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ORIGINAL ARTICLE

First mitogenome for the tribe Saccharosydnini (Hemiptera: Delphacidae: Delphacinae) and the phylogeny of three predominant rice planthoppers

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Key words. Hemiptera, Delphacidae, Delphacinae, *Saccharosydne procerus*, *Sogatella vibix*, mitochondrial genome, phylogeny, planthopper, rice

Abstract. The mitochondrial genome of *Saccharosydne procerus* (Matsumura) is the first sequenced in the tribe Saccharosydnini (Hemiptera: Delphacidae: Delphacinae). In addition, the mitogenome sequence of *Sogatella vibix* (Haupt) (in Delphacini) is also sequenced. The *Sa. procerus* mitochondrial genome is 16,031 bp (GenBank accession no. MG515237) in length, and *So. vibix* is 16,554 bp (GenBank accession no. MG515238). The existence of purifying selection was indicated by the rate of nonsynonymous and synonymous substitutions. Three species of Delphacini, *Laodelphax striatellus* (Fallén), *Sogatella furcifera* (Horváth) and *Nilaparvata lugens* (Stål), are important pests of rice. The phylogeny of these three rice planthoppers based on the mitochondrial genome sequence was (*L. striatellus* + (*So. vibix* + *So. furcifera*)) + (*N. muiri* + *N. lugens*).

INTRODUCTION

The planthopper subfamily Delphacinae is the most speciose and economically important group in the family Delphacidae. It comprises three tribes (Delphacini, Tropidocephalini and Saccharosydnini) and contains over 80% of all delphacid species (Asche, 1985; Bourgoin, 2017). Some members in this subfamily are pests of crops or vectors of plant pathogens, causing economic losses widely reported around the world, for example, three species of Delphacini, *Laodelphax striatellus* (Fallén), *Sogatella furcifera* (Horváth) and *Nilaparvata lugens* (Stål) as important pests of rice (e.g. Cai et al., 2003; Wilson, 2005; Grilli, 2006; Grimshaw & Donaldson, 2007; Wang et al., 2008; Heong et al., 2014; Zhang et al., 2014). Despite several recent studies on the phylogeny of this group (Asche, 1985, 1990; Yang et al., 1987; Emeljanov, 1996; Dijkstra et al., 2003, 2006; Hamilton, 2006; Urban et al., 2010; Huang et al., 2017), more data (including mitochondrial genomes evidence) are still needed to better understand the evolution of Delphacinae.

Insect mitochondrial genomes (mitogenomes) are small, double stranded, circular DNA molecules, ranging in size from 14 to 19 kb. They are composed of 37 genes (13 protein-coding, 22 transfer RNA, and 2 ribosomal RNA genes), and a control region (A + T-rich region) that is thought to play a role in the initiation of transcription and replication, and is a source of length variation in the genome (Boore, 1999). In addition, mitogenome sequences are increasingly being utilized in insect identification or biogeographic and phylogenetic studies (Hua et al., 2009; Ma et al., 2012; Nelson et al., 2012; Wang et al., 2015). Here we document the complete mitogenome of *Saccharosydne procerus* (Matsumura, 1931), which is the first available for the tribe Saccharosydnini. The complete mitochondrial genome of *Sogatella vibix* (Haupt, 1927) (in Delphacini) was also sequenced. Furthermore, the phylogeny of the Delphacinae based on all the mitogenomes currently in GenBank was reconstructed. The purpose of this study is to investigate the mitogenome differences between members of Delphacini and Saccharosydnini, and provide useful information on the molecular evolution of Delphacinae.

MATERIALS AND METHODS

Sample preparation and DNA extraction

Specimens of *Saccharosydne procerus* and *Sogatella vibix* were collected from Guangxi Province. All the specimens were stored at –20°C in absolute ethanol prior to DNA extraction. Total genomic DNA was extracted using the cetyltrimethyl ammonium bromide (CTAB) method (Shahjahan et al., 1995).

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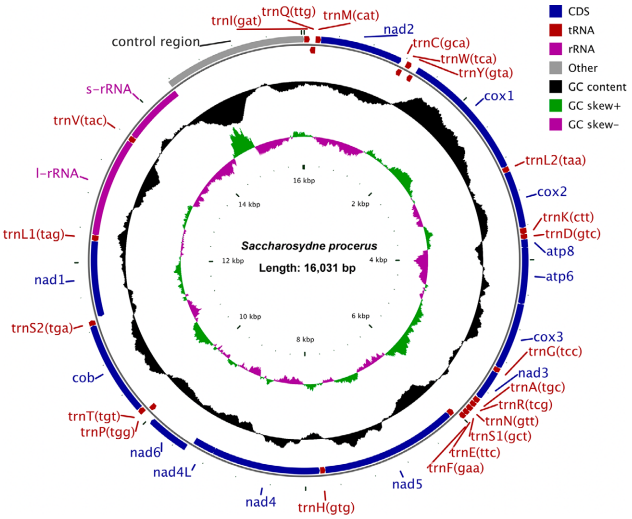

Fig. 1. Mitochondrial genome map of *Saccharosydne procerus*.

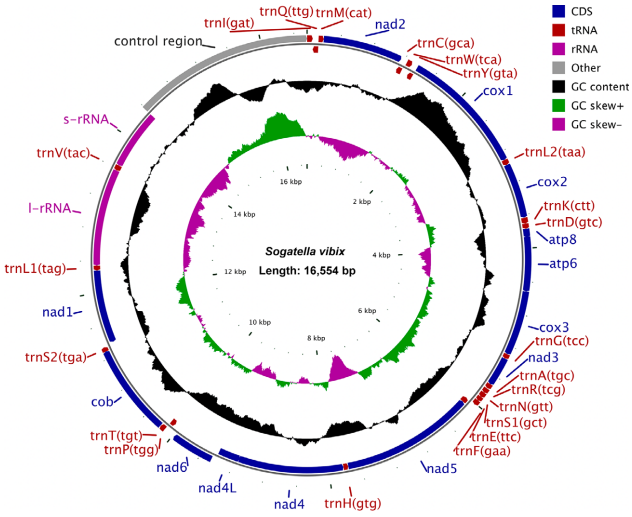

Fig. 2. Mitochondrial genome map of *Sogatella vibix*.

Sequencing and assembly

A whole genome shotgun (WGS) strategy was used with sequencing on the Illumina Miseq platform. The quality of data was checked by FastQC (Andrews, 2016). The adapters of raw data were removed by AdapterRemoval version 2 (Schubert et al., 2016). SOAPec version 2.01 was used for quality correction, setting K-mer to 17. Reads with a length of less than 50 bp were excluded. Assembly of the mitochondrial (mt) genome was done using A5-miseq version 2.0 (Coil et al., 2014).

Mitochondrial genome annotation

The tRNA genes were identified and secondary structures of tRNAs were predicted using MITOS WebSever, setting the parameters with the Invertebrate Mito genetic code (Bernt et al., 2013). Every sequence of tRNA genes was checked separately by eye. Protein-coding genes (PCGs) were identified as open reading frames corresponding to the 13 PCGs in the metazoan mt genomes. The rRNA genes and control region were identified by the boundary of the tRNA genes and by alignment with other Delphacidae mitogenomes. The mitogenome map was produced using CGView (Grant & Stothard, 2008).

Comparative analysis

Base composition and relative synonymous codon usage (RSCU) were analyzed using MEGA 6.0 (Tamura et al., 2013). GC and AT asymmetry were measured in terms of GC and AT skews using the following formulae suggested by Hassanin et al. (2005): AT-skew = (A−T)/(A+T) and GC-skew = (G−C)/(G+C). The number of synonymous substitutions per synonymous site (Ks) and the number of nonsynonymous substitutions per nonsynonymous site (Ka) for each concatenated 13 PCGs of Delphacini mitogenome were calculated by DnaSP 5 (Rozas et al., 2003), with stop codons and codons with alignment gaps excluded, using the sequence of *Sa. procerus* from Saccharosydnini as a reference sequence.

Phylogenetic analysis

Two newly generated mitogenomes and 12 from GenBank (Table 1) were analyzed in this study, with *Sa. procerus* selected as an outgroup. Alignment of PCGs was conducted by using MAFFT 7.3.1 using G-INS-I algorithms (Katoh & Tandley, 2016). Two rRNA segments were aligned by the R-Coffee web server (Moretti, 2008). Subsequently, all alignments were concatenated in a single matrix using DAMBE (Xia, 2013). We used PartitionFinder 1.1.1 (Lanfear et al., 2012) to infer the optimal partitioning strategy; the best-fitting model was selected for each partition using the BIC (Bayesian Information Criterion).

Both ML (Maximum likelihood) and BI (Bayesian inference) analyses were conducted on the concatenated dataset for phylogeny reconstruction. Maximum likelihood analysis was conducted in IQtree v1.4.1 (Lam-Tung et al., 2015) using the best-fit substitution model. An ultrafast bootstrap (UFB) (Bui et al., 2013) of 1000 replications and the SH-aLRT test were used in this analysis to assess branch supports.

Table 1. Taxa included in the phylogenetic analyses in this study.

Family	Subfamily	Tribe	Species	Location / Biotype	Accession No.	Reference
Delphacidae	Delphacinae	Delphacini	*Laodelphax striatellus*	Jiangsu (China)	JX880068	Zhang et al., 2013
			Laodelphax striatellus	Beijing (China)	FJ360695	Song & Liang, 2009
			Nilaparvata lugens	Biotype 1	JN563995	Lv et al., 2015
			Nilaparvata lugens	Biotype 2	JN563996	Lv et al., 2015
			Nilaparvata lugens	Biotype 3	JN563997	Lv et al., 2015
			Nilaparvata lugens	Biotype L	KC333654	Lv & Ge, unpubl.
			Nilaparvata lugens	Biotype Y	KC333653	Lv & Ge, unpubl.
			Nilaparvata lugens	Hainan (China)	JX880069	Zhang et al., 2013
			Nilaparvata muiri	Fujian (China)	JN563998	Lv et al., 2015
			Peregrinus maidis	Guangxi (China)	MG049917	Huang & Qin, 2017
			Sogatella furcifera	Hainan (China)	KC512914	Zhang et al., 2014
			Sogatella furcifera	Yunnan (China)	KC512915	Zhang et al., 2014
			Sogatella vibix	Guangxi (China)	MG515238	In this study
		Saccharosydnini	*Saccharosydne procerus*	Guangxi (China)	MG515237	In this study

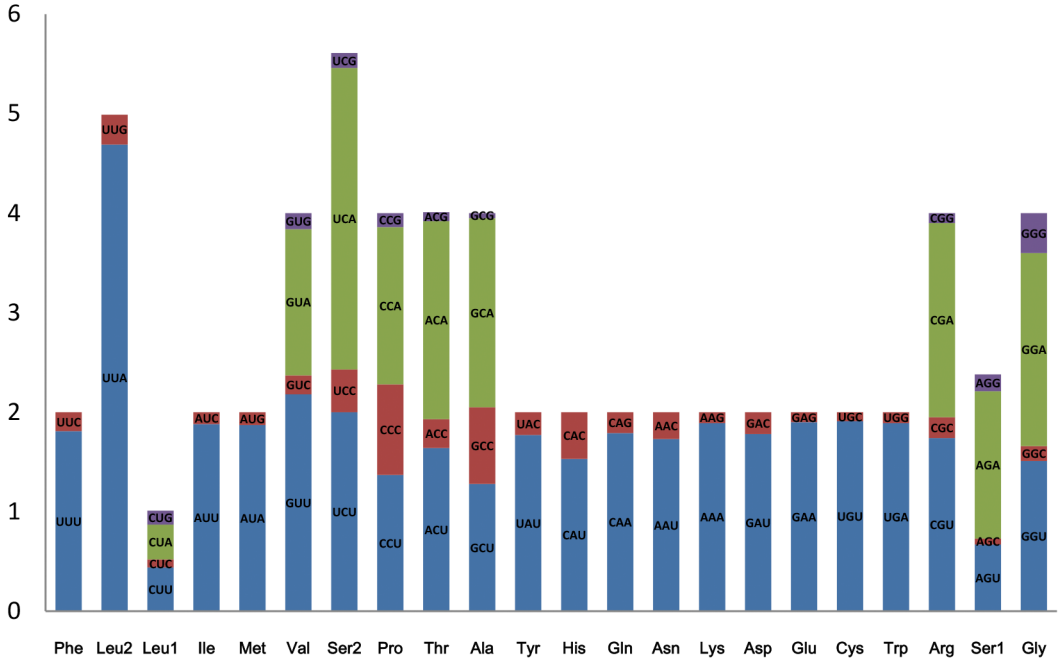

Fig. 3. Relative synonymous codon usage (RSCU) of the mitochondrial genomes of *Saccharosydne procerus*. The stop codon is not given.

Bayesian inference analysis was conducted using BEAST 1.8.0 (Drummond et al., 2012). Chains were run for 20 million generations, with sampling every 2000 generations. Tracer 1.6.0 (Rambaut et al., 2014) was used to verify the posterior distribution and to ensure effective sample sizes (ESSs) > 200 from the Markov Chain Monte Carlo (MCMC) output. TreeAnnotator in the BEAST package was used to summarize tree data with "median height". The first 25% of samples were discarded as burn-in and the remaining samples were used to generate a 50% majority rule consensus tree. FigTree v.1.3.1 (Rambaut, 2009) was used to view the resulting trees.

RESULTS AND DISCUSSION

The *Sa. procerus* mitochondrial genome (GenBank accession no. MG515237) is 16,031 bp in length (Fig. 1), and the overall nucleotide composition exhibits a high A + T

Table 2. Nucleotide composition of the *Saccharosydne procerus* mitochondrial genome.

Feature	Length	Percentage of nucleotides						
		A	C	G	T	G + C	AT-skew	GC-skew
Whole genome	16031	45.6	11.9	7.6	34.9	19.5	0.13	–0.22
PCGs	10835	45.3	12.8	8.0	33.9	20.8	0.14	–0.23
tRNAs	1404	43.9	10.8	9.3	36.0	20.1	0.10	–0.07
rRNAs	1971	45.2	12.0	6.6	36.2	18.6	0.11	–0.29
AT-rich region	1662	48.8	7.5	4.5	39.2	12.0	0.11	–0.25

Table 3. Nucleotide composition of the *Sogatella vibix* mitochondrial genome.

Feature	Length	Percentage of nucleotides						
		A	C	G	T	G + C	AT-skew	GC-skew
Whole genome	16554	41.8	13.9	10.1	34.2	24.0	0.10	–0.16
PCGs	10858	42.4	14.4	10.2	33.0	24.6	0.12	–0.17
tRNAs	1395	42.3	11.9	10.2	35.6	22.1	0.09	–0.08
rRNAs	1976	42.8	14.8	7.7	34.7	22.5	0.10	–0.32
AT-rich region	2167	36.5	12.2	11.9	39.4	24.1	–0.04	–0.01

Table 4. Organization of the mitogenome of *Saccharosydne procerus*.

Name	Product	Strand	Location	Codon		
				Start	Stop	Anti
trnI	tRNA-Ile	J	1–65			GAT
trnQ	tRNA-Gln	N	67–132			TTG
trnM	tRNA-Met	J	132–195			CAT
nad2	NADH2	J	196–1155	ATT	TAA	
trnC	tRNA-Cys	N	1154–1214			GCA
trnW	tRNA-Trp	J	1223–1287			TCA
trnY	tRNA-Tyr	N	1302–1362			GTA
cox1	COX1	J	1368–2901	ATG	T	
trnL2	tRNA-Leu	J	2902–2965			TAA
cox2	COX2	J	2996–3631	ATT	TAA	
trnK	tRNA-Lys	J	3634–3703			CTT
trnD	tRNA-Asp	J	3704–3763			GTC
atp8	ATP8	J	3764–3865	ATT	TAA	
atp6	ATP6	J	3859–4513	ATG	T	
cox3	COX3	J	4514–5294	ATG	T	
trnG	tRNA-Gly	J	5295–5355			TCC
nad3	NADH3	J	5356–5706	ATT	TAA	
trnA	tRNA-Ala	J	5712–5774			TGC
trnR	tRNA-Arg	J	5775–5833			TCG
trnN	tRNA-Asn	J	5835–5897			GTT
trnS1	tRNA-Ser	J	5897–5954			GCT
trnE	tRNA-Glu	J	5954–6015			TTC
trnF	tRNA-Phe	N	6020–6086			GAA
nad5	NADH5	N	6087–7758	ATG	T	
trnH	tRNA-His	N	7759–7822			GTG
nad4	NADH4	N	7826–9142	ATG	TAA	
nad4l	NADH4L	N	9136–9408	ATG	TAG	
nad6	NADH6	J	9458–9964	ATA	TAA	
trnP	tRNA-Pro	N	10029–10092			TGG
trnT	tRNA-Thr	J	10094–10157			TGT
cytb	CYTB	J	10162–11262	ATG	TAA	
trnS2	tRNA-Ser	J	11264–11325			TGA
nad1	NADH1	N	11341–12256	ATG	T	
trnL1	tRNA-Leu	N	12258–12328			TAG
rrnL	16S rRNA	N	12329–13545			
trnV	tRNA-Val	N	13546–13615			TAC
rrnS	12S rRNA	N	13616–14369			
AT-rich			14370–16031			

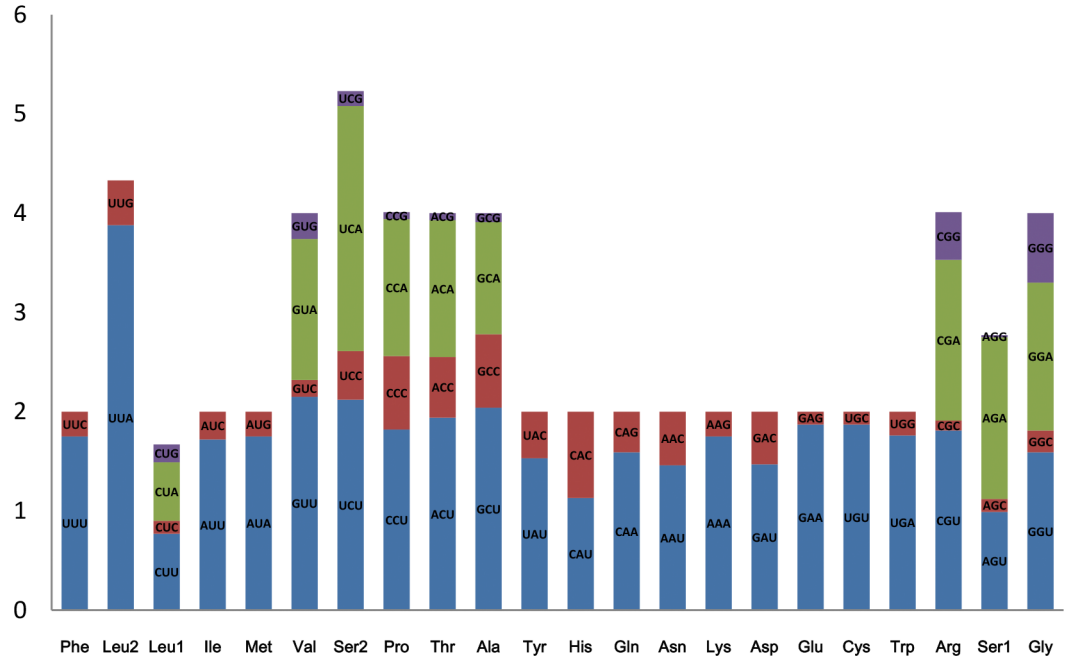

Fig. 4. Relative synonymous codon usage (RSCU) of the mitochondrial genomes of *Sogatella vibix*. The stop codon is not given.

content of 80.5% (Table 2). The mitogenome of *So. vibix* (GenBank accession no. MG515238) is 16,554 bp long with an A + T content of 76.0% (Table 3), likewise heavily biased toward the A and T nucleotides (Fig. 2). The mitogenomes of both species encode a complete set of 37 genes (Tables 4–5) which are usually found in animal mitogenomes, consisting of 13 protein-coding genes (PCG), 2 ribosomal RNA (rRNA) genes and 22 transfer RNA (tRNA) genes (Cameron, 2014). The gene arrangements in the mitochondrial genomes of *Sa. procerus* and *So. vibix* are conserved, similar to other mitogenomes of Delphacidae, with the exception of *Nilaparvata lugens* (Stål). Zhang et al. (2013) found three *trnC* genes in *N. lugens*, but only one *trnC* gene was found by Lv et al. (2015) which corresponds to most hemipteran insects sequenced so far (Wang et al., 2015).

Most PCGs share the start codon ATT or ATG, with *nad6* of *Sa. procerus* starting with ATA. Four genes of *So. vibix* (*cox1*, *atp6*, *cox3*, *nad5*) and fives genes of *Sa. procerus* (*cox1*, *atp6* , *cox3*, *nad5*, *nad1*) use the incomplete stop codon T. Four genes of *So. vibix* (*cox2*, *nad4l*, *cytb*, *nad1*) and *nad4l* of *Sa. procerus* use TAG. The remaining PCGs

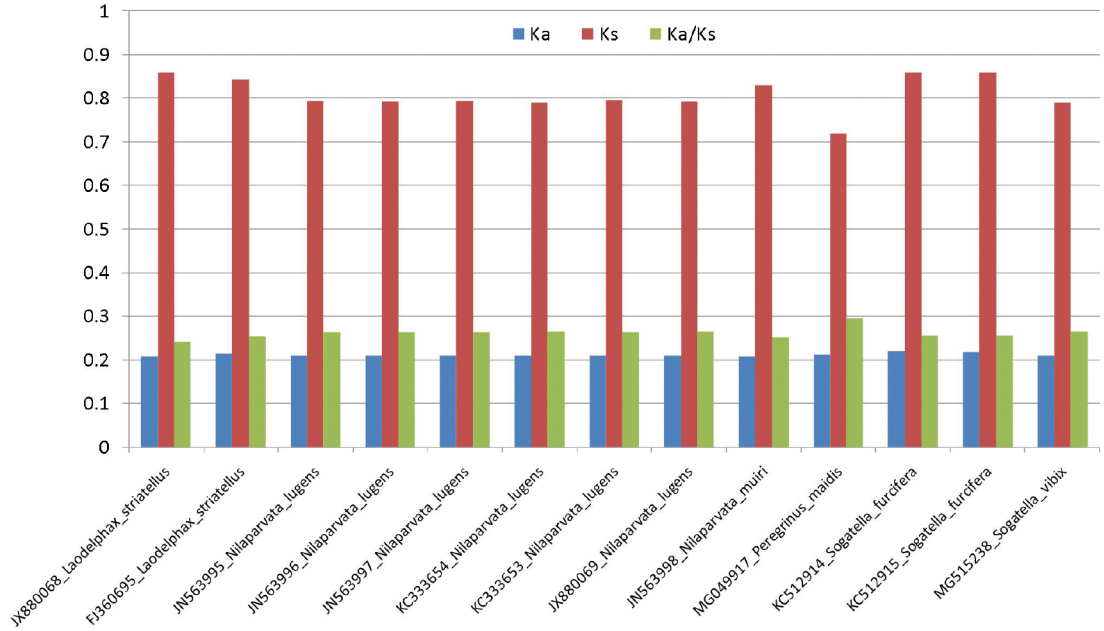

Fig. 5. Evolutionary rates of Delphacini mitochondrial genomes. The number of nonsynonymous substitutions per nonsynonymous site (Ka), the number of synonymous substitutions per synonymous site (Ks), and the ratio of Ka/Ks for each Delphacini mitochondrial genome are given, using that of *Saccharosydne procerus* as a reference sequence.

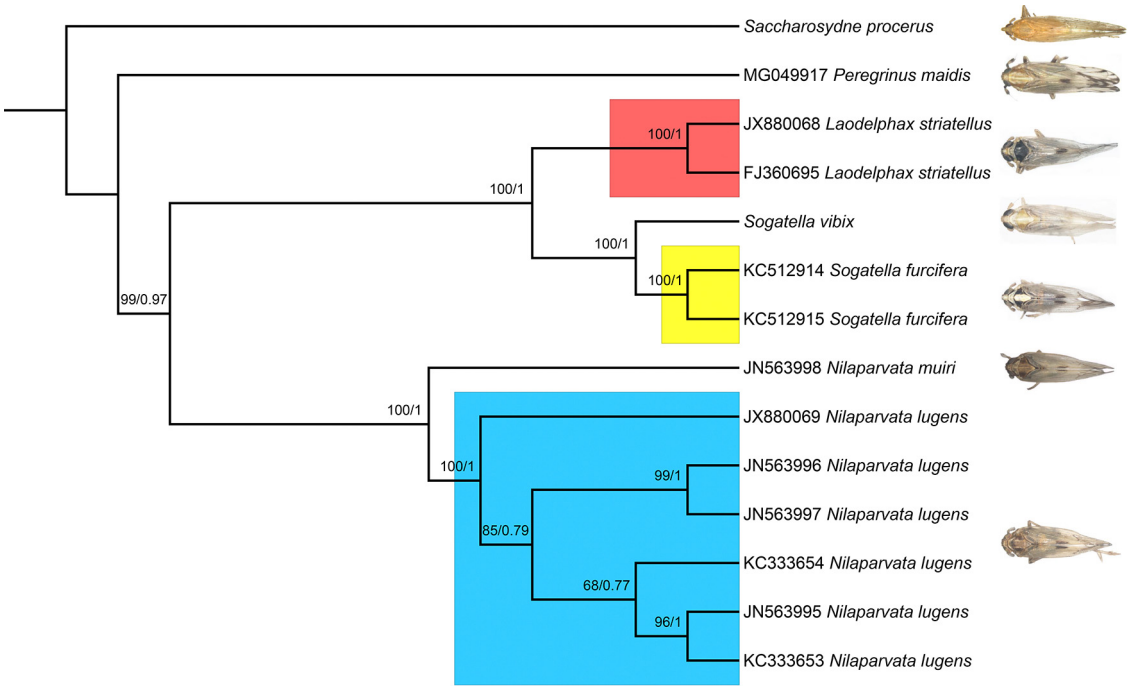

Fig. 6. Phylogenetic tree of three predominant rice planthoppers obtained from ML analysis based on concatenated data of 13 PCGs and two rRNA genes. The numbers at nodes indicate ML bootstrap values/Bayesian posterior probabilities, respectively. Accession numbers are given for species obtained from GenBank.

use the stop codon TAA. The stop codon of *nad1* in *Sa. procerus* (T) is different from those in Delphacini (TAA or TAG). This suggests that during evolution the *nad1* gene in *Sa. procerus* acquired a different mechanism for transcription termination. Further genome sequencing is needed to find out whether this feature exists only in *Sa. procerus* or in the tribe Saccharosydnini. The use of anti-codons for 22 tRNAs are all the same between *So. vibix* and *Sa. procerus*.

The relative synonymous codon usage (RSCU) of *Sa. procerus* and *So. vibix* are shown in Figs 3–4. The codon usage in these mitogenomes shows a high AT content. The most frequently used amino acids were Phe, Leu and Ile, while TTT (Phe), TTA (Leu) and ATT (Ile) were the most frequently utilized codons. All three of these most frequently utilized codons are composed of A and T. Additionally, it is obvious that the preferred codon usage is A or T in the third position rather than G and C. Almost all of the frequently used codons ended with A or T, which may contribute to the significant bias towards A and T.

The rate of nonsynonymous substitutions (Ka), synonymous substitutions (Ks), and the ratio of Ka/Ks were calculated for PCGs of each delphacine mitogenome with *Sa. procerus* as the reference sequence (Fig. 5). All of the Ka, Ks and the ratios of Ka/Ks values were less than 1, indicating the existence of purifying selection in these species.

Saccharosydne procerus (tribe Saccarosydnini) was selected as the outgroup based on results of previous analyses that placed this tribe (plus Tropidocephalini) as sister to Delphacini (Asche, 1985, 1990; Urban et al., 2010; Huang et al., 2017). *Peregrinus maidis* was also included to test the polarity of the phylogeny. The result placed *P. maidis* as sister to the remaining Delphacini, which is concordant with our previous study (Huang et al., 2017). We therefore think the use of *Sa. procerus* as the outgroup taxon is appropriate.

The phylogenetic analyses of ML and BI based on mitogenome datasets yield two identical topologies (Fig. 6) when rooted with *Sa. procerus* (of Saccharosydnini); remaining species form the tribe Delphacini, with *P. maidis* being sister to the remaining species. The conformation of the clade containing the three rice planthoppers (*L. striatellus*, *So. furcifera* and *N. lugens*) was (*L. striatellus* + (*So. vibix* + *So. furcifera*)) + (*N. muiri* + *N. lugens*). Moreover, the relationships among biotypes of *N. lugens* were recovered.

This study documents the first mitogenome of Saccharosydnini and the mitogenome of *So. vibix*, which both contain 37 typical metazoan mitochondrial genes and retain the organization of the most other Delphacidae mitogenomes. The phylogeny based on more taxa is needed to better understand the evolution of Delphacidae. Therefore, more mitogenomes need to be sequenced in further studies.

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Table 5. Organization of the mitogenome of *Sogatella vibix*.

Name	Product	Strand	Location	Codon		
				Start	Stop	Anti
trnI	tRNA-Ile	J	1–68			GAT
trnQ	tRNA-Gln	N	71–138			TTG
trnM	tRNA-Met	J	138–199			CAT
nad2	NADH2	J	200–1156	ATT	TAA	
trnC	tRNA-Cys	N	1155–1219			GCA
trnW	tRNA-Trp	J	1236–1300			TCA
trnY	tRNA-Tyr	N	1310–1371			GTA
cox1	COX1	J	1373–2906	ATG	T	
trnL2	tRNA-Leu	J	2907–2971			TAA
cox2	COX2	J	2972–3634	ATT	TAG	
trnK	tRNA-Lys	J	3636–3706			CTT
trnD	tRNA-Asp	J	3707–3768			GTC
atp8	ATP8	J	3769–3870	ATT	TAA	
atp6	ATP6	J	3864–4518	ATG	T	
cox3	COX3	J	4519–5299	ATG	T	
trnG	tRNA-Gly	J	5300–5359			TCC
nad3	NADH3	J	5360–5710	ATT	TAA	
trnA	tRNA-Ala	J	5710–5770			TGC
trnR	tRNA-Arg	J	5775–5835			TCG
trnN	tRNA-Asn	J	5835–5898			GTT
trnS1	tRNA-Ser	J	5898–5954			GCT
trnE	tRNA-Glu	J	5954–6016			TTC
trnF	tRNA-Phe	N	6017–6083			GAA
nad5	NADH5	N	6084–7758	ATG	T	
trnH	tRNA-His	N	7759–7819			GTG
nad4	NADH4	N	7820–9142	ATG	TAA	
nad4l	NADH4L	N	9136–9408	ATG	TAG	
nad6	NADH6	J	9458–9979	ATT	TAA	
trnP	tRNA-Pro	N	10055–10116			TGG
trnT	tRNA-Thr	J	10119–10182			TGT
cytb	CYTB	J	10187–11290	ATG	TAG	
trnS2	tRNA-Ser	J	11289–11344			TGA
nad1	NADH1	N	11362–12279	ATG	TAG	
trnL1	tRNA-Leu	N	12281–12342			TAG
rrnL	16S rRNA	N	12343–13569			
trnV	tRNA-Val	N	13570–13638			TAC
rrnS	12S rRNA	N	13639–14387			
AT-rich			14388–16554			

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