EUROPEAN JOURNAL OF ENTOMOLOGY
ISSN (online): 1802-8829
http://www.eje.cz
Eur. J. Entomol. **114**: 422–429, 2017
doi: 10.14411/eje.2017.054
ORIGINAL ARTICLE

First mitogenome for the subfamily Miltogramminae (Diptera: Sarcophagidae) and its phylogenetic implications

Liping YAN[1,2], Ming ZHANG[1], Yunyun GAO[1], Thomas PAPE[2] and Dong ZHANG[1,*]

[1] School of Nature Conservation, Beijing Forestry University, Beijing, China; e-mails: yanlp523@qq.com, zmbjfu@163.com, 424208072@qq.com, ernest8445@163.com

[2] Natural History Museum of Denmark, University of Copenhagen, Copenhagen, Denmark; e-mail: tpape@snm.ku.dk

Key words. Diptera, Calyptratae, Sarcophagidae, Miltogramminae, mitogenome, flesh fly, phylogeny

Abstract. The mitochondrial genome of *Mesomelena mesomelaena* (Loew, 1848) is the first to be sequenced in the flesh fly subfamily Miltogramminae (Diptera: Sarcophagidae). The 14,559 bp mitogenome contains 37 typical metazoan mitochondrial genes: 13 protein-coding genes, two ribosomal RNA genes and 22 transfer RNA genes, with the same locations as in the insect ground plan. All the protein-coding genes have the start codon ATN, except for *cox1* (TCG). Eight protein-coding genes have the stop codon TAA, while the remaining five have the stop codon T (*cox1*, *cox2*, *nad5*, and *nad4*) or TAG (*cytb*). Synonymous and non-synonymous substitution rates (Ks and Ka) for each protein-coding gene indicate that these genes evolved primarily under negative (or purifying) selection (Ka < Ks). Phylogeny of Sarcophagidae is proposed based on all the sarcophagid mitogenomes in GenBank, and the subfamily topology is reconstructed as (Sarcophaginae (Paramacronychiinae, Miltogramminae)).

INTRODUCTION

With ~3000 described species worldwide (Pape et al., 2011), the Sarcophagidae (Diptera: Calyptratae), also known as flesh flies, are generally subdivided into three subfamilies, Miltogramminae, Paramacronychiinae and Sarcophaginae (Pape, 1996; Piwczyński et al., 2017). It is a young lineage within the schizophoran super-radiation of Diptera (Wiegmann et al., 2011; Cerretti et al., 2017) with diverse life habits, e.g. kleptoparasitism of Hymenoptera (Spofford et al., 1989), predators of other insects, spider egg sacs and reptile eggs (Pickens, 1981; Lopes, 1982; Mullen et al., 1984; Trauth & Mullen, 1990; Pape, 1996), parasitoids of insects and snails (Pape, 1994; McKillup et al., 2000; Stucky, 2015) and necro/coprophagy (Bänziger & Pape, 2004). Thus, the Sarcophagidae are of important ecological, medical and forensic importance. Mitochondrial genomes (mitogenomes) are thought to be reliable markers for phylogeny reconstruction and taxonomic diagnosis (Nelson et al., 2012; Cameron, 2014). Here we document the nearly-complete mitogenome of *Mesomelena mesomelaena* (Loew, 1848) (Figs 1–2), which is the first nearly-complete mitogenomic data for the Miltogramminae and we reconstruct the phylogeny of the Sarcophagidae based on all the mitogenomes in GenBank.

MATERIALS AND METHODS

Two dry specimens of *M. mesomelaena*, whole body of one specimen (collected in 2014), thorax of another (collected in 2015, voucher BFU-06574), were used for DNA extraction using a QIAGEN DNeasy® Blood and Tissue Kit (Qiagen, Hilden, Germany). The mitogenome was amplified in overlapping fragments by 18 primer pairs (Weigl et al., 2010; Zhang et al., 2013) and a pair of specific primers designed from sequenced fragments (Table 1). The PCR was performed in a reaction volume of 25 µL, which contained 1 µL of genome DNA, 1 µL of each primer (10 µM), 2.5 µL of 10 × Es *Taq* PCR Buffer (Beijing Cowin Biosciencee Co., Ltd., China), 2 µL of dNTPs mixture (2.5 mM each) (Beijing Cowin Biosciencee Co., Ltd., China), 0.3 µL Es *Taq* DNA Polymerase (1.5 U) (Beijing Cowin Biosciencee Co., Ltd., China) and 17.2 µL sterling double distilled water. The PCR cycles for all amplifications were the same as used by Zhang et al. (2016b). Products were resolved in 1% agarose gels and stained with Gold View (Beijing Cool Technology Co., Ltd., China), then purified and sequenced bidirectionally by BGI Sequencing (Beijing, China). After assembly of raw sequences by SeqMan (DNAStar, Steve ShearDown, 1998–2001 version DNASTAR Inc., USA), the annotation of the mitogenome was performed as described in Zhang et al. (2016b). The mitogenome map was produced using CGView (Grant & Stothard, 2008).

All the mitochondrial genomes of Sarcophagidae in GenBank were included in the present study, except for two sequences: one with locus KP861920 [stated to be *Sarcophaga crassipalpis*],

* Corresponding author; e-mail: ernest8445@163.com

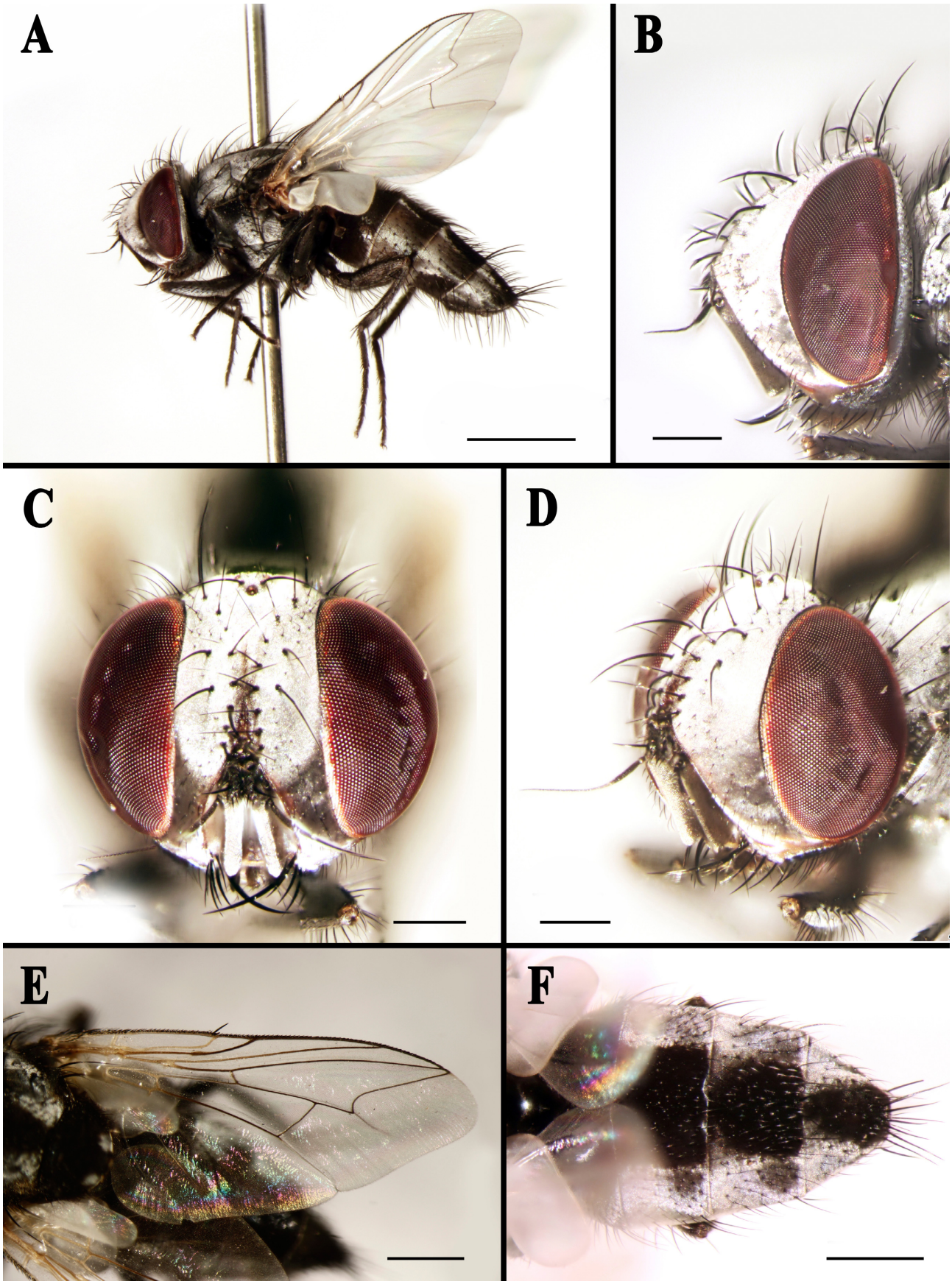

Fig. 1. *Mesomelena mesomelaena* (Loew, 1848), male. A – habitus, lateral view; B – head, lateral view; C – head, anterior view; D – head, anterolateral view; E – right wing, dorsal view; F – abdomen, dorsal view. Scales: A – 2 mm, B–D – 0.5 mm, E and F – 0.5 mm.

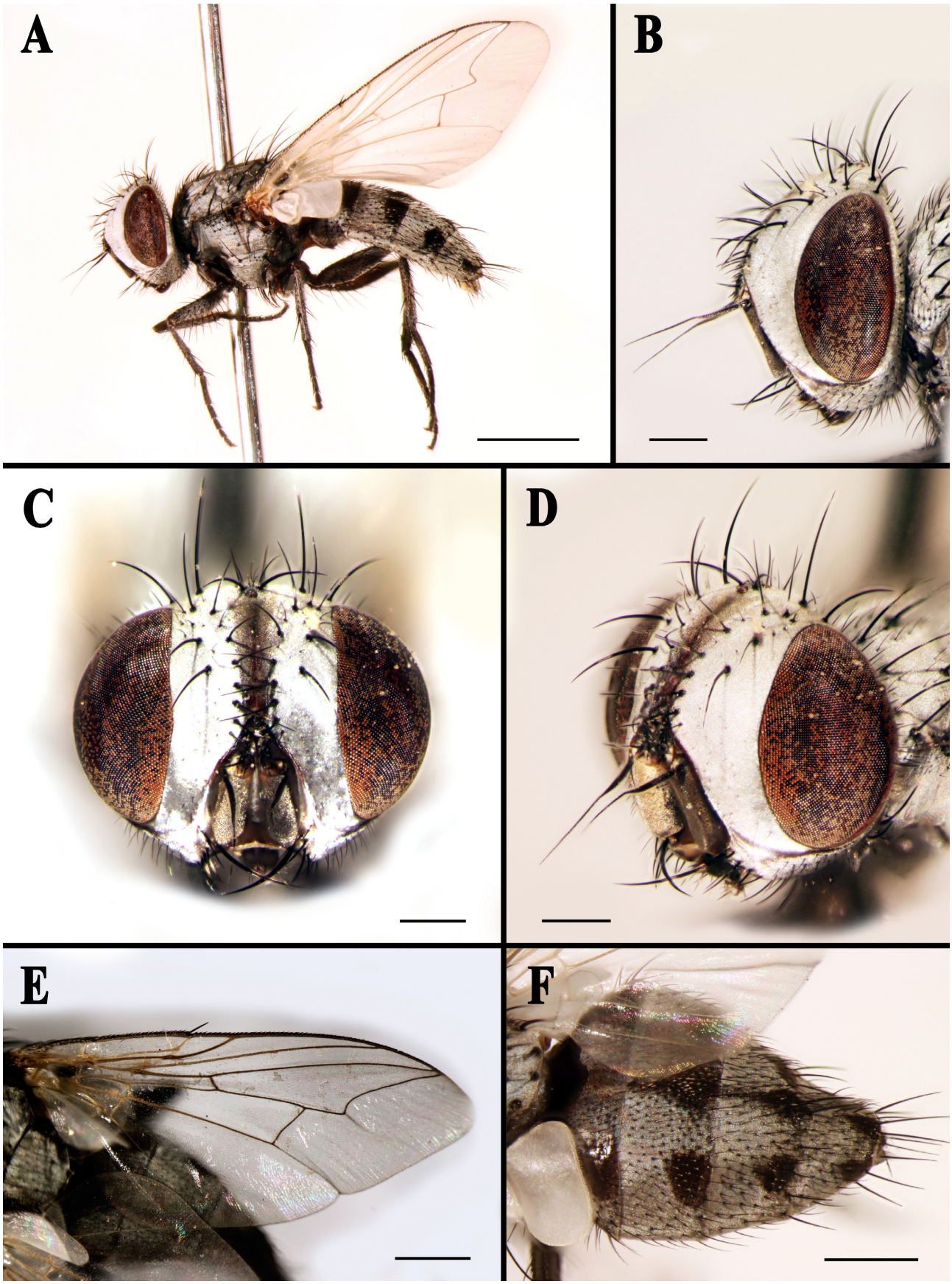

Fig. 2. *Mesomelena mesomelaena* (Loew, 1848), female. A – habitus, lateral view; B – head, lateral view; C – head, anterior view; D – head, anterolateral view; E – right wing, dorsal view; F – abdomen, dorsal view. Scales: A – 2 mm, B–D – 0.5 mm, E and F – 0.5 mm.

Table 1. Primer pairs used to amplify the mitogenome of *Mesomelena mesomelaena* (Loew, 1848).

Primers	Sequence (5'–3')	Size (bp)	Reference
0006_F/R	TGAATTGCCTGATAAAAGG CTCCAATTAAAGCTCCTGGATG	~1500	Weigl et al., 2010
0007_F/R	GGTGGATTACCCCCATTTTTAGG TTAGCTAAAATTACTCCAGTTAATCCTCC	~1400	Weigl et al., 2010
0008_F/R	GAGGAGATCCAATTCTCTATCAACA CAATGACAATTGGTATAAAGCTGTG	~1400	Weigl et al., 2010
0009_F/R	CATTTGATTTGCATTCAAAAAGTATTG GCTGCTATAGCAGCTCCTACKCC	~1200	Weigl et al., 2010
0010_F/R	CCATAAGTAGAAATATAAGGTATAAATCA TATTGATTTGTGGTATCAAAGATAAG	~1450	Weigl et al., 2010
0011_F/R	CAGTAATTTTATTAACATGAATTGGAGC GCGACCTCGATGTTGGATTAAG	~1350	Weigl et al., 2010
0013_F/R	TTCACTTCAAGATAGCTCATCTCCT GGTCATGGACTATAYTCTACTA	~1600	Weigl et al., 2010
0014_F/R	GCAGTTCGATTAACAGCWAA AGTGATAAGCCTCTTTTTGGCTTC	~1500	Weigl et al., 2010
0016_F/R	CAATTCTATTAATTAAAGAAATTTCTCC CTTATTTTTGATTTACAAGACCAATG	~1400	Weigl et al., 2010
0018_F/R	CCTTTACGAATYAAACACCC CTATCTTATGTTTTCAAAACATATGC	~1150	Weigl et al., 2010
0019_F/R	CTAAATTTATTGCACTAATCTGCC TTGTACCTTGTGTATCAGGG	~1150	Weigl et al., 2012
0036F/R	TAGCWGCWGGTAATCAAGA GCTCCTCCWACWTTRAATT	~930	Zhang et al., 2013
0038F/R	TCATATCAYTRACACCACA GAGGKTATCARCCWGAACG	~960	Zhang et al., 2013
0040F/R	GCHCCTTCACAWACTCTAAAWGT CRTAATAWATTCCTCGTCCTA	~1100	Zhang et al., 2013
0043F/R	ATYTATAGGGTCTTCTCGTCT AATATGYACACATCGCCCGTC	~990	Zhang et al., 2013
0044F/R	GACGGGCGATRTGTRCATA CCAGCAGTCGCGGTTATAC	~530	Zhang et al., 2013
0046F/R	AGGAGCWTGAATAGGWTTAGA RTGGCTGAAGTTWAGGCRATA	~1000	Zhang et al., 2013
0049F/R	ATTTTCYGTATTYGACCCYTC TCTCGWGAWACATCTCGTCAT	~830	Zhang et al., 2013
0056F/R	CTTTYACAATACTAWTWMAC WAAACTAGGATTAGATACC	~600	Zhang et al., 2013
0071F/R*	ATGACTGAAAGCAAGTAT ATTAGCTGTTAATCGTAC	~750	

* Primer pair designed using Primer Premier 5.0 (Lalitha, 2000).

which gives a mismatch with the standard *cox1* barcode region for *Sarcophaga crassipalpis* (locus: JN964810) (Meiklejohn et al., 2012) from BOLD (http://www.barcodinglife.org/) and one with locus KT272859, which is stated to be *Sarcophaga bullata*, but which shows 99.96% identity in protein-coding genes (PCGs) to the locus NC_026667 (*Sarcophaga crassipalpis*).

Nineteen mitogenomes of Oestroidea (Table 2) were downloaded from GenBank to reconstruct the phylogeny of Sarcophagidae, with *Lucilia cuprina* as an outgroup. All 15 genes were aligned separately with MAFFT v 7.3.1 (Katoh & Standley, 2016), following Kutty et al. (2014). After alignment, all 13 PCGs and two rRNAs were concatenated using SequenceMatrix v 1.7.8 (Meier et al., 2006). Subsequently, PartitionFinder v 2.1.1 (Lanfear et al., 2016) was used to evaluate the best partitioning schemes based on BIC (Bayesian Information Criterion) using the greedy option with branch lengths estimated as "unlinked", with the dataset partitioned by genes. Phylogenetic analyses were conducted using Maximum Likelihood (ML) and Bayesian Inference (BI) as described in Zhang et al. (2016b).

Synonymous and non-synonymous substitution rates (Ks and Ka) for each species of each protein-coding gene (PCG) alignment were calculated using DnaSP version 5.10.1 (Librado & Rozas, 2009), with stop codons and codons with alignment gaps excluded. A plot of pairwise Ka versus Ks for each gene was then constructed using Sigmaplot v 12.5 (Systat Software Inc. California, USA).

RESULTS AND DISCUSSION

As the control region of *M. mesomelaena* could not be amplified, the small ribosomal RNA gene is incomplete at the 5' end. The nearly-complete mitogenome of *M. mesomelaena* (14,559 bp) was submitted to GenBank (Accession Number: KY003227).

The mitogenome contains 13 PCGs, two ribosomal RNA genes (rRNA) and 22 transfer RNA genes (tRNA), with the same locations as generally in Diptera (i.e., Nelson et al., 2012; Zhang et al., 2016b) and ancestral insects (see Fig. 2 in Cameron, 2014) (Table 3, Fig. 3). The overall nucleotide composition exhibits high AT content (76.9%) similar to other calyptrates (Zhang et al., 2016b).

All PCGs share the start codon of ATT or ATG, except for *cox1* (TCG), *nad3* and *nad1* (ATA). Four genes (*cox1*, *cox2*, *nad5*, and *nad4*) use the incomplete stop codon T, and *cytb* uses TAG. The remaining eight PCGs have the typical stop codon of TAA.

The selection acting on a gene may be detected by comparing the synonymous (Ks) and non-synonymous (Ka) nucleotide distances between gene sequences (Hurst, 2002). Higher Ka than Ks indicates positive selection, and lower Ka than Ks indicates negative selection. The Ka value is obviously lower than the Ks value for all sarcophagid

Table 2. Taxa included in the phylogenetic analyses in this study.

Family	Subfamily	Species	Locus	Reference
Calliphoridae	Luciliinae	*Lucilia cuprina*	NC_019573	Nelson et al., 2012
	Polleniinae	*Pollenia rudis*	JX913761	Nelson et al., 2012
Sarcophagidae	Sarcophaginae	*Sarcophaga melanura*	NC_026112	Zhang et al., 2016a
	Sarcophaginae	*S. portschinskyi*	NC_025574	Shi et al., 2016
	Sarcophaginae	*S. peregrina*	NC_023532	Zhong et al., 2016
	Sarcophaginae	*S. impatiens*	NC_017605	Nelson et al., 2012
	Sarcophaginae	*S. crassipalpis*	NC_026667	Ramakodi et al., 2015
	Sarcophaginae	*S. africa*	NC_025944	Fu et al., 2016
	Sarcophaginae	*S. similis*	NC_025573	Yan et al., 2016
	Sarcophaginae	*S. albiceps*	NC_028413	Liao et al., 2016
	Sarcophaginae	*Ravinia pernix*	NC_026196	Guo et al., 2016
	Sarcophaginae	*Boettcheria latisterna*	KT272848	Junqueira et al., 2016
	Sarcophaginae	*B. bisetosa*	KT272844	Junqueira et al., 2016
	Paramacronychiinae	*Wohlfahrtia magnifica*	KU578263	Zhang et al., 2016b
	Miltogramminae	*Mesomelena mesomelaena*	KY003227	present study
Tachinidae	Exoristinae	*Elodia flavipalpis*	NC_018118	Zhao et al., 2013
	Dexiinae	*Rutilia goerlingiana*	NC_019640	Nelson et al., 2012
Oestridae	Cuterebrinae	*Dermatobia hominis*	NC_006378	Azeredo-Espin et al., 2004
	Hypodermatinae	*Hypoderma lineatum*	NC_013932	Weigl et al., 2010

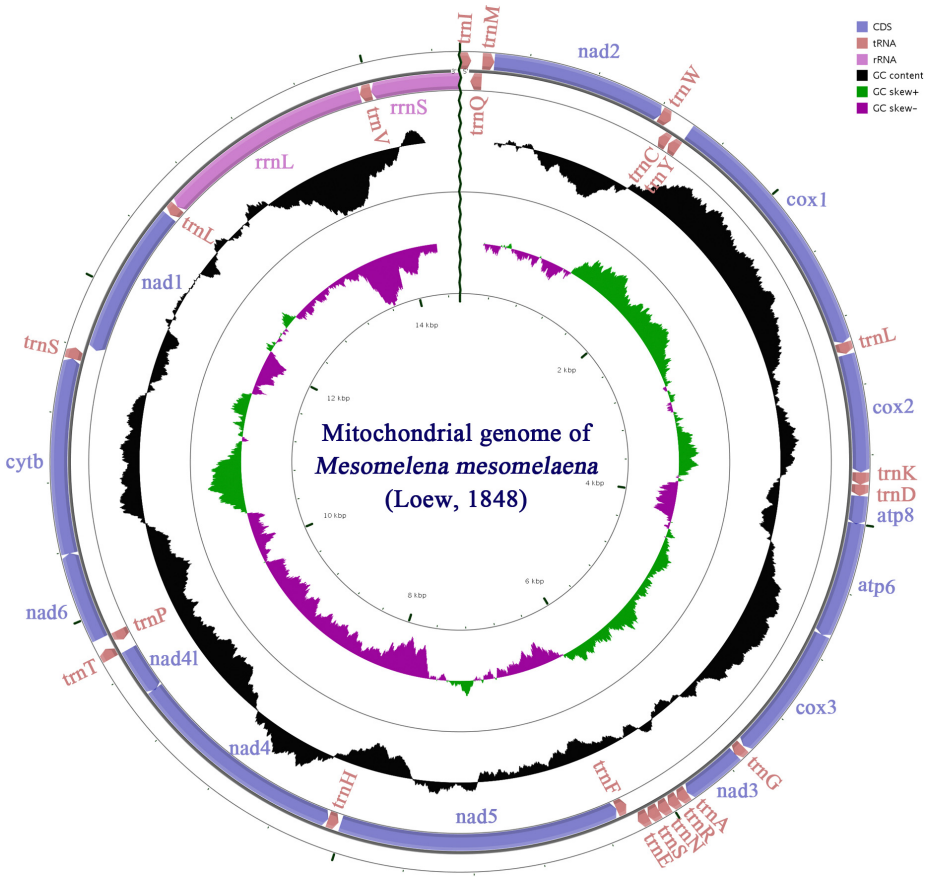

Fig. 3. Mitochondrial genome map of *Mesomelena mesomelaena* (Loew, 1848).

Table 3. Organization of the mitogenome of *Mesomelena mesomelaena* (Loew, 1848).

Gene	Product	Strand	Location	Length (bp)	Codon	
					Start/Anti	Stop
trnI	tRNA-Ile	N	1–65	65	GAT	
trnQ	tRNA-Gln	J	63–131	69	TTG	
trnM	tRNA-Met	N	131–199	69	CAT	
nad2	NADH2	N	200–1216	1017	ATT	TAA
trnW	tRNA-Trp	N	1215–1282	68	TCA	
trnC	tRNA-Cys	J	1275–1337	63	GCA	
trnY	tRNA-Tyr	J	1345–1410	66	GTA	
cox1	COX1	N	1409–2942	1534	TCG	T
trnL	tRNA-Leu	N	2943–3008	66	TAA	
cox2	COX2	N	3014–3701	688	ATG	T
trnK	tRNA-Lys	N	3702–3772	71	CTT	
trnD	tRNA-Asp	N	3772–3837	66	GTC	
atp8	ATP8	N	3838–4002	165	ATT	TAA
atp6	ATP6	N	3996–4673	678	ATG	TAA
cox3	COX3	N	4673–5461	789	ATG	TAA
trnG	tRNA-Gly	N	5467–5531	65	TCC	
nad3	NADH3	N	5529–5885	357	ATA	TAA
trnA	tRNA-Ala	N	5887–5951	65	TGC	
trnR	tRNA-Arg	N	5951–6013	63	TCG	
trnN	tRNA-Asn	N	6015–6080	66	GTT	
trnS	tRNA-Ser	N	6080–6149	70	GCT	
trnE	tRNA-Glu	N	6149–6214	66	TTC	
trnF	tRNA-Phe	J	6233–6298	66	GAA	
nad5	NADH5	J	6299–8018	1720	ATT	T
trnH	tRNA-His	J	8034–8099	66	GTG	
nad4	NADH4	J	8100–9438	1339	ATG	T
nad4l	NADH4L	J	9432–9728	297	ATG	TAA
trnT	tRNA-Thr	N	9731–9795	65	TGT	
trnP	tRNA-Pro	J	9796–9860	65	TGG	
nad6	NADH6	N	9863–10387	525	ATT	TAA
cytb	CYTB	N	10387–11523	1137	ATG	TAG
trnS2	tRNA-Ser	N	11522–11589	68	TGA	
nad1	NADH1	J	11606–12544	939	ATA	TAA
trnL	tRNA-Leu	J	12555–12619	65	TAG	
rrnL	16S rRNA	J	12620–13941	1322		
trnV	tRNA-Val	J	13942–14013	72	TAC	
rrnS	12S rRNA	J	14013–14559	547		

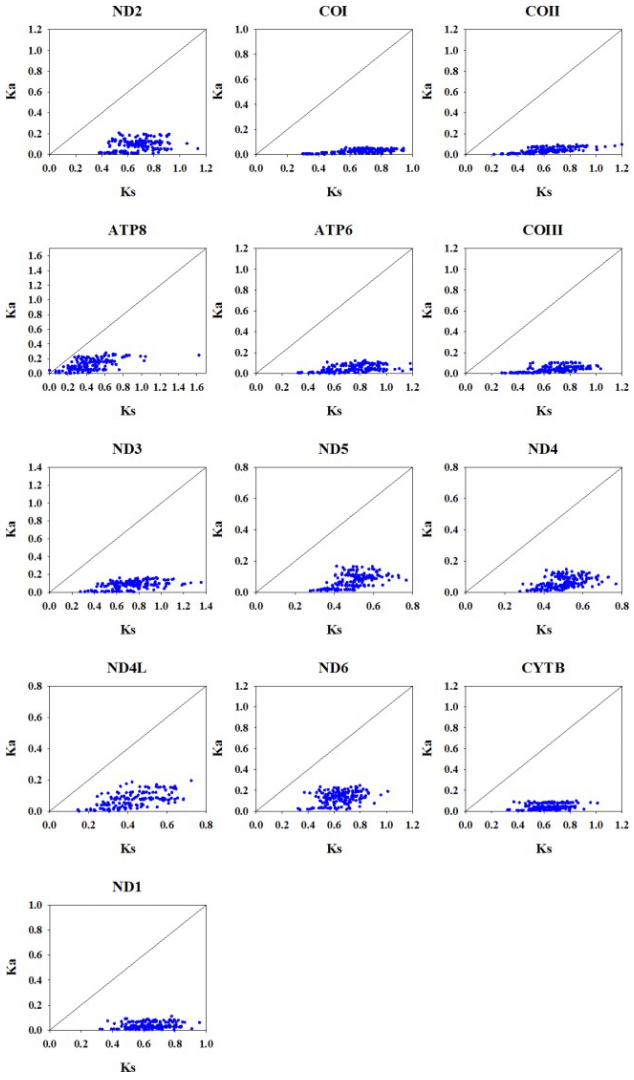

Fig. 4. Plot of pairwise Ka versus Ks of the mitochondrial genes of Sarcophagidae.

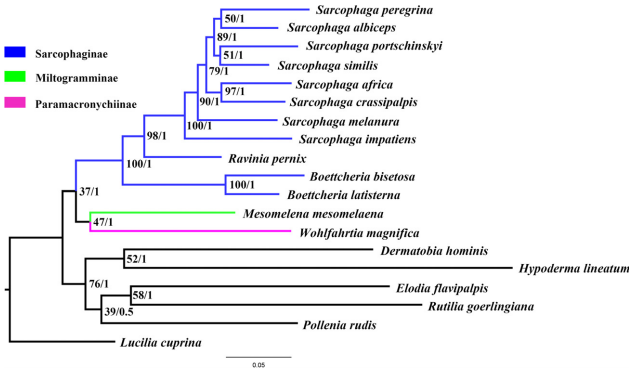

Fig. 5. Phylogeny of Sarcophagidae inferred from a mitochondrial dataset comprising 13 protein-coding genes and 2 rRNA genes. Numbers at nodes are bootstrap values (ML trees) / posterior probabilities (Bayesian trees).

mitochondrial genes (Fig. 4), except *atp8*, for which only non-synonymous substitutions between *Sarcophaga africa* (locus: NC_025944) (Fu et al., 2016) and *S. similis* (locus: NC_025573) (Yan et al., 2016) were detected. The lower values of Ka than Ks indicate negative selection on sarcophagid mitochondrial genes. Specifically, the *cox1* gene has undergone strong negative selection, indicated by the extremely low Ka value compared to Ks value, which also implies the conservativeness of *cox1* gene.

ML and BI analyses give an identical result, with Sarcophagidae being monophyletic and Sarcophaginae as the sister group to (Paramacronychiinae + Miltogramminae) (Fig. 5). According to previous research the relationship of these three subfamilies is still unresolved. Pape (1996: 9) proposed a probable sister-group relationship between the Paramacronychiinae and Sarcophaginae, based on "the shared possession of a ventrally displaced acrophallus, lack of epiphallus and perhaps spherical female accessory glands", which was corroborated by Giroux et al. (2010) in an explicit morphology-based phylogenetic analysis. This relationship was corroborated by Kutty et al. (2010) using a combination of mitochondrial and nuclear genes, although with low support. However, based on a large-scale (in terms of taxa) molecular phylogeny, Piwczyński et al. (2014) suggest a sister-group relationship of Sarcophaginae to (Paramacronychiinae + Miltogramminae), with Paramacronychiinae being paraphyletic, and Piwczyński et al.'s (2017) results are fully concordant with the above, with each subfamily being monophyletic.

Within the Sarcophaginae, *Boettcheria* is located as a basal branch, forming a sister group to (*Ravinia* + *Sarcophaga*). This is in conflict with morphology-based phylogenies of this subfamily, where *Ravinia* is subordinate to *Boettcheria* and *Sarcophaga* (Pape, 1994; Giroux et al., 2010). The monophyly of *Sarcophaga* is well supported (ML bootstrap = 100; BI posterior probability = 1), but the few taxa sampled and inclusion of only Old World species do not allow the testing of any of the biogeographic hypotheses proposed by Buenaventura et al. (2016) and Buenaventura & Pape (2017).

This study documents the first mitogenome of Miltogramminae, which contains 37 typical metazoan mitochondrial genes and retains the organization of the ancestral insect mitogenome. The subfamily relationship within Sarcophagidae is reconstructed for the first time as (Sarcophaginae (Paramacronychiinae, Miltogramminae)) based on mitogenomic data.

ACKNOWLEDGEMENTS. This work was supported by the Fundamental Research Funds for the Central Universities (No. JC2015-04), and National Science Foundation of China (No. 31572305).

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Received July 6, 2017; revised and accepted October 3, 2017
Published online October 23, 2017