Nuclear and plastid phylogenomic analyses provide insights into the reticulate evolution, species delimitation and biogeography of the Sino-Japanese disjunctive *Diabelia* (Caprifoliaceae)

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Abstract: Understanding biological diversity and the mechanisms of the Sino-Japanese disjunctions are major challenges in eastern Asia biogeography. The Sino-Japanese flora has been broadly studied as an ideal model for plant phylogeography. *Diabelia* (Caprifoliaceae) is an East Asian genus, with a disjunctive distribution across the Sino-Japanese region. However, relationships within *Diabelia* remain elusive. In this study, we reconstructed the phylogeny of *Diabelia* and inferred historical biogeography and evolutionary patterns based on nuclear and plastid sequences from target enrichment and genome skimming approaches, respectively. We found that the main clades within *Diabelia* were discordant between nuclear and plastid trees. Both nuclear and plastid phylogenetic analyses supported five main clades: *D. serrata*, *D. tetrasepala*, *D. sanguinea*, *D. spathulata* var. *stenophylla* and *D. spathulata* var. *spathulata*. Species network analyses revealed that *Diabelia tetrasepala* is likely the result of a hybridization event. Divergence time estimation and ancestral area reconstructions showed that *Diabelia* originated in Japan during the early Miocene, with subsequent vicariance and dispersal events between Japan and Korea, and between Japan and China. Overall, our results support the division of *Diabelia* into five main clades and the recognition of five species in the genus. This research provides new insights in the species delimitation and speciation processes of taxonomically complex lineages such as *Diabelia*.

Keywords: *Diabelia;* Phylogenomics; Gene tree discordance; Cytonuclear discordance; Hybridization

1 Introduction

Understanding how different factors have shaped current biological diversity is a major challenge for evolutionary biology (Jiang et al., 2016; Casebolt & Kowalewski, 2018; Wang et al., 2018; Martínez-Espinosa, 2021; Maguilla et al., 2021). The Sino-Japanese floristic region (SJFR) of East Asia was an important glacial sanctuary during the Quaternary and harbors the highest diversity of temperate plant species in the world, warranting much attention to understand its origin and diversification (Mitsui et al., 2008; Qiu et a1., 2009; 2011; Zhao et al., 2019; Tian et al. 2020; Zhang et al., 2020). The SJFR extends widely over an area from southwest China to northern Japan, with complex topography and multiple climatic zones (Qiu et a1., 2011; Lu et al., 2020). The eastern edge of the SJFR experienced dramatic changes in the palaeo-landscape during the Miocene and Pliocene (Ota, 1988; Lu et al., 2020), which may have played key roles in isolating ancient Japanese plant species from continental East Asian species.

Diabelia Landrein (Caprifoliaceae) is an East Asian endemic genus and was recently segregated from *Abelia* based on the paired flowers appearing at the end of short shoots (Landrein, 2010; Wang et al., 2020). This genus of shrubs belongs to the subfamily Linnaeoideae (Landrein, 2010; Wang et al., 2015; Landrein and Farjon, 2020; Wang et al., 2020) and traditionally included three species: *Diabelia serrata* (Siebold & Zucc.) Landrein with two sepals, *D. tetrasepala* (Koidz.) Landrein with four big and one smaller sepal, and *D. spathulata* (Siebold & Zucc.) Landrein with five sepals, which is further subdivided into three varieties, var. *spathulata*, var. *sanguinea* (Makino) Landrein, and var. *stenophylla* (Honda) Landrein (Fig. 1; Hara, 1983). *Diabelia* shows a disjunct distribution in the SJFR (Hara, 1983; Landrein, 2010; Zhao et al., 2019; Landrein and Farjon, 2020; Wang et al., 2020): *D. serrata* is widely distributed in southern Japan as well as on the southeastern coast of China; *D. spathulata* is distributed in south, central and northern areas of Japan, but rare in China and Korea; *D. tetrasepala* is distributed in the area from Fukushima to Fukuoka Prefectures in Japan, and its distribution range partly overlaps with that of *D.*

spathulata and *D. serrata*. Based on morphological characters (the number of sepals, nectary cushion position, and corolla color), Landrein and Farjon (2020) have proposed the recognition of four species: *D. serrata*, *D. spathulata*, *D. sanguinea* (Makino) Landrein, and *D. stenophylla* (Honda) Landrein.

There have been several previous studies on disjunct distributions between China and Japan (e.g., Lu et al., 2020; Haq et al., 2020; Takano et al., 2020), with most studies focusing on species that are widely distributed in Japan. Disjunct distribution patterns typically have been attributed to vicariance or long-distance dispersal events (Doyle et al., 2004; Baenfer et al., 2006; Bobo-Pinilla et al., 2018; Torres-Cambas et al., 2019; Wang et al., 2020; Nge et al., 2021). The disjunct distribution of *Diabelia* can be dated back to the middle Oligocene, spanning the long geological history of the formation of the flora in China and Japan (Yang et al., 2011; Shin et al., 2012; Zhao et al., 2019; Wang et al., 2020; Zhang et al., 2020). Overall, exploring the internal phylogenetic relationships and biogeographic diversification of *Diabelia* is conducive for further inference of the mechanisms leading to the disjunct distribution of SJFR in East Asia.

Several previous molecular phylogenetic studies have been conducted on *Diabelia* (Zhou et al., 2004; Landrein et al., 2012; Wang et al., 2015). However, relationships within *Diabelia* remain controversial due to limited markers and sampling. Zhou et al. (2004) conducted an Amplified Fragment Length Polymorphism (AFLP) analysis including six *Diabelia* samples and found that *D. serrata* from China was closely related to accessions of the same species from Japan. Using the nuclear internal transcribed spacer (ITS) and plastid markers (*rbcL, ndhF, matK, trnL* intron and *trnL-F* intergenic spacer), Landrein et al. (2012) found a close relationship between *D. serrata* and *D. spathulata*. Based on nine plastid markers, Wang et al. (2015) constructed a phylogeny recovering a close relationship of *D. serrata* between China and Japan. Subsequent molecular phylogenetic studies have enriched sampling across the SJFR to further investigate the phylogenetic relationships within *Diabelia*. Using plastid fragments from 37 *Diabelia* samples, Zhao et al. (2019) found the non-monophyly of several *Diabelia* species. Yet based on complete plastomes, Wang et al. (2020) recovered the monophyly of *D. serrata* while the relationships of the other species remained unresolved. Overall, sufficient informative molecular data from both nuclear and plastid genomes and a large taxonomic sampling are essential for the comprehensive reconstruction of phylogenetic relationships within *Diabelia*.

Organelle genes often exhibit phylogenetic patterns significantly different from nuclear markers (Toews and Brelsford, 2012; Leducq et al., 2017; Ji et al., 2019; Yao et al., 2019; Wang et al., 2021). Currently, target enrichment is emerging as the method of choice to obtain target sequence for numerous nuclear orthologs of many complex taxa (Wanke et al., 2017; Buys et al., 2019; Schneider et al., 2020; Granados Mendoza et al., 2020; Wang et al., 2021). Many studies have applied this method to obtain data sets for analyzing cyto-nuclear discordance, speciation, hybridization, and polyploidy (e.g., Bogarin et al., 2018; Morales-Briones et al., 2018; 2021). Given that the species-level phylogeny of *Diabelia* has remained largely unresolved, we obtained data through target enrichment and genome skimming of broadly sampled *Diabelia* accessions across the SJFR, which allowed us to (1) robustly explore intrageneric phylogenetic relationships and compare them against previous phylogenies, and (2) to elucidate the biogeography and evolution of the genus to offer a comprehensive phylogenetic framework for future studies.

2 Materials and Methods

2.1 Sampling

A data set of 47 accessions was analyzed including 42 *Diabelia* samples (encompassing all four currently recognized species of *Diabelia* and one variety of *Diabelia stenophylla* (Honda) Landrein var. *tetrasepala* (Koidz.) Landrein) (Landrein et al., 2012; Zhao et al. 2019; Landrein and Farjon, 2020; Wang et al., 2020) and five outgroup samples representing Linnaeoideae (*Abelia macrotera* var. *macrotera*, *Dipelta floribunda* Maxim., *Kolkwitzia amabilis* Graebn., *Vesalea floribunda* M.Martens & Galeotti, *Linnaea borealis* L.). Voucher specimens have been deposited in the herbarium of the Institute of Tropical Agriculture and Forestry of Hainan

University (HUTB), Haikou, China. Detailed information on the geographical distribution and voucher details for the 47 samples and the localities of the populations sampled in this study are shown in Table S1.

2.2 DNA extraction and sequencing

We used a modified CTAB method (Doyle & Doyle, 1987) to extract total genomic DNA from silica gel-dried tissue or herbarium accessions. The concentration of each extraction was checked with a Qubit 2.0 Fluorometer (Thermo Fisher Scientific, Waltham, MA, USA). A total of 400 ng of DNA was sonicated with a Covaris S2 (Covaris, Woburn, MA) to produce fragments ~150-350 bp in length prior to library preparation. Libraries of genomic DNA were made following Weitemier et al. (2014). To ensure that genomic DNA was sheared to the appropriate fragment size, all samples were evaluated on a 1.2% (w/v) agarose gel.

To obtain nuclear data we used a target enrichment approach (Weitemier et al., 2014) and plastid data we used genome skimming (Wang et al., 2020). Baits designed across Dipsacales (Wang et al., 2021) were used to target 428 putatively single-copy genes. Hybridization, enrichment, and sequencing followed Wang et al. (2021).

2.3 Reads processing and assembly

Trimmomatic v.0.36 (Bolger et al., 2014) was used to remove adaptor sequences and low-quality bases from the raw reads (ILLUMINACLIP: TruSeq_ADAPTER: 2:30:10 SLIDINGWINDOW: 4:5 LEADING: 5 TRAILING: 5 MINLEN: 25). HybPiper v.1.3.1 (Johnson et al., 2016) was employed to assemble the nuclear loci. Exons were assembled individually to avoid chimeric sequences in multi-exon genes produced by potential paralogy (Morales-Briones et al., 2018), in which exons longer than 150 bp were set as a reference. Paralog detection was undertaken for all exons using the 'paralog_investigator' option in HybPiper. To obtain 'monophyletic outgroup'(MO) orthologs (Yang and Smith, 2014), all assembled loci (with and without paralogs detected) were processed following Morales-Briones et al. (2021).

For the plastome assemblies, clean reads were extracted from the raw sequencing reads by using SOAPfilter_v2.2 to remove adapter sequences and low-quality reads. The resulting reads were used as the input to assemble plastomes using MITObim v1.8 (Hahn et al. 2013) following Wang et al. (2020).

2.4 Phylogenetic analyses

Nuclear data sets. We used concatenation and coalescent-based methods to analyze the nuclear data. For concatenation analyses, sequences of individual nuclear exons were aligned with MAFFT v.7.407 (Katoh & Standley, 2013) and columns with more than 90% missing data were removed using Phyutility (Smith and Dunn, 2008). A maximum likelihood tree from the concatenated matrix was inferred with RAxML v.8.2.20 (Stamatakis, 2014) using a partition-by-locus scheme and the GTRGAMMA substitution model for all partitions. We assessed clade support with 100 rapid bootstrap replicates (BS). For coalescent species tree estimation, ASTRAL-III v.5.7.1 (Zhang et al., 2018) was used to estimate a species tree based on individual exon trees constructed using RAxML with a GTRGAMMA model. We used local posterior probabilities (LPP) to calculate branch support (Sayyari and Mirarab, 2016). To evaluate nuclear gene tree discordance, we used Quartet Sampling (QS; Pease et al., 2018) to distinguish strong conflict from weakly supported branches with 1000 replicates. Additionally, we calculated the internode certainty all (ICA) score (Salichos et al., 2014) and the number of conflicting and concordant bipartitions on each node of the species trees with Phyparts (Smith et al., 2015).

Plastome data set. Complete plastomes were aligned using MAFFT v.7.407 (Katoh and Standley, 2013). A ML tree was inferred with IQ-TREE v.1.6.1 (Nguyen et al., 2015) under the extended model and 200 non-parametric BS replicates for branch support. In addition, branch support was evaluated using QS with 1000 replicates.

2.5 Species network analysis

We used PhyloNet (Wen et al., 2018) to infer a maximum pseudo-likelihood species network with the InferNetwork_MPL command (Yu and Nakhleh, 2015). Due to computational restrictions and given that we were primarily concerned with the underlying network between different species, we reduced the 47-taxon data set to one outgroup and 14 ingroup taxa to represent all major clades within *Diabelia*. Network searches were undertaken using only nodes in the gene trees that had at least 50% bootstrap support, allowing up to five hybridization events while optimizing branch lengths and inheritance probabilities of the returned species networks under the full likelihood. The command 'CalGTProb' in PhyloNet was used to infer the maximum likelihood of the concatenated RAxML, ASTRAL, and plastid trees, given the individual gene trees to estimate the optimal number of hybridization events and inspect whether the species network represented a better model than a purely bifurcating tree. The bias-corrected Akaike information criterion (AICc; Sugiura, 1978), Akaike information criterion (AIC; Akaike, 1973), and Bayesian information criterion (BIC; Schwarz, 1978) were used for model selection, with the best-fit-species network having the lowest AICc, AIC and BIC scores.

2.6 Divergence time estimation

Divergence times were estimated with BEAST v.2.4.0 (Bouckaert et al., 2014) using the concatenated nuclear data set. The root age was set to 50 Ma (lognormal prior distribution 32.66 - 57.81 Ma) following Wang et al. (2021). We selected the fruit fossil of *Diplodipelta* Manchester & Donoghue (Bell & Donoghue, 2005) that could confidently be placed in our tree as an internal calibration point, with the constraint set to 36 Ma (offset 36 Ma, lognormal prior distribution 34.07 - 37.20 Ma). Dating analyses were carried out using an uncorrelated lognormal relaxed clock under the GTR + G model for each marker partitioned separately and a Yule tree prior. The MCMC chains were run for 500,000,000 generations and sampling every 5,000 generations. Tracer v.1.7 (Drummond et al., 2012) was used to check convergence with the first 10% of trees removed as burn-in and to assess that all effective sample size (ESS) values were $\geqslant$ 200. The produced tree files were combined using

LogCombiner v1.8.2 and the maximum clade credibility tree was generated in TreeAnnotator v1.8.4 (Drummond et al., 2012).

2.7 Ancestral area reconstruction

The ancestral area reconstruction was done using the Statistical Dispersal - Vicariance Analysis (S - DIVA) in RASP version 4.2 (Yu et al., 2015) based on Bayesian Binary Method (BBM) with the concatenated nuclear data set. To prevent biased inferences towards wide or unlikely distributions for the crown node of the ingroup (only *Diabelia* species) due to the uncertainty in the root area of the outgroup, we pruned the five outgroups for our ancestral state reconstructions. Three areas were defined to cover the present distribution range of *Diabelia*: (A) Japan, (B) Korea, and (C) China. Distribution areas of all populations in this study were defined according to field observations (Table S1). The BBM analyses ran for 500,000,000 generations using 10 MCMC chains.

2.8 Data accessibility

Raw Illumina data from target capture are available in the Sequence Read Archive (SRA) under accession SUB10211626 (see Table S1 for individual sample SRA accession numbers). DNA alignments, phylogenetic trees and results from all analyses and data sets can be found in the Dryad data repository XXXXXX.

3 Results

3.1 Exon assembly

The number of assembled exons per species (with > 75% of the target length; except the outgroups) ranged from 587 (*D. serrata* E314) to 989 (*D. sanguinea* E301), with an average of 889 exons per sample (Table S2; Fig. S1). The number of exons with paralog warnings (except the outgroups) ranged from 34 in *D. serrata* E314 to 619 in *D. sanguinea* E301 (Table S2). The concatenated alignment had a length of 392,600 bp, including 18,057 parsimony-informative sites, and a matrix occupancy of

86.7% (Table 1). The plastid alignment resulted in a matrix of 159,365 bp with 4,693 parsimony-informative sites and a matrix occupancy of 98.2% (Table 1).

3.2 Phylogenetic reconstruction

Our nuclear phylogenetic analyses recovered the monophyly of *Diabelia* with maximum support (BS = 100; LPP = 1) and recognized five main clades: *D. serrata*, *D. stenophylla* var. *tetrasepala*, *D. sanguinea*, *D. stenophylla* and *D. spathulata*. However, the relationships of the five main groups within *Diabelia* varied among analyses and data sets.

With respect to the nuclear concatenated ML tree, the phylogeny was recovered with moderate ($50 < BS \leqslant 70$) to high ($BS > 70$) support along the five main clades (Figs. 2, S3 - S4). The monophyly of *Diabelia* was supported by 313 gene trees (out of 439 informative gene trees; ICA = 0.41) and full QS support (1.0/–/1.0; i.e., all sampled quartets supported that node). *Diabelia serrata* forms a clade with strong QS support (0.91/0.4/1) and only 34 concordant trees (out of 427; ICA = 0.02). The monophyly of *D. stenophylla* var. *tetrasepala* was supported by 158 out of 316 informative trees (ICA = 0.24) and full QS support. The sister relationship of *D. stenophylla* var. *tetrasepala* and *D. serrata* was supported by only 12 gene trees (out of 478; ICA = 0.01) and had moderate QS support with a signal of a possible alternative topology (0.21/0.35/0.99). *Diabelia sanguinea* was supported by only 24 gene trees (out of 395; ICA = 0.03) but had full QS support. The sister relationship of *D. sanguinea* and the clade of *D. serrata* + *D. stenophylla* var. *tetrasepala* was supported by only 4 gene trees (out of 490; ICA = -0.02) and moderate QS support, with a signal for a possible alternative topology (0.21/0.49/0.99). The clade of *D. stenophylla* had 43 concordant trees (out of 376; ICA =0.04) and high QS support (0.91/0.33/1). *Diabelia spathulata* was supported by 26 gene trees (out of 304; ICA = 0.06) and moderate QS support (0.22/0.29/0.98), with the sister relationship to the remainder of *Diabelia*.

The ASTRAL species tree (Fig. 3, S2) presented a largely congruent topology compared to the nuclear ML tree with all five major groupings recovered, each being respectively monophyletic. The main clades were highly supported ($LPP \geq 0.93$)

except for the sister node of *D. sanguinea* and *D. serrata* (LPP = 0.44). The monophyly of *D. serrata* had strong QS support with a signal for a possible alternative topology (0.92/0.38/1). *Diabelia spathulata* var. *sanguinea* was supported by moderate QS support (0.62/0.78/0.99). The sister relationship of the clade of *D. sanguinea* and *D. serrata* was supported by only four gene trees (out of 496; ICA = - 0.02) and had counter QS support with signal for a possible alternative topology (-0.22/0.21/0.99). *Diabelia stenophylla* var. *tetrasepala* was sister to the clade of *D. serrata* + *D. sanguinea* with moderate QS support (0.2/0.35/0.99). The clade of *D. stenophylla* between China and Japan had strong QS support (0.9/0.2/1).

The phylogenetic relationships in the plastid ML tree of *Diabelia* (Fig. 2 and S5) were also confirmed with full QS support. The clade of *D. sanguinea* + *D. stenophylla* (Japan) was sister to the *D. serrata* + *D. stenophylla* var. *tetrasepala* clade, and the combined clade had strong support (BS = 98) and moderate QS score (0.14/0.57/0.98). There were some observed topological differences between the plastid and nuclear trees. For example, the plastid trees showed that *D. stenophylla* var. *tetrasepala* was nested within *D. serrata* with strong support (BS = 98) and full QS support; *D. sanguinea* was not-monophyletic; and *D. stenophylla* from Zhejiang was *s*ister to the remainder of *Diabelia*, rather than to *D. spathulata*.

3.3 Species network analysis

The species network analyses (15-taxa data set) recovered topologies with one to five reticulation events, which appear to be a better model than a strictly bifurcating tree (Table 2; Fig. S6). Model selection preferred the network with two reticulation events (Fig. 4). With this preferred network, the first reticulation event involved *D. serrata* and *D. spathulata*. The inheritance probabilities of this event showed that the ancestral lineage of *D. stenophylla* var. *tetrasepala* had the largest genomic contribution of 65.9 % from the clade of *D. spathulata*, and a smaller portion (34.1 %) came from the *D. serrata* clade. Another reticulation event was observed indicating the clade of *D. spathulata* + *D. stenophylla* had genetic contributions (79.3%) from the lineage leading to *D. sanguinea.*

3.4 Divergence time estimation

Our dating estimates based on the nuclear data suggested an early Miocene crown age for *Diabelia* of 22.53 Ma (95% Highest Posterior Density (HPD): 17.89 - 27.73 Ma, node 1 in Fig. 5). The sister relationships of *D. serrata* and *D. stenophylla* var. *tetrasepala* diverged during the early Miocene 18.17 Ma (95% HPD: 14.07 - 22.41 Ma, node 4 in Fig. 5). The crown age of *D. serrata* was dated to 14.88 Ma (95% HPD: 11.10 - 18.91 Ma, node 5 in Fig. 5). The split between *D. spathulata* (E271) and *D. sanguinea* occurred between 3.90 and 9.41 Ma (node 7 in Fig. 5). The diversification of *D. spathulata* between Korea and Japan was estimated as 4.78 Ma (95% HPD: 3.02 - 6.84 Ma, node 8 in Fig. 5). The divergence time of *D. stenophylla* between China and Japan was 6.30 Ma (95% HPD: 3.90 - 9.41 Ma, node 6 in Fig. 5).

3.5 Ancestral area reconstruction

The reconstruction results of the ancestral distribution of *Diabelia* were presented in Fig. 6. There were three dispersal events and three vicariance events identified within the three defined biogeographic areas (Fig. 6). Our analyses revealed that the ancestor of *Diabelia* was present throughout Japan (region A) in the early Miocene (Fig. 6), followed by dispersal or vicariance events across Japan, Korea, and China. Migration events occurred primarily during the Neogene. *Diabelia spathulata* from Korea was suggested to have originated in Northeast Japan. However, one vicariance and one dispersal event were detected for the ancestral nodes of *D. stenophylla* from China, supporting their origin from Japan.

4 Discussion

4.1 Phylogenetic incongruence and hybridization, and implications for species delimitation

Our phylogenetic analyses retrieved the same five main clades of *Diabelia* in the nuclear ML tree, which are also supported in the ASTRAL tree, but the relationships among these clades are incongruent between the nuclear and plastid data (Figs. 2 and 3). For example, *D. serrata* and *D. stenophylla* var. *tetrasepala* were recovered as monophyletic in the nuclear ML tree, while *D. stenophylla* var. *tetrasepala* was nested within *D. serrata* in the plastid ML tree (Fig. 2). We not only detected widespread cytonuclear discordance across *Diabelia* (Fig. 2), but our results also showed extensive conflict among individual gene trees and the species trees (Figs. 3 and S2). Several processes can lead to gene tree inconsistencies between closely related groups, including incomplete lineage sorting (ILS), hybridization, horizontal gene transfer, or gene duplication and loss (Morales-Briones et al., 2018; Bogarin et al., 2018; Carter et al., 2019; Stull et al., 2020; Wang et al., 2021). Ancestral polymorphisms may lead to incomplete genealogical classification, therefore phylogenetic relationships between organelle markers may fail to capture the true process of population differentiation, or inconsistencies in gene trees may reflect interspecies hybridization and cytoplasmic infiltration (Lee-Yaw et al., 2019; Wielstra & Arntzen, 2020; Tkach et al., 2020). Therefore, exploring the causes of inconsistencies in gene trees may help explain the relative influences of drift, gene flow and selection on the maintenance of organelle variation within and between groups, which is helpful for revealing the evolutionary process of inter-group relationships (Mao et al., 2020; Dufresnes et al., 2020).

Comparing the topologies between the nuclear and plastid data, we found that the topology from the nuclear gene data was more stable. The nuclear data recovered five strongly supported clades (Figs. 2 and 3), with *D. serrata* forming a stable monophyletic group that was consistent with previous studies supporting the monophyletic nature of *D. serrata* (Wang et al., 2020). *Diabelia stenophylla* and *D. spathulata* were each also recovered as monophyletic based on the nuclear data. While *D. sanguinea* was not recovered as a monophyletic group in the plastid tree (Fig. 2), the possibility exists that the non-monophyly of *D. sanguinea* is due to plastid capture events or ILS (Liu et al., 2017; Renoult et al., 2009; Wang et al., 2020). Notably, the placement of *D. sanguinea* in the nuclear data had full LPP support with low ICA value and moderate QS score, which suggests that ILS and/or unidentified hybrid lineages continue to obscure our understanding of the relationship of *D. sanguinea* within the genus, and even the relationships of *Diabelia* as a whole*,* due to strong signals of gene tree discordance. Previous phylogenetic relationships of *Diabelia* based on only plastid data have also been unstable (Zhao et al., 2019; Wang et al., 2020). In the present study, the nuclear data provide a more robust estimate of the species tree compared to plastid data, suggesting that sufficiently informative molecular data are important to our understanding of relationships in *Diabelia*.

A previous study (Zhao et al., 2019) reported gene introgression events between *Diabelia* species and speculated that *D. stenophylla* var. *tetrasepala* (four big and one small sepals) may have resulted from hybridization between *D. serrata* (two sepals) and *D. spathulata* (five sepals). However, this hypothesis has not been confirmed. In this study, we conducted network analyses for *Diabelia* and our results support the existence of reticulation events within the genus (Fig. 4). Concerning the reticulate evolution of the *D. stenophylla* var. *tetrasepala* clade, the inheritance contributions (34.1 % and 65.9 %) support the hybridization event between *D. serrata* and *D. spathulata.* Based on two similar morphologies but different origins of taxa within *Melastoma*, Zou et al. (2017) suggested that it is difficult to infer the origins of hybrid taxa based only on morphology, and the hybrids may be the result of small range overlaps among parental species. Morales-Briones et al. (2018), based on the extensive history of hybridization and network results in *Lachemilla*, showed the potential of phylogenetic species network methods to investigate phylogenetic discordance caused by ILS and hybridization. Given our network results and the distribution of *D. stenophylla* var. *tetrasepala* partly overlaps with those of parental populations, we argue that *D. stenophylla* var. *tetrasepala* may be of hybrid origin between *D. serrata* and *D. spathulata*. As noted by Morales-Briones et al. (2018), additional biological information is necessary for a robust interpretation of values from the phylogenetic networks. Hence, we will include more samples to obtain a more robust inference of relationships for future studies.

Despite the strong signals of gene tree discordance, our nuclear and plastid phylogenies strongly supported five major clades in *Diabelia*: *Diabelia serrata*, *D. stenophylla* var. *tetrasepala*, *D. spathulata*, *D. sanguinea*, and *D. stenophylla* (Figs. 2, 3).

Especially in the nuclear data, all five major branches are monophyletic. These correspond to the species of *D. serrata*, *D. spathulata*, *D. sanguinea*, and *D. stenophylla*, but the clade of *D. stenophylla* var. *tetrasepala* does not form a monophyletic lineage with *D. stenophylla*. To resolve the non-monophyly of *D. stenophylla*, and to clarify the phylogenetic relationship within *Diabelia*, we raise *D. stenophylla* var. *tetrasepala* to the species level, recognizing it as *Diabelia tetrasepala* (Hara, 1983; Landrein, 2010). Hara (1983) also recognized *Diabelia tetrasepala* as a distinct species. Additionally, this taxon can be easily distinguished by the form of sepals (sepals 4 plus a reduced adaxial sepal lobe in *D. tetrasepala*, sepals 5 of similar size in *D. stenophylla*) (Zhao et al., 2019; Landrein and Farjon, 2020; Wang et al., 2020). Overall, based on our phylogenetic inferences (nuclear), we recognize five species in the genus (i.e., *D. serrata*, *D. tetrasepala*, *D. spathulata*, *D. sanguinea*, and *D. stenophylla*).

4.2 Molecular dating and demographic analyses

Based on our nuclear chronogram (Fig. 5), all major *Diabelia* lineages differentiated 22.53-18.17 Ma (Fig. 5). Notably, this point estimate broadly coincides with the isolation of the Japanese island (24-22 Ma) (Hotta, 1974; Iijima and Tada, 1990; Li et al., 1996; Maekawa, 1998) and the estimated dates are earlier than previous estimates based on chloroplast data (Wang et al., 2020). The East China Sea (ESC) land bridge likely acted as a barrier to the dispersal of plant species during the LGM and earlier cold periods, despite its repeated exposure during the Miocene (7.0-5.0 Ma) and Quaternary (2.0-1.3 Ma, 0.2-0.015 Ma) (Harrison, 2001). Even though the Japanese archipelago was not covered by a major ice sheet during the last glacial period (Ono, 1984), the mean annual temperature was 5℃-9℃ cooler and the precipitation was less than at present (Yasuda and Narita, 1981; Tsukada, 1988). In addition, because of lower sea levels (ca. 100 m below present), Shikoku and Kyushu were continuous with Honshu, and the continental shelf, ca. 20-30 km from the present coastline, emerged around the archipelago (Ohta and Yonekura, 1987). The distribution data of *D. serrata* suggests a wide distribution in Japan except for Hokkaido. As the climate warmed, the species recovered and expanded northward or towards higher altitudes (Tsukada, 1988; Takahara et al., 2000), therefore, forming the current isolated distribution.

Diabelia species are relatively tolerant to cold and arid climates, which might have facilitated gene exchange across the glacially exposed ECS land bridge up until its latest submergence. All *Diabelia* species have fruits forming samaras, which increase long-distance dispersal abilities (Landrein, 2010). Our molecular dating indicates that *Diabelia* originated in the Japanese archipelago (Fig. 5) and the onset of diversification of *D. stenophylla* from Japan and *D. stenophylla* from China occurred during the early Pliocene. Our results suggest a vicariance event and a dispersal event associated with *D. stenophylla* from China (Fig. 6). Under the hypothesis of long-distance dispersal, a predicted lineage in one region should nest within a lineage from a separate disjunctive region. In contrast, under vicariance, lineages from different geographic regions would each be monophyletic with relatively comparable levels of genetic diversity in each region of the distribution (Yoder & Nowak, 2006; Liao et al., 2016; Thomas et al., 2017). The disjunction between *D. stenophylla* in Japan and *D. stenophylla* from China may have resulted from migration across this land bridge followed by vicariance.

Our results show that that the interchanges of the populations of *D. spathulata* between Korea and Japan are frequent. The close relationships between Japan and Korea have also been observed in other taxa such as *Meehania urticifolia* (Takano et al., 2020) and *Kirengeshoma koreana* (Qiu et a1., 2011). Furthermore, our results also suggest that populations of *D. spathulata* in Korea originated from Japan and are likely due to recent vicariance and dispersal events (Fig. 6), which is largely congruent with the previous conclusions by Wang et al. (2020). Wang et al. (2020) showed that the populations between Korea and the northern Japan may have resulted from a vicariance event. Our results further suggest an early and a later dispersal event, supporting a highly dynamic biogeographic relationships between Japan and Korea. Our divergence time estimates suggest that species differentiation in *D. spathulata* occurred during the late Miocene to the early Pliocene (4.78 Ma, 95% HPD: 3.02 – 6.84 Ma), suggesting that extant populations likely differentiated well before the LGM.

The cooling and drying climate in the late Miocene drove the formation of *D. spathulata*. The changing climate in the late Pliocene and Pleistocene is related to lineage differentiation, genetic diversity, and population contraction and expansion, which have also been observed in *Cercidiphyllum japonicum* (Qi et al., 2012) and *Euptelea* (Cao et al., 2016). This study adds another example of this well-documented pattern.

5 Conclusions

A robust phylogeny of *Diabelia* was reconstructed with nuclear and plastid data based on target enrichment and genome skimming approaches. The inferred phylogenies from both nuclear and plastome data indicate that *Diabelia* can be divided into five main clades, which are further supported by morphological traits such as number of sepals, nectary cushion position, and corolla color. Our results show clear cytonuclear discordance and strong conflict between individual gene trees and species trees in *Diabelia*. The PhyloNet results further confirmed the existence of reticulation events in *Diabelia*, supporting that *D. tetrasepala* was the result of a hybridization event. The divergence time and biogeographic analyses further support the differentiation and propagation of *Diabelia* with multiple vicariance events from the perspective of time and space, further supporting the complex natural hybridization and evolutionary network of the disjunctive flora of Japan and China. Tree-like and reticulate evolution should be considered when reconstructing phylogenetic relationships among closely related species. The appropriate choice of data to construct phylogenetic trees is important in the era of genomics. Further studies are needed to clarify the origin, dispersal and evolution of Sino-Japanese disjunct species with nuclear and plastid data at the population level. Finally, our results shed light on the species delimitation, supporting the recognition of five species in *Diabelia*, corresponding to the five main clades within the genus in the nuclear phylogeny.

Taxonomic treatment

Based on our results, we formally recognize five species in *Diabelia*. Landrein &

Farjon (2019) treated four of the five species, i.e., *D. sanguinea*, *D. serrata*, *D. stenophylla*, and *D. spathulata*. Below we provide the synoptic treatment for *Diabelia tetrasepala*.

Diabelia tetrasepala (Koidz.) Landrein, Phytotaxa 3: 37. 2010.

Basionym: *Abelia spathulata* Siebold & Zucc. var. *tetrasepala* Koidz., Bot. Mag. (Tokyo) 29 (348): 311. 1915.

Abelia tetrasepala (Koidz.) H. Hara & S. Kuros. in Kurosawa & Hara, J. Jap. Bot. 30: 296. 1955; *Diabelia stenophylla* (Honda) Landrein var. *tetrasepala* (Koidz.) Landrein, Kew Bull. 74(4)-70: 186. 2019.

Abelia spathulata Siebold & Zucc. var. *subtetrasepala* Makino, J. Jap. Bot. 1: 18. 1917.

Abelia spathulata Siebold & Zucc. var. *subtetrasepala* Makino f. *flavescens* Honda, J. Jap. Bot. 11: 569. 1935.

Acknowledgements

The work was funded by Hainan Provincial Natural Science Foundation of China (421RC486) and National Natural Science Foundation of China (31660055). We thank Gabriel Johnson for his help with the target enrichment experiment, and the United States National Herbarium for permission to sample some collections. We acknowledge the staff in the Laboratories of Analytical Biology at the National Museum of Natural History, the Smithsonian Institution for support and assistance.

Author contributions

H.-F.W. and J.W. conceived the study. H.-F.W. and D.F.M-B. performed the research and analyzed the data. X.-R.K., H.-F.W., D.F.M-B., J.W., H.-X.W., Q.-H.S. and J.B.L. wrote and revised the manuscript.

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Figure Legends

Fig. 1. Floral diversity of *Diabelia*. (A) *Diabelia serrata* (Photograph by Difei Wu), (B) *D. serrata var. buchwaldii* (Photograph by Shota Sakaguchi), (C) *D. stenophylla* var. *tetrasepala* (Photograph by Shota Sakaguchi), (D) *D. spathulata* (Photograph by Kyoungsu Choi), (E) *D. spathulata* (Photograph by Sven Landrein), (F) *D. sanguinea* (Photograph by Sven Landrein).

Fig. 2. Tanglegram of the nuclear concatenated (left) and plastid (right) phylogenies of *Diabelia*. Dotted lines connect taxa between the two phylogenies. Maximum likelihood bootstrap support values are shown above branches. The asterisks indicate maximum likelihood bootstrap support of 100%. Major taxonomic groups or main clades in the family as currently recognized are indicated by branch colors as a visual reference to relationships.

Fig. 3. ASTRAL species tree of *Diabelia*; Clade support is depicted as: Local posterior probability (LPP)/Quartet concordance (QC)/Quartet differential (QD)/Quartet informativeness (QI).

Fig. 4. Best supported species network inferred with PhyloNet for the 15-taxa. Numbers next to the inferred hybrid branches indicate inheritance probabilities. Blue curved lines represent major hybrid edges. Red curved lines represent minor hybrid edges (edges with an inheritance contribution < add space 0.50).

Fig. 5. BEAST analysis of divergence times based on the nuclear data set. Calibration points are indicated by A, B. Numbers 1-8 represent major divergence events in *Diabelia*; mean divergence times and 95% highest posterior densities (HDP) are provided for each node of interests. Blue bars represent 95% HDP.

Fig. 6. Ancestral area reconstruction for *Diabelia*. Areas of endemism are as follows: (A) Japan, (B) Korea, (C) China. The numbered nodes represent crown nodes of important colonization events.

Table 1. Data set statistics, including the number of taxa, number of characters, number of PI characters, missing data.

Table 2. Model selection of the different species networks and bifurcating trees.

Fig. S1. Heatmaps showing gene recovery efficiency for the nuclear genes in 42 species of *Diabelia*. Columns represent genes, and each row is one sample. Shading indicates the percentage of the reference locus length coverage.

Fig. S2. ASTRAL species tree. Numbers above branches indicate the number of gene trees concordant/conflicting with that node in the species tree. Numbers below the branches are the Internode Certainty All score. Pie charts next to the nodes present the proportion of gene trees that supports that clade (blue), the proportion that supports the main alternative for that clade (green), the proportion that supports the remaining alternatives (red), light gray means missing data, and dark gray means uninformative (BS < 50%).

Fig. S3. Results of the Quartet Sampling of the nuclear RAxML tree; Clade support is depicted as: Local posterior probability (LPP)/Quartet concordance (QC)/Quartet differential (QD)/Quartet informativeness (QI).

Fig. S4. Nuclear RAxML tree. Numbers above branches indicate the number of gene trees concordant/conflicting with that node in the species tree. Numbers below the branches are the Internode Certainty All score. Pie charts next to the nodes present the proportion of gene trees that supports that clade (blue), the proportion that supports the main alternative for that clade (green), the proportion that supports the remaining alternatives (red), light gray means missing data, and dark gray means uninformative (BS < 50%).

Fig. S5. Results of the Quartet Sampling of the plastid IQ-tree tree; Clade support is depicted as: Local posterior probability (LPP)/Quartet concordance (QC)/Quartet differential (QD)/Quartet informativeness (QI).

Fig. S6. Best species networks of the selective nuclear data set estimated with PhyloNet for the 15-taxa data set. A: One hybridization event; B: Two hybridization events; C: Three hybridization events; D: Four hybridization events; F: Five hybridization events. Blue branches connect the hybrid nodes. Numbers next to blue branches indicate inheritance probabilities.

Table S1. List of species and vouchers used in this study.

Table S2. HybPiper assembly statistics.

Table 1. Data set statistics, including the number of taxa, number of characters, number of PI characters, missing data.

Alignment	No. of taxa	No. sites	Missing data (%)	No. of variable/Parsimony informative sites
Nuclear	47	392,600	13.2	43,250/18,057
Plastid	47	159,365	1.8	8,243/4,693

Table 2. Model selection of the different species networks and bifurcating trees.

					Information criteria		
Topology	lnL	Parameters	Loci	Number of hybridizations	AIC	AICc	BIC
15 taxa							
Nuclear ASTRAL	-6134.788576	27	241	N/A	12323.577153	12330.675744	12417.666670
Nuclear RAxML	-6137.811629	27	241	N/A	12329.623259	12336.721850	12423.712776
Plastid	-6427.555081	27	241	N/A	12909.110161	12916.208753	13003.199679
Network 1	-6079.839883	29	241	1	12217.679766	12225.926212	12318.738877
Network 2	**-6006.511111**	**31**	**241**	**2**	**12075.022221**	**12084.515044**	**12183.050926**
Network 3	-6079.836581	33	241	1	12225.673162	12236.513742	12340.671461
Network 4	-6038.368637	35	241	4	12146.737274	12159.029957	12268.705166
Network 5	-6088.526401	37	241	5	12251.052802	12264.905019	12379.990288

890

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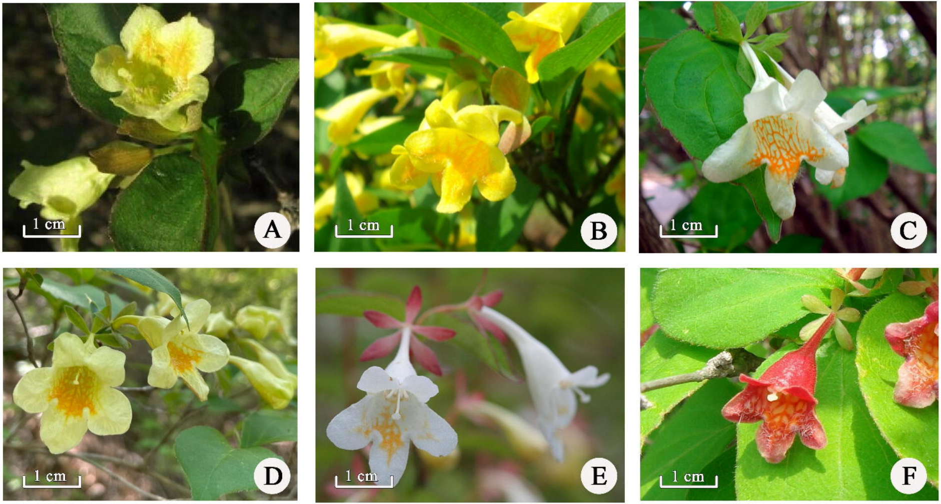
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F

Nuclear concatenated
Plastome
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D. stenophylla var. tetrasepala
D. sanguinea
D. stenophylla
D. spathulata
Outgroups
Diabelia serrata E314
D. serrata var. buchwalddi E324
D. serrata E137
D. serrata E140
D. serrata E138
D. serrata E139
D. serrata E123
D. serrata E122
D. serrata E126
D. serrata E125
D. serrata E321
D. serrata E128
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D. sanguinea E303
D. sanguinea E301
D. sanguinea E131
D. sanguinea E306
D. sanguinea E308
D. stenophylla E204
D. stenophylla E202
D. stenophylla E201
D. stenophylla E203
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D. stenophylla E170
D. stenophylla E132
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D. stenophylla E240
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D. spathulata E190
D. spathulata E200
D. spathulata E141
D. spathulata E129
Abelia macrotera var. macrotera E45
Kolkwitzia amabilis E9
Dipelta floribunda E55
Linnaea borealis E59
Vesalea floribunda E112
0.004
0.008

Diabelia serrata E138
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0.42/0.22/0.19/0.99
D. serrata E125
0.82/0.16/0.58/0.99
D. serrata E140
0.66/-0.47/0.06/1
D. serrata E137
0.6/0.43/0/1
0.59/0.22/0.55/0.99
D. serrata var. buchwalddi E324
D. serrata E126
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0.68/0.43/0.06/0.99
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0.52/-0.03/0.85/1
D. serrata E122
0.57/0.45/0.13/0.99
D. serrata E321
1/0.92/0.38/1
D. serrata E314
D. serrata E123
0.99/0.04/0.76/0.98
D. serrata E124
D. serrata
D. sanguinea E130
0.44/-0.22/0.21/0.99
0.47/-0.09/0/0.98
D. sanguinea E301
0.87/0.39/0.63/1
D. sanguinea E303
0.6/-0.35/0.52/0.99
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0.96/0.59/0.38/1
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1/1/-/1
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D. sanguinea
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1/0.59/0/1
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1/1/-/1
D. stenophylla var. tetrasepala E311
1/1/-/1
D. stenophylla var. tetrasepala E312
D. stenophylla var. tetrasepala
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D. stenophylla E204
0.71/0.05/0.77/0.97
D. stenophylla E202
0.41/0.39/0.25/0.99
D. stenophylla E201
0.98/0.48/0.75/1
D. stenophylla E205
1/1/-/1
D. stenophylla E172
0.54/1/-/1
D. stenophylla E170
0.93/0.63/0.17/0.97
1/1/-/1
D. stenophylla E171
1/0.9/0.2/1
D. stenophylla
D. stenophylla E240
0.62/0.42/0.18/1
D. stenophylla E295
0.97/0.36/0.01/0.98
D. stenophylla E132
0.99/0.32/0.05/1
1/1/-/1
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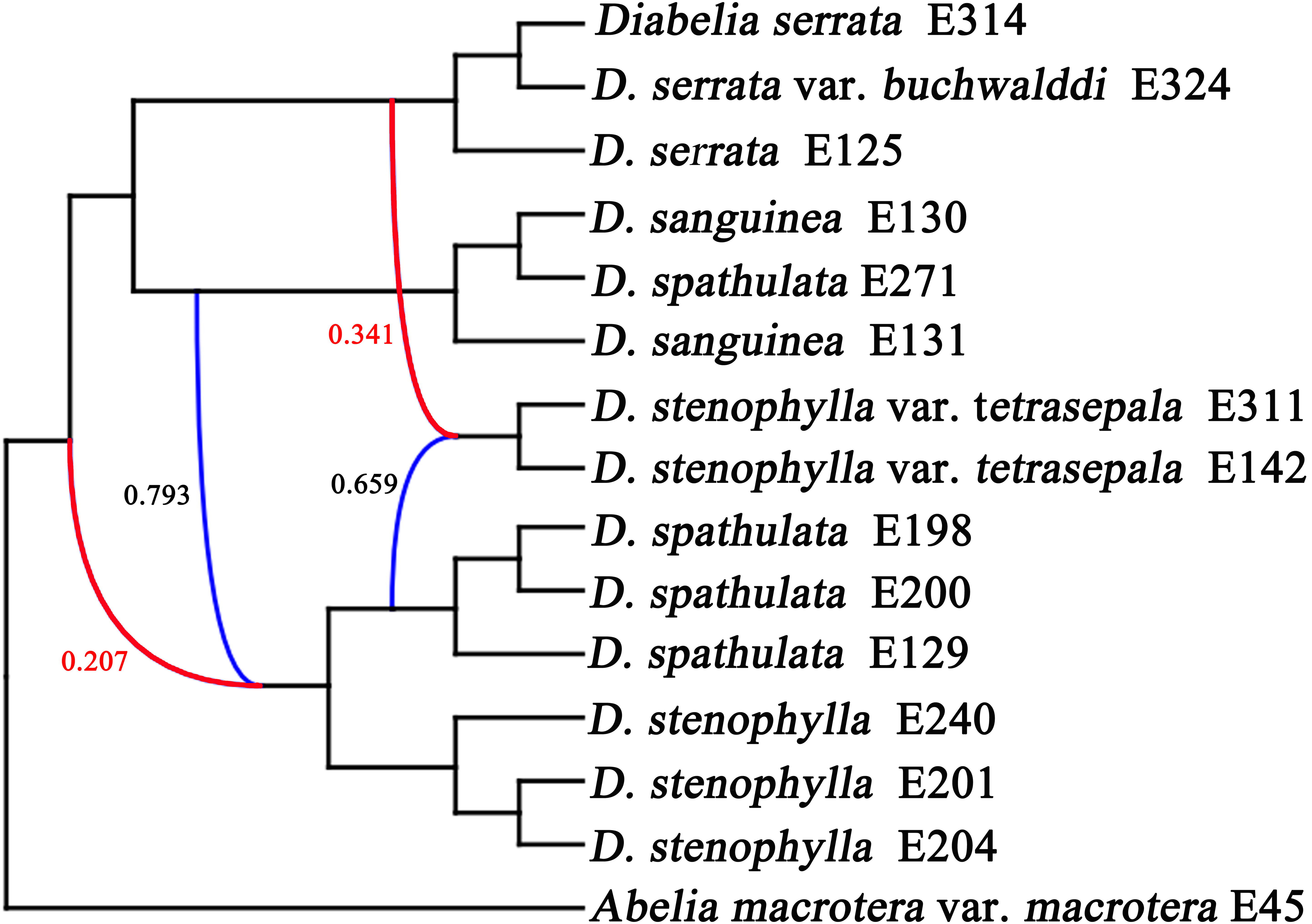
D. spathulata E190
0.41/0.36/0.25/0.98
D. spathulata E200
1/1/-/1
D. spathulata E198
D. spathulata
0.99/0.22/0.29/0.98
D. spathulata E129
1/1/-/1
Abelia macrotera var. macrotera E45
Kolkwitzia amabilis E9
Dipelta floribunda E55
Outgroups
Vesalea floribunda E112
1/1/-/1
Linnaea borealis E59
0.4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D. serrata E125
D. sanguinea E130
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D. stenophylla var. tetrasepala E311
D. stenophylla var. tetrasepala E142
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D. spathulata E200
D. spathulata E129
D. stenophylla E240
D. stenophylla E201
D. stenophylla E204
Abelia macrotera var. macrotera E45
0.341
0.659
0.793
0.207

50.0 MA
36.0 MA
❶ 22.53 [17.89 - 27.73] MA
❷ 21.05 [16.72 - 25.96] MA
❸ 19.90 [15.74 - 24.52] MA
❹ 18.17 [14.07 - 22.41] MA
❺ 14.88 [11.10 - 18.91] MA
❻ 14.78 [10.79 - 19.11] MA
❼ 6.30 [3.90 - 9.41] MA
❽ 4.78 [3.02 - 6.84] MA
Diabelia serrata E314
D. serrata var. *buchwalddi* E324
D. serrata E137
D. serrata E140
D. serrata E138
D. serrata E139
D. serrata E122
D. serrata E321
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D. serrata E126
D. serrata E125
D. serrata E124
D. serrata E123
D. stenophylla var. *tetrasepala* E143
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D. spathulata E271
D. sanguinea E294
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D. stenophylla E202
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D. stenophylla E172
D. stenophylla E171
D. stenophylla E132
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D. stenophylla E240
Abelia macrotera var. *macrotera* E45
Kolkwitzia amabilis E9
Dipelta floribunda E55
Linnaea borealis E59
Vesalea floribunda E112
1
2
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4
5
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7
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Oligocene
Miocene
Pliocene
Ple.
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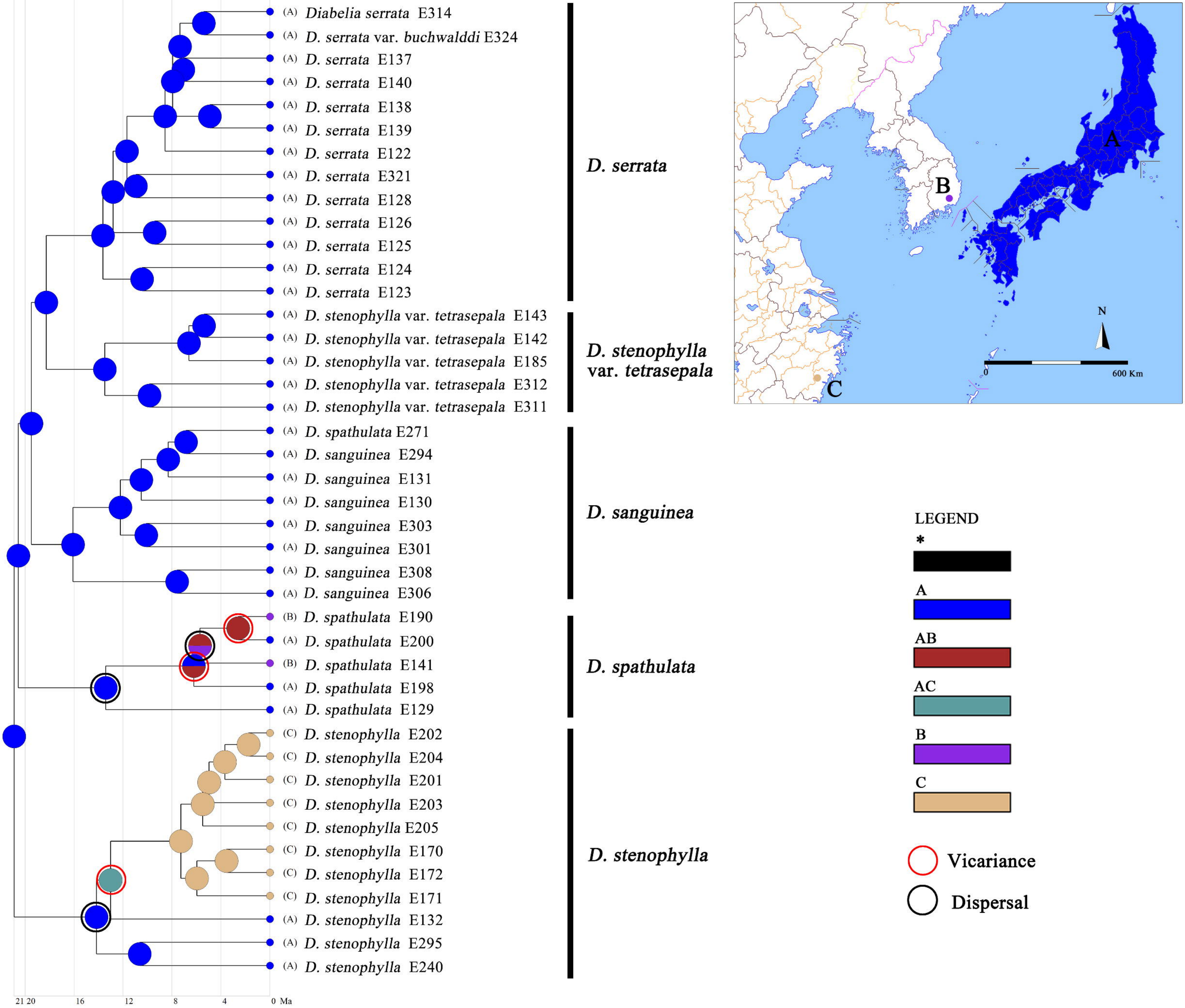
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(A) D. serrata E139
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(A) D. sanguinea E131
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(A) D. spathulata E198
(A) D. spathulata E129
(C) D. stenophylla E202
(C) D. stenophylla E204
(C) D. stenophylla E201
(C) D. stenophylla E203
(C) D. stenophylla E205
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(C) D. stenophylla E171
(A) D. stenophylla E132
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(A) D. stenophylla E240
D. serrata
D. stenophylla var. tetrasepala
D. sanguinea
D. spathulata
D. stenophylla
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AB
AC
B
C
Vicariance
Dispersal

Vesalea floribunda E112
Linnaea borealis E59
Kolkwitzia amabilis E9
Dipelta floribunda E55
Diabelia spathulata E200
D. spathulata E198
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D. spathulata E141
D. serrata E140
D. stenophylla E132
D. sanguinea E131
D. spathulata E271
D. serrata E321
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D. stenophylla var. tetrasepala E143
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D. sanguinea E308
D. sanguinea E306
D. spathulata E129
value
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0.75
0.50
0.25
0.00

10/274
-0.03
10/323
0.02
5/432
-0.02
71/184
0.12
6/342
0.03
1/463
-0.02
12/261
0.03
1/344
-0.02
0/446
-0.01
1/432
-0.01
36/393
0.02
27/236
0.04
4/492
-0.02
22/221
0.08
14/277
0.05
10/303
-0.04
16/293
0.04
54/271
0.05
24/371
0.03
161/107
0.37
4/486
-0.02
54/188
0.15
56/196
0.14
158/158
0.24
124/109
0.35
18/436
0.03
49/167
0.12
12/257
-0.05
12/311
-0.04
14/314
0.04
123/189
0.18
39/219
0.08
13/285
0.04
45/333
0.04
40/257
0.07
31/300
0.04
313/126
0.41
35/166
0.18
38/206
0.18
290/76
0.57
26/278
0.06
82/155
0.35
87/171
0.30
130/48
0.49
Diabelia serrata E137
D. serrata E140
D. serrata var. buchwalddi E324
D. serrata E139
D. serrata E138
D. serrata E125
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D. serrata E122
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D. sanguinea E301
D. sanguinea E130
D. sanguinea E303
D. sanguinea E294
D. spathulata E271
D. sanguinea E131
D. sanguinea E306
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D. spathulata E129
Abelia macrotera var. macrotera E45
Kolkwitzia amabilis E9
Dipelta floribunda E55
Linnaea borealis E59
Vesalea floribunda E112
D. serrata
D. sanguinea
D. stenophylla var. tetrasepala
D. stenophylla
D. spathulata
Outgroups

0.99/0.67/0.5/0.98
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D. serrata var. *buchwalddi* E324
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D. serrata E140
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D. serrata E138
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D. serrata E139
D. serrata E123
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D. serrata E122
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D. serrata E126
0.86/0.62/0.2/0.94
1/0.91/0.4/1
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0.69/-0.2/0.22/0.99
D. serrata E128
0.6/-0.55/0.13/1
D. serrata E321
1/0.21/0.35/0.99
D. serrata E124
D. serrata
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D. stenophylla var. *tetrasepala*
D. stenophylla var. *tetrasepala* E312
1/1/-/1
D. stenophylla var. *tetrasepala* E311
0.71/0.21/0.49/0.99
D. sanguinea E294
1/0.58/0.33/1
D. spathulata E271
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1/0.23/0/1
D. sanguinea E303
0.99/0.22/0/0.98
D. sanguinea
D. sanguinea E301
1/0.89/0.44/1
D. sanguinea E131
1/1/-/1
D. sanguinea E308
1/1/-/1
D. sanguinea E306
0.56/0.5/0.63/0.98
D. stenophylla E204
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D. stenophylla
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D. stenophylla E240
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1/1/-/1
D. spathulata E141
D. spathulata
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D. spathulata E129
Abelia macrotera var. *macrotera* E45
Kolkwitzia amabilis E9
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Dipelta floribunda E55
Outgroups
Linnaea borealis E59
1/1/-/1
Vesalea floribunda E112
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5/210
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4/388
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3/431
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71/184
0.12
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D. serrata E138
0/502
-0.02
3/291
-0.02
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7/247
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0/403
-0.02
14/268
-0.03
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12/466
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D. serrata E124
D. serrata
44/181
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64/196
0.14
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158/158
0.24
D. stenophylla var. tetrasepala E185
124/109
0.35
D. stenophylla var. tetrasepala E311
D. stenophylla var. tetrasepala E312
D. stenophylla var. tetrasepala
4/486
-0.02
17/186
0.06
D. spathulata E271
8/269
-0.05
D. sanguinea E294
22/293
0.04
D. sanguinea E130
37/210
0.10
D. sanguinea E301
54/271
0.05
D. sanguinea E303
24/371
0.03
D. sanguinea E131
161/107
0.37
D. sanguinea E306
D. sanguinea E308
D. sanguinea
18/436
0.03
13/240
0.06
D. stenophylla E202
4/322
-0.06
D. stenophylla E204
13/311
0.05
D. stenophylla E201
14/314
0.04
D. stenophylla E203
10/339
-0.04
D. stenophylla E205
121/219
0.17
D. stenophylla E171
39/219
0.08
D. stenophylla E172
29/329
0.04
D. stenophylla E170
313/126
0.41
43/333
0.04
D. stenophylla E132
40/257
0.07
D. stenophylla E240
D. stenophylla E295
D. stenophylla
82/155
0.35
37/177
0.20
D. spathulata E200
35/206
0.16
D. spathulata E190
290/76
0.57
D. spathulata E141
26/278
0.06
D. spathulata E198
155/48
0.51
D. spathulata E129
D. spathulata
Abelia macrotera var. macrotera E45
59/167
0.26
Dipelta floribunda E55
Kolkwitzia amabilis E9
Vesalea floribunda E112
Linnaea borealis E59
Outgroups

1/1/-/1
1/1/-/1
Diabelia stenophylla var. tetrasepala E311
D. stenophylla var. tetrasepala E312
D. stenophylla var. tetrasepala E143
1/1/-/1
D. stenophylla var. tetrasepala E142
1/1/-/1
D. stenophylla var. tetrasepala E185
0.98/-0.003/0/0.99
D. stenophylla var. tetrasepala
D. serrata E321
0.98/-0.24/0.27/0.99
D. serrata E122
0.97/-0.29/0.1/1
1/0.62/0.96/1
D. serrata E314
0.98/-0.34/0.05/1
D. serrata E139
D. serrata E125
0.97/0.49/0/1
D. serrata E126
1/0.89/0/1
D. serrata var. buchwalddi E324
1/1/-/1
D. serrata E124
0.72/-0.29/0.62/0.93
D. serrata E128
0.72/-0.05/0/0.93
D. serrata E138
0.74/-0.16/0.4/0.97
D. serrata E140
0.7/-0.52/0/0.99
D. serrata E137
1/1/-/1
D. serrata E123
D. serrata
0.98/0.14/0.57/0.98
D. stenophylla E132
0.81/0.08/0.76/1
D. stenophylla E295
1/1/-/1
D. stenophylla E240
0.6/-0.54/0/1
D. stenophylla
D. sanguinea E294
0.8/-0.06/0.58/0.97
0.98/0.1/0/1
0.63/0.66/0.15/0.96
D. sanguinea E303
D. sanguinea E130
1/1/-/1
D. sanguinea E301
0.37/0.36/0.07/1
0.98/0.35/0.05/0.99
D. sanguinea E131
D. spathulata E271
D. sanguinea E306
1/0.93/0/1
D. sanguinea E308
D. sanguinea
0.98/0.18/0.74/0.98
D. spathulata E141
1/1/-/1
D. spathulata E200
0.99/0.77/0.4/1
D. spathulata E190
1/1/-/1
0.66/0.71/0.51/1
D. spathulata E198
D. spathulata E129
D. spathulata
1/1/-/1
D. stenophylla E201
0.81/0.73/0/1
D. stenophylla E205
1/1/-/1
D. stenophylla E204
0.99/0.45/0.45/0.99
D. stenophylla E171
0.95/0.34/0.04/0.99
1/1/-/0.98
D. stenophylla E172
1/1/-/1
D. stenophylla E202
1/1/-/1
1/0.56/0/1
D. stenophylla E203
0.81/-0.07/0.54/0.91
D. stenophylla E170
D. stenophylla
1/1/-/1
Dipelta floribunda E55
Kolkwitzia amabilis E9
Abelia macrotera var. macrotera E45
Outgroups
Linnaea borealis E59
1/1/-/1
Vesalea floribunda E112
0.003

A
Diabelia stenophylla E240
D. stenophylla E204
D. stenophylla E201
D. stenophylla var. tetrasepala E142
D. stenophylla var. tetrasepala E311
D. serrata E125
D. serrata var. buchwalddi E324
D. serrata E314
D. sanguinea E131
D. spathulata E271
D. sanguinea E130
D. spathulata E129
D. spathulata E200
D. spathulata E198
Abelia macrotera var. macrotera E45
0.843
0.157
B
Diabelia serrata E314
D. serrata var. buchwalddi E324
D. serrata E125
D. sanguinea E130
D. spathulata E271
D. sanguinea E131
D. stenophylla var. tetrasepala E311
D. stenophylla var. tetrasepala E142
D. spathulata E198
D. spathulata E200
D. spathulata E129
D. stenophylla E240
D. stenophylla E201
D. stenophylla E204
Abelia macrotera var. macrotera E45
0.341
0.793
0.659
0.207
C
Diabelia stenophylla E240
D. stenophylla E204
D. stenophylla E201
D. stenophylla var. tetrasepala E142
D. stenophylla var. tetrasepala E311
D. serrata E125
D. serrata var. buchwalddi E324
D. serrata E314
D. sanguinea E131
D. spathulata E271
D. sanguinea E130
D. spathulata E129
D. spathulata E200
D. spathulata E198
Abelia macrotera var. macrotera E45
0.843
0.157
D
Abelia macrotera var. macrotera E45
Diabelia stenophylla E240
D. stenophylla E204
D. stenophylla E201
D. sanguinea E130
D. sanguinea E131
D. spathulata E271
D. spathulata E198
D. spathulata E200
D. spathulata E129
D. serrata E314
D. serrata E125
D. serrata var. buchwalddi E324
D. stenophylla var. tetrasepala E142
D. stenophylla var. tetrasepala E311
0.181
0.819
0.817
0.183
0.106
0.894
0.001
0.999
E
Abelia macrotera var. macrotera E45
Diabelia spathulata E198
D. spathulata E200
D. spathulata E129
D. stenophylla var. tetrasepala E142
D. stenophylla var. tetrasepala E311
D. sanguinea E130
D. spathulata E271
D. sanguinea E131
D. serrata E314
D. serrata var. buchwalddi E324
D. serrata E125
D. stenophylla E201
D. stenophylla E204
D. stenophylla E240
0.579
0.421
0.347
0.164
0.653
0.237
0.134
0.763
0.866
0.836

Nuclear concatenated
Plastome
D. serrata
D. stenophylla var. tetrasepala
D. sanguinea
D. stenophylla
D. spathulata
Outgroups
Diabelia serrata E314
D. serrata var. buchwalddi E324
D. serrata E137
D. serrata E140
D. serrata E138
D. serrata E139
D. serrata E123
D. serrata E122
D. serrata E126
D. serrata E125
D. serrata E321
D. serrata E128
D. serrata E124
D. stenophylla var. tetrasepala E142
D. stenophylla var. tetrasepala E143
D. stenophylla var. tetrasepala E185
D. stenophylla var. tetrasepala E312
D. stenophylla var. tetrasepala E311
D. sanguinea E294
D. spathulata E271
D. sanguinea E130
D. sanguinea E303
D. sanguinea E301
D. sanguinea E131
D. sanguinea E306
D. sanguinea E308
D. stenophylla E204
D. stenophylla E202
D. stenophylla E201
D. stenophylla E203
D. stenophylla E205
D. stenophylla E171
D. stenophylla E172
D. stenophylla E170
D. stenophylla E132
D. stenophylla E295
D. stenophylla E240
D. spathulata E198
D. spathulata E190
D. spathulata E200
D. spathulata E141
D. spathulata E129
Abelia macrotera var. macrotera E45
Kolkwitzia amabilis E9
Dipelta floribunda E55
Linnaea borealis E59
Vesalea floribunda E112
0.004
0.008

Table. S1 **List of species and vouchers used in this study.**

Order	Ingroup/ Outgroup	Taxon	Coding	Locality	Voucher specimen number	SRA accession
1	Ingroup	*Diabelia serrata*	A	Ogawara plateau,Tokushima , Japan	HUTB, E314	SRR15731354
2	Ingroup	*Diabelia serrata* var. *buchwaddi*	A	Takanose-kyo gorge, Kito, Naka-cho, Kochi, Japan	HUTB, E324	SRR15731353
3	Ingroup	*Diabelia serrata*	A	Mt. Shiraga, Motoyama-cho, Kochi, Japan	HUTB, E137	SRR15731342
4	Ingroup	*Diabelia serrata*	A	Kochi, Japan	HUTB, E140	SRR15731331
5	Ingroup	*Diabelia serrata*	A	Kakiki-mura, Kanoashi-gun, Shimane, Japan	HUTB, E122	SRR15731324
6	Ingroup	*Diabelia serrata*	A	Anan, Tokushima, Japan	HUTB, E123	SRR13705758
7	Ingroup	*Diabelia serrata*	A	Mt. Shiraga, Motoyama-cho, Kochi, Japan	HUTB, E138	SRR15731323
8	Ingroup	*Diabelia serrata*	A	Mt. Shiraga, Motoyama-cho, Kochi, Japan	HUTB, E139	SRR15731322
9	Ingroup	*Diabelia serrata*	A	Takanose-kyo gorge, Kito, Naka-cho, Kochi, Japan	HUTB, E128	SRR15731321
10	Ingroup	*Diabelia serrata*	A	Takakuma, Kagoshima, Japan	HUTB, E321	SRR13890747
11	Ingroup	*Diabelia serrata*	A	Mt. Shozanji, Kamiyama, Tokushima, Japan	HUTB, E125	SRR15731320
12	Ingroup	*Diabelia serrata*	A	Ogawara plateau,Tokushima , Japan	HUTB, E126	SRR15731319
13	Ingroup	*Diabelia serrata*	A	Takaga, Seki city, Gifu, Japan	HUTB, E124	SRR15731352
14	Ingroup	*Diabelia stenophylla var. tetrasepala*	A	Mt. Takamaru, Kamikatsu, Tokushima, Japan	HUTB, E142	SRR15731351
15	Ingroup	*Diabelia stenophylla var. tetrasepala*	A	Mt. Takamaru, Kamikatsu, Tokushima, Japan	HUTB, E143	SRR15731350
16	Ingroup	*Diabelia stenophylla var. tetrasepala*	A	Mt. Takamaru, Kamikatsu, Tokushima, Japan	HUTB, E185	SRR15731349
17	Ingroup	*Diabelia stenophylla var. tetrasepala*	A	Mt. Takamaru, Kamikatsu, Tokushima, Japan	HUTB, E312	SRR15731348
18	Ingroup	*Diabelia stenophylla var. tetrasepala*	A	Mt. Takamaru, Kamikatsu, Tokushima, Japan	HUTB, E311	SRR15731347
19	Ingroup	*Diabelia spathulata*	A	Tochigi, Japan	HUTB, E271	SRR15731346
20	Ingroup	*Diabelia sanguinea*	A	Yumoto, Nasu-cho, Nasu-gun, Tochigi, Japan	HUTB, E130	SRR15731345

21	Ingroup	*Diabelia sanguinea*	A	Mt. Takamaru, Kamikatsu, Tokushima, Japan	HUTB, E294	SRR15731344
22	Ingroup	*Diabelia sanguinea*	A	Zike, Toyama city, Toyama, Japan	HUTB, E131	SRR15731343
23	Ingroup	*Diabelia sanguinea*	A	Sendai, Miyagi, Japan	HUTB, E301	SRR13705755
24	Ingroup	*Diabelia sanguinea*	A	Mt. Kinkan, Numadzu city, Shizuoka, Japan	HUTB, E303	SRR13890746
25	Ingroup	*Diabelia sanguinea*	A	Tanyama, Nagano, Japan	HUTB, E308	SRR15731341
26	Ingroup	*Diabelia sanguinea*	A	Tanyama, Nagano, Japan	HUTB, E306	SRR13705756
27	Ingroup	*Diabelia spathulata*	B	Naewon temple forests,Yangsan-si, Gyeongsangnam-do, Korea	HUTB, E190	SRR15731340
28	Ingroup	*Diabelia spathulata*	A	Kowaki-cho, Higashiomi city, Shiga, Japan	HUTB, E200	SRR15731339
29	Ingroup	*Diabelia spathulata*	B	Naewon temple forests,Yangsan-si, Gyeongsangnam-do, Korea	HUTB, E141	SRR15731338
30	Ingroup	*Diabelia spathulata*	A	Kowaki-cho, Higashiomi city, Shiga, Japan	HUTB, E198	SRR13705757
31	Ingroup	*Diabelia spathulata*	A	Hatasawa, Obanasawa city, Yamagata, Japan	HUTB, E129	SRR15731337
32	Ingroup	*Diabelia stenophylla*	C	Wenzhou, Zhejiang, China	HUTB, E204	SRR13705754
33	Ingroup	*Diabelia stenophylla*	C	Wenzhou, Zhejiang, China	HUTB, E203	SRR15731336
34	Ingroup	*Diabelia stenophylla*	C	Wenzhou, Zhejiang, China	HUTB, E201	SRR15731335
35	Ingroup	*Diabelia stenophylla*	C	Wenzhou, Zhejiang, China	HUTB, E202	SRR15731334
36	Ingroup	*Diabelia stenophylla*	C	Wenzhou, Zhejiang, China	HUTB, E205	SRR15731333
37	Ingroup	*Diabelia stenophylla*	C	Wenzhou, Zhejiang, China	HUTB, E170	SRR15731332
38	Ingroup	*Diabelia stenophylla*	C	Wenzhou, Zhejiang, China	HUTB, E172	SRR15731330
39	Ingroup	*Diabelia stenophylla*	C	Wenzhou, Zhejiang, China	HUTB, E171	SRR15731329
40	Ingroup	*Diabelia stenophylla*	A	Saitama, Japan	HUTB, E240	SRR15731328
41	Ingroup	*Diabelia stenophylla*	A	Tabitomachi, Iwaki-shi, Fukushima Pref, Japan	HUTB, E295	SRR15731327
42	Ingroup	*Diabelia stenophylla*	A	Kami-sanbonmatsu, Honzyuku-cho, Okazaki city, Aichi, Japan	HUTB, E132	SRR15731326
43	Outgroup	*Abelia macrotera* var. *macrotera*		Yichang, Hubei, China	HUTB, E45	SRR13890750

44	Outgroup	*Dipelta floribunda*	Cambridge, UK.	HUTB, E55	SRR13705794
45	Outgroup	*Kolkwitzia amabilis*	Weinan, Shanxi, China	HUTB, E9	SRR13705797
46	Outgroup	*Vesalea floribunda*	Oaxaca, Mexico	HUTB, E112	SRR15731325
47	Outgroup	*Linnaea borealis*	Yili, Xinjiang, China	HUTB, E59	SRR13705788

Table S2. HybPiper assembly statistics

Species	Number of reads	Number of reads on target	Percent reads on target	Number of exons with reads	Number of exons with contigs	Number of exons with sequences	Number of exons with sequences > 25% of the target length	Number of exons with sequences > 50% of the target length	Number of exons with sequences > 75% of the target length	Number of exons with sequences > 150% of the target length	Number of exons with paralog warnings
D. spathulata E129	16390784	4958995	0. 303	1114	1025	994	992	982	934	1	101
D. sanguinea E306	9313351	1888267	0. 203	1119	1007	977	974	960	889	0	79
D. sanguinea E308	5571741	780542	0. 14	1097	981	960	956	936	875	0	69
D. stenophylla var. tetrasepala E142	14145605	1023090	0. 072	1089	987	963	962	952	899	1	79
D. stenophylla var. tetrasepala E143	4395804	228392	0. 052	1050	900	878	878	851	783	0	54
D. stenophylla var. tetrasepala E185	5533465	1430420	0. 259	1114	1008	978	977	959	898	0	90
D. sanguinea E294	1071353	238126	0. 222	1021	876	862	861	841	779	0	56
D. stenophylla E295	9507905	2627497	0. 276	1138	1024	992	992	971	904	0	92
D. tetrasepala E311	12638082	3514670	0. 278	1144	1030	995	994	982	937	2	98
D. tetrasepala E312	26768128	7923496	0. 296	1130	1022	995	994	984	940	2	102
D. stenophylla E170	8333538	2519416	0. 302	1127	1017	995	994	979	922	1	90
D. stenophylla E171	8838954	2672116	0. 302	1108	1017	987	985	972	923	1	96
D. stenophylla E172	6849894	2064638	0. 301	1103	1008	983	981	962	908	1	92
D. stenophylla E201	10281957	3225974	0. 314	1112	1015	988	987	973	922	1	86
D. stenophylla E202	7944302	2326039	0. 293	1109	1012	986	985	968	915	1	86
D. stenophylla E203	8895646	3097609	0. 348	1122	1022	996	995	980	924	1	85
D. stenophylla E204	6642696	2077347	0. 313	1103	1006	983	982	962	908	1	76
D. stenophylla E205	9630997	2810192	0. 292	1128	1020	995	993	972	920	1	80

D. sanguinea E130	4766791	879875	0.185	1065	981	958	956	942	887	0	79
D. stenophylla E240	8121657	922592	0.114	1098	988	963	961	933	838	0	66
D. sanguinea E301	12028399	2724711	0.227	1151	1062	1032	1032	1021	989	3	619
D. sanguinea E303	10970170	3075238	0.28	1134	1025	991	988	973	914	0	91
D. serrata var. *buchwaddi* E324	6665872	419228	0.063	1093	872	852	849	803	683	0	39
D. serrata E122	5880405	1892938	0.322	1064	999	978	977	962	895	0	85
D. serrata E123	21639680	7331755	0.339	1120	1033	998	996	980	933	1	136
D. serrata E124	22914349	9714647	0.424	1116	1031	1000	999	984	940	2	97
D. serrata E125	15011394	6415541	0.427	1105	1034	1003	1002	986	938	0	88
D. serrata E126	30652021	9145847	0.298	1124	1028	1002	1000	984	937	0	112
D. serrata E128	13934333	2581418	0.185	1091	999	975	974	959	909	1	102
D. serrata E137	4273733	735627	0.172	1060	974	952	950	933	871	0	79
D. serrata E138	14148609	3912863	0.277	1100	1020	993	992	979	924	1	83
D. serrata E139	10112962	2465780	0.244	1102	1002	983	982	968	910	0	96
D. serrata E314	5056940	378381	0.075	1050	877	850	839	746	587	1	36
D. serrata E321	13220295	4190116	0.317	1138	1037	1002	1000	986	934	0	93
D. spathulata E271	3089596	212920	0.069	992	827	809	806	762	661	0	39
D. sanguinea E131	13699360	3897086	0.284	1107	1018	991	990	979	930	1	87
D. stenophylla E132	7051574	1749371	0.248	1081	1000	976	974	958	905	1	86
D. serrata E140	6481952	1399052	0.216	1081	992	967	966	949	888	0	88
D. spathulata E141	6471860	1497704	0.231	1075	992	966	965	952	900	0	87
D. spathulata E190	8953298	2806002	0.313	1124	1022	989	986	973	928	2	86
D. spathulata E198	9267804	3459777	0.373	1130	1022	993	992	981	928	1	92
D. spathulata E200	8307344	2742274	0.33	1118	1018	991	990	980	922	1	86
Abelia macrotera var. *macrotera* E45	1833543	32422	0.018	825	436	424	417	355	253	0	6

Dipelta floribunda E55	4636783	105360	0．023	924	660	642	639	601	507	0	27
Kolkwitzia amabilis E9	9779050	2641147	0．27	1097	1005	984	983	967	916	0	75
Linnaea borealis E59	3831881	51899	0．014	867	536	516	507	443	333	0	11
Vesalea floribunda E112	3834861	805440	0．21	1061	970	947	946	915	856	0	52