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Complete mitochondrial genome of *Bactrocera limbifera* (Insecta: Tephritidae) and phylogenetic relationship with its congeners

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Abstract

Bactrocera limbifera is a dacine fruit fly found across Southeast Asia. The complete mitochondrial genome and phylogenetic relationships of other *Bactrocera* species have been extensively studied except for *B. limbifera*. We report here its complete mitochondrial genome determined by next-generation sequencing and phylogenetic relationship with other congeners. The whole mitogenome possessed 37 genes (13 protein-coding genes – PCGs, 2 rRNA and 22 tRNA genes) and a control region. It had a total length of 15,860 bp. Six PCGs (*atp6*, *cob, cox2*, *cox3*, *nad4*, *nad4l*) had ATG start codon, four (*nad2*, *nad3*, *nad5*, *nad6*) had ATT, and one each had ATA (*nad1*), GTG (*atp8*) and TCG (*cox1*). Seven PCGs (*atp6*, *atp8*, *cox2*, *cox3*, *nad2*, *nad4l*, *nad6*) had TAA stop codon, three (*cob*, *nad3*, *nad4*) had TAG, and three had incomplete stop codon (*cox1* – TA; *nad1*, *nad5* – T). The DHU-loop of tRNA was absent in *trnS1* while *trnF* lacked the TΨC-loop. Phylogenetic analysis based on 15 mt-genes (13 PCGs + 2 rRNA genes) using maximum likelihood method indicated *B. limbifera* forming a sister group with *B. ritsemai* in the lineage containing also *B. umbrosa* and the subgenus *Bactrocera* was monophyletic.

Keywords: *Bactrocera limbifera,* mitogenome, molecular phylogeny, fruit fly, Indonesia

Introduction

Fruit flies of the genus *Bactrocera* are represented by some 144 species (NCBI Taxonomy). Many of them are of economic importance in agriculture (White and Elson-Harris, 1992; Vargas et al., 2015). The genus is well represented in Southeast Asia, and many are endemic to the region (Drew, 2004). Among them, *Bactrocera limbifera* (Bezzi) is found across Southast Asia (Hardy and Adachi, 1954; Hardy, 1983; Drew and Romig, 2013).

B. limbifera is not known as an economic pest. Its larva has been recorded to infest *Aglaia* sp. (Meliaceae), *Draconomelum dao* (Anacardiaceae), *Inocarpus fagifer* (Fabaceae), *Sterculia* sp. (Sterculiaceae) and *Terminalia catappa* (Combretaceae) (Hardy and Adachi, 1954; Ranganath and Veerakumari, 1995; Allwood et al., 1999; Suputa et al., 2010; Drew and Romig, 2013). It has been recorded to be parasitised by several parasitoids, including *Diachasmimorpha longicaudata*, *Fopius skinneri*, *Pachycrepoideus dubius* and *Psyttalia fletcheri* (Hardy and Adachi, 1954). The adult males are attracted to Cue lure (Hardy, 1983).

To date, there has been scanty reports on the phylogenetics of *B. limbifera* (Leblanc et al., 2015). The NCBI GenBank lists only three entries for the partial cytochrome *c* oxidase subunit I (*cox1*) gene sequence, and one each for internal transcribed spacer 1 (*ITS1*), elongation factor 1 alpha (*EF-1α*), and period (*PER*) gene. Its mitochondrial genome has not been studied. We report here its complete mitogenome determined by next-generation sequencing and its phylogenetic relationship with other congeners.

Materials and methods

Specimen and mitochondral DNA extraction

Male fruit fly of *B. limbifera* was collected in Lombok, Indonesia by means of Cue lure according to the method of Yong et al. (2015). The specimen was preserved in absolute ethanol and stored in -20°C freezer until use. It is not endangered or protected by law. No permits are required to study this fruit fly.

Mitochondria were isolated from a small piece of the alcohol-preserved tissue by the standard differential centrifugation method (White and Densmore, 1992), and mitochondrial DNA was extracted using Mitochondrial DNA Isolation Kit (Abnova, Taiwan) following the manufacturer's instructions.

Genome sequencing and analysis

Library was prepared using Nextera DNA Sample Preparation Kit and mitochondrial genome was sequenced using the Illumina MiSeq Desktop Sequencer (2 × 150 bp paired-end reads) (Illumina, USA). De novo assembly was performed using the CLC Genomic Workbench v.8.0.1 (https://www.qiagenbioinformatics.com/) after quality trimming of sequence reads. The assembled contig was then annotated by manual validation of the coding regions using the NCBI ORF Finder (https://www.ncbi.nlm.nih.gov/orffinder). The circular mitogenome of *B. limbifera* was visualized with Blast Ring Image Generator (BRIG) (Alikhan et al., 2011). Details on the analysis were as described in Yong et al. (2016a).

Table 1 Gene order and features of mitochondrial genome of *Bactrocera limbifera*. The anticodon of each tRNAs is shown in bracket. J (+) or N (-) indicates gene directions.

Gene	Location	Strand	Size (bp)	Intergenic Sequence	Start/stop codon
trnI(atc)	1 – 66	J	66	-3	
trnQ(caa)	64 – 132	N	69	45	
trnM(atg)	178 – 246	J	69		
nad2	247 – 1269	J	1023	12	ATT/TAA
trnW(tga)	1282 – 1350	J	69	-8	
trnC(tgc)	1343 – 1406	N	64	30	
trnY(tac)	1437 – 1503	N	67	-2	
cox1	1502 – 3036	J	1535		TCG/TA
trnL2(tta)	3037 – 3102	J	66	4	
cox2	3107 – 3793	J	687	5	ATG/TAA
trnK(aag)	3799 – 3869	J	71	1	
trnD(gac)	3871 – 3937	J	67		
atp8	3938 – 4099	J	162	-7	GTG/TAA
atp6	4093 – 4770	J	678	-1	ATG/TAA
cox3	4770 – 5558	J	789	9	ATG/TAA
trnG(gga)	5568 – 5632	J	65		
nad3	5633 – 5986	J	354	-2	ATT/TAG
trnA(gca)	5985 – 6049	J	65	9	
trnR(cga)	6059 – 6122	J	64	27	
trnN(aac)	6150 – 6214	J	65		
trnS1(agc)	6215 – 6282	J	68		
trnE(gaa)	6283 – 6349	J	67	18	
trnF(ttc)	6368 – 6432	N	65		
nad5	6433 – 8152	N	1720	15	ATT/T
trnH(cac)	8168 – 8233	N	66		
nad4	8234 – 9574	N	1341	-7	ATG/TAG
nad4l	9568 – 9864	N	297	2	ATG/TAA
trnT(aca)	9867 – 9931	J	65		
trnP(cca)	9932 – 9997	N	66	2	
nad6	10000 – 10524	J	525	-1	ATT/TAA
cob	10524 – 11660	J	1137	-2	ATG/TAG
trnS2(tca)	11659 – 11725	J	67	15	
nad1	11741 – 12680	N	940	10	ATA/T
trnL1(cta)	12691 – 12755	N	65		
rrnL	12756 – 14085	N	1330		
trnV(gta)	14086 – 14157	N	72		
rrnS	14158 – 14944	N	787		
Control region	14945 – 15860	J	916		

Mitogenomes from GenBank and phylogenetic analysis

The mitogenomes of genus *Bactrocera* available in GenBank – *B. arecae* NC_028327 (Yong et al., 2015); *B. carambolae* NC_009772 (unpublished); *B. correcta* NC_018787 (unpublished); *B. dorsalis* complex [*B. dorsalis* NC_008748 (unpublished); *B. papayae* NC_009770 (unpublished); *B. philippienensis* NC_009771 (unpublished); *B. invadens* NC_031388 (Zhang L.-J. et al., 2016)]; *B. latifrons* NC_029466 (Yong et al., 2016b); *B. melastomastos* NC_029467 (Yong et al., 2016b); *B. ritsemai* MF668132 (Song et al., 2018); *B. tryoni* NC_014611 (Nardi et al., 2010); *B. umbrosa* NC_029468 (Yong et al., 2016b); *B. zonata* NC_027725 (Choudhary et al., 2015); *B.* (*Daculus*) *oleae* NC_005333 (Nardi et al., 2003); *B.* (*Tetradacus*) *minax* NC_014402 (unpublished) – were used for phylogenetic comparison.

Species of *Zeugodacus* – *Z. caudatus* Malaysia KT625491 and *Z. caudatus* Indonesia KT625492 (Yong et al., 2016c) – were used as outgroup taxa.

The nucleotide sequences of 15 mt-genes (13 PCGs and 2 rRNA gnes) were aligned by MAFFT v.7 (Katoh and Standley, 2013) and subsequently edited and trimmed using BioEdit v.7.0.5.3 (Hall, 1999). The best-fit nucleotide substitution model for maximum likelihood (ML) using the corrected Akaike Information Criterion (Akaike, 1973) was determined by Kakusan v.3 (Tanabe, 2007). Phylograms of 15 mt-genes were constructed using TreeFinder (Jobb et al., 2004). Phylogenetic trees were viewed and edited by FigTree v.1.4 (Rambaut, 2012). The total nucleotide sequences of 15 mt-genes was 13,343 bp with AIC model = GTR+Gamma. The aligned sequences consisted of 13,206 characters (excluding sites with gaps / missing data), of which 8531 were invariable (monomorphic), 4675 were variable (polymorphic) of which 3157 were parsimony informative sites (2016 two variants, 900 three variants and 241 four variants) and 1518 were singleton variable sites (1304 two variants, 191 three variants and 23 four variants).

Table 2 Nucleotide composition of whole mitogenome, protein-coding genes, rRNA genes and control region of *Bactrocera limbifera.*

Region	A/%	C/%	G/%	T/%	A+T/%	G+C/%	AT skew	GC skew
Whole mitogenome	39.4	16.8	10.1	33.7	73.1	26.9	0.078	-0.249
nad2	34.2	17.0	8.8	40.0	74.2	25.8	-0.078	-0.318
cox1	30.0	20.3	15.5	34.2	64.2	35.8	-0.065	-0.134
cox2	33.9	19.7	13.2	33.2	67.1	32.9	0.010	-0.198
atp8	35.2	19.7	9.9	35.2	70.4	29.6	0.000	-0.331
atp6	30.1	20.5	12.4	37.0	67.1	32.9	-0.103	-0.246
cox3	30.8	21.0	14.4	33.8	64.6	35.4	-0.046	-0.186
nad3	32.2	18.1	9.9	39.8	72.0	28.0	-0.106	-0.293
nad5	46.4	17.2	8.8	27.6	74.0	26.0	0.254	-0.323
nad4	47.8	18.1	9.0	25.1	72.9	27.1	0.311	-0.336
nad4l	50.5	15.1	7.1	27.3	77.8	22.2	0.298	-0.360
nad6	38.5	15.2	6.5	39.8	78.3	21.7	-0.017	-0.401
cob	32.2	20.0	13.1	34.7	66.9	33.1	-0.037	-0.208
nad1	48.8	18.5	8.4	24.3	73.1	26.9	0.335	-0.375
rrnS	40.6	15.3	9.0	35.1	75.7	24.3	0.073	-0.259
rrnL	42.7	13.5	6.9	36.9	79.6	20.4	0.073	-0.324
Control region	47.0	7.1	5.1	40.8	87.8	12.2	0.071	-0.164

Results and discussion

Mitogenome features

Mitochondrial genomes of tephritid fruit flies have been applied particularly to study systematics, phylogeny and evolution (Yong et al., 2015, 2016b, c, 2017). To date, there are 27 entries of complete mitogenomes of tephritid fruit flies in the GenBank – 15 from genus *Bactrocera* (Dacinae, Dacini), 8 from genus *Zeugodacus*, 2 from genus *Ceratitis* (Dacinae, Ceratitidini), and 1 each from genus *Dacus* (Dacinae, Dacini), genus *Anastrepha* (Trypetinae, Toxotrypanini) and genus *Procecidochares* (Tephritinae, Cecidocharini). We report here the complete mitogenome of *B. limbifera* and its phylogenetic relationship with other congeners.

The gene order of the mitogeneome of *B. limbifera* conforms to other tephritid mitogenomes (Drosopoulou et al., 2017; Isaza et al., 2017; Jeong et al., 2017; Jiang et al., 2016; Yong et al., 2015, 2016b,c, 2017). It had a total length of 15,860 bp, comprising 37 genes – 13 protein-coding genes (PCGs), 2 ribosomal ribonucleic acid (rRNA) and 22 transfer ribonucleic acid (tRNA) genes – and a control region (D-loop) (Table 1, Figure. 1).

There were 16 intergenic regions with spacing sequence ranging from 1 to 45 bp, and 9 regions with overlapping sequence ranging from -1 to -8 bp (Table 1). As in other members of the subgenus *Bactrocera* of genus *Bactrocera* (Yong et al., 2015, 2016b), the largest intergenic sequence (45 bp in *B. limbifera*) was between *trnQ* and *trnM*. This large intergenic space is variable in size, for example, 55 bp in *B. arecae* (Yong et al., 2015), 94 bp in *B. latifrons*, 82 bp in *B. melastomatos* and 79 bp in *B. umbrosa* (Yong et al., 2016b).

Six (*atp6*, *cob, cox2*, *cox3*, *nad4*, *nad4l*) of the 13 PCGs in *B. limbifera* mitogenome had ATG start codon, four (*nad2*, *nad3*, *nad5*, *nad6*) had ATT, and one each had ATA (*nad1*), GTG (*atp8*) and TCG (*cox1*). Seven PCGs (*atp6*, *atp8*, *cox2*, *cox3*, *nad2*, *nad4l*, *nad6*) had TAA stop codon, three (*cob*, *nad3*, *nad4*) had TAG, and three had incomplete stop codon (*cox1* – TA; *nad1*, *nad5* – T) (Table 1, Figure. 1). Incomplete stop codons can be converted to TAA by post-translational polyadenylation (Ojala et al., 1981; Yong et al., 2015, 2016b,c) and have been reported in other taxa of tephritid fruit flies (Yong et al., 2015, 2016b,c, 2017).

Table 2 summarizes the nucleotide compositions of the mitochondrial whole genome, protein-coding genes, rRNA genes and control region of *B. limbifera*. All were A+T rich as in other *Bactrocera* fruit flies (Yong et al., 2016b). The A+T content for PCGs was lowest in *cox1* (64.2%) and highest in *nad6* (78.3%); in other *Bactrocera* fruit flies *nad4l* had the highest A+T content (Yong et al., 2016b). As in other *Bactrocera* fruit flies (Yong et al., 2016b), the ribosomal operon *rrnL* had a higher A+T content than *rrnS* (79.6% vs 75.7%). The A+T content of the non-coding control region was 87.8%. As in other *Bactrocera* fruit flies (Yong et al., 2016b), the GC skew content of the whole genome, PCGs, rRNA genes and control region was negative indicating a bias toward the use of Cs over Gs. The AT skewness value, as in other fruit flies (Yong et al., 2016b), was positive for the whole mitogenome, both the rRNA genes and control region, but variable in the individual PCGs.

As in other tephritid fruit flies and other insects, the mitogenome of *B. limbifera* had three main tRNA clusters: (1) I-Q-M; (2) W-C-Y; and (3) A-R-N-S1-E-F (Figure. 1). The DHU-loop was absent in *trnS1* while *trnF* lacked the TΨC-loop (Figure. 2). Similar condition was found in other members of genus *Bactrocera* (*B. correcta*, *B. latifrons*, *B. melastomatos*, *B. ritsemai*, *B. zonata*), as well as in *Zeugodacus caudatus*, *Z. diaphorus* and *Z. tau* (Yong et al., 2015, 2016b,c, 2017; Song et al., 2018). Deviant tRNA secondary structures are not unusual in Arthropoda (Jühling et al., 2012), although misacylation of tRNA can affect the survivability of an organism (Hendrickson, 2001).

Phylogenetic relationships

B. limbifera is a member of the subgenus *Bactrocera* (Drew and Romig, 2013; Hardy, 1983). The subgenus *Bactrocera* is represented by some 100 species (NCBI Taxonomy). Based

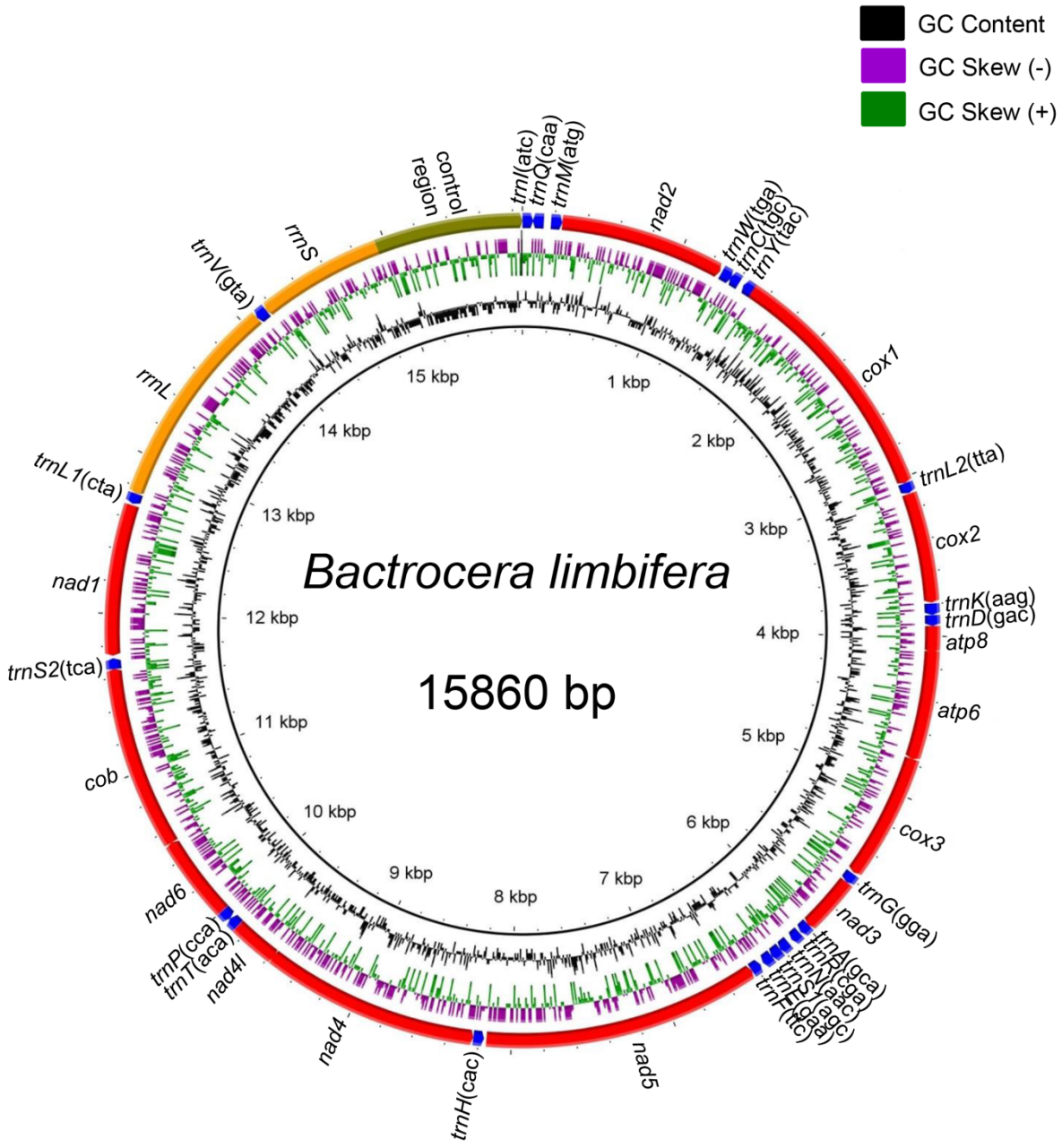

Figure 1. Complete mitogenome of *Bactrocera limbifera* with BRIG visualization showing the protein-coding genes, rRNAs and tRNAs. GC skew is shown on the outer surface of the ring whereas GC content is shown on the inner surface. The anticodon of each tRNA is shown in bracket.

on three gene (*cox1, period, EF-1α*) dataset, *B. limbifera* formed a sister group with *B. kohkongiae* in the lineage containing also *B. latifrons* and *B. bryoniae* (Leblanc et al., 2015).

In the present study, based on 15 mt-genes (13 PCGs + 2 rRNA genes) *B. limbifera* formed a sister group with *B. ritsemai* in the lineage containing also *B. umbrosa* (Figure. 3). This lineage did not include *B. arecae* reported in an earlier study (Song et al., 2018). *B. arecae* in the present study was basal to the *B. dorsalis* complex. *B. latifrons* was basal to the other members of the subgenus *Bactrocera*. In the phylogeny based on *cox1*, *period* and *EF-1α* sequences,

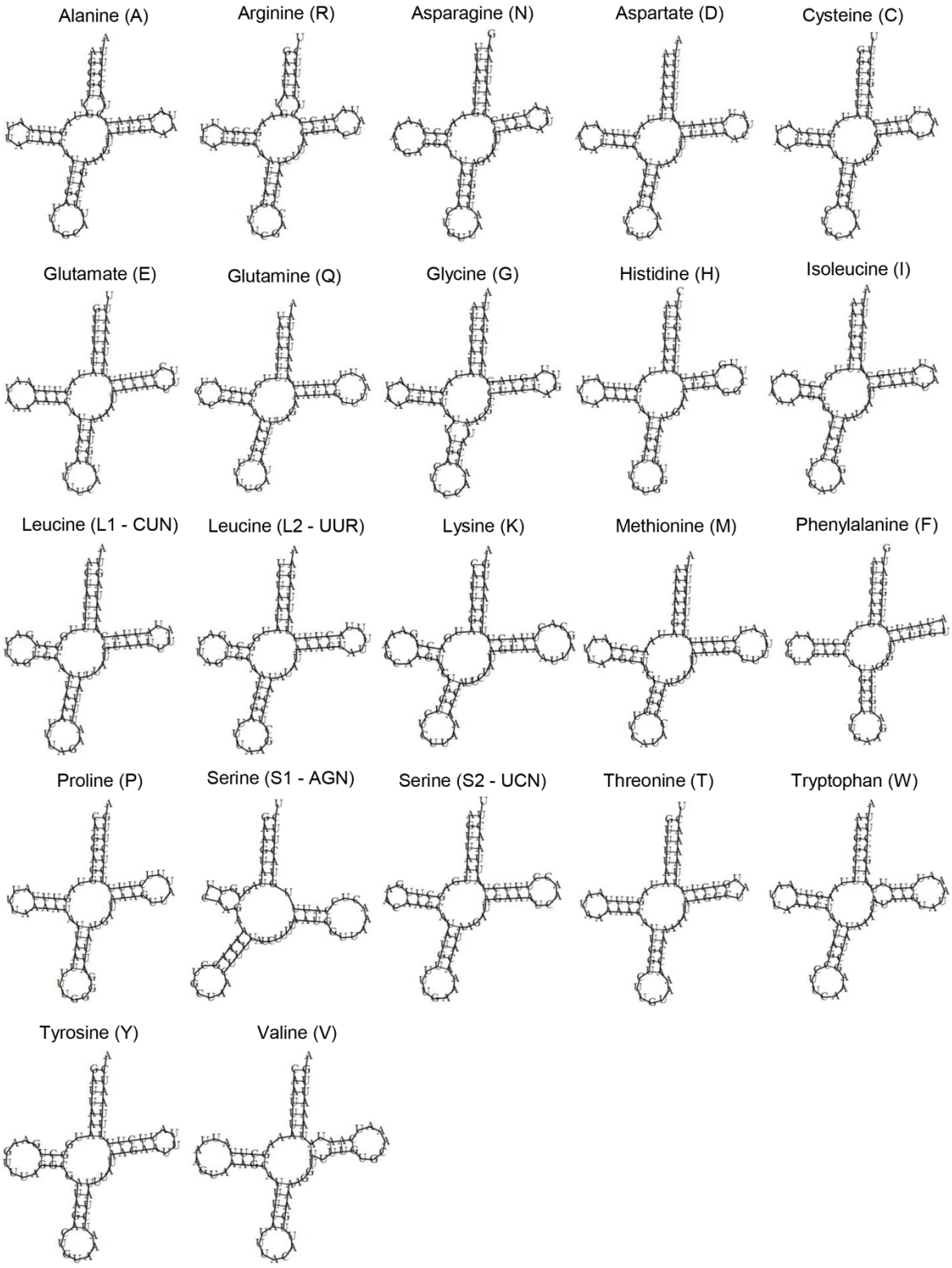

Figure 2. Cloverleaf structure of the 22 inferred tRNAs in the mitogenome of *Bactrocera limbifera*. The cloverleaf structure for *trnF* lacked the TψC-loop, and *trnS1* lacked the DHU-loop

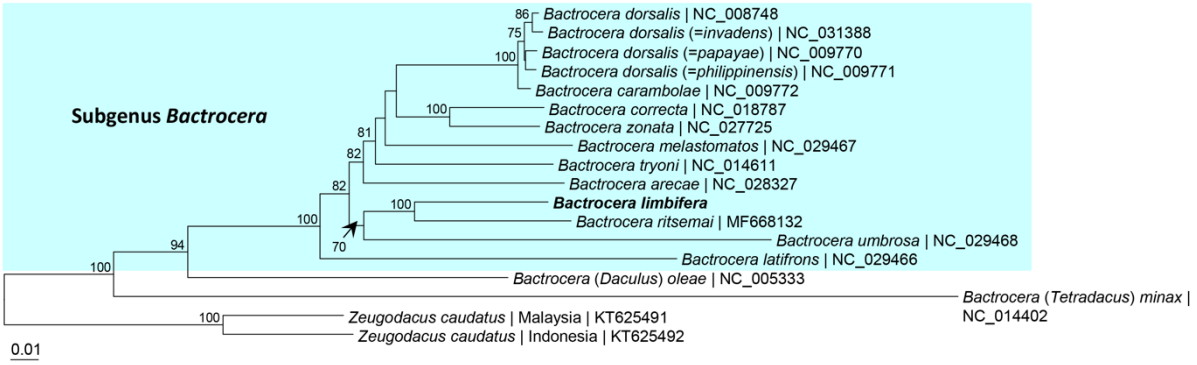

Figure 3. Maximum likelihood tree based on 15 mt-genes (13 PCGs and 2 rRNA genes) of the whole mitogenome of *Bactrocera limbifera* and congeners with *Zeugodacus* spp. as outgroup. Numeric values at the nodes are ML bootstrap values with 1000 replicates.

B. umbrosa formed a lineage with *B. fuscitibia* in the same clade as *B. limbifera*, *B. kohkongiae*, *B. latifrons* and *B. bryoniae*, and *B. dorsalis* was not clearly separated from *B. carambolae* (Leblanc et al., 2015). As in other studies on mitogenome of *Bactrocera* fruit flies (Yong et al., 2015, 2016b,c), *B. carambolae* in the present phylogenetic analysis was distinctly separated from *B. dorsalis*. The different phylogenetic relationship may be attributed to taxon sampling and use of larger number of genes. Nonetheless, the subgenus *Bactrocera* was monophyletic and distinctly separated from the subgenera *Daculus* and *Tetradacus* of genus *Bactrocera* (Figure. 3). This concurs with earlier findings on the molecular phylogeny of *Bactrocera* fruit flies (Leblanc et al., 2015; Yong et al., 2015, 2016b; Isaza et al., 2017; Jeong et al., 2017).

In summary, the use of 15 complete mt-genes (13 PCGs and 2 rRNA genes) in the present study indicated close phylogenetic relationship of *B. limbifera*, *B. ritsemai* and *B. umbrosa*. The use of large number of genes such as mitogenome and a broader taxa sampling will better elucidate the phylogenetics and systematics of *Bactrocera* fruit flies.

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Disclosure statement

The authors report no conflicts of interest.

Ethics statement

Bactrocera limbifera is an insect pest of the fruits of *Aglaia* sp. (Meliaceae), *Draconomelum dao* (Anacardiaceae), *Inocarpus fagifer* (Fabaceae), *Sterculia* sp. (Sterculiaceae) and *Terminalia catappa* (Combretaceae). It is not endangered or protected by law. No permits are required to study this fruit fly.

Author contributions

HSY and IWS designed the experiment, HSY and SLS conducted the experiment, HSY, SLS, IWS and PEL analyzed data, all authors reviewed the manuscript.

Accession Code

The whole mitochondrial genome sequence of *Bactrocera limbifera* is available in GenBank database (accession number: MG566056).

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