhoff, 1984b: 270, figs 1–3, 10a, 11a, b. Type host: *Ploceus cucullatus cucullatus* (Müller, 1776). **New synonymy.**

Myrsidea textoris Klockenhoff, 1984b: Lindholm et al. (1998: 147); Price et al. (2003: 132); Halajian et al. (2012: 65, 2014: 770); Sychra et al. (2014b: 599).

Myrsidea viduae Tendeiro, 1993: 57, figs 2, 4, 6. Type host: *Vidua macroura* (Pallas, 1764). **New synonymy.**

Myrsidea viduae Tendeiro, 1993: Price et al. (2003: 133).

Myrsidea anoxanthi Price and Dalgleish, 2007: 13, figs 40–44. Type host: *Loxipasser anoxanthus* (Gosse, 1847). **New synonymy.**

Myrsidea darwini Palma and Price, 2010: 136, figs 1–5. Type host: *Geospiza fuliginosa* Gould, 1837. **New synonymy.**

Type host. *Passer domesticus* (Linnaeus, 1758) (Passeridae).

Type locality. Unknown (most likely Netherlands).

Differential diagnosis. In both sexes showing the characteristics of the "*M. serini*-Artengruppe" (Klockenhoff 1984b), or *serini* species-group (Price and Dalgleish 2007). It is well characterized with 1) weakly developed hypopharyngeal sclerites; 2) abdominal segments with continous row of tergal setae across segments I–II, and with well-defined median gap in row of tergal setae on other segments; 3) the females with non enlarged and unmodified tergites (except tergites II–III with slight medioposterior curvature) (Figs 1–3); 4) the females with

a strongly spiculate posterior margin of the subgenital plate; and 5) the males with characteristic genital sac sclerites (Figs 4–18).

Description. The following overall description is based on a large number of specimens from different hosts. Data for the most important morphometric characteristics for specimens according to their hosts are presented in supplement Tables S3–S12. For better orientation and to avoid repetition of lists of hosts in the following text we refer to *Myrsidea* from particular hosts under their previous names in quotation marks, for example, "*M. serini*", "*M. textoris*", etc. (for specification see Table S1).

To evaluate the status of "*M. argentina*" we also examined available nymphs of 3rd instar: 1) two nymphs from *Spinus magellanicus* – type host of "*M. argentina*", and 2) one nymph from *Passer montanus* – host of *M. quadrifasciata*. These nymphs differ from previous descriptions of "*M. argentina*" by Kellogg (1906) and "*M. serini*" by Cicchino and Valim (2015). Here the essential characters are given, with data from Kellogg (1906) and Cicchino and Valim (2015) in parentheses as (Kellogg/ Cicchino and Valim).

FEMALE (n=167) (as in Fig. 19): *Head*. Hypopharyngeal sclerites weakly developed. Length of *dhs* 10, 0.05–0.10; *dhs* 11, 0.07–0.11; ratio *dhs* 10/11, 0.70–1.10. *Ls5* 0.06–0.07 long, latero-ventral fringe with 9–10 setae. Gula with a total of 7–11 setae (3–6 setae on each side). *Thorax*. Pronotum with 6 setae on posterior margin and 3 short spiniform setae at each lateral corner. Prosternal plate with rounded anterior margin. First tibia with 3–4 outer ventro-lateral and 3–4 dorsolateral setae. Mesonotum divided. Metanotum not enlarged, with 6–13 marginal setae; metasternal plate with 4–8 setae; metapleurites with 3–4 short strong spiniform setae. Femur III with 14–21 setae in ventral setal brush. *Abdomen*. Tergites not enlarged, all with straight posterior margin, only tergites II–III slightly convex medioposteriorly. Abdominal segments with continous row of tergal setae across segments I–II, and with small, but noticeable, median gap in row of tergal setae on other segments. Tergal setae: I, 7–18; II, 8–18; III, 7–19; IV, 7–17; V, 6–15; VI, 5–14; VII, 4–11; VIII, 3–8. Postspiracular setae long to extremely long on II, IV, VII and VIII and shorter on I, III, V and VI with length as in Table S9. Inner posterior seta of last tergum as long as or longer than anal fringe setae with length 0.09–0.10; length of short lateral marginal seta of last segment, 0.03–0.05. Pleural setae: I, 2–6; II, 5–8; III, 5–9; IV, 5–8; V, 4–7; VI, 4–6; VII, 3–5; VIII, 2–4. Pleurites I–II with only short spine-like setae; pleurites III–VII also with 1–2 slender and longer setae; without anterior pleural setae. Pleurite VIII with inner setae (0.02–0.03) as long as outer (0.02–0.04). Anterior margin of sternal plate II with a medial notch. Sternal setae: I, 0; II, 3–5 in each aster, aster setae length: *s1*, 0.09–0.11; *s2*, 0.05–0.07; *s3*, 0.04–0.06; *s4*, 0.03–0.05; with 9–20 marginal setae between asters, 4–14 medioanterior; III, 16–31; IV, 27–45; V, 27–49; VI, 12–39; VII, 11–22; VIII–IX, 6–22; and 6–14 setae on deeply serrated vulval margin; sternites III–VII without medioanterior setae. Anal fringe formed by 27–43 dorsal

and ventral setae. *Measurements*. TW, 0.34–0.46; POW, 0.30–0.34; HL, 0.25–0.32; PW, 0.18–0.30; MW, 0.36–0.51; AWIV, 0.51–0.71; ANW, 0.19–0.24; TL, 1.26–1.80.

MALE (n=90) (as in Fig. 20). Similar to female except as follows. *Head*. Length of *dhs* 10, 0.05–0.10; *dhs* 11, 0.06–0.11; ratio *dhs* 10/11, 0.70–1.10. *Ls5* 0.05–0.06 long. *Thorax*. Metanotum not enlarged with 6–14 marginal setae; metasternal plate with 4–6 setae; metapleurites with 3 strong, short spiniform setae. Femur III with 15–20 setae in ventral setal brush. *Abdomen*. Abdominal segments with continous row of tergal setae at least across segments I–III, with small median gap in row of tergal setae on other segments. Tergal setae: I, 9–18; II, 9–21; III, 9–22; IV, 7–26; V, 9–23; VI, 8–24; VII, 6–19; VIII, 4–14. Length of inner posterior seta of last tergum, 0.07–0.08; short lateral marginal seta of last segment, 0.03. Pleural setae: I, 3–5; II, 5–8; III, 5–9; IV, 5–7; V, 4–8; VI, 3–6; VII, 3–6; VIII, 2–3. Pleurites I–II with only short spine-like setae; pleurites III–VII also with 1–4 slender and longer setae; without anterior pleural setae. Pleurite VIII with inner setae (0.03) as long as outer (0.03–0.04). Sternal setae: I, 0; II, 3–4 in each aster, aster setae length: *s1*, 0.07–0.08; *s2*, 0.04–0.06; *s3*, 0.03–0.04; *s4*, 0.02; with 8–16 marginal setae between asters, 4–14 medioanterior; III, 16–34; IV, 24–44; V, 24–45; VI, 21–39; VII, 12–24; VIII, 4–19; remainder of plate, 6–8; and with 3–6 setae posteriorly; sternites III–VII without medioanterior setae. With 6–12 internal anal setae. Genital sac sclerite as in Figs 4–18. *Measurements*. TW, 0.33–0.42; POW, 0.28–0.33; HL, 0.23–0.30; PW, 0.20–0.29; MW, 0.28–0.41; AWIV, 0.37–0.54; GW, 0.09–0.10; GL, 0.34–0.43; ParL, 0.06–0.08; GSL, 0.03; TL, 1.05–1.41.

THIRD INSTAR NYMPH. Marginal seta of metanotum 7 (4/6). Tergocentral setae of abdomen: I, 7–10 (10/8–9); II, 8–9 (11/8); III, 8 (11/8–9); IV, 8 (11/8–9); V, 6–7 (10/6–7); VI, 6 (10/6–7); VII, 5–6 (9/6); VIII, 4–5 (4/4). Number of setae of dorsal anal fringe, 16–21 (cca 15/15). Dimensions: HL, 0.25–0.29 (0.27/0.28–0.30); TW, 0.35–0.36 (0.35/0.39–0.40); TL, 1.20–1.29 (1.20/1.40–1.41).

Material examined. Ex *Passer domesticus* (Passeridae): 1♂ (designated as a neotype), **England**: Cheshire, Great Budworth, 5.xii.1934, A.W. Boyd leg. (NHML: B.M.1955–616); 2♂, 2♀, **USA**: Mississippi, Tibbee, 15.iii.1936, E.W. Stafford leg. (KCEM: 8170, 8172–74); 1♂, 1♀, **USA**: Hawaii, Honolulu, 8.ii.–8.iii.1947, J. Alicata leg. (USNM: Lot 47-4795, vial 2). — Ex *Passer montanus* (Passeridae): 1♀ (paratype of *M. balati*), **Czech Republic**, Nesyt, 9.xi.1973, P. Macháček leg. (ZFMK: 1986/15), 1♂, **Czech Republic**, Jinačovice (49°15′N 16°31′E), 13.i.2006, O. Sychra and I. Literak leg. (MMBC), 1♀, **Czech Republic**, Moravské Knínice (49°17′N 16°29′E), 8.ii.2009, O. Sychra and I. Literak leg. (MMBC), 1♀, **Czech Republic**, Kardašova Řečice, 19.vii.1938, K. Pfleger leg. (SNMB); 1♀, **Hungary**, Nagykanizsa, 28.vi.1952, Balát coll. (MMBC: B185), 1♀, **Hungary**, Bajcza (Zala m.), 19.iv.1953, Balát coll. (MMBC: C579); 1♀, 1 nymph, **Slovakia**, Gabčíkovo, 22.vii.1953, Balát coll. (MMBC: 1380), 2♂, 1♀, **Slovakia**, Gbelce (47°51′N 18°30′E), 10.vii.2019, O. Sychra and L. Oslejskova leg.; 3♂, 3♀, **Thailand**, San Sai, Ban Pong, 16.ii.1962, Kitti Thonglongya leg. (KCEM: 8183–85); 1♀, **W. Java**, Bogor, 8.xi.1968 (KCEM: 9E 0414); 2♀, no data (NHML: 840). — Ex *Agelaius phoeniceus* (Linnaeus, 1766) (Icteridae): 9♀, 3♂, **USA**: South Carolina, Charleston,
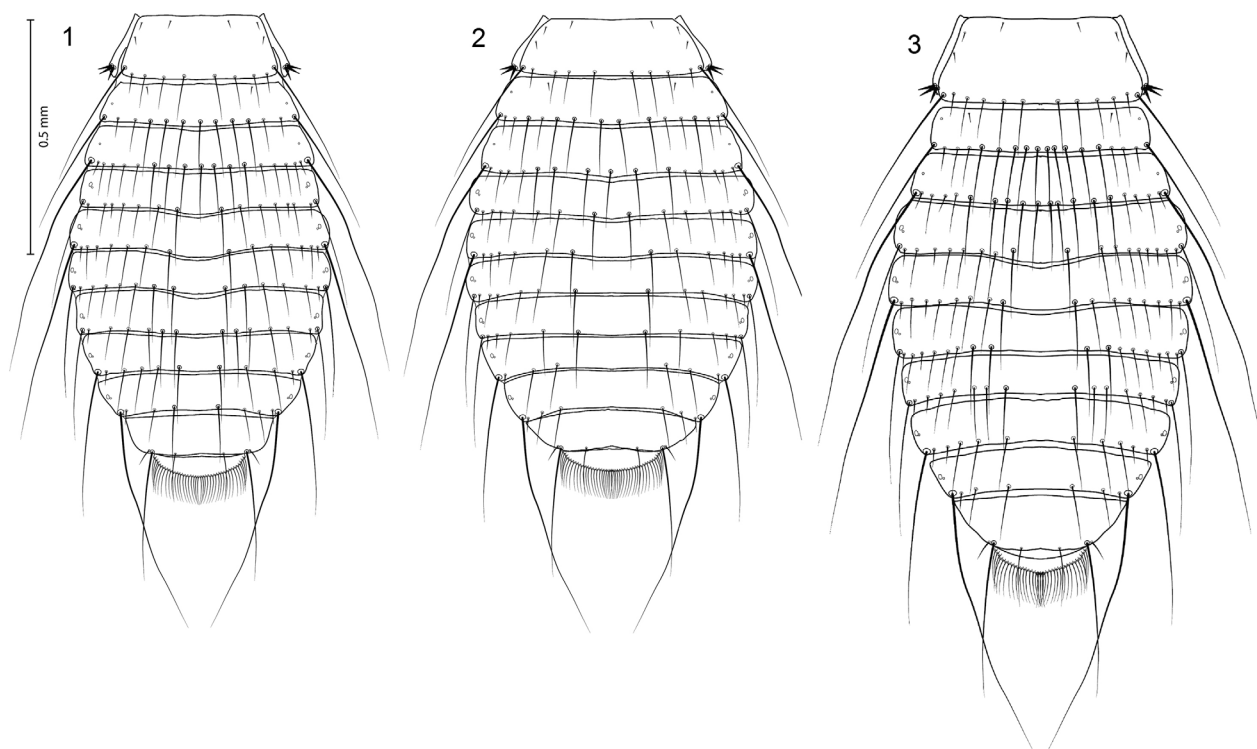
Figures 1–3. Dorsal view of female metathorax and abdomen. **1**: *Myrsidea quadrifasciata quadrifasciata* ex *Passer domesticus*. **2**: *M. q. quadrifasciata* ex *Passer montanus*. **3**: *M. q. queleae* ex *Quelea quelea*.
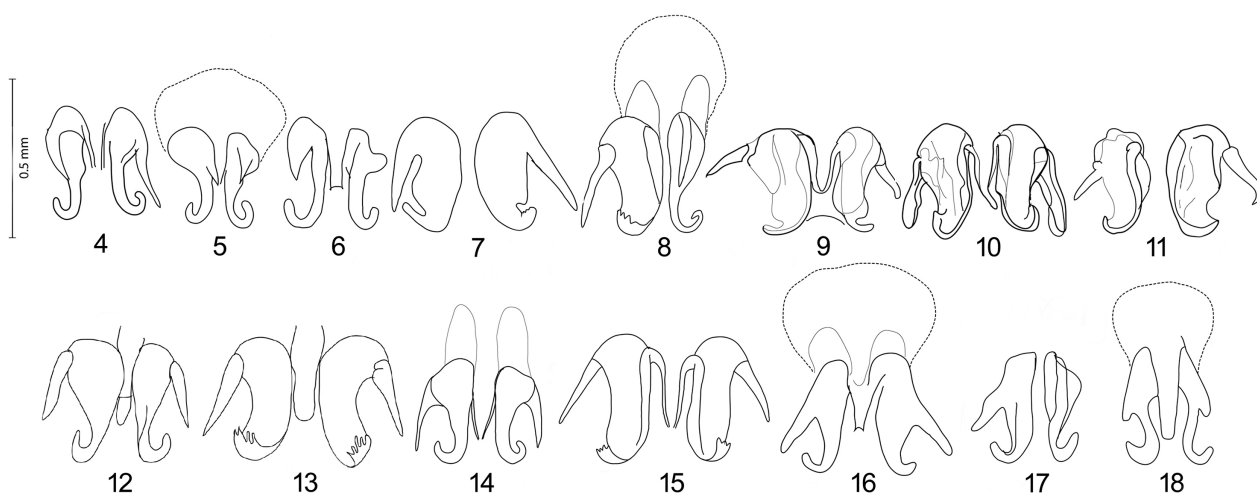
Figures 4–18. Male genital sac sclerites of *Myrsidea quadrifasciata*. **4–5**: *M. q. quadrifasciata* ex *Passer domesticus*. **6–7**: *M. q. quadrifasciata* ex *Passer montanus*. **8**: *M. q. argentina* ex *Agelaoides badius* from Paraguay. **9–11**: *M. q. argentina* according to Cicchino and Valim (2015). **12–13**: *M. q. serini* according to Klockenhoff (1984a). **14**: *M. q. darwini* according to Palma and Price (2010). **15**: *M. q. anoxanthi* according to Price and Dalgleish (2007). **16**: *M. q. textoris* ex *Ploceus cucullatus*. **17–18**: *M. q. queleae* ex *Quelea quelea*.

1934, 27.iii.1933, H.S. Peters leg. (USNM: Bish. 1934 #20711). — Ex ***Agelaoides badius badius*** (Vieillot, 1819) (Icteridae): 1♀, 4♂, **Paraguay**, Los Tres Gigantes Biological Station in the Pantanal (20°04′S 50°09′W), 6.ix.2012, I. Literak leg. (MMBC: PG357). — Ex ***Emberiza citrinella caliginosa*** Clancey, 1940 (Emberizidae): 1♀, 1♂, **New Zealand**, Raoul I., Kermadec Is., 11.xii.1972; J. Ireland leg., R.L.C. Pilgram Collection (MONZ). — Ex ***Euplectes franciscanus*** (Isert, 1789) (Ploceidae): 2♂, 2♀, **Senegal**, Niokolo Koba National Park, Simenti (13°02′N 13°18′W), 8.ii.2005, P. Prochazka leg. (MMBC). — Ex ***Euplectes jacksoni*** (Sharpe, 1891) (Ploceidae): 1♂, 3♀, **Kenya**, i.1936,

Meinertzhagen coll. (NHML: No.6081). — Ex ***Euplectes orix*** (Linnaeus, 1758) (Ploceidae): 2♀, **South Africa**, Pietermaritzburg, Scottsville (29°39′S 30°23′E), 7. and 19.ii.1994, A. Lindholm leg. (slide no. 57A, 106A). — Ex ***Euplectes progne delamerei*** (Shelley, 1903) (Ploceidae): 2♂, **Kenya**, iii.1936, Meinertzhagen coll. (NHML: No.7462); 1♂, 3♀, **Kenya**, ii.1936, Meinertzhagen coll. (NHML: No.6715). — Ex ***Foudia madagascariensis*** (Linnaeus, 1766) (Ploceidae): 1♂, 2♀, **Madagascar**, Diego Suarez, 1921, G. Melow Coll. (NHML: 1921–200). — Ex ***Passer luteus*** (Lichtenstein, M.H.C., 1823) (Passeridae): 3♀, **Senegal,** Matam (15°37′N 13°20′W), 6.ix.2007, I. Literak and M. Capek leg. (MMBC).

Figures 19–20. *Myrsidea quadrifasciata quadrifasciata* ex *Passer domesticus*. **19**: Female. **20**: Neotype male.

— Ex *Ploceus cucullatus cucullatus* (Statius Müller, 1776) (Ploceidae): 1♂, 3♀, **Senegal,** Kaolack (14°09′N 16°06′W), 7.ix.2007, I. Literak and M. Capek leg. (MMBC). — Ex *Microspingus melanoleucus* (d'Orbigny and Lafresnaye, 1837) (Thraupidae): 1♀, **Paraguay**, Los Tres Gigantes Biological Station in the Pantanal (20°04′S 50°09′W), 6.ix.2012, I. Literak leg. (MMBC: PG359). — Ex *Ploceus cucullatus nigriceps* (Layard, 1867) (Ploceidae): 1♂, **Mozambique**, Zambue, Tete District, 3.ix.1964, A.L.Moore leg. (KCEM: A36). — Ex *Ploceus nigricollis brachypterus* Swainson, 1837 (Ploceidae): 1♂, 1♀, **Cameroon**, Yaounde, 1955, J. Mouchet (NHML: B.M.1955–737). — Ex *Ploceus philippinus* (Linnaeus, 1766) (Ploceidae): 1♂, 5♀, 1 nymph, **India**, Deccan, ii.1937, Meinertzhagen coll. (NHML: No.8615–17); 2♀, **India**, Daulatabad, Maharastra, 25.vi.1969, (KCEM: S.No.XE–363, XE–193, AB–24042); 1♀, **India**, Daulatabad, Aurangabad, 20.vii.1968, (KCEM: 9E 0250, A81348); 1♀, **Thailand**, Doi Pha Hom Pok Chiengmai 22.xii.1965, (KCEM: MAPS–3658). — Ex *Ploceus velatus tahatali* A. Smith, 1836 (Ploceidae): 1♂, **South Africa**, Limpopo province, Polokwane Game Reserve (23°58′S 29°28′E), 11.ii.2012, A. Halajian leg. (MMBC). — Ex *Quelia cardinalis* (Hartlaub, 1880) (Ploceidae): 1♂ (paratype of *M. queleae*), Bechuanaland (now **Botswana**), Mababe, 6.x.1952, F. Zumpt leg. (NHML: B.M. 1959–273). — Ex *Quelea quelea aethiopica* (Sundevall, 1850) (Ploceidae): 1♂, 1♀, **Sudan,** May 1936, Meinertzhagen coll. (NHML: No.7836). — Ex *Quelea quelea*

lathami (Ploceidae): 1♂, Southern Rhodesia (now **Zimbabwe**), Matopos, 30.iii.1952 (NHML: B.M.1980–40, coll.691); 1♂, 1♀, Transvaal (now **South Africa**), Nr. Komatipoort, 18.i.1961, F. Zumpt leg. (NHML: B.M.1965–526); 4♂, 3♀, **South Africa**, Limpopo province, De Loskop (23°30′S 29°18′E), 7.xii.2012, Halajian leg. (MMBC). — Ex *Quelea quelea quelea* (Linnaeus, 1758) (Ploceidae): 1♂, 1♀, North **Cameroon**, Marona, J.Mouchet leg. (NHML); 2♂, 2♀, **Senegal,** Matam (15°37′N 13°20′W), 6.ix.2007, I. Literak and M. Capek leg. (MMBC). — Ex *Serinus canaria* (Linnaeus, 1758)–captive bird (Fringillidae): 1♀, 1♂, **New Zealand**, Christchurch, 20.xii.1944, R.L.C. Pilgram Collection (MONZ). — Ex *Spinus magellanicus* (Fringillidae): 4♀, 2♂, 2 nymphs, **Peru**, Cascay, Huanuco (9°50'S 76°08'W), 20. and 22.viii.2011, I. Literak leg (MMBC: O. Sychra PE16–19). — Ex *Sporophila nigricollis* (Vieillot, 1823) (Thraupidae): 1♂, **Peru**, Cascay, Huanuco (9°50'S 76°08'W), 21.viii.2011, I. Literak leg (MMBC: O. Sychra PE20). — Ex *Vidua macroura* (Viduidae): 2♀, **São Tomé and Príncipe**, Missão Zoológica a São Tomé, loc. 41, São João dos Angolares (MZUL: 23/6/984).

Remarks. Piaget (1880) gave only a short description of *M. quadrifasciata* based on 13 females and 11 males from *Passer domesticus*. Later Thompson (1937) in his review of Piaget's collection referred to the presence of

Table 1. Summary of published records of examined sparrows and collected *Myrsidea quadrifasciata quadrifasciata* from *Passer domesticus* and *Passer montanus* within and out of their native range. — **Abbreviations**: E=number of examined birds; P=number of parasitised birds; %=prevalence; MA=mean abundance; ?=not mentioned.

Host / Country	E	P	%	MA	Number of collected lice	Reference
Passer domesticus						
Azerbaijan	514	21	4.1	0.078	40	Gadzhiev and Mustafaeva (1981)
Belarus	93	0	0	0	–	Zhuk and Nikalaeva (1987)
Bulgaria	118	1	0.8	0.008	1♀	Touleshkov (1974)
Czech Republic	436	1	0.2	0.002	1♂	Macháček (1977a)
Czech Republic	86	0	0	0	–	present study
England	473	0	0	0	–	Brown and Wilson (1975)
England	237	0	0	0	–	Thompson (1957)
India	100	20	20	?	Range 2–28 lice per bird	Saxena et al. (2007)
Iran	9	0	0	0	–	Moodi et al. (2013)
Pakistan	129	39	30.2	0.66	85	Naz et al. (2021)
Romania	492	0	0	0	–	Pap et al. (2013)
Turkey	22	0	0	0	–	Dik et al. (2013)
TOTAL (within native range)	2709	82	3.0	?		
Canada, Manitoba	455	0	0	0	–	Galloway (pers. comm.)
Panama	58	0	0	0	–	Martin et al. (2007)
USA, Indiana	300	0	0	0	–	McGroarty and Dobson (1974)
USA, Kansas	567	0	0	0	–	Hoyle (1938)
USA, Kentucky	77	0	0	0	–	Wilson (1958)
USA, Massachusetts	34	0	0	0	–	Brown and Wilson (1975)
USA, New Hampshire	44	0	0	0	–	Keirans (1966)
USA, New Jersey	62	0	0	0	–	Martin et al. (2007)
USA, Oklahoma	127	0	0	0	–	Weddle (2000)
USA, Wisconsin	391	0	0	0	–	Woodmann and Dickie (1954)
TOTAL (out of native range)	1660	0	0	0		
Passer montanus						
Belarus	235	0	0	0	–	Zhuk and Nikalaeva (1987)
Czech Republic	433	2	0.5	0.021	2♂, 2♀, 5 nymphs	Macháček (1977a)
Czech Republic	15	2	13	0.133	1♂, 1♀	present study
Iran	8	0	0	0	–	Moodi et al. (2013)
Thailand	140	70	50	?	?	Boonkong and Meckvichai (1987)
TOTAL (within the native range)	831	74	9.0	?		

only one slide with two females of *M. quadrifasciata*, but mentioned *Passer montanus* as host. He also stated: "A male is mentioned in the original description, but there is no male in the collection." Subsequently Clay (1949b) specified that there is no original Piaget's specimen of *M. quadrifasciata* from the type host, either in the NHML or in the museum in Leiden and confirmed the presence of two females from *Passer montanus* in the NHML.

We were able to examine slide no. 840 mentioned by Thompson (1937) and Clay (1949b), labeled as *Menopon fasciatum*, that is deposited in NHML and originally from Piaget's collection. Moreover, there were also three slides labeled as "*Myrsidea 4fasciata*" from *Passer domesticus* in the collections of NHML; but in fact, there is actually only one slide (No. B.M.1955–616) with one male (here designated as neotype) belonging to this species. On the next two slides (both under the same number, B.M.1980-40) there are two females of *Menacanthus eurysternus* (Burmeister, 1838) collected from the same locality as *Myrsidea*, i. e. England: Cheshire, Great Bud-

worth and Plumbey by A.W. Boyd (10.ix.1932), and J.S. Booth (8.10.1932), respectively. It is probably the same situation concerning the record of *Menacanthus quadrifasciatum* Piag. from house sparrow (collected by A.W. Boyd (13.3.1923) in Great Budworth) reported by Britten (1932). The name of this species is manually rewritten as *Menacanthus spinosus* Piaget, 1880 (now *M. eurysternus*) in the available copy of this paper on phthiraptera. info web page (http://phthiraptera.info/sites/phthiraptera. info/files/44361.pdf).

There are few reports about the occurrence of *M. quadrifasciata* on *P. domesticus* and *P. montanus* (see Table 1). It is quite prevalent in Asia with prevalence 20–50% and mean intensity only about 2 specimens per infested bird (Table 1).

Table 2. Genetic distance between available specimens of *Myrsidea quadrifasciata* (= *M. q.*, in **bold** type) and six related species; upper right and lower left distance collected from *COI* and *EF-1α* partial gene pairwise comparisons. GenBank numbers for *COI* and *EF-1α*, respectively: 1) KY113129, MT515729; 2) KY113130, MT515731; 3) MT526017, MT515735; 4) *COI* not available, MT968994; 5) DQ887256, DQ887220; 6) DQ887257; DQ887221; 7) KF768813, *EF-1α* not available; 8) KF768814, *EF-1α* not available; 9) KF768815, *EF-1α* not available; 10) MG682397, *EF-1α* not available; 11) MG682394, *EF-1α* not available; 12) MG765498, *EF-1α* not available; 13) FJ171275, FJ171301; 14) KY359403, KY359392; 15) AF545733, AF320428; 16) AF545731, AF320429. * denotes amblycerans examined in this study.

	(sub)Species	EF-1α															
		1)	2)	3)	4)	5)	6)	7)	8)	9)	10)	11)	12)	13)	14)	15)	16)
	*1) **M. q. argentina** ex *Spinus magellanicus*		0.0	0.0	0.0	0.0	0.3	N/A	N/A	N/A	N/A	N/A	N/A	7.8	5.5	8.1	7.4
	*2) **M. q. argentina** ex *Agelaoides badius*	6.6		0.0	0.0	0.0	0.3	N/A	N/A	N/A	N/A	N/A	N/A	7.8	5.5	8.1	7.4
	*3) **M. q. argentina** ex *Microspingus melanoleucus*	5.5	5.8		0.0	0.0	0.3	N/A	N/A	N/A	N/A	N/A	N/A	7.8	5.5	8.1	7.4
	*4) **M. q. anoxanthi** ex *Sporophila nigricollis*	N/A	N/A	N/A		0.0	0.3	N/A	N/A	N/A	N/A	N/A	N/A	7.8	5.5	8.1	7.4
	5) **M. q. viduae** ex *Vidua macroura*	7.7	7.4	6.6	N/A		0.3	N/A	N/A	N/A	N/A	N/A	N/A	7.8	5.5	8.1	7.4
	6) **M. q. viduae** ex *Vidua macroura*	7.7	7.9	6.6	N/A	0.5		N/A	N/A	N/A	N/A	N/A	N/A	8.1	5.8	8.4	7.7
	*7) **M. q. textoris** ex *Ploceus intermedius*	5.3	5.6	6.1	N/A	7.7	8.2		N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
COI	*8) **M. q. textoris** ex *Ploceus velatus*	5.6	5.8	6.4	N/A	7.9	8.5	0.3		N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
	*9) **M. q. textoris** ex *Ploceus velatus*	5.3	5.6	6.1	N/A	7.7	8.2	0.0	0.3		N/A	N/A	N/A	N/A	N/A	N/A	N/A
	10) **M. q. textoris** ex *Ploceus ocularis*	6.9	6.6	7.7	N/A	8.7	9.3	1.6	1.9	1.6		N/A	N/A	N/A	N/A	N/A	N/A
	11) *M.* cf. *bubalornithis* ex *Bubalornis niger*	14.3	15.6	16.4	N/A	16.9	16.9	16.1	16.4	16.1	16.4		N/A	N/A	N/A	N/A	N/A
	12) *Myrsidea* sp. ex *Linurgus olivaceus*	16.1	15.3	13.7	N/A	14.7	14.7	14.5	14.8	14.5	15.0	18.2		N/A	N/A	N/A	N/A
	13) *Myrsidea seminuda* ex *Thraupis palmarum*	18.2	18.5	19.0	N/A	19.8	19.8	17.7	17.5	17.7	18.3	20.8	19.5		4.9	7.5	6.6
	14) *Myrsidea* sp. ex *Ploceus nigricollis*	22.2	21.2	21.2	N/A	21.7	21.7	20.6	20.4	20.6	21.2	21.4	18.7	20.9		7.0	5.7
	15) *Myrsidea ledgeri* ex *Philetairus socius*	23.2	24.0	23.0	N/A	21.4	21.4	22.8	23.0	22.8	23.5	22.4	23.7	26.4	22.2		8.0
	16) *Myrsidea eisentrauti* ex *Sporopipes squamifrons*	24.0	22.4	23.2	N/A	22.4	22.4	22.5	22.2	22.5	23.5	23.8	23.2	21.1	23.0	24.5	

3.2. Molecular genetic and sequence analysis

Within the *M. quadrifasciata* complex, we found genetic divergences of 0.0–6.6% among the obtained sequences of *COI* from six *Myrsidea* samples examined in this study (Table 2, lines 1–3, 7–9). In comparison with GenBank, we found three other sequences with < 10% divergence (*Myrsidea* cf. *textoris* ex *Ploceus ocularis*; two *Myrsidea* sp. ex *Vidua macroura*), while the interspecific genetic distance from other species always exceeded 13%, the three closest species being *M.* cf. *bubalornithis*, *M. seminuda* and *Myrsidea* sp. ex *Linurgus olivaceus* (Table 2). Sequences for the *EF-1α* gene for all our examined *Myrsidea* specimens were identical, while sequences for all other species (with the exception of the *Myrsidea* sp. ex *Vidua macroura*) showed divergence over 5% (Table 2). Phylogenetic relationships

among *Myrsidea* sequences obtained during this study and other *Myrsidea* sequences are presented in Fig. 21 and Fig. S1.

3.3. Louse-host body size correlation

Principal Component Analysis (Fig. 22) using morphological data showed that there is no significant difference between the individuals of the different species in both males and females. Body size of 33 hosts was positively correlated with size of their *Myrsidea* (Table S1): bird size in centimetres (cm) vs. louse female TW: R=0.6703, P < 0.001; bird size in cm vs. louse female TL: R=0.4358, P < 0.01; bird body mass in grams (g) vs. louse female TW: R=0.7058, P < 0.001; bird body mass in g vs. louse female TL: R=0.5305, P < 0.01 (Fig. 23). Contrary to this, there is no correlation between host size and total number
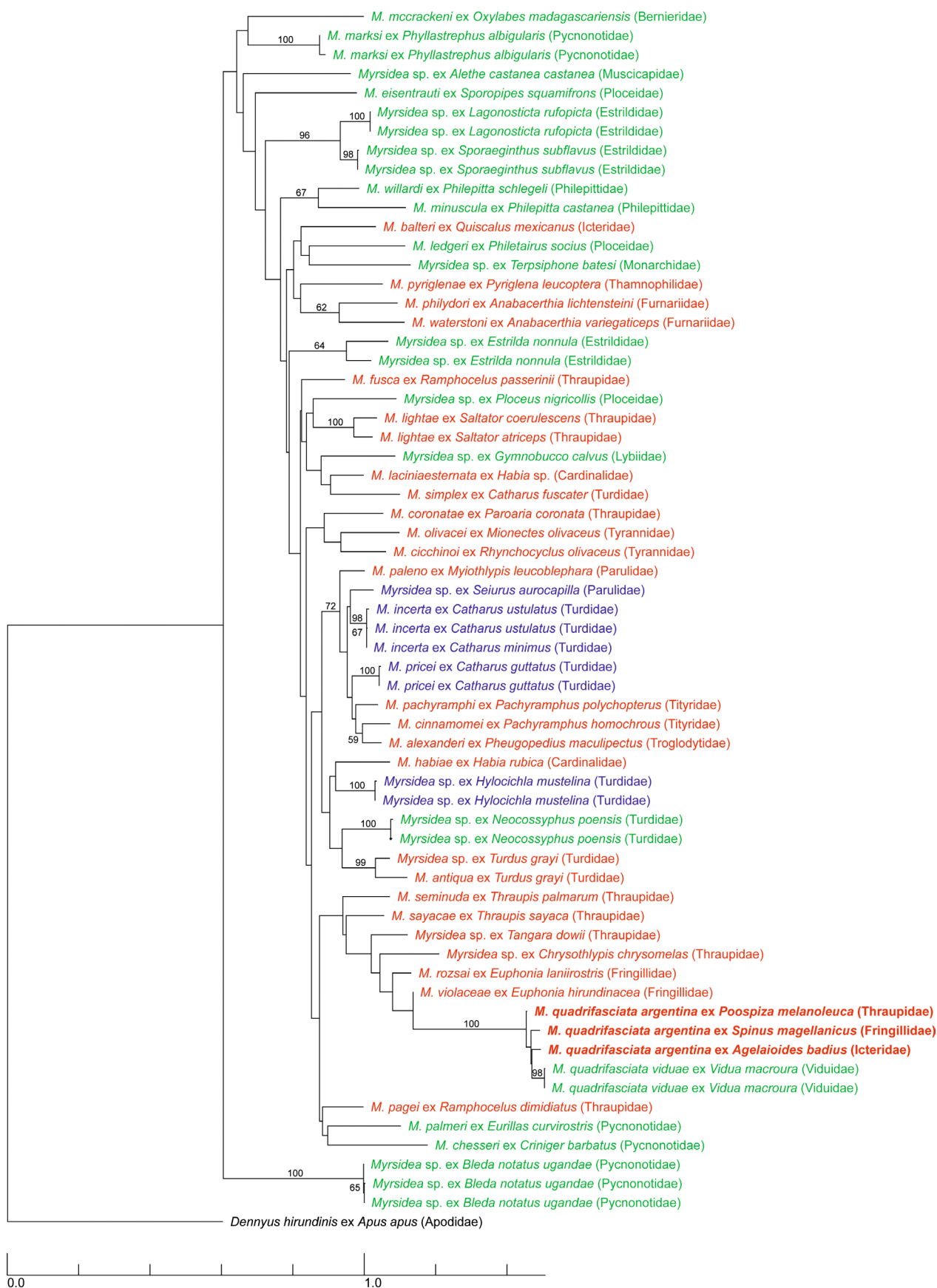
Figure 21. Phylogenetic tree of the *Myrsidea* species based on concatenated partial *COI* and *EF-1α* sequences. The tree was inferred using the maximum likelihood method based on the GTR+G+I model. The tree with the highest log likelihood is shown. Bootstrap support is shown next to the branches (values < 50% not shown). The tree is drawn to scale, with branch lengths in proportion to expected number of substitutions per site, as represented by the scale bar. Samples of *M. quadrifasciata* discussed in the present paper are in **bold** type. — ***Colours***: green – samples from Ethiopian Region; red – samples from Neotropical Region; blue – samples from Nearctic Region.
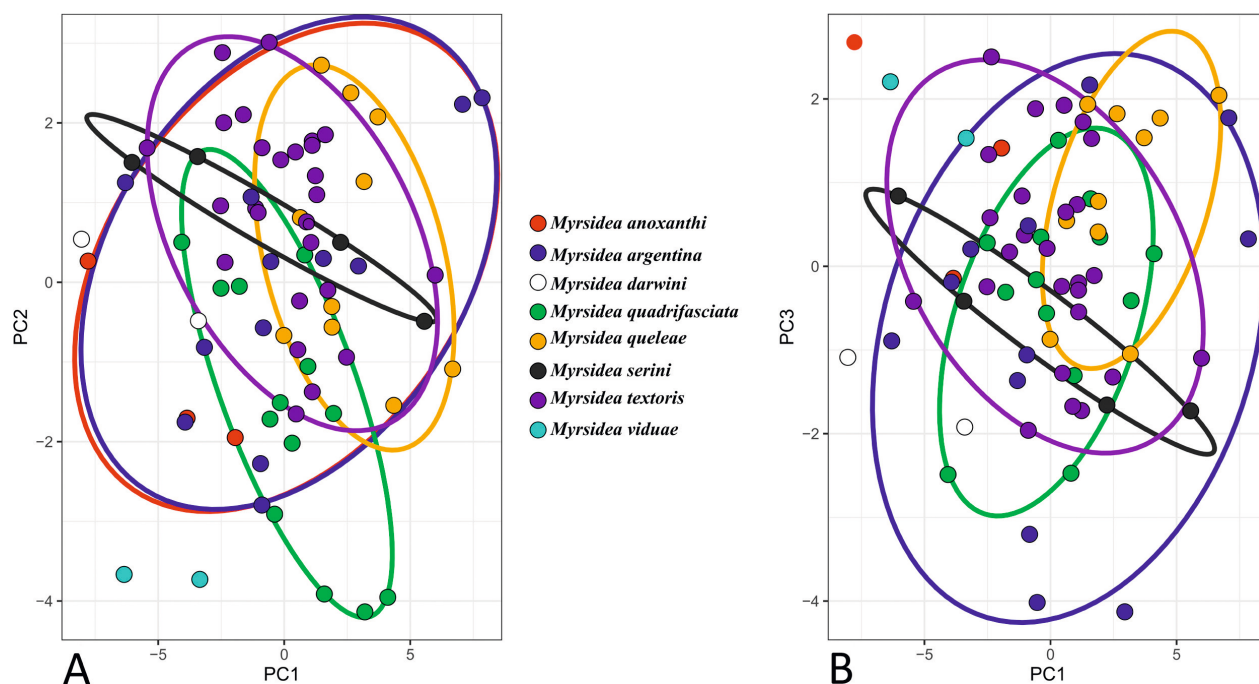
Figure 22. Principal Component Analyses (PCA) using 26 morphological traits of 43 males and 71 females. **A:** PC1 and PC2; **B:** PC1 and PC3. PC1 explains 44.36%, PC2 13.01% and PC3 9.37%.
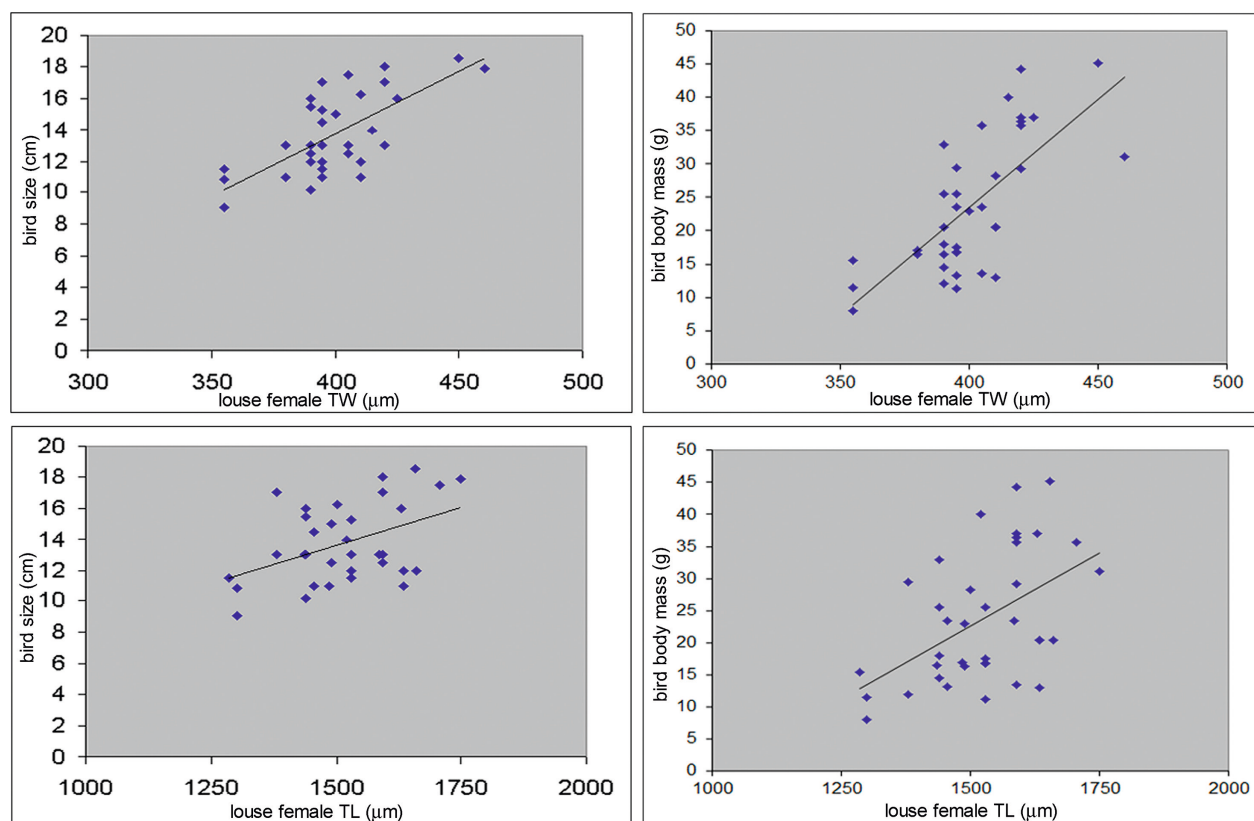
Figure 23. Host-parasite body size correlation. Birds are characterized by the body size in centimetres and body mass in grams. Lice are characterized by the female temple width (TW) and total length (TL) (source data in Table S1).

of louse female tergal setae (bird size in cm vs. louse female total number of tergal setae: R=0.2338, P=0.16; bird body mass in g vs. louse female total number of tergal setae: R=0.1486, P=0.38).

4. Discussion

4.1. *Myrsidea quadrifasciata*

Passer domesticus, the type host of *M. quadrifasciata*, is a widespread species. Its native range includes the Palearctic and Oriental Regions, but it was also introduced to the Nearctic and Neotropical Regions and the southern parts of the Afrotropical and Australasian Regions (Summers-Smith 2009). A total of six species of chewing lice were recorded on this host (Price et al. 2003) and according to our experience, *M. quadrifasciata* is the rarest and the least known species. There are only a few scarce reports about its occurrence (see Table 1), with no record out of its original range (Brown and Wilson 1975; Paterson et al. 1999; see also references in Table 1). The finding of a slide with *M. quadrifasciata* from *Passer domesticus* from Hawaii deposited in USNM (reported as *Myrsidea* sp. by Alicata et al. 1948) shows that this species was introduced out of its original range and that is why we can not exclude the possibility that it may also occur in other regions where its host has been introduced. It is interesting that all House Sparrows in Hawaii are believed to have descended from nine sparrows imported from New Zealand in 1871 (Caum 1933). But to date, no records of *Myrsidea* from this host have been reported from New Zealand (Paterson et al. 1999; Galloway 2005; Palma 2017), where House Sparrows were introduced from England sometime between 1862–1871 (Baker 1980). The hypothesis of its Palearctic-Oriental origin is supported by a slide with *M. quadrifasciata* from *Passer domesticus* from the USA (Mississippi, Tibbee) that is deposited in KCEM. On the other hand, the occurrence of *Myrsidea* from this species-complex on *Agelaius phoeniceus* from South Carolina deposited in USNM opens the possibility for the hypothesis that this species of *Myrsidea* may be common in the USA on icterid hosts and that *Myrsidea* on *P. domesticus* could be stragglers from these hosts.

Myrsidea quadrifasciata is prevalent in Asia with a prevalence 20–50% (Table 1). It is in accordance with Bush et al. (2009) who suggested that *Myrsidea* is probably adapted to more humid habitats, and thus, it is mainly present in the wetter subtropical and tropical areas (such as India and Thailand in our case). Scarce reports from Europe may be because the type host, *P. domesticus* probably spread spontaneously from Central and southern Asia to Europe thousands of years ago (Johnston and Klitz 1977; Šefrová and Laštůvka 2005). Probably thanks to that, some authors considered *M. quadrifasciata* as an alien species in Europe (Šefrová and Laštůvka 2005; Kenis and Roques 2010). We disagree with this idea. If *P. domesticus* spread to Europe thousands of years ago it

can be already considered as native species. Moreover, as we are reporting here, *M. quadrifasciata* also occurs on *P. montanus* that is native in Europe (Summers-Smith 2009).

4.2. Proposed synonymies

"*Myrsidea anoxanthi*". Price and Dalgleish (2007) placed *M. anoxanthi* into the "*serini* species group" and mentioned the following differences between this species and *M. serini*: 1) "Both sexes of *M. anoxanthi* are consistently smaller than those of *M. serini*, generally being at or below the lowest values of the ranges given by Klockenhoff (1984a)"; 2) "the females tend to have fewer abdominal setae, especially on the anterior tergites and sternites"; 3) "Males are not as clearly separated by these quantitative data, but the metanotal margin of *M. anoxanthi* has only 10 setae versus 11–15 for *M. serini*." (according to the setal counting system used in this paper, the last sentence should be changed as: *M. anoxanthi* has only 8 setae versus 9–13 for *M. serini*, see Table S3). In their remarks, Price and Dalgleish (2007) stated: „These two species are clearly closely related, but the new species quantitatively is sufficiently distinct to justify its recognition." When we compared morphometric characteristics of these species according to their original descriptions and all examined specimens, we can definitively say that there are no significant differences either in number of abdominal setae of female or metanotal marginal setae of male (see Tables S3, S4). Thus, the remaining differences between these two species are only in their dimensions (Tables S11, S12). It is also true for males collected from *Sporophila nigricollis* (a bird species related to known host of "*M. anoxanthi*", *Sporophila minuta*) that is at or below the lowest values of the ranges of "*M. anoxanthi*" given by Price and Dalgleish (2007). We believe that this difference can be affected by host size, because seedeaters of the genus *Sporophila* are the smallest hosts of *M. quadrifasciata* (Table S1). Harrison's Rule supports that smaller hosts harbour smaller lice (Johnson et al. 2005; Harnos et al. 2016). According to these data, we believe that *M. anoxanthi* is conspecific with *M. quadrifasciata*. Therefore, we place *M. anoxanthi* as a junior synonym of *M. quadrifasciata*.

"*Myrsidea argentina*". *Myrsidea argentina* was described by Kellogg (1906) on the basis of a single specimen, supposedly a female, from Argentina. On the basis of Kellogg's figure and description, Cicchino and Valim (2015) discussed morphological relationships between *M. argentina* and *M. serini*. They supported the note by Clay (1968) that Kellogg's specimen was most likely a third instar nymph, not a female (Cicchino and Valim 2015). After comparison of morphometric characteristics of our specimens with the description of *M. serini* by Cicchino and Valim (2015), we suggest that *M. argentina* is most likely conspecific with *M. serini*. As we synonymize *M. serini* with *M. quadrifasciata* (see below), we also place *M. argentina* as a junior synonym of latter species.

"*Myrsidea balati*". *Myrsidea balati* was described on the basis of two males and two females found on two of 434 examined *Passer montanus* by Macháček (1977a), who was able to compare them with one male of *Myrsidea quadrifasciata* that he found on one of 436 examined *Passer domesticus* in the Czech Republic. Unfortunately, the slides with holotype male (No. 2–320a) and allotype female (No. 2–320c) are probably lost (Vladimir Jansky, Slovak National Museum, Bratislava, Slovakia, pers. comm. 2017). There is only the second and last paratype male available in the collection of ZFMK.

Contrary to ischnoceran lice, where Macháček (1977b) correctly suggested that both species of sparrows share the same species of lice, *Brueelia cyclothorax* (Burmeister, 1838), *Philopterus fringillae* (Scopoli, 1772) and *Sturnidoecus ruficeps* (Nitzsch, 1866), in the case of *Myrsidea*, unfortunately he was wrong. As main diagnostic characteristics of *M. balati*, he used the ratio of lengths of setae in asters, head ratio and total length, and he compared only three males. When we compared our examined specimens, we found that all aforementioned characteristics of *Myrsidea* from both species of sparrows overlap. Since all other characters are almost identical (Tables S3–S12), we place *M. balati* as a junior synonym of *M. quadrifasciata*. It is also in accordance with Touleshkov (1962), who mentioned *M. quadrifasciata* from *Passer montanus* from Bulgaria.

"*Myrsidea darwini*". Palma and Price (2010) placed *M. darwini* into the "*serini* species group" and mentioned that it can be separated from the three species in that group (*M. anoxanthi*, *M. major* and *M. serini*) by 1) having "fewer metanotal and abdominal setae"; 2) "the relative length of the postspiracular setae"; and 3) "details of the male genital sac sclerite: compare fig. 3 (in Palma and Price 2010) with fig. 2B in Klockenhoff (1984a) for *Myrsidea serini* (Seguy, 1944), and fig. 44 in Price and Dalgleish (2007) for *Myrsidea anoxanthi* Price and Dalgleish, 2007."

When we compared morphometric characteristics of these species according to their original descriptions and all examined specimens, there are no more significant differences either in number of abdominal setae of both sexes or in the relative length of the postspiracular setae (see Tables S3–S12). Slight differences of the male genital sac sclerites mentioned by Palma and Price (2010) may be caused by distortion of this tiny structure. When we compare drawings of male genital sac sclerites in the original descriptions or redescriptions, we can see variability in their shape even in the case of different males from the same host (Figs 4–18). The best example of this is a male from *Agelaoides badius* from Paraguay (Fig. 8), where we can see differences even between the left and right sides of the single sclerite. Therefore, the only unique character is the small number of metanotal setae of the male (Table S4) and slight differences in dimensions (Table S12). According to these data we believe that *M. darwini* is conspecific with *M. quadrifasciata*. Therefore, we place *M. darwini* as a junior synonym of *M. quadrifasciata*.

"*Myrsidea major*". Piaget (1880) gave only a short description of this species based on 16 females and 13 males. Later Thompson (1937), in his review of Piaget's collection, referred to the presence of only two slides with five males of *M. quadrifasciata* var. *major*. He also stated: „Females are mentioned in the original description, but there are no females in the collection." Contrary to this, Clay (1949a) indicated that there are two slides (No. 841 and 842) with six females. She also designated the female on slide 842 as the lectotype and other females as paratypes. All six females were examined by Price and Dalgleish (2007). These authors stated that this species is: "morphologically closest to *M. serini*, differing principally in having longer postspiracular setae on tergites V–VII, somewhat greater total length, and fewer setae on tergite VII. While these differences are not profound, we have opted to continue to recognize this as a valid species pending additional collections from the type host and the study of male specimens." When we compared characteristics of *M. major* by Price and Dalgleish (2007) with our examined specimens of *M. quadrifasciata*, we found that all aforementioned characteristics overlap. Since all other characters are almost identical (Tables S3–S11), we place *M. major* as a junior synonym of *M. quadrifasciata*.

"*Myrsidea queleae*". This species was described by Tendeiro (1964) from *Quelea quelea* from the family Ploceidae from South Africa. Later it was redescribed by Klockenhoff (1984b), who also provided statistical evaluation of populations of "*M. queleae*", "*M. serini*" and "*M. textoris*" (see discussion about subspecies concept below).

"*Myrsidea serini*". This species was described by Séguy (1944) from *Serinus serinus* from the family Fringillidae from France. Later, it was redescribed by Klockenhoff (1984a), Price and Dalgleish (2007), and Cicchino and Valim (2015). Descriptions and illustrations of both sexes presented by these authors are almost completely consistent with that of *M. quadrifasciata* (Tables S3–S12), so we place *M. serini* as a junior synonym of this species. As stated by Price and Dalgleish (2007) and Cicchino and Valim (2015) "*M. serini*" represents: "atypical species, considering the host distribution patterns presented in *Myrsidea* genus, due to its occurrence" on eight bird species from families Emberizidae, Fringillidae and Icteridae. Since the only practical manner to deal with the taxonomy of such a large genus as *Myrsidea* was, and still is, to treat lice from each host family as a unit, it is easy to overlook similarity of *Myrsidea* parasitizing hosts from different families and regions. We expect that a more complex review of the genus will reveal more similar cases.

"*Myrsidea textoris*". This species was described by Klockenhoff (1984b) from *Ploceus cucullatus* from the family Ploceidae from Ghana. Klockenhoff (1984b) also provided statistical evaluation of populations of "*M. queleae*", "*M. serini*" and "*M. textoris*" (see discussion about subspecies concept below).

"*Myrsidea viduae*". This species was described on the basis of only two females found on *Vidua macroura* from Sao Tomé e Principe by Tendeiro (1993). Since all characters are almost identical with those of *M. quadrifasciata* (Tables S3–S11), and we found also low genetic differentiation, we place *M. viduae* as a junior synonym of *M. quadrifasciata*.

Myrsidea from *Microspingus melanoleucus*. We found only one female of *Myrsidea* on this host in Paraguay (see material examined). At the same day when we collected this female on *Microspingus melanoleucus* (bird no. PG359), we also examined one *Agelaoides badius* (bird no. PG357) with a few *Myrsidea* (reported as "*M. serini*" by Kolencik et al. 2016). Therefore, it is most likely that this is the result of contamination while collecting. On the other hand, we can not completely exclude that this case represents an example of natural host-switching because as we have shown, *M. quadrifasciata* also occurs on birds from the family Thraupidae. As shown by Weckstein (2004) or Kounek et al. (2011), host-switching between different host species is possible at one location between birds with similar behaviour and ecology.

4.2. Subspecies concept

Klockenhoff (1984b) provided statistical evaluation of populations of "*M. queleae*", "*M. serini*" and "*M. textoris*". He found significant differences between these populations and he supposed that these differences show interspecific rather than intraspecific variation. Thus, he considered these taxa separate species. When we compared our material of "*M. queleae*" with Klockenhoff's data, we found only few differences in setal counts on both sexes (Tables S13, S14). Since we have material from the same host species as Klockenhoff (*Quelea cardinalis* and *Q. quelea*), we believe these differences are related to intraspecific morphological variability in the species. Unfortunately, Klockenhoff (1984b) did not provide statistical data for measurements of this species, so we could not evaluate them. Similarly, differences in some setal counts for our specimens of "*M. textoris*" can, by our opinion, be attributed to intraspecific variation. Beside the type host (*Ploceus cucullatus*), we examined *Myrsidea* from five other Afrotropical ploceids (*Euplectes franciscanus*, *E. jacksoni*, *E. progne*, *Ploceus madagascariensis* and *P. nigricollis*) and one Asian species (*Ploceus philippinus*). Different sizes of these hosts correlated with different sizes of their *Myrsidea* (Fig. 23, Table S1). This observation, known as as Harrison's Rule, is well known within chewing lice and has been documented also in a wide variety of other parasitic organisms (Harnos et al. 2016). This biological rule can also explain the observed differences in measurements of our and Klockenhoff's material. Contrary to "*M. queleae*" and "*M. textoris*", we found more significant differences between our samples of "*M. serini*" from Neotropical hosts and data provided by Klockenhoff (1984b) for "*M. serini*" from hosts from the Palearctic Region. Similarly,

when we compared characteristics of *M. quadrifasciata* from *Passer domesticus* and *P. montanus*, we found significant differences between specimens of *Myrsidea* from these hosts and specimens from all aforementioned taxa. Recorded differences show the following pattern:

In cases where there is a larger number of examined females, such as for *M. quadrifasciata* from *Passer montanus* (n=11) or "*M. serini*" reported by Klockenhoff (1984a) (n=35), we can find higher variability in the number of metanotal setae, 8–13 and 7–13, respectively (Table S3). We can see the same pattern in the case of males of "*M. serini*" (n=25), where Klockenhoff (1984a) reported 9–13 metanotal setae. One exception is "*M. darwini*" from Galápagos Islands with uniformly only 6 metanotal setae in both sexes (n=22 females and 7 males). In general, in the case of "*M. darwini*", there is also a tendency to a smaller number of setae on tergites. Together with "*M. anoxanthi*" from the Neotropics and "*M. viduae*" from Africa, it lies at the lower limit of the range of tergal setae (Tables S3 and S4), and this is true for both sexes (the exception is "*M. viduae*" where only females are known, and for "*Myrsidea* cf. *anoxanthi*" from *Sporophila nigricollis*, where only one male is known).

On the other hand, there are "*M. serini*" from *Agelasticus thilius petersii* from Argentina and "*M. queleae*" from Africa with their numbers of tergal setae at the upper limit of the range (Tables S3 and S4). Moreover, females of "*M. serini*" from *Agelasticus thilius petersii* differ from all examined specimens by 8 setae on tergite VIII (vs. 3–6 setae; Table S3). Due to this fact, we have doubts as to whether these individuals really represent the species under consideration. More specimens from this host are needed to resolve this problem.

In the case of males, the highest numbers of tergal setae are recorded mainly on males of "*M. queleae*" and "*M. textoris*" from Africa. The most conspicuous differences are visible on tergite VIII: while specimens from Neotropical ("*M. anoxanthi*", "*M. darwini*" and "*M. serini*") and Palearctic ("*M. balati*" and "*M. quadrifasciata*") have 4–8 setae (one exception is again "*M. serini*" from *Agelasticus thilius petersii* with 11 setae), specimens from Africa ("*M. queleae*" and "*M. textoris*") have 8–14 setae (Table S4). Conversely, "*M. serini*" from Palearctic shows wide range of number of setae (6–12 setae) that overlap range of setae found on both aforementioned examples. Unfortunately, Klockenhoff (1984a) did not mention characteristics separately for particular hosts, so it is necessary to re-examine his material and re-evaluate these parameters according to hosts.

When we compare sternal chaetotaxy, we see a similar pattern as for tergites: 1) Neotropical specimens lie at the lower limit of the range of these setae; 2) African specimens, in this case including specimens from sparrows ("*M. balati*" and "*M. quadrifasciata*"), lie at the upper limit of the range of these setae; and 3) cases where there are larger numbers of examined specimens, i.e. "*M. serini*" reported by Klockenhoff (1984a) (n=35), and "*M. textoris*" reported by Klockenhoff (1984b) (n=28), which show high variability over almost the entire range of re-

corded values. So what is missing for other taxa above is a large range of specimens, which will likely support highly variable morphology in terms of number of setae.

Postspiracular setae show the same pattern in their ratio of lengths, with high variability in the lengths of these setae on a particular segment. In general, there are long to extremely long postspiracular setae on II, IV, VII and VIII and shorter with variable length setae on I, and shortest on III, V and VI (Tables S9 and S10).

Concerning different body sizes, in general, "*M. anoxanthi*" and "*M. viduae*" are represented by the smallest individuals (for example, TW of females 0.34–0.37 and TW of males 0.33–0.34), while *Myrsidea* from the Icteridae are represented by the largest ones (for example TW of females 0.44–0.46 and TW of males 0.40–0.42). Similarly, as in the case of setal counts, "*M. serini*" reported by Klockenhoff (1984a) for 35 individuals from five hosts of different size show the highest variability in measurements with values overlapping both of the mentioned limits (for example TW of females 0.36–0.43 and TW of males 0.34–0.39) (Tables S11, S12). Contrary to these data, there is no correlation between host size and total number of tergal setae in females.

Observing the PCA plots for PC1 and PC2 and the PC1 and PC3 revealed the overlapping of all examined groups of *Myrsidea*, supporting that all analysed individuals of *M. quadrifasciata* complex form one morphological group with a few outliers.

Taking into consideration all these parameters, host associations and geographic distribution, we suggest that the only way to deal with these taxa is to follow the concept of subspecies. Palma and Price (2010) applied it to two morphologically distinct populations of *Myrsidea nesomimi* from the Galápagos Islands, which were later confirmed by genetic data by Štefka et al. (2011). Štefka et al. (2011) reported that *M. nesomimi* from one locality or from a few close ones showed minimal genetic differences (0.1–0.6%), while lice of the two subspecies from different hosts and distant localities showed increasing genetic variability (4.5–5.1%). Our molecular data support these subspecies concepts, since we found divergences of 0.0–6.6% among the newly obtained sequences of *COI* from six *Myrsidea* samples examined in this study (Table 2: lines 1–3, 7–9), and up to 9.3% inside the whole proposed *M. quadrifasciata* complex (Table 2), while the interspecific genetic distance from other species always exceeded 13%. Even species collected from other birds belonging to families in which lice from the *M. quadrifasciata* complex occur (e.g., Ploceidae) ranged over 20% in distance (Table 2). It is also in accordance with Kolencik et al. (2017), who proposed a limit of interspecific genetic diversity at 12% divergence. Similarly, concerning the *EF-1α* gene, all our examined *Myrsidea* sequences were identical and the divergence within the proposed species did not exceed 0.3% (Table 2), while sequences for other species showed divergence over 5%. We propose these low divergences are a limit of interspecific genetic diversity in this gene.

Because for most *Myrsidea* species, only a relatively short sequence of the *COI* gene is available, all conclu-

sions inferred from the phylogenetic analyses are necessarily limited; no deeper phylogenetic conclusions can be reached and we can not speculate about the definitive position of the *M. quadrifasciata* complex in context of the genus *Myrsidea*. This necessary caution is further supported by relatively low bootstrap supports in the majority of tree branches (see Figs 21, S1). Nevertheless, it is true for both trees that our *M. quadrifasciata* sequences always group together, which supports the hypothesis of species identity of the proposed *M. quadrifasciata* complex.

Klockenhoff (1984b) discussed relationships between species from the "*serini* species group" (namely "*M. queleae*", "*M. serini*" and "*M. textoris*") and three other species of *Myrsidea* from hosts from the family Ploceidae (*M. bubalornithis* Klockenhoff, 1984, *M. eisentrauti* Klockenhoff, 1982 and *M. ledgeri* Klockenhoff, 1984). Our results corroborate with Klockenhoff's (1984b) opinion that none of them belonged to the "*serini* species group", i.e., the *M. quadrifasciata* complex presented in this study. While *M. eisentrauti* and *M. ledgeri* have a completely different type of male genital sac sclerite compared with *M. quadrifasciata*, *M. bubalornithis* share the same one. Despite this morphological similarity, the net average p-distances between *M. bubalornithis* and *M. quadrifasciata* are 14.3–16.9%. This genetic divergence allows us to exclude this species from the *M. quadrifasciata* complex.

The subspecies concept we are using here is accepted for other chewing lice, for example lice from the genera *Gyropus* (Gyropidae), *Actornithophilus*, *Dennyus*, *Menacanthus* (Menoponidae), *Lunaceps*, *Saemundssonia* (Philopteridae), *Geomydoecus*, *Procaviphilus* (Trichodectidae) (Price et al. 2003; Mey 2004). Our results also demonstrate the importance of geography in multi-host, polyxenous parasites. We suggest that overlapping distribution (sympatry) and the same habitat preferences (syntopy) of the hosts seem to be the most important factors maintaining genetic connectivity within geographic areas, because they provide a good opportunity for host-switching that can lead to establishment of naturally occurring populations of the same louse species on two or more distantly related hosts.

We propose the following subspecies (a list of their hosts and their geographic distributions is given in Table 3):

Palearctic Region:
M. q. quadrifasciata (Piaget, 1880) comb. nov.
M. q. serini (Séguy, 1944) comb. nov.

Paleotropic Region:
M. q. queleae Tendeiro, 1964 comb. nov.
M. q. textoris Klockenhoff, 1984 comb. nov.
M. q. viduae Tendeiro, 1993 comb. nov.

Neotropical Region:
M. q. anoxanthi Price and Dalgleish, 2007 comb. nov.
M. q. argentina (Kellogg, 1906) comb. nov.
M. q. darwini Palma and Price, 2010 comb. nov.

Table 3. List of hosts of *Myrsidea quadrifasciata* and their geographic distribution.

Hosts family Host species	Location	References
Myrsidea quadrifasciata anoxanthi		
Thraupidae		
Loxipasser anoxanthus (Gosse, 1847)	Jamaica	Price and Dalgleish (2007)
Sporophila minuta (Linnaeus, 1758)	Venezuela	Price and Dalgleish (2007)
Sporophila nigricollis (Vieillot, 1823)	Peru	present study
Myrsidea quadrifasciata argentina		
Fringillidae		
Spinus barbatus (Molina, 1782)	Chile	Cicchino and Valim (2015)
Spinus magellanicus (Vieillot, 1805)	Peru	present study
Icteridae		
Agelaioides badius badius (Vieillot, 1819)	Argentina	Cicchino and Valim (2015)
<< ,, ,, ,, >>	Paraguay	Kolencik et al. (2016)
Agelasticus thilius petersii (Laubmann, 1934)	Argentina	Cicchino and Valim (2015)
Agelaius phoeniceus (Linnaeus, 1766)	USA: South Carolina	present study
Thraupidae		
Microspingus melanoleucus (d'Orbigny and Lafresnaye, 1837)	Paraguay	present study
Myrsidea quadrifasciata darwini		
Thraupidae		
Camarhynchus psittacula Gould, 1837	Galápagos Islands	Palma and Price (2010)
Geospiza fuliginosa Gould, 1837	Galápagos Islands	Palma and Price (2010)
Geospiza magnirostris Gould, 1837	Galápagos Islands	Palma and Price (2010)
Myrsidea quadrifasciata quadrifasciata		
Emberizidae		
Plectrophenax nivalis (Linnaeus, 1758)	no location data	Piaget (1880), Price and Dalgleish (2007)
Passeridae		
Passer domesticus (Linnaeus, 1758)	Netherlands?	Piaget (1880)
<< ,, ,, ,, >>	Azerbaijan	Gadzhiev and Mustafaeva (1981)
<< ,, ,, ,, >>	Bulgaria	Touleshkov (1974)
<< ,, ,, ,, >>	Czech Republic	Macháček (1977a)
<< ,, ,, ,, >>	England	Thompson (1957), present study
<< ,, ,, ,, >>	France	Séguy (1944)
<< ,, ,, ,, >>	Germany	Mey (2004)
<< ,, ,, ,, >>	Hungary?	Fauna Europaea (www.fauna-eu.org) - but not confirmed by Vas et al. (2012)
<< ,, ,, ,, >>	Italy	Manilla (2000)
<< ,, ,, ,, >>	India	Saxena et al. (2007)
<< ,, ,, ,, >>	Pakistan	Lakshminarayana (1979)
<< ,, ,, ,, >>	Sweden	present study (Daniel Gustafsson, pers. comm.)
<< ,, ,, ,, >>	USA, Mississippi	present study
<< ,, ,, ,, >>	USA, Hawaii	Alicata et al. (1948), present study
Passer montanus (Linnaeus, 1758)	Czech Republic	Macháček (1977a), present study
<< ,, ,, ,, >>	Bulgaria	Touleshkov (1962)
<< ,, ,, ,, >>	Hungary	present study
<< ,, ,, ,, >>	Slovakia	present study
<< ,, ,, ,, >>	Romania	Adam (2007), Adam et al. (2009)
<< ,, ,, ,, >>	Thailand	Boonkong and Meckvichai (1987), McClure and Ratanaworabhan (1973), present study
<< ,, ,, ,, >>	W. Java	present study
Myrsidea quadrifasciata queleae		
Ploceidae		
Quelea cardinalis (Hartlaub, 1880)	Botswana	Tendeiro (1964)
Quelea quelea aethiopica (Sundevall, 1850)	Kenya, Sudan,	Klockenhoff (1984b)
Quelea quelea quelea (Linnaeus, 1758)	Senegal	Sychra et al. (2010)
<< ,, ,, ,, >>	Cameroon	present study
Quelea quelea lathami (Smith)	Congo, South Africa, Zambia	Tendeiro (1964), Klockenhoff (1984b), Halajian et al. (2014)

Hosts family Host species	Location	References
Passer luteus (Lichtenstein M.H.C., 1823)* – probably stragglers	Senegal	present study
Myrsidea quadrifasciata serini		
Emberizidae		
Emberiza citrinella caliginosa Clancey, 1940	New Zealand	Klockenhoff (1984a), Price and Dalgleish (2007)
Fringillidae		
Carduelis carduelis britannica (Hartert, 1903)	New Zealand	Klockenhoff (1984a)
Carduelis carduelis parva Tschusi, 1901	Spain	Klockenhoff (1984a)
Chloris chloris chloris (Linnaeus, 1758)	New Zealand	Klockenhoff (1984a)
Serinus canaria (Linnaeus, 1758) – domesticated form	England, New Zealand	Klockenhoff (1984a)
<< ,, ,, ,, >>	Netherlands	RMNH.INS.UT.479; No. B01/1887; 12-09-2001 (parasites_collection_utrecht_naturalis.xls)
<< ,, ,, ,, >>	Czech Republic	present study
Serinus serinus (Linnaeus, 1766)	France	Séguy (1944)
<< ,, ,, ,, >>	Morocco	Klockenhoff (1984a)
<< ,, ,, ,, >>	Romania	Negru (1963, 1965)
Myrsidea quadrifasciata textoris		
Ploceidae		
Euplectes franciscanus (Isert, 1789)	Senegal	present study
Euplectes jacksoni (Sharpe, 1891)	Kenya	present study
Euplectes orix (Linnaeus, 1758)	South Africa	Lindholm et al. (1998), present study
Euplectes progne delamerei (Shelley, 1903)	Kenya	present study
Foudia madagascariensis (Linnaeus, 1766)	Madagascar	present study
Ploceus capensis (Linnaeus, 1766)	South Africa, Mozambique	Klockenhoff (1984b)
Ploceus cucullatus cucullatus (Müller, 1776)	Ghana, Senegal	Klockenhoff (1984b), present study
Ploceus cucullatus nigriceps (Layard, 1867)	South Africa Mozambique	Klockenhoff (1984b) present study
Ploceus cucullatus spilonotus Vigors, 1831	South Africa	Klockenhoff (1984b)
Ploceus intermedius cabanisii (W.K.H. Peters, 1868)	South Africa	Linholm et al. (1998), Sychra et al. (2014)
Ploceus nigricollis brachypterus Swainson, 1837	Cameroon	present study
Ploceus ocularis A. Smith, 1828	South Africa	Takano et al. (2019)
Ploceus philippinus (Linnaeus, 1766)	India, Thailand	present study
Ploceus velatus tahatali A. Smith, 1836	South Africa	Halajian et al. (2012), Sychra et al. (2014)
Ploceus velatus velatus (Vieillot, 1819)	South Africa, Botswana	Klockenhoff (1984b)
Myrsidea quadrifasciata viduae		
Viduidae		
Vidua macroura (Pallas, 1764)	Sao Tomé e Príncipe	Tendeiro (1993)
<< ,, ,, ,, >>	Cameroon	Balakrishnan and Sorenson (2006)

4.   Conclusions

Our results revealed an interesting case of a cosmopolitan, polyxenous species of *Myrsidea*. *Myrsidea quadrifasciata* is unique within the genus that primarily includes, according to our knowledge, highly host-specific lice. This is similar to the case of *Menacanthus eurysternus* (Burmeister, 1838), another widespread species closely related to host-specific *Menacanthus* species. Despite the fact that this cosmopolitan host generalist has been recorded from almost 170 species of passerines belonging to 20 families, it possesses a relatively low level of differentiation, with sequences (*COI* and *EF-1α*) differing only in approximately 4% of nucleotide positions (Martinu et

al. 2015). Similarly as in the case of *M. eurysternus* there are some general features that may predispose also *Myrsidea* to maintain a wider host spectrum. They are agile lice capable of moving quickly across the skin of its host, and they can leave their host when actively looking for a new one (Price et al. 2003; pers. obs.). As we showed *M. quadrifasciata* is found on hosts that allow for inter-specific transmission such as colonial nesters, birds which often build intricately woven nests and birds that form mixed-species feeding flocks. As stated Martinu et al. (2015) there is no common biological pattern apparent for all hosts of *M. eurysternus*. The same is true for *M. quadrifasciata*. We can only speculate that the ecological proximity of hosts can explain the transmission of lice through active dispersal to a new host after escaping

preening. On the other hand, *P. domesticus*, a type host of *M. quadrifasciata*, has secondary cosmopolitan distribution, because it was introduced by human almost around the world. If this is the primary reason for the cosmopolitan distribution of *M. quadrifasciata* or if its distribution is naturally cosmopolitan thanks to host switching between phylogenetically unrelated hosts is the question that needs another research, especially with more comprehensive genetic data.

In our study, we demonstrated the importance of a comprehensive approach in taxonomy of such a large genus as *Myrsidea*. Since the only practical manner to deal with this genus was, and still it is, to treat lice from each host family as a unit it is easy to overlook similarity of *Myrsidea* parasitizing hosts from different families and regions. We expect that more complex review not only in this genus, but other genera of lice, will reveal additional similar cases.

5. Acknowledgements

6. References

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Supplementary material 1

File 1

Authors: Sychra et al. (2021)

Data type: .xlsx

Explanation note: Table S1. List of hosts of *Myrsidea quadrifasciata*, their geographic distribution, body size (cm) and body mass (g) with data about louse female temple width (TW), total length (TL), and total number of tergal setae.

Link: https://doi.org/10.3897/asp.79.e63975.suppl1

Supplementary material 2

File 2

Authors: Sychra et al. (2021)

Data type: .xlsx

Explanation note: Table S2. List of *COI* and *EF-1α* sequences included in the phylogenetic analyses in this study. 64 samples with A/Ns for both markers were included in the concatenated tree; 186 samples, i.e. all samples minus four noted as „concatenated tree only", were included in the *COI* tree.

Link: https://doi.org/10.3897/asp.79.e63975.suppl2

Supplementary material 3

File 3

Authors: Sychra et al. (2021)

Data type: .docx

Explanation note: Tables S3–S16. Morphometric characteristics: number of setae on gula, metanotum, metasternal plate and tergites of **female** of *Myrsidea quadrifasciata* from different hosts (T=tergites). — **Table S4.** Morphometric characteristics: number of setae on gula, metanotum, metasternal plate and terg- ites of **male** of *Myrsidea quadrifasciata* from different hosts (T=tergites). — **Table S5.** Morphometric characteristics: number of setae on sternites and anal fringe of **female** of *Myrsidea quadrifasciata* from different hosts (S=sternites; marg.=marginal; m.a.=medioanterior; AFD=anal fringe dorsal; AFV=anal fringe ventral). — **Table S6.** Morphometric characteristics: number of setae on sternites and ventral terminalia of **male** of *Myrsidea quadrifasciata* from different hosts (S=sternites; marg.=marginal; m.a.=medioanterior). — **Table S7.** Morphometric characteristics: number of setae on pleurites of **female** of *Myrsidea quadrifasciata* from different hosts (P=pleurites). — **Table S8.** Morphometric characteristics: number of setae on pleurites of **male** of *Myrsidea quadrifasciata* from different hosts (P=pleurites). — **Table S9.** Morphometric characteristics: length of dorsal head setae 10, 11 and postspiracular setae (in mm) of **female** of *Myrsidea quadrifasciata* from different hosts (DHS=dorsal head seta; PsS=postspiracular seta). — **Table S10.** Morphometric characteristics: length of dorsal head setae 10, 11 and postspiracular setae (in mm) of **male** of *Myrsidea quadrifasciata* from different hosts (DHS=dorsal head seta; PsS=postspiracular seta). — **Table S11.** Morphometric characteristics: dimensions (in mm) of **female** of *Myrsidea quadrifasciata* from different hosts (TW=temple width; POW=preocular width; HL=head length at midline; PW=prothorax width; MW=metathorax width; AWIV=abdomen width at level of segment IV; ANW=anus width; TL=total length). — **Table S12.** Morphometric characteristics: dimensions (in mm) of **male** of *Myrsidea quadrifasciata* from different hosts (TW=temple width; POW=preocular width; HL=head length at midline; PW=prothorax width; MW=metathorax width; AWIV=abdomen width at level of segment IV; GW=male genitalia width; GL=male genitalia length; ParL=paramere length; GSL=genital sac sclerite length.; TL=total length). — **Table S13.** Comparison of morphometric characteristics of **female** of *Myrsidea quadrifasciata* from different subspecies. — ***Abbreviations***: M=metanotal posterior setae; S=sternal setae; T=tergal setae. — ***Symbols***: After each comparison of our data with those mentioned by Klockenhoff (1984b) statistically significant differences are marked as: * P < 0.05; ** P < 0.01; *** P < 0.001. — **Table S14.** Comparison of measurements of **female** of *Myrsidea quadrifasciata* from different subspecies (in mm). — ***Symbols***: After each comparison of our data with those mentioned by Klockenhoff (1984b) statistically significant differences are marked as: * P < 0.05; ** P < 0.01; *** P < 0.001 (data used by Klockenhoff 1984b for *M. queleae* are not available). — **Table S15.** Comparison of morphometric characteristics of **male** of *Myrsidea quadrifasciata* from different subspecies. — ***Abbreviations***: M=metanotal posterior setae; S=sternal setae; T=tergal setae. — ***Symbols***: After each comparison of our data with those mentioned by Klockenhoff (1984b) statistically significant differences are marked as: * P < 0.05; ** P < 0.01; *** P < 0.001. — **Table S16.** Comparison

of measurements of **male** of *Myrsidea quadrifasciata* from different subspecies (in mm). — ***Symbols***: After each comparison of our data with those mentioned by Klockenhoff (1984b) statistically significant differences are marked as: * P < 0.05; ** P < 0.01; *** P < 0.001 (data used by Klockenhoff 1984b for *M. queleae* are not available).

Link: https://doi.org/10.3897/asp.79.e63975.suppl3

Supplementary material 4

File 4

Authors: Sychra et al. (2021)
Data type: .pdf
Explanation note: Figure S1. Phylogenetic tree of the *Myrsidea* species based on partial *COI* sequences. The tree was inferred using the maximum likelihood method based on the GTR+G+I model. The tree with the highest log likelihood is shown. Bootstrap support is shown next to the branches (values < 50% not shown). The tree is drawn to scale, with branch lengths measured in the number of substitutions per site. Samples of *M. quadrifasciata* discussed in the present paper are in **bold** type. — ***Colours***: blue – samples from Nearctic Region; light blue – samples from Palearctic Region; green – samples from Ethiopian Region; red – samples from Neotropical Region; violet – samples from Oriental Region.

Link: https://doi.org/10.3897/asp.79.e63975.suppl4