

Article

# Comparative Plastome Analyses and Phylogenetic Applications of the *Acer* Section *Platanoidea*

Tao Yu <sup>1</sup>, Jian Gao <sup>2</sup>, Bing-Hong Huang <sup>3</sup>, Buddhi Dayananda <sup>4</sup> , Wen-Bao Ma <sup>5</sup>,  
Yu-Yang Zhang <sup>1</sup>, Pei-Chun Liao <sup>3,\*</sup> and Jun-Qing Li <sup>1,\*</sup>

<sup>1</sup> Forestry College, Beijing Forestry University, 35 Qinghua East Road, Haidian District, Beijing 100083, China; yutao123@bjfu.edu.cn (T.Y.); yuyangzhang@bjfu.edu.cn (Y.-Y.Z.)

<sup>2</sup> Faculty of Resources and Environment, Baotou Teachers' College, No.3, Kexue Rd., BaoTou, Inner Mongolia 014030, China; gaojian5688@163.com

<sup>3</sup> School of Life Science, National Taiwan Normal University, No. 88, Sec. 4, TingChow Rd., Wunshan Dist., Taipei 116, Taiwan; sohjiro4321@yahoo.com.tw

<sup>4</sup> School of Agriculture and Food Sciences, The University of Queensland, Brisbane QLD 4072, Australia; buddhi6@gmail.com

<sup>5</sup> Key Laboratory of National Forestry and Grassland Administration on Sichuan Forest Ecology, Resources and Environment Sichuan Academy of Forestry, Chengdu 610081, China; mawenbao\_2000@126.com

\* Correspondence: pcliao@ntnu.edu.tw (P.-C.L.); lijq@bjfu.edu.cn (J.-Q.L.); Tel.: +886-2-77346330 (P.-C.L.)

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**Abstract:** The *Acer* L. (Sapindaceae) is one of the most diverse and widespread genera in the Northern Hemisphere. Section *Platanoidea* harbours high genetic and morphological diversity and shows the phylogenetic conflict between *A. catalpifolium* and *A. amplum*. Chloroplast (cp) genome sequencing is efficient for the enhancement of the understanding of phylogenetic relationships and taxonomic revision. Here, we report complete cp genomes of five species of *Acer* sect. *Platanoidea*. The length of *Acer* sect. *Platanoidea* cp genomes ranged from 156,262 bp to 157,349 bp and detected the structural variation in the inverted repeats (IRs) boundaries. By conducting a sliding window analysis, we found that five relatively high variable regions (*trnH-psbA*, *psbN-trnD*, *psaA-ycf3*, *petA-psbJ* and *ndhA* intron) had a high potential for developing effective genetic markers. Moreover, with an addition of eight plastomes collected from GenBank, we displayed a robust phylogenetic tree of the *Acer* sect. *Platanoidea*, with high resolutions for nearly all identified nodes, suggests a promising opportunity to resolve infrasectional relationships of the most species-rich section *Platanoidea* of *Acer*.

**Keywords:** *Acer*; sect. *Platanoidea*; chloroplast genome; sequence divergence; structural variation; phylogenetics

## 1. Introduction

Chloroplasts (cp) are essential organelles in plant cells for the processes of photosynthesis and carbon fixation [1]. They possess uniparental inheritance and their genome has a high conservation structure in most land plants [2]. Generally, cp genomes in most angiosperms are circular DNA molecules composed of four parts, namely two inverted repeats (IRs) at approximately 20–28 kb, a vast single-copy region (LSC) at 80–90 kb and a small single-copy region (SSC) at 16–27 kb [3]. The composition of angiosperm cp genomes is relatively conserved and encodes four ribosomal RNAs (rRNAs), roughly 30 transfer RNAs (tRNAs) and approximately 80 single-copy genes [4]. With the rapid development of next-generation sequencing (NGS) and other methods for obtaining the cp genome sequences, the availability of cp genome sequences has increased dramatically for land plants, offering opportunities for the comprehensive structure comparison, improvement of horticultural plant breeding [5,6] and reconstruction of evolutionary relationships [7,8]. In most angiosperms,

the cp genome is inherited from the patrilineal lineage and exhibits little or no recombination [9]. Due to its relatively conserved features, cp sequences are commonly used as DNA barcodes for genetic identification, plant systematic studies, and research into plant biodiversity, biogeography, adaptation, etc. [10,11].

*Acer* L. (Maple), a diverse genus of family Sapindaceae L., contains more than 124 species [12]. Most extant species of the genus are native to Asia, whereas others occur in North America, Europe and North Africa [12–14]. Most *Acer* species are famous ornamental plants [13], and also another usage for pharmaceutical and chemical products [15]. To date, 17 species belonging to the *Acer* section *Platanoidea* have been recognised in China, in which the section shows high genetics and morphology diversity. [12]. Among them, four species are widespread in various vegetation regions (*A. amplum*, *A. longipes*, *A. mono* and *A. truncatum*) [16], and some are endangered, such as *A. catalpifolium*, *A. miaotaiense*, and *A. yangjuechi*.

However, some species with diversified leaf morphology have taxonomic controversy due to unresolved phylogenetic relationships (for example, *A. longipes* and *A. amplum*) and require further studies and clarification [17]. The comparative plastome analysis allows detailed insights to affirm the phylogenetic placement of these plants and will be useful for species identification, to verify taxonomic levels and identify phylogenetic relationships [8,18]. Recently, cp genomes of *A. miaotaiense* and *A. truncatum* have been reported, but merely the sequence information was provided without further analyses [19,20]. Thus, a comparative study among these two published cp genomes and five newly generated plastomes of sect. *Platanoidea* is conducted and applied to address phylogenetic and taxonomic validity.

Firstly, we reported newly completed cp genomes of five species of the *Acer* sect. *Platanoidea* (*A. catalpifolium*, *A. amplum*, *A. longipes*, *A. yangjuechi* and *A. mono*). Then, we compared the gene contents and the plastomic organisation with two published cp genomes in the sect. *Platanoidea* to identify variable loci that can apply to the species or population-level studies on *Acer*. The aims of this study are: (i) to deepen our understanding of the genetic and structural diversity within the sect. *Platanoidea*, (ii) to increase our understanding of phylogenetic relationships of species within the sect. *Platanoidea*, and (iii) to reconstruct a phylogenetic tree based on these plastomes. Our study also provides genetic resources for future research in this genus.

## 2. Materials and Methods

### 2.1. Sampling and DNA Extraction

Young leaves of five *Acer* species (*A. catalpifolium*, *A. amplum*, *A. longipes*, *A. yangjuechi* and *A. mono*) were collected and dried immediately with silica gel for preservation, for each species we collected the leaves from one healthy plant. Collection information of the plant materials is showed in Table S1. Vouchers taxonomical determination was by the Beijing Forestry University herbarium and deposited at the College of Forestry, Beijing Forestry University, China. We isolated total genomic DNA from silica gel-dried leaves according to the modified CTAB method [21].

### 2.2. Chloroplast Genome Sequencing, Assembling and Annotation

Purified genomic DNA was sequenced using an Illumina MiSeq sequencer at Shanghai OE Biotech. Co., Ltd. A paired-end library was constructed with an insert size of 300 bp, yielding at least 8 GB of 150 bp paired-end reads for each species. Clean reads were obtained with NGS QC Toolkit v2.3.3 (cut-off read length for HQ = 70%, cut-off quality score = 20, trim reads from 5' = 3, trim reads from 3' = 7) [22]. We used MITObim v. 1.8 [23] to assemble the five new *Acer* cp sequences with the reference cp genomes, *A. miaotaiense* (KX098452) [19], *A. davidii* (KU977442) [24] and *A. morrisonense* (KT970611) [25]. Gene functions were annotated using DOGMA [26], and the protein-encoding genes (PCG), tRNAs and rRNA were determined and verified using the BLAST searches (<https://blast.ncbi.nlm.nih.gov/Blast.cgi>).

### 2.3. Divergence Hotspot Identification

In order to determine the divergence level, a MAFFT: multiple sequence alignment program [27] was used to align cp sequences of seven *Acer* sect. *Platanoidea* species, and then sliding windows of the nucleotide variability ( $\pi$ ) was conducted using DnaSP 5.0 with 600-bp window length and 200-bp step size [28].

### 2.4. Phylogenomic Reconstruction

To determine the phylogenetic relationship of the *Acer* sect. *Platanoidea*, we performed phylogenetic analyses using 13 cp genome sequences, which comprised five plastome sequences generated in this study, six plastomes of the *Acer* species collected from GenBank, and two of the *Dipteronia* species as an outgroup (Table S2). Consequently, a total length of 160,886 bp was aligned using MAFFT [27]. The best-fitting substitution model (GTR + I + G) was inferred using Modeltest 3.7 [29]. Finally, phylogenomic relationships were reconstructed with Bayesian Inference (BI) and Maximum Likelihood (ML) using MrBayes 3.2 [30] and phyML v3.0 [31], respectively. For the BI tree, 10 million generations were simulated using two parallel Markov Chain Monte Carlo (MCMC) simulations, sampled every 1000 generations. The first 25% of the simulations were discarded (burn-in) to generate a consensus tree. For the ML tree, 1000 bootstrap replicates were conducted to evaluate the supporting values of each node.

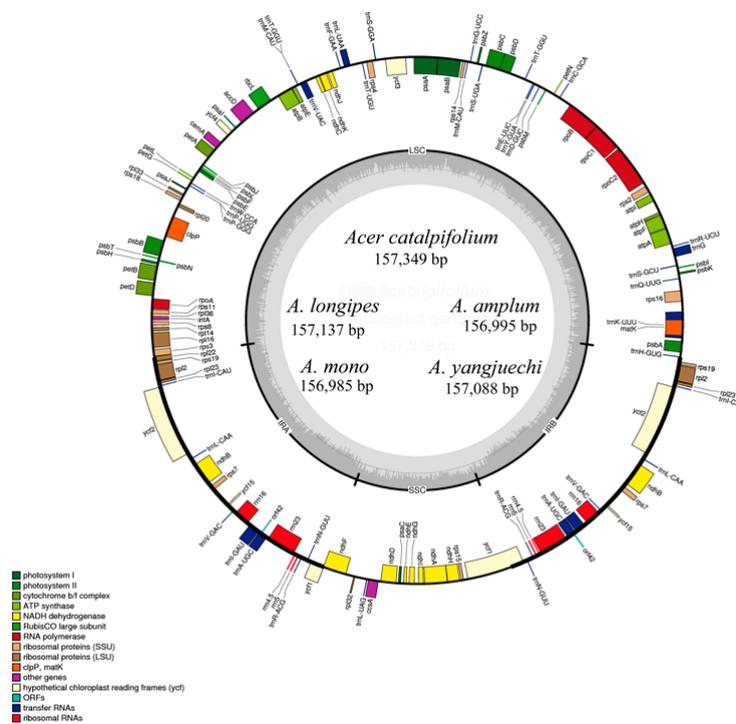
## 3. Results and Discussion

### 3.1. Chloroplast Genome Organisation of the *Acer* sect. *Platanoidea*

The nucleotide sequences of the seven *Acer* sect. *Platanoidea* cp genomes ranged from 156,262 bp to 157,349 bp in length (Figure 1, Table 1), which are similar to other reported cp genomes of *Acer* [19,25]. The variation of chloroplast genome length is mainly caused by the change of LSC region length. The quadripartite structures of these cp genomes were identical to most angiosperms containing a LSC region, SSC region and two inverted repeat regions (IRa and IRb) [32]. The overall GC content of these cp genomes accounts for 37.9% and the GC content of IR regions accounts for 42.8% higher than the LSC (35.9%) and the SSC (32.3%). The new sequences possess 117 genes, including four unique rRNAs, 31 tRNAs, and 82 PCGs, respectively (Table 2). Among them, most cp genes were single copy, while 23 genes exhibited double copies, including four rRNA (4.5S, 5S, 16S and 23S rRNA), nine tRNA (*trnA-UGC*, *trnI-CAU*, *trnI-GAU*, *trnL-CAA*, *trnM-CAU*, *trnN-GUU*, *trnR-ACG*, *trnT-GGU* and *trnV-GAC*) and 10 PCGs (*ndhB*, *rpl2*, *rps12*, *rpl23*, *rps19*, *rps7*, *ycf1*, *orf42*, *ycf2* and *ycf15*). Additionally, a total of 18 genes harboured introns, and three genes (*ycf3*, *clpP* and *rps12*) contained two introns.

**Table 1.** General features of the *Acer* sect. *Platanoidea* chloroplast genomes compared in this study.

Name	Total (bp)	LSC (bp)	SSC (bp)	IR (bp)	GC%
<i>A. catalpifolium</i>	157,349	85,745	18,066	26,769	37.9
<i>A. miaotaiense</i>	156,595	86,327	18,068	26,100	37.9
<i>A. longipes</i>	157,137	85,531	18,068	26,769	37.9
<i>A. amplum</i>	156,995	85,386	18,077	26,766	37.9
<i>A. mono</i>	156,985	85,378	18,069	26,769	37.9
<i>A. yangjuechi</i>	157,088	85,483	18,069	26,768	37.9
<i>A. truncatum</i>	156,262	86,019	18,073	26,085	37.9



**Figure 1.** Merged gene map of the complete chloroplast genomes of five *Acer* sect. *Platanioidea* species. Genes belonging to different functional groups are colour-coded. The genes drawn inside the circle are transcribed clockwise, while those outside are transcribed counter-clockwise. Darker grey in the inner circle corresponds to the GC content of the chloroplast genome.

**Table 2.** Genes presented in the *Acer* sect. *Platanioidea* chloroplast genome.

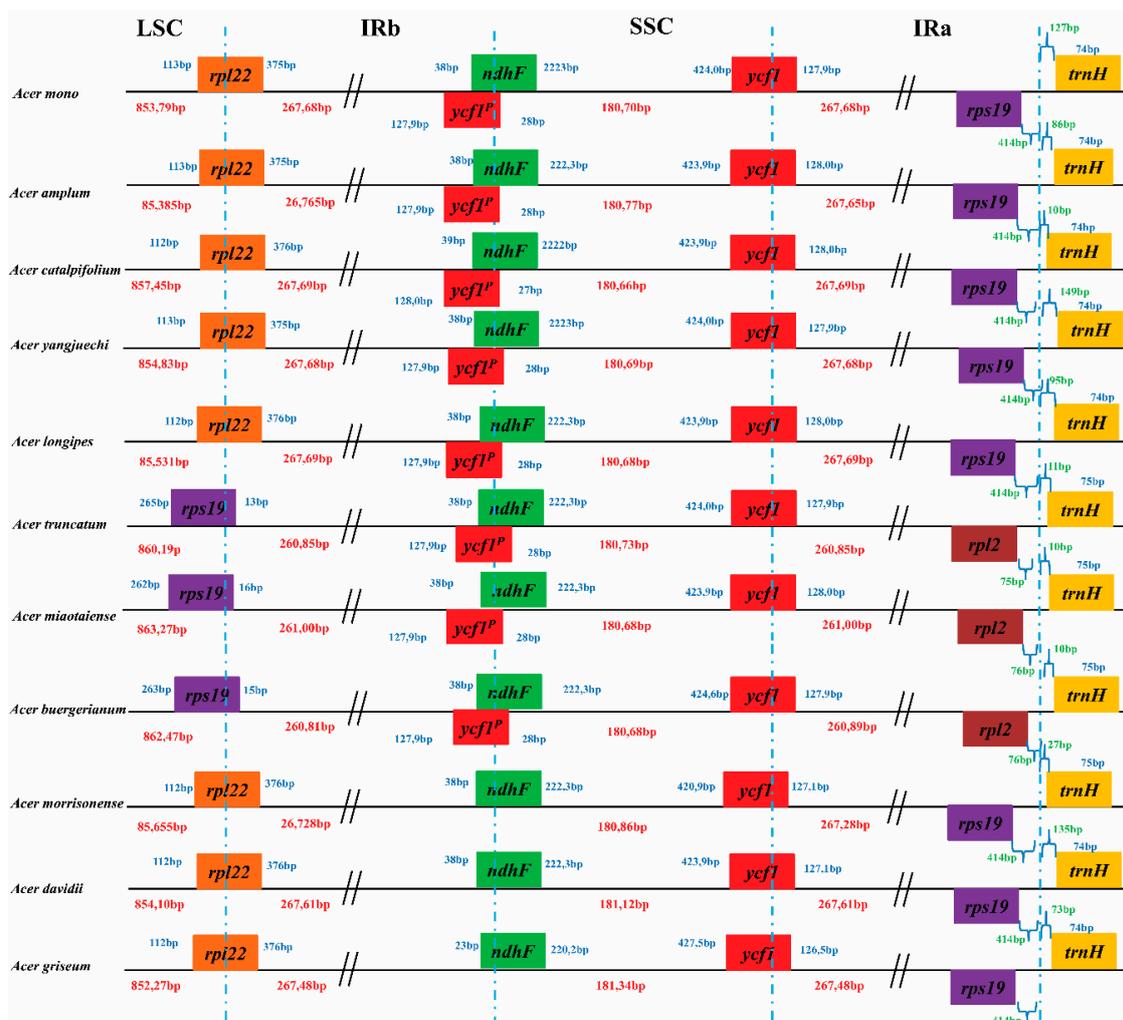
Group of Gene	Genes Name
1 Photostsyem I	<i>psaA, psaB, psaC, psaI, psaJ</i>
2 Photostsyem II	<i>psbA, psbB, psbC, psbD, psbE, psbF, psbH, psbI, psbJ, psbK, psbL, psbM, psbN, psbT, psbZ</i>
3 Cytochrome b/f complex	<i>petA, petB*, petD*, petG, petL, petN</i>
4 ATP synthase	<i>atpA, atpB, atpE, atpF*, atpH, atpI</i>
5 NADH dehydrogenase	<i>ndhA*, ndhB*, ndhC, ndhD, ndhE, ndhF, ndhG, ndhH, ndhI, ndhJ, ndhK</i>
6 RubisCO large subunit	<i>rbcL</i>
7 RNA polymerase	<i>ropA, ropB, ropC1*, ropC2</i>
8 Ribosomal proteins(SSU)	<i>rps2, rps3, rps4, rps7, rps8, rps11, rps12**, rps14, rps15, rps16*, rps18, rps19</i>
9 Ribosomal proteins (LSU)	<i>rpl2*, rpl14, rpl16*, rpl20, rpl22, rpl23(x2), rpl32, rpl33, rpl36</i>
10 Other gene	<i>clpP**, matK, accD, ccsA, infA, cemA</i>
11 Proteins of unknown function	<i>ycf1, ycf2, ycf3**, ycf4, ycf15</i>
12 ORFs	<i>Orf42</i>
13 Transfer RNAs	31 tRNAs(six contain a single intron)
14 Ribosomal RNAs	<i>rrn4.5, rrn5, rrn16, rrn23</i>

Note: a single asterisk (\*) following after gene names indicate intron-containing genes, and double asterisks (\*\*) following after gene names indicate two introns in the gene.

### 3.2. Comparative Analysis of the Genomic Structure

Contraction and expansion of the IRs, LSC and SSC are important to the evolution of cp genomes [33,34], which is the leading cause of gene order and the size changes of the cp genome [35]. Detailed structure comparisons among the 13 cp genomes of the *Acer* species were presented in Figure 2. *rpl22* in the LSC/IR boundary and *rps19* was the last gene in most *Acer* sect. *Platanioidea* cp genomes included *A. mono*, *A. amplum*, *A. catalpifolium*, *A. yangjuechi*, *A. longipes*, *A. morrisonense*, *A. davidii* and *A. griseum*. However, the different structures of *rps19* in the LSC/IR boundary and the last gene *rpl2* were found in *A. truncatum*, *A. miaotaiense* and *A. buergerianum*. Among the Arcoideae species,

*rpl22* and *rps19* gene order changes in the IRA/LSC borders were also observed and has become the most varied rearrangement in this section [36]. Similarly, the rearrangement has been reported in the *Apiales* species, which also has two structure types of *rpl23* and *rps19* in the LSC/IR boundary [37]. Length variations of the *Acer* cp genomes were found by contraction and expansion of the LSC and IRs, the length of the LSC varies from 85,379 bp to 86,327 bp, and the length of the IR varies from 26,085 bp to 26,769 bp (Figure 2). Moreover, the type of unique structural borders of the cp genome (*A. truncatum*, *A. miaotaiense*, and *A. buergerianum*) also show a contraction of IRs, which indicates variations in boundary genes may be caused by variations in length.

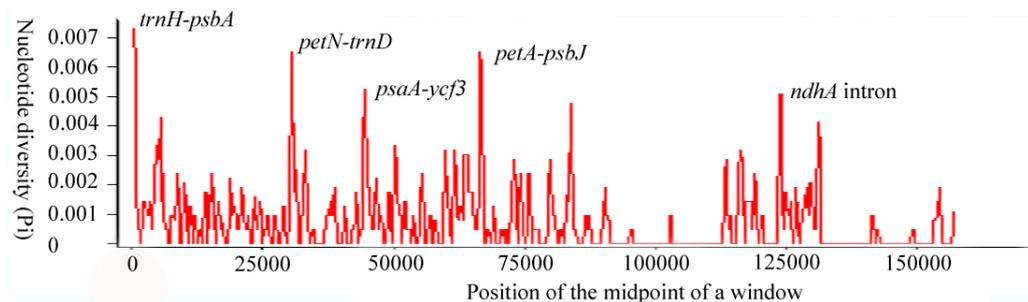


**Figure 2.** Comparison of the junction sites of the LSC, IRs and SSC regions among 13 *Acer* sect. *Platanioidea* species chloroplast genomes. Different colour boxes indicate specific genes and those above the genome lines indicate their transcriptions in a forward direction, while the under-line boxes are in the reverse direction. The length of the LSC, SSC, and IR regions is shown in red, the length of the gene distance from the boundary is shown in green, the length of the gene is shown in blue, and the P represents the pseudogene.

### 3.3. Divergence Hotspot of the *Acer* sect. *Platanioidea* Species

Sliding window analysis of the whole cp genome was performed to identify hotspots of the *Acer* sect. *Platanioidea* species. In Figure 3, it is apparent that the *trnH-psbA*, *psbN-trnD*, *psaA-ycf3*, *petA-psbJ* and *ndhA* intron nucleotide variability was higher than other regions. Most divergent hotspot loci are located in the LSC region, which allows for the proper design of the genetic markers. Only one hotspot *ndhA* intron was located in the SSC region. The IR regions were much more conserved. This result

was similar to other cp genomes [37,38]. The general barcode *trnH-psbA* has demonstrated extreme variation in plant groups [39,40]. Thus, the highest variation *trnH-psbA* has the potential to be used in DNA barcoding in the *Acer* sect. *Platanoidea*. Additionally, the evolutionary history of *A. mono* has been inferred by using *psbA-trnH*, *trnL-trnF* and an intron of *rpl16* [16]. The regions of the *psaA-ycf3*, *petA-psbJ* and *ndhA* intron have been indicated as high variations in previous studies. In witch-hazel (genus *Hamamelis* L., Hamamelidaceae), appropriate variations of *psaA-ycf3* were used to reconstruct phylogenetic relationships [41]. In *Scutellaria*, *petA-psbJ* was one of six fast-evolving DNA sequences in the cp genome [42], while a systematic study shows that Muhlenbergiinae has high variation at the *ndhA* intron [43].



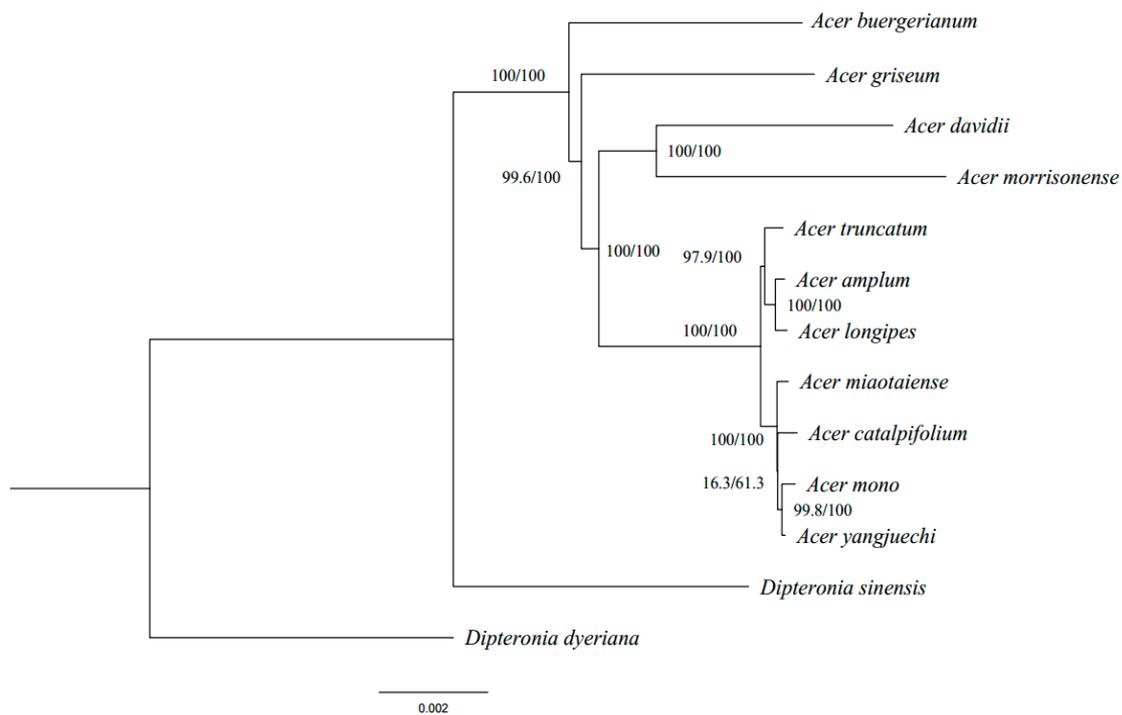
**Figure 3.** Sliding-window analysis on the cp genomes for seven *Acer* sect. *Platanoidea* species.

The endangered plants, *A. catalpifolium*, *A. yangjuechi* and *A. miaotaiense* in the *Acer* sect. *Platanoidea*, have small population sizes [44]. Population genetics studies of these species are relatively weak, and with limited conservation goals [45,46]. These high variability regions can provide alternative sites for subsequent studies and will contribute to the conservation of endangered plants.

### 3.4. Phylogenetic Analysis

The phylogenomic inference based on cp genomes shows high bootstrap supports in most nodes that provided robust evolutionary placement and relationship of the *Acer* species (Figure 4). The results showed that seven sampled species of the *Acer* sect. *Platanoidea* formed a single clade, which is consistent with previous studies of the *Acer* phylogeny [14,47]. In this clade, *A. catalpifolium*, *A. mono*, *A. miaotaiense* and *A. yangjuechi* had the closest phylogenetic relationship and formed a subclade, while *A. truncatum*, *A. longipes*, *A. amplum* formed another one. Previous phylogenetic inference of the *Acer* did not contain species with a small population size in the sect. *Platanoidea* (such as *A. catalpifolium* and *A. yangjuechi*) [14,47]. Phylogenetic analysis exhibited in this study for the issue of *A. longipes* *A. amplum* complex in the sect. *Platanoidea* raised earlier [17], and the phylogenetic position of *A. catalpifolium* was also redefined.

It is somewhat surprising that *A. mono* is not a sister with *A. truncatum* but with *A. yangjuechi*, which differs from some published studies [13]. Since *A. mono* is widespread in Asia and comprised of multiple local varieties, we cannot rule out that the possibility of the grouping of *A. mono* and *A. yangjuechi* due to adjacent sampling localities of *A. mono* and *A. yangjuechi* in Lin'an, Zhejiang province of China, the only extant habitat of *A. yangjuechi* [48]. Liu et al. [49] showed that the population composition of the Lin'an population is significantly different from the neighbouring populations of *A. mono*. The clustering of *A. mono* and *A. yangjuechi* inferred in this study may not only reflect the truth of geographic divergence in the genetics of *A. mono* but also implies the chloroplast capture by ancient hybridisation events between the two species in Lin'an.



**Figure 4.** Phylogenetic tree of 13 *Acer* species inferred by Maximum Likelihood (ML) and Bayesian Inference (BI) methods, based on the whole cp genome sequences. The numbers above the branches are the bootstrap values of ML methods and the posterior probabilities of BI.

#### 4. Conclusions

In this study, we firstly reported complete cp genomes of five *Acer* sect. *Platanoidea* species (*A. catalpifolium*, *A. amplum*, *A. longipes*, *A. yangjuechi* and *A. mono*) using the NGS technology. In comparison with other published *Acer* species from NCBI, we found that the *Acer* species have similar cp genome structure and gene content. The divergence hotspots identified in the cp genome of the *Acer* sect. *Platanoidea* could be applied to develop molecular markers for further population genetics studies. The high variation at the IR/LSC and IR/SSC boundaries were also reported. The phylogenetic analysis strongly supported that *A. catalpifolium* has the closest relationship with *A. miaotaiense*, followed by *A. mono*, and *A. yangjuechi*, which confirms the species-complex relationship of *A. longipes* and *A. amplum*. The available genomic data presented in this paper provides a basis for further research on the evolutionary history and conservation genetics of endangered species of genus *Acer*.

**Supplementary Materials:** The following are available online at <http://www.mdpi.com/1999-4907/11/4/462/s1>, Table S1: General features of the *Acer* sect. *Platanoidea* chloroplast genomes compared in this study. Table S2: *Acer* taxa sampled in this study.

**Author Contributions:** T.Y. and J.G. conceived and designed the work; J.G. and Y.-Y.Z. collected samples; T.Y., J.G. and B.-H.H. performed the experiments and analysed the data; T.Y. and J.G. wrote the manuscript; P.-C.L., W.-B.M., B.D. and J.-Q.L. critically reviewed the manuscript. All authors have read and agreed to the published version of the manuscript.

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**Conflicts of Interest:** The authors declare no conflict of interest.

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