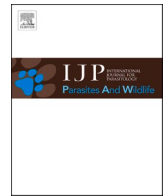




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Diversity and host associations of *Myrsidea* chewing lice (Phthiraptera: Menoponidae) in the tropical rainforest of Malaysian Borneo

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ABSTRACT

The tropical rainforests of Sundaland are a global biodiversity hotspot increasingly threatened by human activities. While parasitic insects are an important component of the ecosystem, their diversity and parasite-host relations are poorly understood in the tropics. We investigated parasites of passerine birds, the chewing lice of the speciose genus *Myrsidea* Waterston, 1915 (Phthiraptera: Menoponidae) in a natural rainforest community of Malaysian Borneo. Based on morphology, we registered 10 species of lice from 14 bird species of six different host families. This indicated a high degree of host specificity and that the complexity of the system could be underestimated with the potential for cryptic lineages/species to be present. We tested the species boundaries by combining morphological, genetic and host speciation diversity. The phylogenetic relationships of lice were investigated by analyzing the partial mitochondrial cytochrome oxidase I (*COI*) and the nuclear elongation factor alpha (*EF-1α*) genes sequences of the species. This revealed a monophyletic group of *Myrsidea* lineages from seven hosts of the avian family Pycnonotidae, one host of Timaliidae and one host of Pelloroneidae. However, species delimitation methods supported the species boundaries hypothesized by morphological studies and confirmed that four species of *Myrsidea* are not single host specific. Cophylogenetic analysis by both distance-based test ParaFit and event-based method Jane confirmed overall congruence between the phylogenies of *Myrsidea* and their hosts. In total we recorded three cospeciation events for 14 host-parasite associations. However only one host-parasite link (*M. carmenae* and their hosts *Terpsiphone affinis* and *Hypothymis azurea*) was significant after the multiple testing correction in ParaFit.

Four new species are described: *Myrsidea carmenae* sp.n. ex *Hypothymis azurea* and *Terpsiphone affinis*, *Myrsidea franciscaae* sp.n. ex *Rhipidura javanica*, *Myrsidea ramoni* sp.n. ex *Copsychus malabaricus stricklandii*, and *Myrsidea victoriae* sp.n. ex *Turdinus sepiarius*.

1. Introduction

Tropical rainforests harbour the greatest concentration of biological biodiversity on the planet (Mittermeier et al., 2003; Brooks et al., 2006; Schmitt et al., 2009). The tropical forest of Borneo belongs to the

Sundaland biodiversity hotspot, featuring exceptional species richness and endemism (Mittermeier et al., 1998). Many rainforest regions are under heavy pressure due to deforestation and other disturbances (Geist and Lambin, 2001), and Malaysian Borneo has experienced one of the highest relative rates of deforestation in the tropics (Wilkove et al.,

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2013). This means that many species in the region, including as yet undescribed species, are facing the threat of extinction and require an inventory of their diversity (Webb et al., 2010).

Parasitic insects, such as many ectosymbionts of birds and mammals, are poorly known in the tropics and often face co-extinction with their hosts. This occurs even before their host is threatened, because reduction in continuity and fragmentation of remaining areas of forest have a negative effect on parasite richness and can result in extinction even while the host species is still present (Bush et al. 2013). One group of parasitic insects, the chewing lice, are permanent ectoparasites that complete their entire life cycle on the body of the host. Recent studies have revealed high levels of chewing lice diversity in tropical regions, of which only a small fraction has been identified (Clayton et al., 1992; Johnson and Price, 2006; Valim and Weckstein, 2013; Najer et al., 2014; Light et al., 2016; Kolencik et al., 2017; Takano et al., 2019). Information about chewing lice diversity in the Oriental region and particularly Sundaland is very limited (Najer et al., 2012; Sychra et al., 2014), so the identification and description of chewing lice assemblages in the Sundaland region represents an essential task.

Close relationships between parasites and hosts at the species, population and individual level is one of the major factors determining chewing lice diversity and, in the tropics, host-parasites relationships are predominantly known from the Neotropics (Johnson et al., 2002a, b; Bueter et al., 2009; Bush et al., 2016). Chewing lice are generally transmitted to new hosts from parent birds to their young in the nest and during direct contact between birds. Specific chewing lice adaptations to particular hosts can lead to reproductive isolation among parasite populations and limit their ability to colonize new host species (Johnson et al., 2002b; Clayton et al., 2004; Martinů et al., 2015). The determination of host distribution and specificity of chewing lice species is often used to investigate host-parasite relations in this group of parasitic insects (Clayton et al., 2004).

We focused on the chewing lice genus *Myrsidea* Waterson, 1915 (Insecta: Psocodea: Phthiraptera: Menoponidae), which are ubiquitous parasites of passerine birds. *Myrsidea* have been found on the majority of tropical passerine species (they are also present on non-passerines), and 80 percent of *Myrsidea* species are known from a single host species

(Price et al., 2003). However, to date, most *Myrsidea* species in Asia have been identified by morphological methods alone and their associations with hosts remain largely undescribed. For instance, there are 322 species of passerine birds recorded in Borneo (Lepage, 2020, according to taxonomy in Clements et al., 2019), of which 45 (14%) are known to host 47 species of *Myrsidea* chewing lice in other parts of their range. From Borneo itself, only seven species of *Myrsidea* from nine hosts have been recorded (Klockenhoff, 1971; Hellenthal and Price, 2003; Price et al. 2003, 2006).

Here, we studied the diversity and host specificity of chewing lice of the genus *Myrsidea* in the tropical rainforest avian community of Sabah, Malaysian Borneo, using morphology, phylogenetics, species delimitation algorithms and cophylogenetic analysis. Four new species of *Myrsidea* were described. We sampled several groups of wild passerine birds common in the tropical forest community studied: bulbuls (Pycnonotidae), fantails (Rhipiduridae), monarch flycatchers (Monarchidae), old world flycatchers (Muscicapidae), ground babbler (Pellorneidae), and tree babbler, scimitar-babbler and allies (Timaliidae). Thus, we hope to augment our knowledge of chewing lice parasite diversity and host interactions in this particular understudied community.

2. Material and methods

2.1. Study area

The fieldwork was carried out from June to August 2014 and 2015 within the Yayasan Sabah Forest Management Area (YSFMA) in Sabah, Malaysia (4°58'N, 117°4'E) (Fig. 1). This area contains both primary unlogged and selectively logged dipterocarp forest (Reynolds et al., 2011).

2.2. Louse specimen collection

Three plots in primary and three plots in selectively twice-logged forest were sampled, with each plot comprising of two transects 250 m apart (Edwards et al. 2009; Hill and Hamer 2004; Whitman et al. 1998).

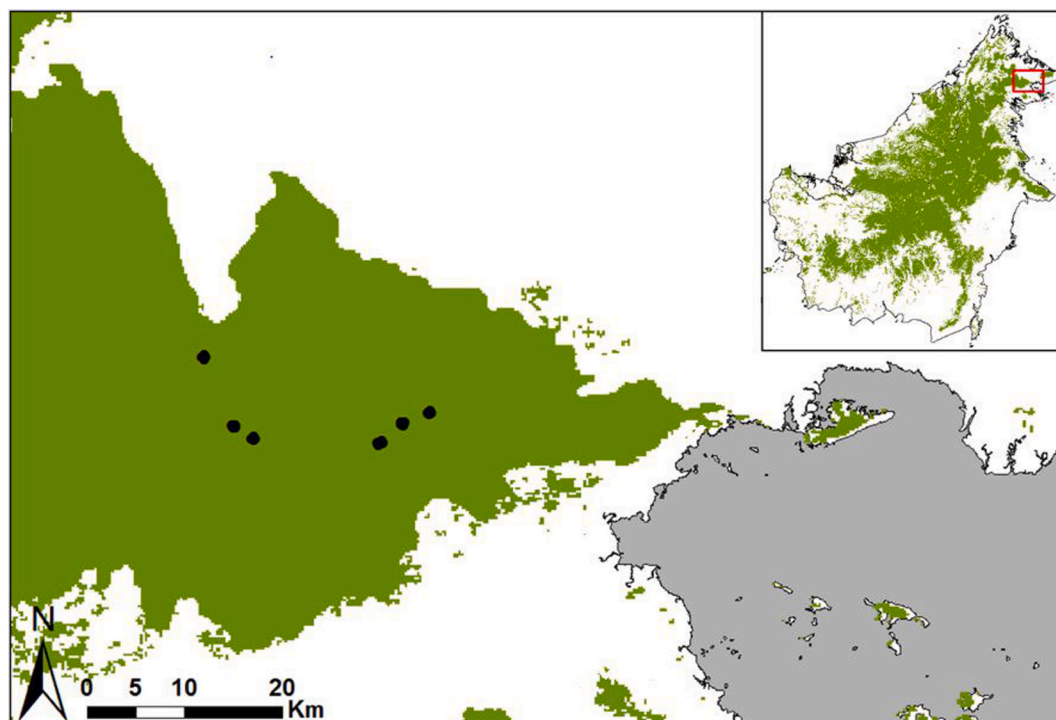


Fig. 1. Map of sampling localities (black dots) in the Yayasan Sabah Forest Management Area, Malaysian Borneo.

At each transect, 15 mist nets (12 × 2.7 m; 25 mm size) were erected end-to-end in a straight line and opened from 06:00 to 12:00 for two consecutive days. The mist-netting was carried out by two teams of 2 or 3 people and team visits were alternated between the different transects. Sampling was rotated among forest types to diminish temporal effects (Edwards et al. 2009). After capture, each bird was put in a cloth bag and then dust-ruffled to collect ectoparasites (Koop and Clayton, 2013; Walther and Clayton, 1997). Each bag was only used once a day to avoid cross contamination and was washed with detergent between uses. Insecticide powder containing effective permethrin (Johnsons Pigeon Mite and Insect Powder) was applied to the bird feathers. With a paint brush, powder was applied to the legs, wings, belly, neck and back. On the head, the powder was applied very carefully to avoid contact with the eyes, which can cause irritation. Subsequently, each bird was dust-ruffled for a standardised 3 min. All the powder and particles visible to the naked eye were collected in a 5 ml vial containing 2.5 ml of 95% ethanol (Walther and Clayton, 1997).

2.3. Lice identification and description

Subsequently, chewing lice were slide-mounted in Canada balsam as permanent preparations in the laboratory, following the technique by Palma (1978). Identification of the lice was based on existing literature (Tandan, 1972; Hellenthal and Price, 2003; Price et al., 2006; Halajian et al., 2012). Bird taxonomy follows that in Clements et al. (2019).

Some of the louse specimens obtained belong to previously described species, but differ from their original descriptions or redescrptions by setal counts and dimensions. In these cases, we present our data together with those from the original descriptions or redescrptions. If our setal counts and dimensions are fully consistent with those in the original descriptions, the latter are not repeated here.

In the following descriptions, all dimensions are given in millimetres, numbers of metanotal marginal setae do not include the most posterolateral setae, and the postspiracular setae - as well as short associated setae on tergites II–VIII - are not included in tergal setal counts. Abbreviations for measured features are: DHS, dorsal head seta; *ls*5, labial seta 5; *s*1–*s*6, aster setae length (setae are counted from the longest inner seta to the shortest outer one); TW, temple width; POW, preocular width; HL, head length at midline; PW, prothorax width; MW, metathorax width; AW, abdomen width at level of segment IV; TL, total length; ANW, female anus width; GW, male genitalia width; ParL, paramere length; GSL, male genital sac sclerite length (Clay, 1966; Valim and Weckstein, 2013). Line drawings of habitus show the dorsal view on the left side, the ventral view on the right side.

The new species are attributed to the first two authors only. The ten species dealt with below are arranged in alphabetical order with initial note to *Myrsidea* from Pycnonotidae. All specimens, including the type specimens of the new species described, are deposited in the Moravian Museum, Brno, Czech Republic (MMBC).

2.4. Phylogenetic study

DNA was extracted from specimens fixed in 95% ethanol with addition of proteinase K and mercaptoethanol in the lysing solution (Holterman et al., 2006). Voucher slides were retained for each louse specimen as described above. Two fragments of two genes were selected for phylogenetic analysis based on the availability of sequenced markers for *Myrsidea* in GenBank. The mitochondrial protein coding gene: cytochrome oxidase I (*COI*) (381 bp) and the nuclear protein coding gene: elongation factor-1 α (*EF-1 α*) (345 bp) were used. All sequences obtained were compared to the GenBank database using the BLAST algorithm (Altschul et al., 1990). P-distances of sequences from all *Myrsidea* were computed in Mega X (Kumar et al., 2018), and the information is summarized in Supplement 1 together with the 10 closest sequences from GenBank for all new species described.

For *COI* amplification, we used primers L6625 and H7005 (Hafner

et al., 1994) and for *EF-1 α* , we used following primers: TEF1_F TAA GAC TAT TTC GGT TAA GGA ATT GCG CC and TEF1_R ACG AAC GGC GAA ACG TCC CAA. *COI* and *EF-1 α* sequences were amplified using an EncycloPlus PCR Kit (Evrogen, Russia). Polymerase chain reaction (PCR) products were visualized in gel, cut out, and cleaned using the SV Gel and PCR CleanUp System kit (Evrogen, Russia). DNA sequencing was performed at the Genome Centre for Collective Use in the Severtsov Institute of Ecology and Evolution of Russian Academy of Science (Moscow, Russia). Molecular markers used and GenBank (Thompson et al., 1997) accession numbers for the sequences of the species studied are presented in Table 1.

Sequences were aligned with MAFFT <https://mafft.cbrc.jp/alignment/server/> and L-INS-I method (Katoh et al., 2019) and were concatenated in Mesquite 2.3.0 software. Partitioning schemes and models of molecular evolution were defined with PartitionFinder 2 (Lanfear et al., 2017) using the following settings: branch length linked, all models and Bayesian Information Criterion. Estimated models of molecular evolution (HKY + G for *COI* and K80+G for *EF-1 α*) were set during the Bayesian analysis with Mr. Bayes 3.2.7 (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003). Phylogenetic analyses were performed using two independent runs with four incrementally heated chains (Metropolis-coupled Markov chain Monte Carlo; Ronquist and Huelsenbeck, 2003), run for 10 million generations, and sampled every 1000 generations. The first 25% of trees from each run were discarded as burn-in. The remaining trees were used to create a 50% majority consensus tree and calculate posterior probabilities. Then the effective sample sizes of all parameters were calculated using Tracer v1.5 (Rambaut and Drummond, 2009).

Sequences of the partial *COI* sequence (GenBank accession number AF385013.1) and *EF-1 α* (Accession number AF320391.1) of *Dennyus hirundinis* were selected as outgroups for phylogenetic reconstructions (Kolencik et al., 2017; Marshall 2003).

2.5. Species delimitation

We used several methods for identifying potential cryptic lineages/species. We tested the congruence of operational taxonomic units (OTUs) by the application of three analytical methods: Automatic Barcode Gap Discovery (ABGD) (Puillandre et al., 2012), Generalized Mixed Yule Coalescent (GMYC) (Pons et al., 2006), and Poisson tree processes model (PTP) (Zhang et al., 2013). The ABGD approach was conducted at the ABGD web server (<https://bioinfo.mnhn.fr/abi/public/abgd/abgdweb.html>) with the relative gap width value equal to 0.5 and Jukes-Cantor model. The GMYC and bPTP analyses were performed with Bayesian trees with default parameters at the Exelixis Lab web-server (<http://species.h-its.org>), the tree was converted to ultrametric using the ape package (Paradis and Schliep, 2019) in R (R Core Team, 2020). We considered a population of *Myrsidea* species from a single host species in the community studied as a *Myrsidea* lineage. Three samples of lice from different host individuals per *Myrsidea* lineage were used to test the molecular OTUs if possible.

2.6. Cophylogenetic analysis

TreeMap V.3 was used for visualisation of the cophylogeny of the studied *Myrsidea* species and their hosts. We used concatenated *Myrsidea* phylogeny, which was pruned so that each species was represented by a single tip, with outgroup taxa removed. The phylogeny of the hosts species was extracted from the BirdTree.org database (<http://www.birdtree.org>) using the study by Hackett et al. (2008) as the backbone for phylogenetic reconstruction. Two species of Pycnonotidae, *Pycnonotus erythroththalmos* and *P. eutilotus*, which are absent in the database of BirdTree.org were placed in the clade of *Pycnonotus* with non-zero branch lengths, which might potentially affect cospeciation tests. A total of 1000 trees were downloaded from BirdTree.org, which is enough to obtain robust phylogenies (Rubolini et al. 2015). The resultant MCC

Table 1

Bornean *Myrsidea* species and their avian host species (family) used for phylogenetic analysis and GenBank accession numbers of the sequences.

Louse species	Avian host	EF-1 α sequences number	COI sequences number
<i>Myrsidea johnsoni</i>	<i>Pycnonotus melanoleucos</i> (Pycnonotidae)	MG252736	KY066744
<i>Myrsidea johnsoni</i>	<i>Pycnonotus melanoleucos</i> (Pycnonotidae)	MG252737	KY066745
<i>Myrsidea johnsoni</i>	<i>Pycnonotus melanoleucos</i> (Pycnonotidae)	MG252738	KY066746
<i>Myrsidea macronoi</i>	<i>Stachyris poliocephala</i> (Timaliidae)	MG252739	KY066747
<i>Myrsidea macronoi</i>	<i>Stachyris poliocephala</i> (Timaliidae)	KX423043	KX423041
<i>Myrsidea macronoi</i>	<i>Stachyris poliocephala</i> (Timaliidae)	KX423044	KX423042
<i>Myrsidea ochracei</i>	<i>Alophoixus bres</i> (Pycnonotidae)	MG252740	KY066748
<i>Myrsidea ochracei</i>	<i>Alophoixus bres</i> (Pycnonotidae)	MG252741	KY066749
<i>Myrsidea ochracei</i>	<i>Alophoixus bres</i> (Pycnonotidae)	MG252742	KY066750
<i>Myrsidea eutiloti</i>	<i>Pycnonotus erythropthalmos</i> (Pycnonotidae)	MG252743	KY066751
<i>Myrsidea eutiloti</i>	<i>Pycnonotus erythropthalmos</i> (Pycnonotidae)	MG252744	KY066752
<i>Myrsidea eutiloti</i>	<i>Pycnonotus erythropthalmos</i> (Pycnonotidae)	MG252745	KY066753
<i>Myrsidea eutiloti</i>	<i>Pycnonotus eutilotus</i> (Pycnonotidae)	MG252746	KY066754
<i>Myrsidea eutiloti</i>	<i>Pycnonotus eutilotus</i> (Pycnonotidae)	MG252747	KY066755
<i>Myrsidea eutiloti</i>	<i>Pycnonotus eutilotus</i> (Pycnonotidae)	MG252748	KY066756
<i>Myrsidea ramoni</i>	<i>Copsychus malabaricus</i> (Muscicapidae)	MG252749	KY066757
<i>Myrsidea ramoni</i>	<i>Copsychus malabaricus</i> (Muscicapidae)	MG252750	KY066758
<i>Myrsidea ramoni</i>	<i>Copsychus malabaricus</i> (Muscicapidae)	MG252751	KY066759
<i>Myrsidea johnsoni</i>	<i>Pycnonotus atriceps</i> (Pycnonotidae)	MG252752	KY066760
<i>Myrsidea johnsoni</i>	<i>Pycnonotus atriceps</i> (Pycnonotidae)	MG252753	KY066761
<i>Myrsidea johnsoni</i>	<i>Pycnonotus atriceps</i> (Pycnonotidae)	MG252754	KY066762
<i>Myrsidea victoriae</i>	<i>Turdinus sepiarius</i> (Pycnonotidae)	MG252755	KY066763
<i>Myrsidea victoriae</i>	<i>Turdinus sepiarius</i> (Pycnonotidae)	MG252756	KY066764
<i>Myrsidea victoriae</i>	<i>Turdinus sepiarius</i> (Pycnonotidae)	MG252757	KY066765
<i>Myrsidea ochracei</i>	<i>Alophoixus finschii</i> (Pycnonotidae)	MG252758	KY066766
<i>Myrsidea ochracei</i>	<i>Alophoixus finschii</i> (Pycnonotidae)	MG252759	KY066767
<i>Myrsidea ochracei</i>	<i>Alophoixus finschii</i> (Pycnonotidae)	MG252760	KY066768
<i>Myrsidea pycnonoti</i>	<i>Tricholestes criniger</i> (Pycnonotidae)	MG252761	KY066769
<i>Myrsidea pycnonoti</i>	<i>Tricholestes criniger</i> (Pycnonotidae)	MG252762	KY066770
<i>Myrsidea pycnonoti</i>	<i>Tricholestes criniger</i> (Pycnonotidae)	MG252763	KY066771
<i>Myrsidea franciscaae</i>	<i>Rhipidura javanica</i> (Rhipiduridae)	MG252764	KY066772
<i>Myrsidea franciscaae</i>	<i>Rhipidura javanica</i> (Rhipiduridae)	MG252765	KY066773
<i>Myrsidea franciscaae</i>	<i>Rhipidura javanica</i> (Rhipiduridae)	MG252766	KY066774
<i>Myrsidea carmenae</i>	<i>Hypothymis azurea</i> (Monarchidae)	MG252767	KY066775
<i>Myrsidea carmenae</i>	<i>Hypothymis azurea</i> (Monarchidae)	MG252768	KY066776
<i>Myrsidea carmenae</i>	<i>Hypothymis azurea</i> (Monarchidae)	MG252769	KY066777

Table 1 (continued)

Louse species	Avian host	EF-1 α sequences number	COI sequences number
<i>Myrsidea carmenae</i>	<i>Terpsiphone affinis</i> (Monarchidae)	MG252770	KY066778
<i>Myrsidea carmenae</i>	<i>Terpsiphone affinis</i> (Monarchidae)	MG252771	KY066779
<i>Myrsidea carmenae</i>	<i>Terpsiphone affinis</i> (Monarchidae)	MG252772	KY066780

consensus tree was obtained by Treeannotator of BEAST 1.8.2 (Drummond et al. 2012). Both event-based and distance-based cophylogenetic analyses were used for cophylogenetic analysis as described by Sweet and Johnson (Sweet and Johnson, 2016; Sweet et al., 2016). ParaFit (Legendre et al., 2002) was used for the distance-based cophylogenetic analyses, we applied the Benjamini-Hochberg (1995) multiple testing correction to individual host-parasite link p-values. Jane v4 (Conow et al., 2010) was used for event-based approach.

3. Results

3.1. Morphological studies

Based on morphology, we registered 10 species of lice from 14 bird species of six different host families.

Systematics.

Order Phthiraptera Haeckel, 1896.

Suborder Amblycera Kellogg, 1896.

Family Menoponidae Mjöberg, 1910.

Genus *Myrsidea* Waterston, 1915.

3.1.1. *Myrsidea* from bulbuls (*Pycnonotidae*)

Myrsidea from bulbuls were revised by Hellenenthal and Price (2003). Here we would like to update morphometric characters omitted by these authors. Because these characters are common to all the *Myrsidea* species from bulbuls mentioned below, they will not be repeated under these species.

Length of DHS 10, 0.025–0.045; DHS 11, 0.075–0.095; ratio DHS 10/11, 0.29–0.57. Labial setae 5 (ls5) short 0.02–0.04 long, latero-ventral fringe with 9–11 setae. First tibia with 3 outer ventro-lateral and 4 dorso-lateral setae. Metapleurites of females with 3 (rarely 4), those of males with only 2 short strong spiniform setae. Femur III with 12–18 setae in ventral setal brush.

Abdominal segments with well-defined median gap in each row of tergal setae. Postspiracular setae of females: very long on II, IV, VII and VIII (0.33–0.59); long to very long on III (0.27–0.52) and VI (0.25–0.44); and long on I (0.21–0.32). Contrary to Hellenenthal and Price (2003) who mentioned very long postspiracular setae on all segments we found variable length of these setae on segment V: short (0.14–0.19) for *M. eutiloti*, *M. johnsoni* and *M. ochracei* from *Alophoixus finschii*; long (0.28–0.30) for *M. pycnonoti*; and very long (0.33–0.44) for *M. ochraceus* from *Alophoixus bres*. Similarly, postspiracular setae of males: very long on II, IV, VII and VIII (0.30–0.51); long to very long on III (0.22–0.49) and VI (0.20–0.36); long on I (0.19–0.31); and variably long on V: short (0.11–0.13) for *M. johnsoni* and *M. ochracei* from *Alophoixus finschii*; long (0.19–0.25) for *M. eutiloti*, *M. pycnonoti* and *M. ochraceus* from *Alophoixus bres*.

Inner posterior seta of last tergum with length 0.06–0.14; length of short lateral marginal seta of last segment, 0.03–0.06. Pleurites I–VI with only short spine-like setae; pleurite VII with one conspicuously longer seta. Pleural setae: I, 2–4; II–V, 5–8; VI–VII, 4–7; VIII of female, 4 (rarely 5); and VIII of male, 3 (rarely 4). Anterior margin of sternal plate II with a medial notch. Aster setae length: s1, 0.07–0.13; s2, 0.05–0.10; s3, 0.03–0.07; s4, 0.03–0.06; s5 (rarely s6), 0.02–0.05. Remainder of subgenital plate of male (except those setae counted for sternite VIII) with 6–7 setae; with 3–4 setae on posterior margin and with 8–9 internal

anal setae.

3.1.2. *Myrsidea carmenae* Soto Madrid & Sychra, new species

(Fig. 2A–D, 6A–B).

Type host. *Hypothymis azurea* (Boddaert, 1783) – Black-naped Monarch (Monarchidae).

Type locality. YSFMA in Sabah, MALAYSIA (4°58'N, 117°4'E).

Type material. Holotype, ♀, MALAYSIA: YSFMA in Sabah (4°58'N, 117°4'E), ex *Hypothymis azurea*, 7.viii.2015 (Ramón Soto Madrid) (MMBC). Paratypes, 1♀, 1♂ with the same data as holotype.

Other material. 1♀, 1♂, MALAYSIA: YSFMA in Sabah (4°58'N, 117°4'E), ex *Terpsiphone affinis* (Blyth, 1846) – Blyth's Paradise-flycatcher (Monarchidae), 6.viii.2015 (Ramón Soto Madrid) (MMBC).

Diagnosis. According to male genital sac sclerites (Fig. 2D) *M. carmenae* sp.n. is morphologically closest to *Myrsidea ishizawai* Uchida (1926) from *Zoothera dauma* (Latham, 1790). Both sexes of *M. carmenae* can be easily separated from those of *M. ishizawai* by: 1) small number of outer dorso-lateral setae of first tibia (4 vs. more than 10), 2) smaller number of setae on sternites III–V (13–30 vs. 35–81), and 3) conspicuously smaller dimensions (for example TW 0.38–0.44 vs. 0.49–0.61; and TL of male 1.09–1.17 vs. 1.43–1.64, and TL of female 1.28–1.30 vs. 1.79–2.17).

Female (n = 3). As in Figs. 2A and 6A. Hypopharyngeal sclerites fully developed. Shape of head as in Fig. 2B. Length of DHS 10, 0.04–0.05; DHS 11, 0.09–0.10; ratio DHS 10/11, 0.38–0.48. *Ls*5, 0.05–0.06 long, latero-ventral fringe with 9–10 setae. Gula with 4–6 setae on each side. Pronotum with 6 setae on posterior margin and 3 short spiniform setae at each lateral corner. Prosternal plate with rounded anterior margin (Fig. 2A). First tibia with 3 outer ventro-lateral and 4 dorso-lateral setae. Mesonotum divided. Metanotum not enlarged, with 4–6 marginal setae; metasternal plate with 6–7 setae; metapleurites

with 3 short strong spiniform setae. Femur III with 12–15 setae in ventral setal brush. Tergites not enlarged, all with straight posterior margin. Abdominal segments with well-defined median gap in each row of tergal setae (Fig. 2A). Tergal setae (postspiracular setae and on tergites II–VIII also short associated setae are not included): I, 9–11; II, 9–10; III, 9–11; IV, 10–12; V, 9–10; VI, 7–9; VII, 4; VIII, 4. Postspiracular setae very long on II, IV, VII and VIII (0.39–0.54); long on I (0.24–0.31); and short on III, V and VI (0.14–0.19). Inner posterior seta of last tergum longer than anal fringe setae with length 0.10–0.13; length of short lateral marginal seta of last segment, 0.05–0.06. Pleural setae: I, 5–6; II, 5–7; III, 6–9; IV, 7–8; V, 6–7; VI, 5; VII, 4–5; VIII, 3. Pleurites with only short spine-like setae. Pleurite VIII with inner setae (0.06–0.10) as long as outer (0.04–0.06). Anterior margin of sternal plate II with a medial notch. Sternal setae: I, 0; II, 4 in each aster, aster setae length: s1, 0.08–0.09; s2, 0.06–0.09; s3, 0.05–0.06; s4, 0.03–0.04; with 10–12 marginal setae between asters, 4–6 medioanterior; III, 20–21; IV, 23–26; V, 28–30; VI, 21–25; VII, 9–10; VIII–IX, 8–12; and 8 setae on deeply serrated vulval margin; sternites III–VII without medioanterior setae. Anal fringe formed by 27–32 dorsal and 26–30 ventral setae.

Dimensions: TW, 0.42–0.44; POW, 0.33–0.35; HL, 0.28–0.29; PW, 0.26–0.27; MW, 0.36–0.38; AW, 0.50–0.52; ANW, 0.17–0.18; TL, 1.28–1.36.

Male (n = 2). As in Fig. 6B. Similar as female except as follows. Length of DHS 10, 0.03–0.04; DHS 11, 0.08–0.09; ratio DHS 10/11, 0.35–0.45. *Ls*5, 0.04–0.05 long, latero-ventral fringe with 9 setae. Gula with 4–5 setae on each side. Metanotum not enlarged with 3–4 marginal setae (the most posterolateral setae are not counted); metasternal plate with 5–6 setae; metapleurites with 3 short spiniform strong setae. Femur III with 10–12 setae in ventral setal brush. Abdominal segments with well-defined median gap in each row of tergal setae. Tergal setae (postspiracular setae and on tergites II–VIII also short associated setae are not included): I, 5; II, 6–7; III, 6–9; IV, 6–9; V, 7; VI, 6; VII, 4; VIII, 4;

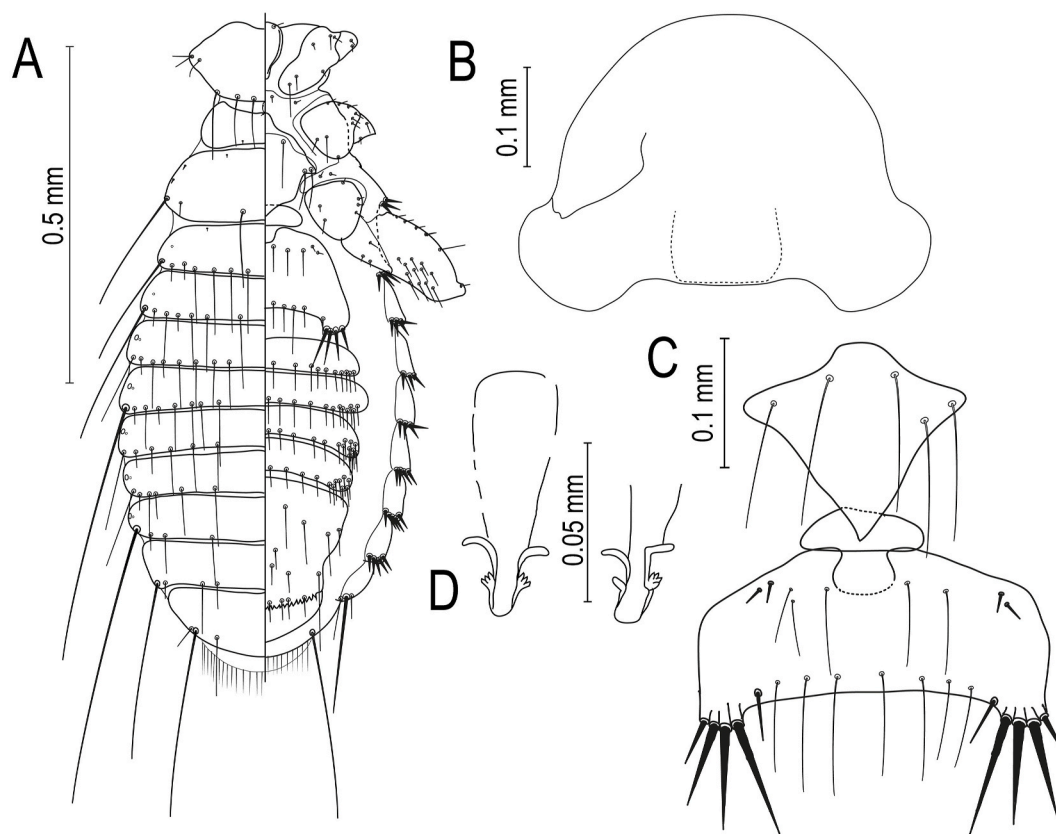


Fig. 2. *Myrsidea carmenae* sp.n. A, dorso-ventral view of female thorax and abdomen; B, head shape; C, male metasternal plate and sternites I–II; D, male genital sac sclerites.

length of longer inner tergal seta on abdominal segment VII (as defined in Hellenthal and Price, 2003), 0.06. Postspiracular setae very long on II, IV, VII and VIII (0.31–0.51); long on I (0.20–0.26); and short on III, V and VI (0.10–0.19); Length of inner posterior seta of last tergum, 0.03–0.05; short lateral marginal seta of last segment, 0.02. Pleural setae: I, 3–4; II, 5–6; III, 5–6; IV, 5; V, 5; VI, 4–5; VII, 3–4; VIII, 3. Pleurites with only short spine-like setae. Pleurite VIII with inner setae (0.04) as long as outer (0.03). Anterior margin of sternal plate II with a medial notch (Fig. 2C). Sternal setae: I, 0; II, 4 in each aster, aster setae length: s1, 0.07–0.08; s2, 0.06; s3, 0.05–0.06; s4, 0.03–0.04; with 8–9 marginal setae between asters, 4–6 medioanterior; III, 13–14; IV, 13–20; V, 20–25; VI, 15–16; VII, 5–7; VIII, 4; remainder of plate, 6; and with 4 setae posteriorly; sternites III–VII without medioanterior setae. With 8 internal anal setae. Genital sac sclerites in Fig. 2D.

Dimensions: TW, 0.38–0.42; POW, 0.30–0.33; HL, 0.27–0.28; PW, 0.23–0.25; MW, 0.31–0.34; AW, 0.39–0.42; GW, 0.10; GL, 0.36–0.38; ParL, 0.07–0.08; GSL, 0.30–0.32; TL, 1.09–1.17.

Etymology. This species epithet is named in honor of Carmen Madrid Martínez, mother of the first author.

3.1.3. *Myrsidea eutiloti* Hellenthal and Price (2003)

Myrsidea eutiloti Hellenthal and Price (2003): 11. Type host: *Pycnonotus eutilotus* (Jardine and Selby, 1837) – Puff-backed Bulbul (Pycnonotidae).

Material studied. 1♀, 1♂, MALAYSIA: YSFMA in Sabah (4°58'N, 117°4'E), ex *Pycnonotus erythroptalmus* (Hume, 1878) – Spectacled Bulbul (Pycnonotidae), 24.vii.2015 (Ramón Soto Madrid) (MMBC). 1♂, MALAYSIA: YSFMA in Sabah, ex *Pycnonotus eutilotus*, 3.vii.2015 (Ramón Soto Madrid) (MMBC).

Remarks. Our specimens differ from the description of *M. eutiloti* presented by Hellenthal and Price (2003) by setal counts and dimensions

as follows [setal counts and dimensions mentioned by Hellenthal and Price (2003) are in parentheses]:

Female (n = 1). Postspiracular setae very long on II, III, IV, VII and VIII (0.33–0.48); long on I and VI (0.26–0.28); and conspicuously shorter on V (0.19) (according to Hellenthal and Price (2003) very long on all segments).

Dimensions: LSVII, 0.14 (0.20–0.30).

Male (n=2). Pronotum with 3–4 (3) short spiniform setae at each lateral corner. Tergal setae: V, 8–11 (6–10); VI, 10 (6–9). Postspiracular setae very long on II–IV and VI–VIII (0.30–0.44); and shorter on I and V (0.20–0.25) (according to Hellenthal and Price (2003) very long on all segments). Sternal setae: III, 6–8 (7–12).

Dimensions: LSVII, 0.10–0.15 (0.12–0.22).

3.1.4. *Myrsidea franciscaae* Soto Madrid & Sychra, new species

(Fig. 3A–D).

Type host. *Rhipidura javanica* (Sparrman, 1788) – Malaysian Pied Fantail (Rhipiduridae).

Type locality. YSFMA in Sabah, MALAYSIA (4°58'N, 117°4'E).

Type material. Holotype, ♀, MALAYSIA: YSFMA in Sabah (4°58'N, 117°4'E), ex *Rhipidura javanica*, 22.viii.2015 (Ramón Soto Madrid) (MMBC). Paratypes, 2♂ with the same data as holotype.

Diagnosis. This new species is well recognized by the male genital sac sclerite (Fig. 3D) that is, to our knowledge, unique within all oriental *Myrsidea* in its shape and structure with only small simple lateral lobe-like structures. Both sexes are characterised by the following combination of characters: 1) abdominal segments with well-defined median gap in each row of tergal setae; 2) small number of tergal setae, especially tergites VII–VIII with only 4 setae; 3) small number of sternal setae, especially sternite III with 10–14 setae and sternite VII with 6–8 setae. These characters place *M. franciscaae* sp.n. very close to *M. carmenae* sp.

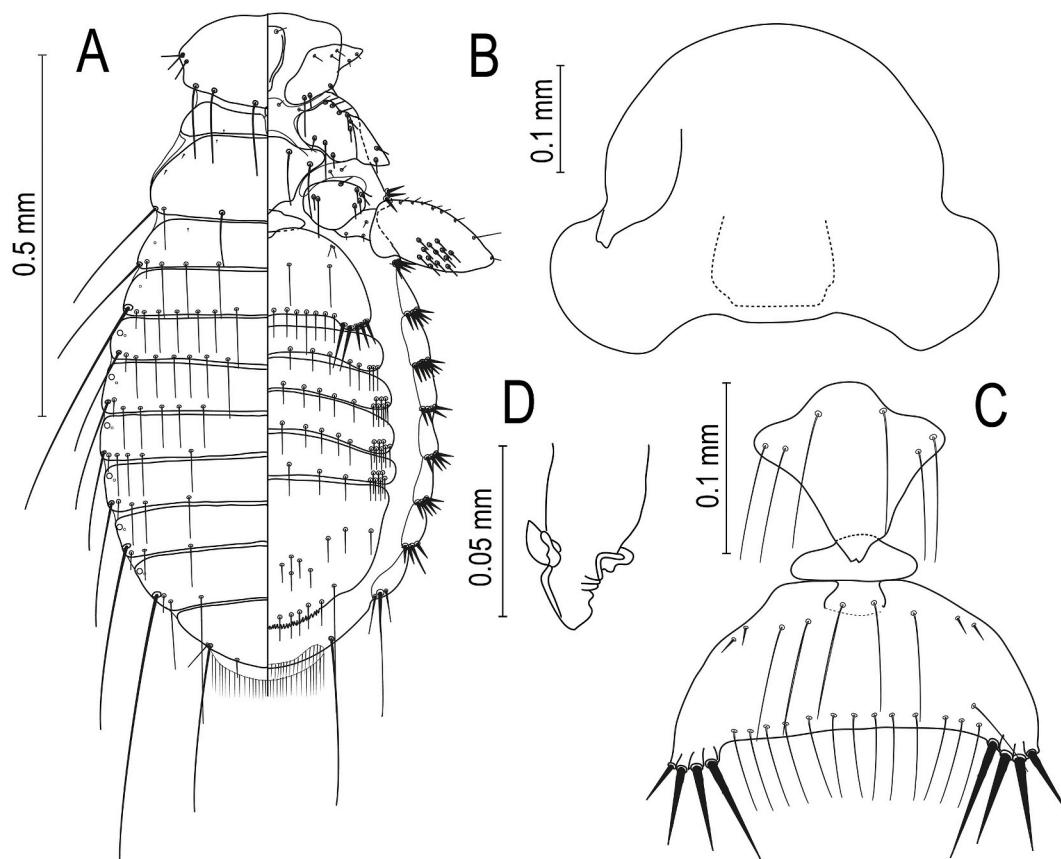


Fig. 3. *Myrsidea franciscaae* sp.n. A, dorso-ventral view of female thorax and abdomen; B, head shape; C, male metasternal plate and sternites I–II; D, male genital sac sclerite.

n. Except different male genital sac sclerite (compare Fig. 3D vs. Fig. 2D) these two species can be separate by: 1) inner posterior seta of last tergum of female not longer than anal fringe setae with length 0.03 (vs. 0.10–0.13), and 2) quite long inner tergal seta on abdominal segment VII (0.10–0.12 vs. 0.06).

Female (n = 1). As in Figs. 3A and 6C. Hypopharyngeal sclerites fully developed. Shape of head as in Fig. 3B. Length of DHS 10, 0.05; DHS 11, 0.10; ratio DHS 10/11, 0.49. *Ls5*, 0.04 long, latero-ventral fringe with 9 setae. Gula with 3–4 setae on each side. Pronotum with 6 setae on posterior margin and 3 short spiniform setae at each lateral corner. Prosternal plate with rounded anterior margin (Fig. 3A). First tibia with 3 outer ventro-lateral and 4 dorso-lateral setae. Mesonotum divided. Metanotum not enlarged, with 4 marginal setae; metasternal plate with 6 setae; metapleurites with 3 short strong spiniform setae. Femur III with 13 setae in ventral setal brush. Tergites not enlarged, all with straight posterior margin. Abdominal segments with well-defined median gap in each row of tergal setae (Fig. 3A). Tergal setae (postspiracular setae and on tergites II–VIII also short associated setae are not included): I, 7; II, 12; III, 10; IV, 7; V, 11; VI, 6; VII, 4; VIII, 4. Postspiracular setae very long on II, IV, VII and VIII (0.35–0.48); long on I, III V and VI (0.20–0.25). Inner posterior seta of last tergum not longer than anal fringe setae with length 0.03; length of short lateral marginal seta of last segment, 0.03. Pleural setae: I, 4; II, 6–7; III, 6–7; IV, 6–7; V, 6; VI, 5; VII, 4; VIII, 3. Pleurites with only short spine-like setae. Pleurite VIII with inner setae (0.06–0.07) as long as outer (0.04). Anterior margin of sternal plate II with a medial notch. Sternal setae: I, 0; II, 4–5 in each aster, aster setae length: s1, 0.08–0.09; s2, 0.06–0.08; s3, 0.04; s4, 0.04; s5, 0.04; with 14 marginal setae between asters, 4 medioanterior; III, 10; IV, 20; V, 22; VI, 20; VII, 7; VIII–IX, 10; and 11 setae on deeply serrated vulval margin; sternites III–VII without medioanterior setae. Anal fringe formed by 30 dorsal and 30 ventral setae.

Dimensions: TW, 0.43; POW, 0.33; HL, 0.29; PW, 0.27; MW, 0.38; AW, 0.51; ANW, 0.16; TL, 1.30.

Male (n = 2). As in Fig. 6D. Similar as female except as follows. Length of DHS 10, 0.05; DHS 11, 0.09–0.10; ratio DHS 10/11, 0.50–0.57. *Ls5*, 0.03–0.04 long, latero-ventral fringe with 9 setae. Gula with 3–4 setae on each side. Pronotum with 6–7 setae on posterior margin. Metanotum not enlarged with 4 marginal setae (the most posterolateral setae are not counted); metasternal plate with 7 setae; metapleurites with 2–3 short spiniform strong setae. Femur III with 14–15 setae in ventral setal brush. Abdominal segments with well-defined median gap in each row of tergal setae. Tergal setae (postspiracular setae and on tergites II–VIII also short associated setae are not included): I, 5–6; II, 9–10; III, 9–11; IV, 7–8; V, 7–8; VI, 6; VII, 4; VIII, 4; length of longer inner tergal seta on abdominal segment VII (as defined in Hellenthal and Price, 2003), 0.10–0.12. Postspiracular setae very long on II, IV, VII and VIII (0.31–0.45); long on I, III V and VI (0.14–0.19). Length of inner posterior seta of last tergum, 0.02–0.05; short lateral marginal seta of last segment, 0.13. Pleural setae: I, 3–4; II, 6; III, 6; IV, 4–6; V, 5; VI, 5–6; VII, 3; VIII, 3. Pleurites with only short spine-like setae. Pleurite VIII with inner setae (0.06–0.08) twice as long as outer (0.03). Anterior margin of sternal plate II with a medial notch (Fig. 3C). Sternal setae: I, 0; II, 4–5 in each aster, aster setae length: s1, 0.07–0.08; s2, 0.06–0.07; s3, 0.05–0.07; s4, 0.04–0.06; s5, 0.03; with 12–14 marginal setae between asters, 5–7 medioanterior; III, 13–14; IV, 23; V, 22–24; VI, 20; VII, 8; VIII, 4; remainder of plate, 4; and with 2–3 setae posteriorly; sternites III–VII without medioanterior setae. With 8 internal anal setae. Genital sac sclerites as in Fig. 3D.

Dimensions: TW, 0.39; POW, 0.29–0.30; HL, 0.26–0.27; PW, 0.23–0.24; MW, 0.32–0.33; AW, 0.41–0.42; GW, 0.09–0.11; GL, 0.32–0.34; ParL, 0.07; GSL, 0.30–0.35; TL, 1.02–1.05.

Etymology. This species epithet is named in honor of Francisca Madrid Martínez, grandmother of the first author.

3.1.5. *Myrsidea johnsoni* Hellenthal and Price (2003)

Myrsidea johnsoni Hellenthal and Price (2003): 13. Type host:

Pycnonotus atriceps (Temminck, 1822) – Black-headed Bulbul (Pycnonotidae).

Material studied. 2♀, 2♂, MALAYSIA: YSFMA in Sabah (4°58'N, 117°4'E), ex *Pycnonotus atriceps* (Pycnonotidae), 7.viii.2015 (Ramón Soto Madrid) (MMBC). 2♀, 2♂, MALAYSIA: YSFMA in Sabah, ex *Pycnonotus melanoleucos* (Eyton, 1839) – Black-and-white Bulbul (Pycnonotidae), 12.viii.2015 (Ramón Soto Madrid) (MMBC).

Remarks. Our specimens differ from the description of *M. johnsoni* presented by Hellenthal and Price (2003) by setal counts and dimensions as follows [setal counts and dimensions mentioned by Hellenthal and Price (2003) are in parentheses]:

Female (n = 4). Tergal setae: II, 4–5 (5–11); III, 11–14 (13–18); IV, 12–16 (13–18). Postspiracular setae very long on II, IV, VII and VIII (0.35–0.59); long on I, III and VI (0.22–0.30); and short on V (0.14–0.19) (according to Hellenthal and Price (2003) very long on all segments). Sternal setae: VII, 11–15 (9–14).

Dimensions: AW, 0.53–0.54 (0.55–0.59); ANW, 0.19–0.20 (0.20–0.22); TL, 1.28–1.31 (1.38–1.50).

Male (n = 4). Postspiracular setae very long on II, IV, VII and VIII (0.30–0.48); long on I, III and VI (0.17–0.26); and short on V (0.11–0.13) (according to Hellenthal and Price (2003) very long on all segments). Sternal setae: II, 4–6 (4–5) in each aster; VI, 20–28 (21–37).

Dimensions: HL, 0.25–0.27 (0.26–0.28); TL, 0.99–1.02 (1.04–1.15).

3.1.6. *Myrsidea macronoi* Price et al. (2006)

(Fig. 5E).

Myrsidea macronoi Price et al. (2006): 371. Type host: *Macronus gularis* = *Mixornis gularis* (Horsfield, 1822) – Pin-striped Tit-babbler (Timaliidae).

Material studied. 1♀, 1♂, MALAYSIA: YSFMA in Sabah (4°58'N, 117°4'E), ex *Stachyris poliocephala* (Temminck, 1836) – Gray-headed Babbler (Timaliidae), 23.vi.2015 (Ramón Soto Madrid) (MMBC).

Remarks. Our specimens differ from the redescription of *M. macronoi* presented by Price et al. (2006) by setal counts and dimensions as follows [setal counts and dimensions mentioned by Price et al. (2006) are in parentheses]:

Female (n = 1). Tergal setae: VI, 12 (9–11).

Dimensions: MW, 0.41 (0.43–0.47); AW, 0.60 (0.62–0.64); ANW, 0.21 (0.22–0.24); TL, 1.45 (1.47–1.58).

Male (n = 1). Metanotum with 3 (4) marginal setae; metasternal plate with 6 (4) setae.

Tergal setae: I, 3 (2); IV, 13 (10–12); VI, 13 (8–11); VIII, 6 (4). Sternal setae: III, 14 (11–13); V, 34 (29–32); VII, 28 (18–27).

Dimensions: HL, 0.26 (0.27–0.30).

There is very simple drawing of male genital sac sclerite in the original description (see Fig. 8 in Price et al., 2006), so we redrew it from another view also here to see its variability (Fig. 5E).

3.1.7. *Myrsidea ochracei* Hellenthal and Price (2003)

Myrsidea ochracei Hellenthal and Price (2003): 12. Type host: *Alophoixus ochraceus* (F. Moore, 1854) – Ochraceus Bulbul (Pycnonotidae).

Material studied. 3♀, 1♂, MALAYSIA: YSFMA in Sabah (4°58'N, 117°4'E), ex *Alophoixus bres* (R. Lesson, 1831) – Gray-cheeked Bulbul (Pycnonotidae), 9 and 13.viii.2015 (Ramón Soto Madrid) (MMBC). 1♀, 1♂, MALAYSIA: YSFMA in Sabah, ex *Alophoixus finschii* (Salvadori, 1871) – Finsch's Bulbul (Pycnonotidae), 3.viii.2015 (Ramón Soto Madrid) (MMBC).

Remarks. Our specimens differ from the description of *M. ochracei* presented by Hellenthal and Price (2003) by setal counts and dimensions as follows [setal counts and dimensions mentioned by Hellenthal and Price (2003) are in parentheses]:

Female (n = 4). Sternal setae: VI, 22–36 (24–35). Ventral anal fringe formed by 28–32 (31–39) setae.

Dimensions: HL, 0.28–0.31 (0.30–0.33); AW, 0.53–0.58 (0.56–0.70); ANW, 0.18–0.21 (0.20–0.23); TL, 1.32–1.39 (1.34–1.65).

Male (n = 2). Sternal setae: 5–6 (4–5) in each aster; V, 24–28

(26–45); VII, 9–11 (10–18).

Dimensions: AW, 0.43–0.45 (0.45–0.53); TL, 1.06–1.11 (1.11–1.28).

3.1.8. *Myrsidea plumosi* Hellenenthal and Price (2003)

Myrsidea plumosi Hellenenthal and Price (2003): 10. Type host: *Pycnonotus plumosus* (Blyth, 1845) – Olive-winged Bulbul (Pycnonotidae).

Material studied. 1♂, MALAYSIA: YSFMA in Sabah (4°58'N, 117°4'E), ex *Pycnonotus brunneus* (Blyth, 1845) – Red-eyed Bulbul (Pycnonotidae), 15.viii.2014 (Marte Fandrem) (MMBC).

Remarks. Our specimen differs from the description of *M. plumosi* presented by Hellenenthal and Price (2003) by setal counts and dimensions as follows [setal counts and dimensions mentioned by Hellenenthal and Price (2003) are in parentheses]:

Male (n = 1). Tergal setae: III, 5 (7–12); V, 6 (7–12); VI, 5 (6–9).

Dimensions: LSVII, 0.08 (0.18–0.28).

3.1.9. *Myrsidea pycnonoti* Eichler (1947)

Myrsidea pycnonoti Eichler (1947): 18. Type host: “*Pycnonotus analis* Horsf.” = *Pycnonotus goavier analis* (Horsfield, 1821) – Yellow-vented Bulbul (Pycnonotidae).

Material studied. 3♀, 1♂, MALAYSIA: YSFMA in Sabah (4°58'N, 117°4'E), ex *Tricholestes criniger* (Blyth, 1845) – Hairy-backed Bulbul (Pycnonotidae), 4 and 9.viii.2015 (Ramón Soto Madrid) (MMBC).

Remarks. Our specimens differ from the redescription of *M. pycnonoti* presented by Hellenenthal and Price (2003) by setal counts and dimensions as follows [setal counts and dimensions mentioned by Hellenenthal and Price (2003) are in parentheses]:

Female (n = 3). Tergal setae: I, 3–4 (4–6); II, 5–6 (6–12). Postspiracular setae very long on II–VIII (0.28–0.51), but conspicuously shorter on I (0.21–0.26) (according to Hellenenthal and Price (2003) very long on all segments). Sternal setae: VI, 19–30 (25–46); VII, 10–12 (11–20). Anal fringe with 24–30 (28–40) ventral setae.

Dimensions: HL, 0.28–0.29 (0.29–0.34); MW, 0.39–0.41 (0.40–0.48); AW, 0.54–0.56 (0.56–0.66); LSVII, 0.13–0.24 (0.12–0.22); ANW, 0.20 (0.21–0.25); TL, 1.30–1.32 (1.38–1.57).

Male (n = 1). Postspiracular setae very long on I–IV and VI–VIII (0.23–0.45); long, but conspicuously shorter on V (0.19) (according to Hellenenthal and Price (2003) very long on all segments). Sternal setae: VII, 10 (11–20).

Dimensions: LSVII, 0.14 (0.09–0.12).

3.1.10. *Myrsidea ramoni* Soto Madrid & Sychra, new species

(Fig. 4A–E, 7A–B).

Type host. *Copsychus malabaricus stricklandii* (Motley and Dillwyn, 1855) – White-crowned Shama (Muscicapidae).

Type locality. YSFMA in Sabah, MALAYSIA (4°58'N, 117°4'E).

Type material. Holotype, ♀, MALAYSIA: YSFMA in Sabah (4°58'N, 117°4'E), ex *Copsychus malabaricus stricklandii*, 9.viii.2015 (Ramón Soto Madrid) (MMBC). Paratypes, 4♀, 2♂ with the same data as holotype.

Diagnosis. Until now, there were only three species of *Myrsidea* described on flycatchers (Muscicapidae) — *Myrsidea subdissimilis* Uchida (1926) from *Cyanoptila cyanomelana* (Temminck, 1829) in Japan (Uchida 1926), *Myrsidea proterva* Złotorzycka (1964) from *Muscicapa striata* (Pallas, 1764) in Poland (Złotorzycka 1964) and *Myrsidea mariquensis* Halajian and Sychra, 2012 from *Bradornis mariquensis* Smith (1847) in South Africa. *Myrsidea ramoni* sp.n. is morphologically very close to *M. mariquensis*. Both species are separated from the first two aforementioned species by a smaller number of tergal setae in the female, especially on tergite I (5–6 vs. more than 10). Female of *M. ramoni* sp.n. is separated from that of *M. mariquensis* by 1) shorter DHS 10, i. e. with ratio DHS10/11 0.27–0.45 (vs. 0.59–0.65 for *M. mariquensis*); higher number on tergites II–VIII, total number 57–77 (vs. 29–38), and 3) postspiracular setae very long on all segments (vs. conspicuously shorter on tergites III and V). While the male of *M. proterva* is unknown,

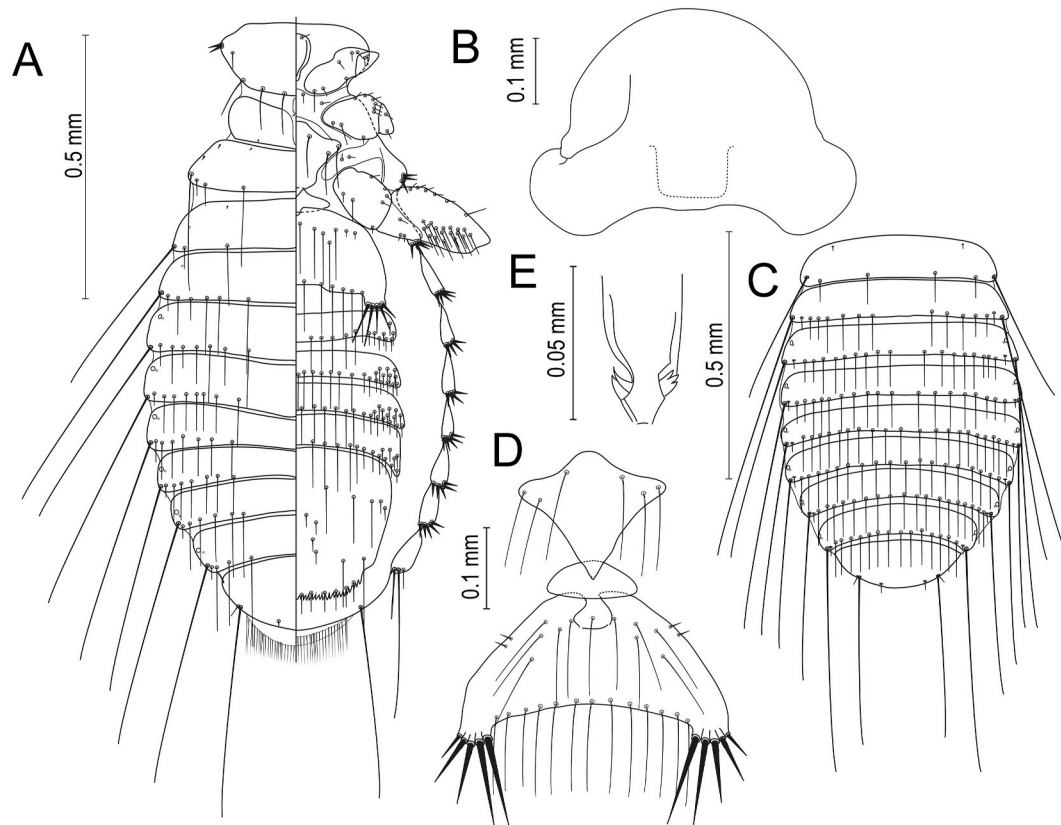


Fig. 4. *Myrsidea ramoni* sp.n. A, dorso-ventral view of female thorax and abdomen; B, head shape; C, dorsal view of male abdomen; D, male metasternal plate and sternites I–II; E, male genital sac sclerite.

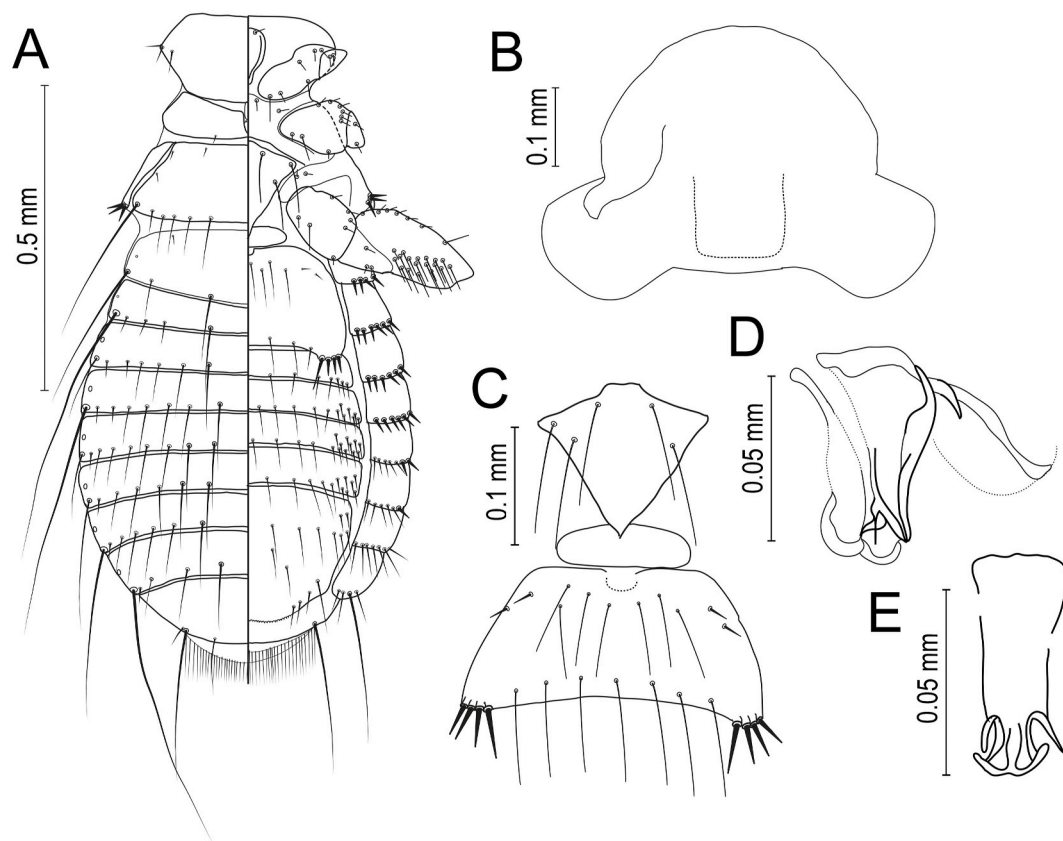


Fig. 5. *Myrsidea victoriae* sp.n. A–D, dorso-ventral view of female thorax and abdomen (A), head shape (B), male metasternal plate and sternites I–II (C), male genital sac sclerite (D); *Myrsidea macronoi* E, male genital sac sclerite.

the male of *M. ramoni* sp.n. differs, together with male of *M. mariquensis*, from that of *M. subdissimilis* by larger dimensions, especially TW (0.44–0.46 vs. 0.40–0.41). Male of *M. ramoni* sp.n. is separated from that of *M. mariquensis* by very high number setae on tergites II–VIII (122–132 vs. 44), arranged into continuous row across each segment. This sexual dimorphism is quite unusual within *Myrsidea*. To our knowledge, it is only known in *Myrsidea* using Hirundinidae as host, but these lice are well-characterised by their strongly flattened frons (Zlotorzyska, 1964).

Female (n = 5). As in Figs. 4A and 7A. Hypopharyngeal sclerites fully developed. Shape of head as in Fig. 4B. Length of DHS 10, 0.03–0.05; DHS 11, 0.10–0.12; ratio DHS 10/11, 0.27–0.45. *Ls*5, 0.06–0.07 long, latero-ventral fringe with 10–12 setae. Gula with 4–5 setae on each side. Pronotum with 6 setae on posterior margin and 3 short spiniform setae at each lateral corner. Prosternal plate with rounded anterior margin (Fig. 4A). First tibia with 3 outer ventro-lateral and 4 dorso-lateral setae. Mesonotum divided. Metanotum not enlarged, with 4–5 marginal setae; metasternal plate with 5–7 setae; metapleurites with 3–4 short spiniform setae. Femur III with 15–21 setae in ventral setal brush. Tergites not enlarged and modified as follows: I–II and V–VIII with straight posterior margin, III and IV with small medio-posterior convexity (Fig. 4A). Abdominal segments with well-defined median gap in each row of tergal setae. Tergal setae (postspiracular setae and on tergites II–VIII also short associated setae are not included): I, 4; II, 6–10; III, 11–12; IV, 10–13; V, 8–11; VI, 9–12; VII, 8–11; VIII, 5–8. Postspiracular setae very long on all segments (0.34–0.53). Inner posterior seta of last tergum not longer than anal fringe setae with length 0.02–0.03; length of short lateral marginal seta of last segment, 0.03–0.04. Pleural setae: I, 5; II, 7–8; III, 7–9; IV, 6–9; V, 6–8; VI, 5–6; VII, 3–5; VIII, 3. Pleurites with only short spine-like setae; pleurites III–V only rarely with 1 anterior seta. Pleurite VIII with inner setae (0.10–0.15) three times as long as outer (0.04–0.05). Anterior margin of

sternal plate II with a medial notch. Sternal setae: I, 0; II, 5–6 in each aster, aster setae length: s1, 0.09–0.10; s2, 0.07–0.09; s3, 0.05–0.06; s4, 0.04–0.06; s5, 0.03–0.06; s6, 0.03; with 10–14 marginal setae between asters, 7–10 medioanterior; III, 22–26; IV, 34–39; V, 38–41; VI, 31–36; VII, 7–11; VIII–IX, 10–14; and 10–13 setae on deeply serrated vulval margin; sternites III–VII without medioanterior setae. Anal fringe formed by 37–44 dorsal and 35–40 ventral setae.

Dimensions: TW, 0.48–0.51; POW, 0.37–0.38; HL, 0.29–0.31; PW, 0.28–0.30; MW, 0.41–0.45; AW, 0.60–0.63; ANW, 0.22–0.23; TL, 1.51–1.57.

Male (n = 2). As in Figs. 4C and 7B. There is strong sexual dimorphism in presence of continuous row of tergal setae across each segment in male, while female has well-defined median gap in each row of tergal setae. Other characteristics of male are similar as for female except as follows. Length of DHS 10, 0.04–0.05; DHS 11, 0.10; ratio DHS 10/11, 0.43–0.45. *Ls*5, 0.07 long, latero-ventral fringe with 11 setae. Metanotum not enlarged with 4 marginal setae (the most posterolateral setae are not counted); metasternal plate with 6 setae; metapleurites with 3 short spiniform strong setae. Femur III with 15–19 setae in ventral setal brush. Abdominal segments with continuous row of tergal setae across each segment. Tergal setae (postspiracular setae and on tergites II–VIII also short associated setae are not included): I, 4; II, 11–12; III, 17–18; IV, 18–22; V, 22; VI, 18–20; VII, 19–22; VIII, 16–17. Postspiracular setae very long on all segments (0.27–0.49). Length of inner posterior seta of last tergum, 0.01–0.02; short lateral marginal seta of last segment, 0.02–0.03. Pleural setae: I, 5; II, 5–7; III, 6–8; IV, 6–8; V, 6–7; VI, 6–7; VII, 4–5; VIII, 3. Pleurites with only short spine-like setae. Pleurite VIII with inner setae (0.12–0.14) three times as long as outer (0.04–0.05). Anterior margin of sternal plate II with a medial notch (Fig. 4D). Sternal setae: I, 0; II, 4–5 in each aster, aster setae length: s1, 0.09; s2, 0.08; s3, 0.06–0.08; s4, 0.05–0.06; s5, 0.03–0.04; with 10–13 marginal setae between asters, 9–10 medioanterior; III, 19–20; IV, 31–33; V, 35–36; VI,

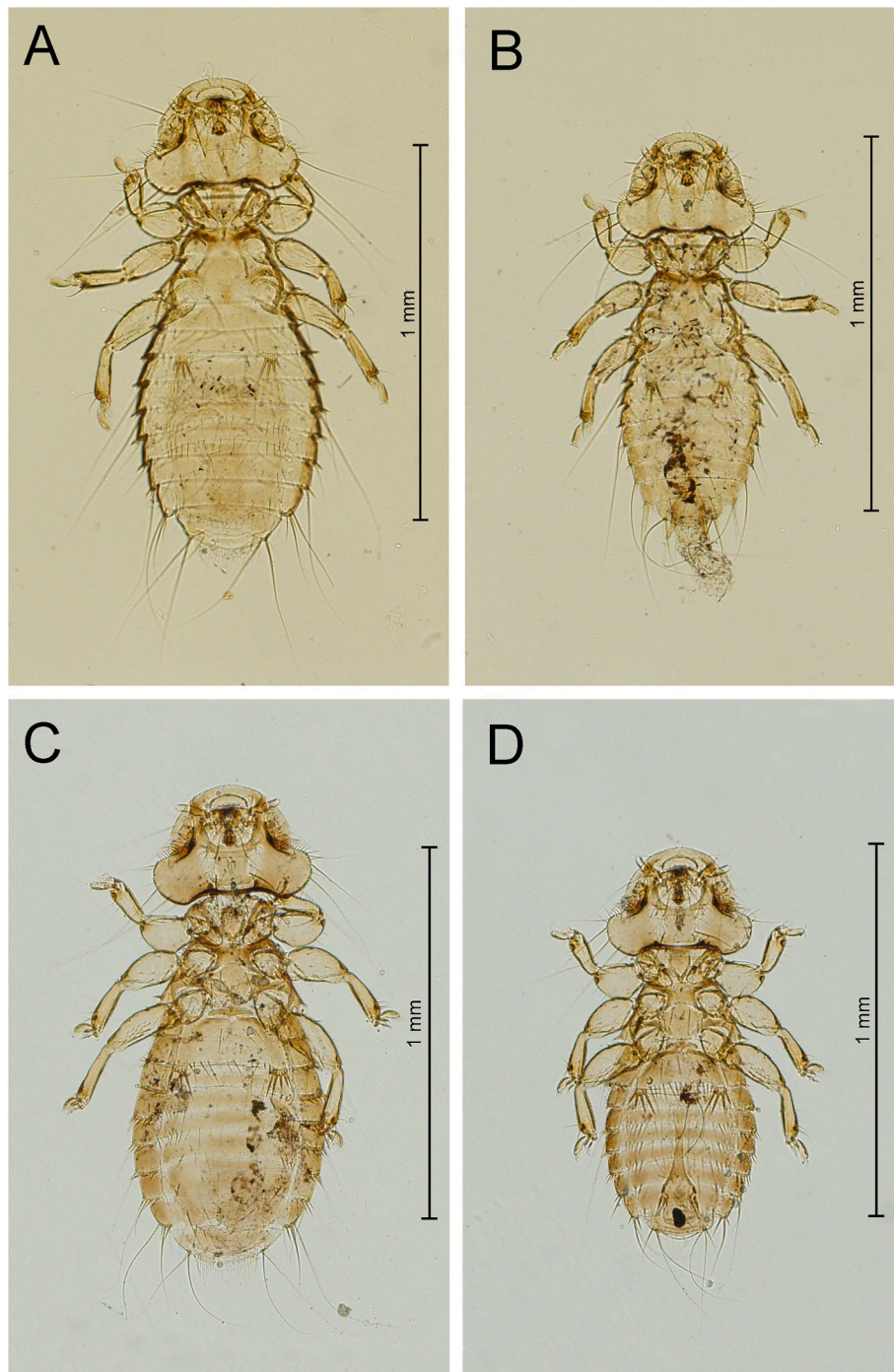


Fig. 6. Habitus. *Myrsidea carmenae* sp.n. A-B, holotype female (A), paratype male (B). *Myrsidea francisca* sp.n. C-D, holotype female (C), paratype male (D).

28–29; VII, 12; VIII, 5–11; remainder of plate, 6–8; and with 4 setae posteriorly; sternites III–VII without medioanterior setae. With 8 internal anal setae. Genital sac scleriteas in Fig. 4E.

Dimensions: TW, 0.46–0.46; POW, 0.34–0.36; HL, 0.28–0.29; PW, 0.27–0.28; MW, 0.37–0.38; AW, 0.49–0.51; GW, 0.11; GL, 0.44–0.45; ParL, 0.09; GSL, 0.37–0.40; TL, 1.33–1.35.

Etymology. This species epithet is named in honor of Ramón Madrid Belizón, cousin of the first author.

3.1.11. *Myrsidea victoriae* Soto Madrid & Sychra, new species (Fig. 5A–D, 7C–D).

Type host. *Turdinus sepiarius* (Horsfield, 1821) – Horsfield's Babbler (Pellorneidae).

Type locality. YSFMA in Sabah, MALAYSIA (4°58'N, 117°4'E).

Type material. Holotype, ♀, MALAYSIA: YSFMA in Sabah (4°58'N, 117°4'E), ex *Turdinus sepiarius*, 15.viii.2014 (Marte Fandrem) (MMBC). Paratypes, 1♀, 1♂ with the same data as holotype.

Diagnosis. According to the male genital sclerite, the male of *Myrsidea victoriae* sp.n. is close to *M. monilegeri* Tandan (1972) that was described on the base of single male from *Garrulax monileger fuscatus* Baker (1918) (Leiothrichidae) from Thailand. Both males can be easily distinguished by (1) the form of hypopharynx (fully developed in *M. victoriae* sp.n. and considerably reduced in *M. monilegeri*), (2) smaller number of tergal setae on segments I–III (4, 6, 8 on *M. victoriae* sp.n. and 7, 11, 13 on *M. monilegeri*), and (3) absence of anterior setae on pleurites (these setae are present on *M. monilegeri*). Except for the male genital sac

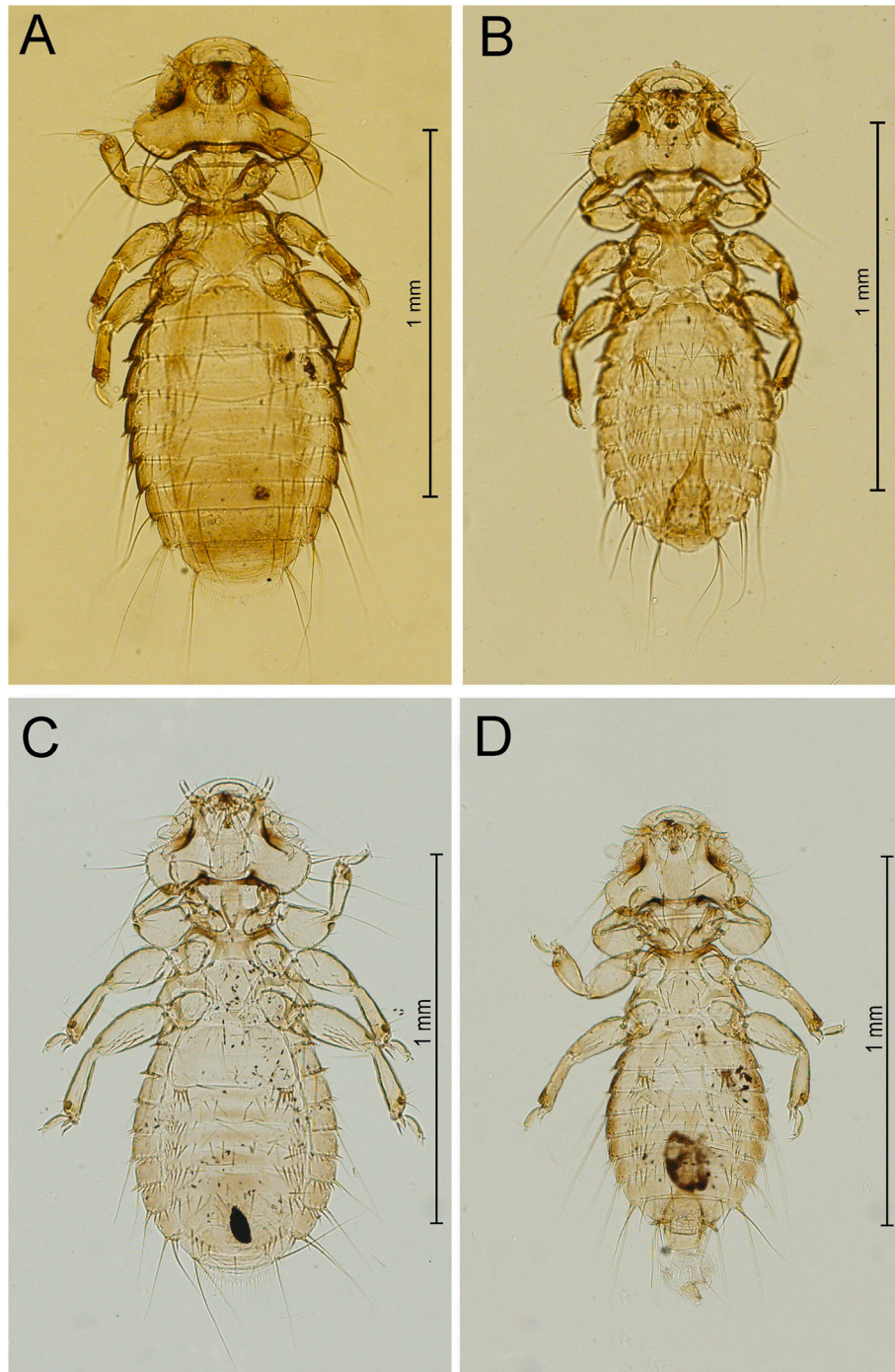


Fig. 7. Habitus. *Myrsidea ramoni* sp.n. A-B, holotype female (A), paratype male (B). *Myrsidea victoriae* sp.n. C-D, holotype female (C), paratype male (D).

sclerite *Myrsidea victoriae* sp.n. is morphologically very close to *M. duplicata* Tandan (1972) from *Pomatorhinus schisticeps* Hodgson (1836) (Timaliidae) from Thailand. Both sexes are well separated from those of *M. duplicata* by 1) smaller number of tergal setae on segments II–VIII (total number of setae, 63–65 vs. 87–90 in female; and 55 vs. 65–76 in male); 2) presence median gap in each row of tergal setae; and 3) smaller dimensions, especially TW (0.45–0.46 vs. 0.47–0.49 in female; and 0.40 vs. 0.45–0.46 in male).

Female (n = 2). As in Figs. 5A and 7C. Hypopharyngeal sclerites fully developed. Shape of head as in Fig. 5B. Length of DHS 10, 0.04–0.05; DHS 11, 0.10; ratio DHS 10/11, 0.42–0.48. Ls5, 0.06 long, latero-ventral fringe with 9 setae. Gula with 3 setae on each side. Pronotum with 6 setae on posterior margin and 3 short spiniform setae at each lateral

corner. Prosternal plate with rounded anterior margin (Fig. 5A). First tibia with 3 outer ventro-lateral and 4 dorso-lateral setae. Mesonotum divided. Metanotum not enlarged, with 8–10 marginal setae; metasternal plate with 6 setae; metapleurites with 2 short strong spiniform setae. Femur III with 14–16 setae in ventral setal brush. Tergites modified as follows: I enlarged with widely rounded posterior margin, II–VIII not enlarged and all with straight posterior margin (Fig. 5A). Abdominal segments with small median gap in each row of tergal setae. Tergal setae (postspiracular setae and on tergites II–VIII also short associated setae are not included): I, 4; II, 7–9; III, 7–10; IV, 11–13; V, 13–14; VI, 11; VII, 11; VIII, 7. Postspiracular setae very long on II, IV, VII and VIII (0.30–0.41); long on I and VI (0.24–0.28); and short on III and V (0.13–0.15). Inner posterior seta of last tergum longer than anal fringe

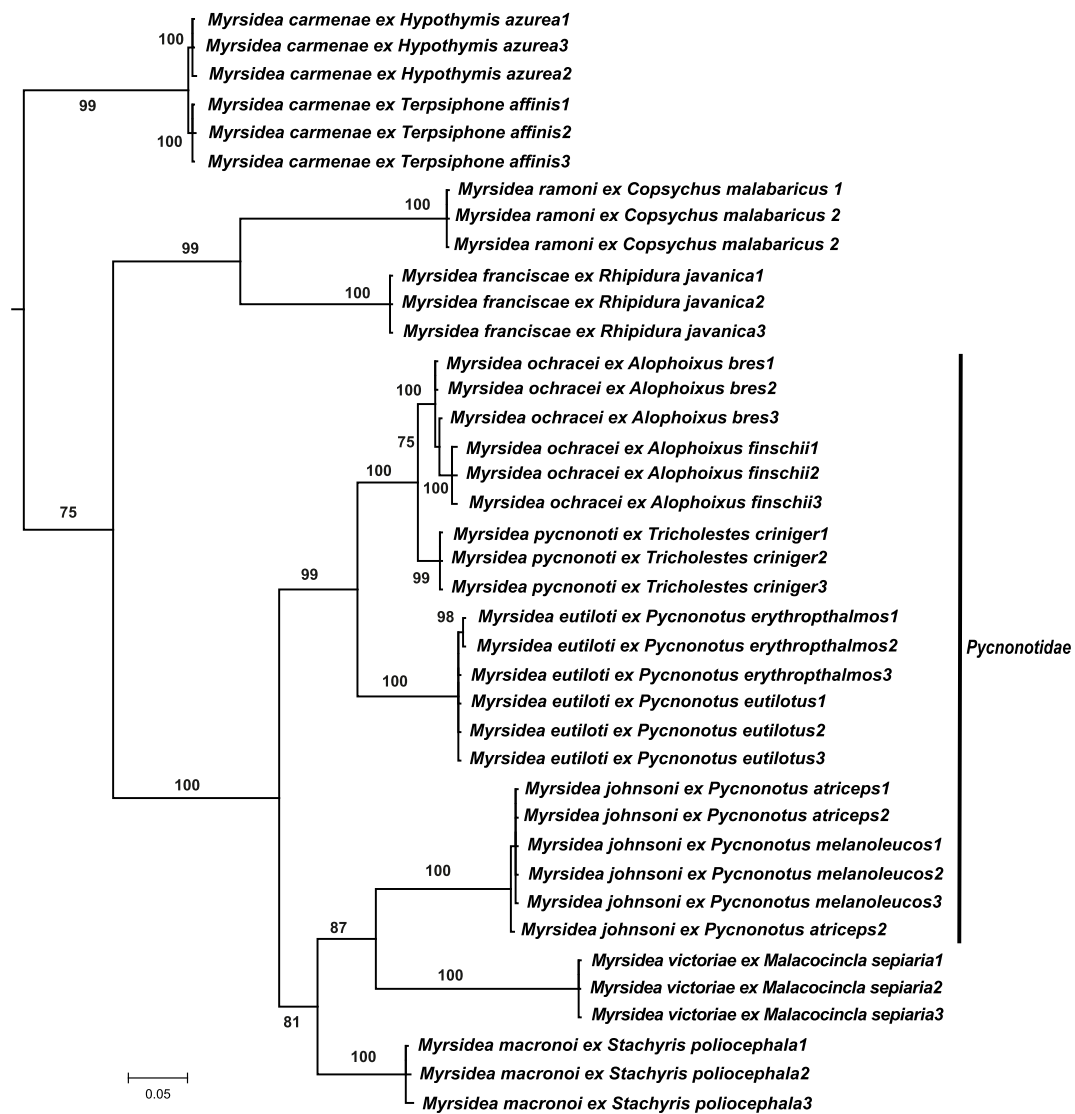


Fig. 8. Bayesian phylogeny of Bornean *Myrsidea* studied based on analysis of the mitochondrial cytochrome *c* oxidase subunit I (*COI*) and elongation factor-1 α (*EF-1 α*) genes. Outgroup taxon was removed from this figure for readability. Hosts belong to family Pycnonotyidae are indicated on the right.

setae with length 0.08; length of short lateral marginal seta of last segment, 0.04. Pleural setae: I, 4–5; II, 6–8; III, 6–8; IV, 7–8; V, 7–8; VI, 7–8; VII, 5–6; VIII, 3–4. Pleurites with only short spine-like setae. Pleurite VIII with inner setae (0.05–0.08) as long as outer (0.04–0.05). Anterior margin of sternal plate II without a medial notch. Sternal setae: I, 0; II, 4 in each aster, aster setae length: s1, 0.05–0.07; s2, 0.04; s3, 0.03; s4, 0.02–0.03; with 7 marginal setae between asters, 7 medioanterior; III, 14; IV, 26–28; V, 32–34; VI, 26–27; VII, 14–17; VIII–IX, 7–9; and 5–6 setae separated by large median gap into two groups of 2–3 setae on deeply serrated vulval margin with slight medioposterior concavity; sternites III–VII without medioanterior setae. Anal fringe formed by 30–31 dorsal and 30–32 ventral setae.

Dimensions: TW, 0.45–0.46; POW, 0.32; HL, 0.28–0.29; PW, 0.28; MW, 0.43; AW, 0.56–0.57; ANW, 0.21; TL, 1.37–1.41.

Male ($n = 1$). As in Fig. 7D. Similar as female except as follows. Length of DHS 10, 0.05; DHS 11, 0.10; ratio DHS 10/11, 0.50. *Ls*5, 0.05 long, latero-ventral fringe with 10 setae. Metanotum not enlarged with 5 marginal setae (the most posterolateral setae are not counted); metasternal plate with 6 setae; metapleurites with 2 short spiniform strong setae. Femur III with 14 setae in ventral setal brush. Abdominal segments with well-defined median gap in each row of tergal setae. Tergal setae (postspiracular setae and on tergites II–VIII also short associated

setae are not included): I, 4; II, 6; III, 8; IV, 11; V, 10; VI, 10; VII, 10; VIII, 6. Postspiracular setae very long on II, IV, VII and VIII (0.30–0.40); long on I and VI (0.21–0.23); and short on III and V (0.11); Length of inner posterior seta of last tergum, 0.07; short lateral marginal seta of last segment, 0.02. Pleural setae: I, 4; II, 6–7; III, 6–7; IV, 7; V, 6; VI, 6; VII, 5; VIII, 3. Pleurites with only short spine-like setae. Pleurite VIII with inner setae (0.06–0.08) as long as outer (0.04–0.05). Anterior margin of sternal plate II without a medial notch (Fig. 5C). Sternal setae: I, 0; II, 4 in each aster, aster setae length: s1, 0.04–0.05; s2, 0.03–0.04; s3, 0.03; s4, 0.02–0.03; with 7 marginal setae between asters, 7 medioanterior; III, 8; IV, 22; V, 26; VI, 23; VII, 13; VIII, 3; remainder of plate, 12; and with 5 setae posteriorly; sternites III–VII without medioanterior setae. With 8 internal anal setae. Genital sac sclerites in Fig. 5D.

Dimensions: TW, 0.40; POW, 0.29; HL, 0.27; PW, 0.25; MW, 0.34; AW, 0.45; GW, 0.11; GL, 0.42; ParL, 0.07; GSL, 0.06; TL, 1.16.

Etymology. This species epithet is name in honor of Victoria Soto Madrid, sister of the first author.

3.2. Phylogeny and OTU delimitation

We obtained 74 sequences for the partial genes *COI* and *EF-1 α* (one of each per specimen) from 37 *Myrsidea* specimens for nine species with

obtained DNA samples (except *Myrsidea plumosi*). Results of the phylogenetic analysis (Fig. 8) showed a well-supported clade of six *Myrsidea* species from hosts of the family Pycnonotidae, Timaliidae and Pellorneidae.

Molecular operational taxonomic unit (MOTU) analysis based on *COI* partial sequence resulted in partitioning our data set into 9–10 MOTUs. Delimitation results between analyses were congruent and highly coincident with our morphological studies (Fig. 9). The GMYC results with single-threshold model suggested the presence of 10 groups, similar to the number of MOTUs estimated with bPTP method and morphology. While the distance-based approach (‘barcode gap analyses’) by the ABGD for the analyzed *COI* region did not support delimitation between *Myrsidea pycnonoti* and *Myrsidea ochracei* ($p > 0.05$). Thus, species delimitation algorithms mostly supported the species boundaries hypothesized by morphological studies and confirmed that four species of *Myrsidea* out of 10 species studied are not specific for a single host.

3.3. Cophylogenetic analysis

To test whether the host specificity corresponded with the congruence of parasite and host phylogenies, we performed cophylogenetic

analysis. Cophylogenetic analyses based on nine *Myrsidea* taxa from the community studied (in total 13 host-parasite links were tested) indicated a certain amount of congruence between the host and parasite phylogenies. Distance-based test ParaFit was significant for the chewing lice/passerine birds links (ParaFit global = 5432.699, p -value = 0,00006 for 9999 permutations), thus rejecting the independence of the host and parasite phylogenies. The ParaFitLink test showed that four species: *M. ochracei*, *M. eutiloti*, *M. franciscae* and *M. carmenae* (Table 2) contributed to the overall congruence the most, however only the latter host-parasite link (*M. carmenae* and their hosts *Terpsiphone affinis* and *Hypothymis azurea*) p -value was significant after the multiple testing correction.

The event-based method of Jane also recovered a global signal of congruence across the whole data set. The event reconstruction recovered three cospeciation events, between *M. carmenae* and *M. franciscae* and their hosts *Terpsiphone affinis*, *Hypothymis azurea* and *Rhipidura javanica*, between *M. macronoi* and *M. victoriae* and their hosts *Stachyris poliocephala* and *Turdinus sepiarius*, and for *M. pycnonoti* and *M. ochracei* and their hosts *Tricholestes criniger* and *Alophoixus bres* and *Alophoixus finschii* (Fig. 10). Jane also recovered two duplications events for *M. macronoi* and *M. victoriae* (not shown) and host switch for *M. ramoni*

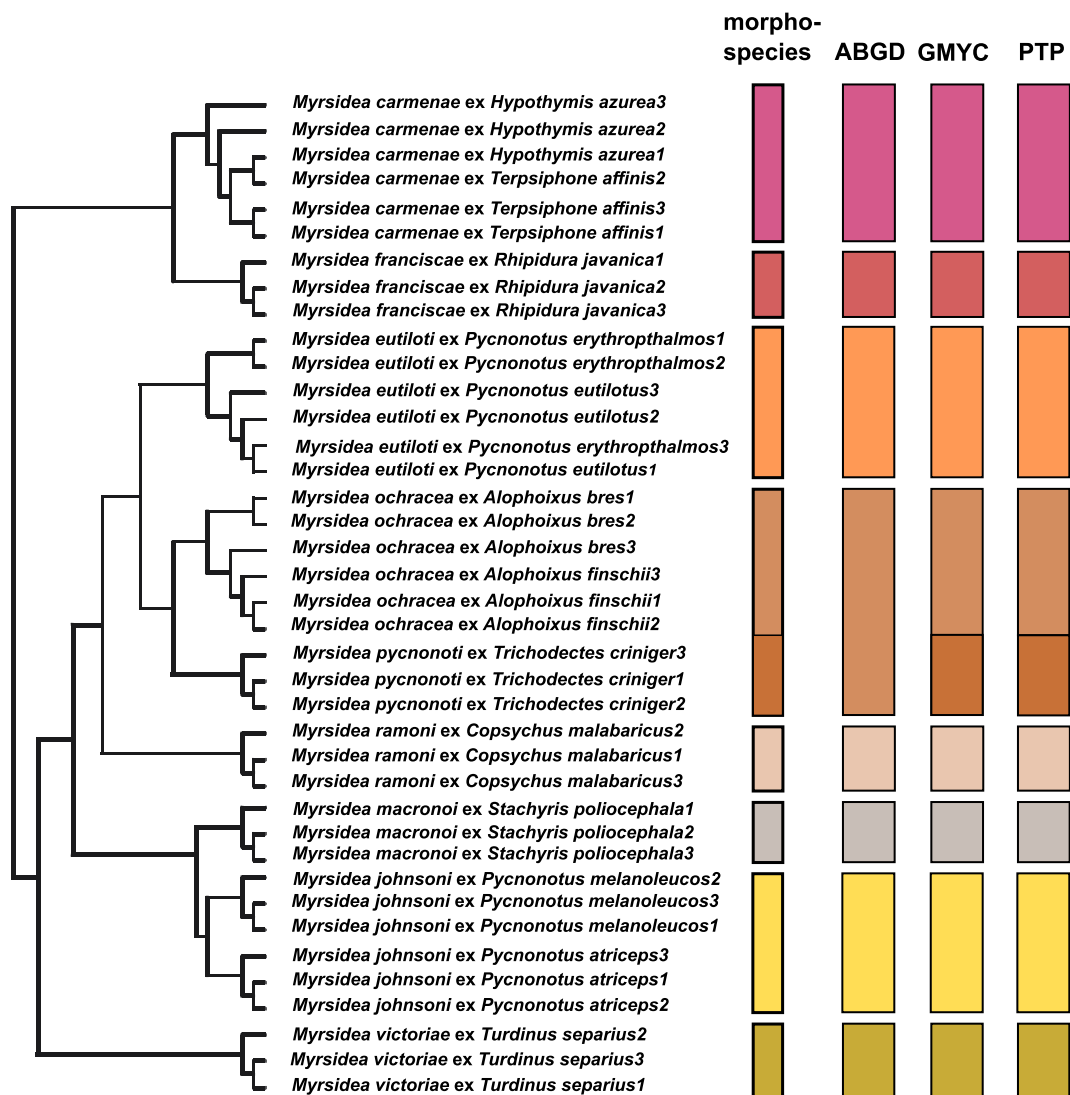


Fig. 9. A species delimitation of Bornean *Myrsidea* studied inferred from a partial sequence of the mitochondrial *COI* gene. Validation methods shown on Bayesian tree of hypothetical species. Colors represent unique partitions and correspond to operational taxonomic units (OTU) by various methods of species delimitation: morphological, Automatic Barcode Gap Discovery (ABGD), Generalized Mixed Yule Coalescent analyses (GMYC), and Poisson Tree Process analyses (PTP) respectively.

Table 2

Results of the ParaFit analysis on Bornean *Myrsidea* lice studied and their avian hosts. The global test results ParaFitGlobal = 5432.699, p-value = 6e-04 (9999 permutations) and each individual link test results are indicated. For the individual link test, values in bold with an asterisk (*) indicate significant values after the Benjamini-Hochberg correction.

Avian host species	<i>Myrsidea</i> species	F1.stat	p.F1	F2.stat	p.F2
<i>Turdinus sepiarius</i>	<i>Myrsidea victoriae</i>	224.1191	0.1575	4.873291e-07	0.1575
<i>Pycnonotus atriceps</i>	<i>Myrsidea johnsoni</i>	320.4024	0.0598	6.966896e-07	0.0598
<i>Pycnonotus melanoleucos</i>	<i>Myrsidea johnsoni</i>	320.4024	0.0607	6.966896e-07	0.0607
<i>Stachyris poliocephala</i>	<i>Myrsidea macronoi</i>	235.6936	0.1423	5.124970e-07	0.1423
<i>Alophoixus bres</i>	<i>Myrsidea ochracei</i>	407.0476	0.0458	8.850927e-07	0.0458
<i>Alophoixus finschii</i>	<i>Myrsidea ochracei</i>	407.0476	0.0416	8.850927e-07	0.0416
<i>Tricholestes criniger</i>	<i>Myrsidea pycnonoti</i>	368.4375	0.0685	8.011380e-07	0.0685
<i>Pycnonotus erythroptalmos</i>	<i>Myrsidea eutiloti</i>	382.3593	0.0476	8.314099e-07	0.0476
<i>Pycnonotus eutilotus</i>	<i>Myrsidea eutiloti</i>	382.3593	0.0478	8.314099e-07	0.0478
<i>Rhipidura javanica</i>	<i>Myrsidea franciscaae</i>	1292.2507	0.0256	2.809896e-06	0.0256
<i>Copsychus malabaricus</i>	<i>Myrsidea ramoni</i>	800.9454	0.0690	1.741592e-06	0.0690
<i>Terpsiphone paradisi</i>	<i>Myrsidea carmenae</i>	1699.4445	0.0003*	3.695307e-06	0.0003*
<i>Hypothymis azurea</i>	<i>Myrsidea carmenae</i>	1699.4445	0.0003*	3.695307e-06	0.0003*

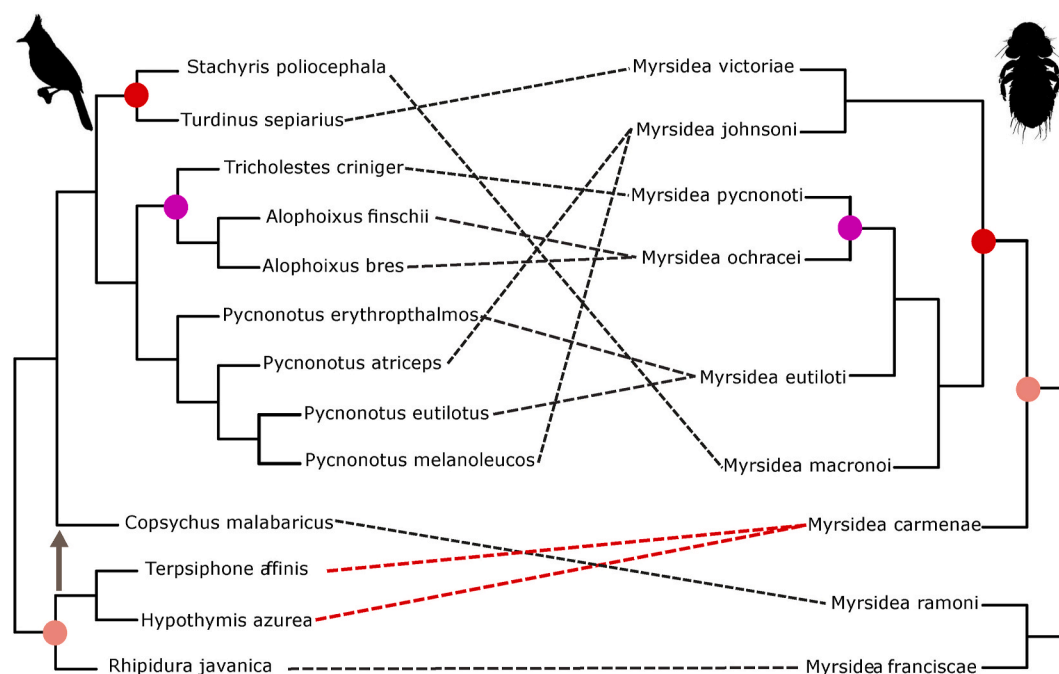


Fig. 10. Tanglegram of phylogenies of Bornean avian host (left) and associated *Myrsidea* lice (right) studied. Colored circles above nodes indicate cospeciation events recovered from Jane (they correspond to 83% of the solutions with p-value of 0.001). Arrow indicates a host switching event recovered by Jane. Red lines indicate significant host-parasite links estimated by the ParaFitLink1 test.

(Fig. 10).

4. Discussion

4.1. Morphology

Besides the description of four new species, this study includes the first records of chewing lice from *Alophoixus finschii*, *Stachyris poliocephala*, *Terpsiphone affinis* and *Turdinus sepiarius*, and two new host-lice associations for previously known species of *Myrsidea*, as follows: *A. finschi* for *M. ochraceus* and *S. poliocephala* for *M. macronoi*. Although there are records of *Myrsidea* sp. from *Hypothymis azurea* and *Copsychus malabaricus* from the Malay Peninsula and Vietnam (Sandosham et al., 1965; Najer et al., 2014, respectively) and from *Rhipidura javanica* from the Malay Peninsula (Sandosham et al., 1965), this is the first determination of a chewing louse from these hosts to the species level.

Our material of six previously described species of *Myrsidea*

(*M. eutiloti*, *M. johnsoni*, *M. macronoi*, *M. ochracei*, *M. plumosi* and *M. pycnonoti*) differs slightly from original descriptions or re-descriptions, particularly in setal counts and dimensions. Our data increase knowledge of both their intraspecific morphological variability and their geographical distribution. *Myrsidea plumosi*, previously known from Thailand and Malay Peninsula (Hellenthal and Price, 2003), is reported for the first time from Borneo. Five other species have already been reported from Sarawak, northwest Borneo (Hellenthal and Price, 2003; Price et al., 2006).

4.2. Phylogenetics

Phylogenetic analyses of *Myrsidea* species from the New World and Africa based on the same partial *COI* and *EF-1 α* genes have previously been performed (Bueter et al., 2009; Gajdošová et al., 2020), although on a very limited number of *Myrsidea* species. No sequences from the oriental *Myrsidea* have been published to date.

Hellenthal and Price (2003) morphologically distinguished three

species groups of *Myrsidea* from bulbuls (Pycnonotidae): *pycnonoti*, *plumosi* and *palmai*. In our data, we had members of two of these groups: *M. pycnonoti* from the *pycnonoti* species group and *M. eutiloti*, *M. johnsoni* and *M. ochracei* from the *plumosi* species group. Our phylogenetic analysis did not support morphological groups suggested by Hellenthal and Price (2003).

Host phylogeny confirmed two large clades within Pycnonotidae, African and Asian, and the sister group of three *Pycnonotus* species (*eutilotus*, *melanoleucos*, and *atriceps*) within the Asian clade (Moyle and Marks, 2006). Our data does not support the sister status of *Myrsidea* species from three *Pycnonotus* species (*eutilotus*, *melanoleucos*, and *atriceps*) within the Asian clade of *Myrsidea*. In our morphological study, we found that the diversity of chewing lice species (10 species of *Myrsidea*) were less diverse than their avian hosts (14 species). However we did not find potential cryptic lineages/species as it was shown for other taxa of chewing lice (Bush et al., 2015; Sweet and Johnson, 2016; Sweet et al., 2018). Morphological keys for *Myrsidea* species are well developed (e.g. Hellenthal and Price, 2003) and our data on species delimitation confirmed that morphospecies diversity reflect the actual diversity of *Myrsidea* species.

In many taxa studied, related chewing lice species tend to live on related host species rather than non-related species (Price et al., 2003). The vast majority of the *Myrsidea* species studied predominantly live on a single host species, suggesting a low level of lice dispersal among hosts (Bueter et al., 2009). Interestingly, we found a significant component of the species studied living on two host species, suggesting that ongoing dispersal and gene flow between sympatric or ecologically similar hosts is relatively common in the tropical community studied.

Our cophylogenetic analysis of the host and *Myrsidea* by both distance-based test ParaFit and event-based method Jane indicated overall congruence between phylogenies of *Myrsidea* and their hosts. In total we recorded three cospeciation events for 14 host-parasite associations. However only one host-parasite link (*M. carmenae* and their hosts *Terpsiphone affinis* and *Hypothymis azurea*) was significant after the multiple testing correction in ParaFit. Similar result with both cospeciation and host switching and duplication events was recently shown for African *Myrsidea* (Gajdošová et al., 2020). Interestingly the congruence of host and *Myrsidea* phylogenies in this study also corresponded with the hosts of family Pycnonotidae.

Thus we showed that even when sampling was limited to one genus, *Myrsidea*, investigation of the chewing lice diversity within this bird community revealed a substantial diversity of parasites, including several undescribed species. Our results highlight the necessity to describe the diversity of parasites in the tropical rainforests and in the Sundaland biodiversity hotspot specifically. This research is especially important for Malaysian Borneo with its high relative rate of deforestation, where many species of parasites, including undescribed species, are facing the extinction.

Declaration of competing interest

None.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ijppaw.2020.10.011>

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