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

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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 quelea 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 distribution: Palearctic Region: M. q. quadrifasciata and M. q. serini, Neotropical Region: M. q. anoxanthi, M. q. argentina, M. q. darwini, Paleotropic Region: M. q. quelea, M. q. textoris and M. q. viduae.

Keywords

Chewing louse, polyxenous, geographic distribution, host specificity, morphometry, parasite

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 (Martín et al. 2015). Also the fact that host switching certainly happens naturally and more often than we expected (Weckstein 2004; Martín 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 species 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 _Agelaioides 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 amlyccean 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 cabanisi_ (W.K.H. Peters, 1868) and _Ploceus velatus tahalati_ 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 quadrispathia_ (Piaget, 1880); 7) _Myrsidea queleae_ Tendeiro, 1964; 8) _M. serini_; 9) _M. textoris_; and 10) _Myrsidea viduas_ 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. quadrispathia_ (Piaget, 1880) as its nominate species and we propose to rename this species group as the “_M. quadrispathia_ complex”.

The aims of this paper are to: 1) re-describe _M. quadrispathia_; 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. quadrispathia_ and designate 8 subspecies; 5) present new host records for _M. quadrispathia_; 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 post-terolateral 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; Tenodeiro 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 millimeters. 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. viduæ. 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, Museu 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 Köning, 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 KF113129), M. serini ex Agelaioides bidus from Paraguay (A/N KF113130), Myrsidea sp. ex Microspingus melanoleucus (A/N MT526017), M. textoris ex Placeus intermedius and Placeus velatus from South Africa (A/N KF768813–KJ768815), 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-1a) gene were obtained from Myrsidea sp. ex Spinus magellanicus from Peru (A/N MT515729), M. serini ex Agelaioides bidus from Paraguay (A/N MT515731), Myrsidea sp. ex Microspingus melanoleucus (A/N MT517355), 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-1a 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 boralis 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

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

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

Menopen 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).

Menopen argentinum 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).

Menopen sereri Séguy, 1944: 80, fig. 84. Type host: Serinus serinus (Linnaeus, 1766). New synonymy.

Myrsidea sereri (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 1–3), Kolencik et al. (2016: 245).

Liquidea sereri (Séguy, 1944): Zlotoryzycka (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 balatii Macháček, 1977a: 1, figs 1a, b, 4, 7–8. Type host: Paser montanus (Linnaeus, 1758). New synonymy.

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

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

Myrsidea testoris 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 macrorra (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. sereri-Artengruppe” (Klockenhoff 1984b), or serini species-group (Price and Dalgleish 2007). It is well characterized with 1) weakly developed hypophyrygeal 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 medio-posterior 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 montanu*us – 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; metapleurites 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 divided. Metanotum not enlarged, with 6–14 marginal setae between asters, 4–16 medioanterior setae; metasternal plate with 4–6 setae; metapleurites I–III, with small median gap in row of 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, 3–5; II, 5–8; III, 5–9; IV, 5–7; V, 4–6; 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, 3–4 in each aster, aster setae length: *sI*, 0.07–0.08; *sII*, 0.04–0.06; *sIII*, 0.03–0.04; *sIV*, 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; *PMW*, 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 seta 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). Length of inner posterior seta of last tergum, 0.07–0.08; short lateral marginal seta of last segment, 0.03–0.04; with 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 seta: 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: *sI*, 0.07–0.08; *sII*, 0.04–0.06; *sIII*, 0.03–0.04; *sIV*, 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; *PMW*, 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.

**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.i.–8.iii.1947, J. Alicata leg. (USNM: Lot 47-4795, vial 2). — *Ex Passer montanus* (Passeridae): 1♂ (paratype of *M. balatii*), Czech Republic, Nasey, 9.xii.1973, P. Macháček leg. (ZFMK: 1986/15, 1♂, Czech Republic, Jinačovice (49°15′N 16°31′E), 13.i.2006, O. Sychra and I. Litarak leg. (MMBC), 1♂, Czech Republic, Moravské Knínice (49°17′N 16°31′E), 1♀, 8.xi.2009, O. Sychra and I. Litarak leg. (MMBC), 1♀, Czech Republic, Kardašova Řečice, 19.vii.1938, K. Pfeiger leg. (SNMB); 1♂, Hungary, Nagykanizsa, 28.vii.1952, Balát coll. (MMBC: B185), 1♀, Hungary, Bajca (Zala m.), 19.iv.1953, Balát coll. (MMBC: C579); 1♀, I. Literak leg. *Slovakia*, Gabčíkovská II. 27.vii.1953, Balát coll. (MMBC: 1380), 2♂, 1♀, *Slovakia*, Gbelye (47°51′N 18°30′E), 10.vii.2019, O. Sychra and L. Olejískova leg.; 3♂, 3♀, Thailand, San Sai, Ban Pong, 16.ii.1962, Kittí Thonglongya leg. (KCEM: 8183–85); 1♀, W. Java, Bogor, 8.xii.1968 (KCEM: 9E 0414); 2♂, no data (NHML: 840). — *Ex Agelaius phoeniceus* (Linnaeus, 1766) (Icteridae): 9♂, 3♀, USA: South Carolina, Charleston,
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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.1994, A. Lindholm leg. (slide no. 57A, 106A). — Ex Euplectes francescianus (Iset, 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 lutetius (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 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.
— 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*, Zambezi, 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 *Quelea quelea* aethiopica (Sundevall, 1850) (Ploceidae): 1♂, 1♀, *Southern Rhodesia* (now *Zimbabwe*), Matabeleland, 30.iii.1952 (NHML: B.M.1980–40, coll.691); 1♂, 1♀, *Transvaal* (now *South Africa*), Nr. Komatiport, 1.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, Halajan leg. (MMBC). — Ex *Ploceus velatus taiti* 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. quinquecincta*), Bechuanaaland (now *Botswana*), Mahabe, 6.x.1952, F. Zumpt leg. (NHML: B.M.1959–273). — Ex *Quelea quelea aethiopica* (Sundevall, 1850) (Ploceidae): 1♂, 1♀, *Sudan*, May 1936, Meinertzahlen coll. (NHML: No.7836). — Ex *Quelea quelea lathami* (Ploceidae): 1♂, Southern Rhodesia (now *Zimbabwe*), Matabeleland, 30.iii.1952 (NHML: B.M.1980–40, coll.691); 1♂, 1♀, *Transvaal* (now *South Africa*), Nr. Komatiport, 1.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, Halajan leg. (MMBC). — Ex *Quelea quelea quelea* (Linnaeus, 1758) (Ploceidae): 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 *Spizorhynchus 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. quadrijasciata* 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...
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 *Meno-pon 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 Budworth and Plumbery 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.

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).

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### 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 Nikolaeva (1987)     |
| Bulgaria        | 118| 1  | 0.8| 0.008 | 1 ♀                      | Touleshev (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.)         |
| USA, Indiana    | 300| 0  | 0  | 0    | –                         | Martin et al. (2007)           |
| 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 Nikolaeva (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| ?    | –                         |                                |
### Table 2. Genetic distance between available specimens of *Myrsidea quadri fasciata* (= *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) KF766813, EF-1α not available; 8) KF766814, EF-1α not available; 9) KF766815, 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)   |
| **COI**      |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |
| *M. q. argentina*  | 0.0   | 0.0   | 0.0   | 0.0   | 0.3   | N/A   | N/A   | N/A   | N/A   | N/A   | 7.8   | 5.5   | 8.1   | 7.4   |       |
| *M. q. argentina*  | 6.6   | 0.0   | 0.0   | 0.0   | 0.3   | N/A   | N/A   | N/A   | N/A   | N/A   | 7.8   | 5.5   | 8.1   | 7.4   |       |
| *M. q. argentina*  | 5.5   | 5.8   | 0.0   | 0.0   | 0.3   | N/A   | N/A   | N/A   | N/A   | N/A   | 7.8   | 5.5   | 8.1   | 7.4   |       |
| *M. q. anoxanthi* | N/A   | N/A   | N/A   | 0.0   | 0.3   | N/A   | N/A   | N/A   | N/A   | N/A   | 7.8   | 5.5   | 8.1   | 7.4   |       |
| *M. g. viduae*    | 7.7   | 7.4   | 6.6   | N/A   | 0.3   | N/A   | N/A   | N/A   | N/A   | N/A   | 7.8   | 5.5   | 8.1   | 7.4   |       |
| *M. g. viduae*    | 7.7   | 7.9   | 6.6   | 0.5   | N/A   | N/A   | N/A   | N/A   | N/A   | N/A   | 8.1   | 5.8   | 8.4   | 7.7   |       |
| *M. q. textoris*  | 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   |       |
| *M. q. textoris*  | 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   |       |
| *M. q. textoris*  | 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   |       |
| *M. q. textoris*  | 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   |       |
| *M. q. textoris*  | 14.3  | 15.6  | 16.4  | N/A   | 16.9  | 16.1  | 16.4  | 16.1  | 16.4  | N/A   | N/A   | N/A   | N/A   | N/A   |       |
| *M. q. textoris*  | 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   |       |
| *M. q. textoris*  | 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   |
| *M. q. textoris*  | 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   |
| *M. q. textoris*  | 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   |
| *M. q. textoris*  | 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. quadri fasciata* 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, 7–10). In comparison with GenBank, we found three other sequences with <10% divergence (*Myrsidea* cf. *textoris* ex *Plocetus oculus*; 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 *Linarus 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 of *Myrsidea* for the 33 host species.
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 cannot 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 of *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 synonyms

“*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 allototype 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 Sturnidoeus 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 Touloukhov (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 Agelaioides 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 Ten-djore (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 São Tomé e Príncipe 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 *Agelaioides 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 cardinals 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 of the Paleartic 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 tergetal 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 thiliius 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 thiliius 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 Paleartic (“*M. balati*” and “*M. quadrifasciata*”) have 4–8 setae (one exception is again “*M. serini*” from *Agelasticus thiliius petersii* with 11 setae), specimens from Africa (“*M. queleae*” and “*M. textoris*”) have 8–14 setae (Table S4). Conversely, “*M. serini*” from Paleartic 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 Šťefka et al. (2011). Šťefka 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 Kolenck 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 conclusions 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. quelea”, “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, Dennysus, Menacanthus (Menoponidae), Lunaceps, Saemundssonia (Philopteridae), Geomydoecus, Procaviophilus (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 (sympathy) 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):

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

**Palearctic Region:**
- M. q. quelea 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) |
| | | *Agelastica thilus petersii* (Laubmann, 1934) | Paraguay | Kolencik et al. (2016) |
| | | *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) |
| | | *Quelea quelea* (Linnaeus, 1758) | Thailand | Boonkong and Meckvichai (1987), McClure and Ratnaworabhan (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 | Kloekenhoff (1984b) |
| | | *Quelea quelea quelea* (Linnaeus, 1758) | Senegal | Sychra et al. (2010) |
| | | | Cameroon | present study |
| | | *Quelea quelea lathami* (Smith) | Congo, South Africa, Zambia | Tendeiro (1964), Kloekenhoff (1984b), Halajian et al. (2014) |
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 interspecific 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 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

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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.
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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.
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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 tergites 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; GW=male genitalia width; GL=male genitalia length; ParL=paramere length; GSL=genital sac sclerite length; 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; 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. — 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).

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**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.

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