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Advancements in Genetic Diversity and Genome Characteristics of Durians (*Durio* spp.)

Tran Gia Huy [a*], Nguyen Kim Hoan [b++], Nguyen Pham Anh Thi [a] and Do Tan Khang [a]

[a] Institute of Food and Biotechnology, Can Tho University, 3/2 Street, Ninh Kieu District, Can Tho City, Vietnam.
[b] Can Tho University, Can Tho City, Vietnam.

Authors' contributions

This work was carried out in collaboration among all authors. Author TGH designed the study, performed the statistical analysis, searched the literature and wrote the first draft of the manuscript. Authors NKH, DTK and NPAT edited the draft. All authors read and approved the final manuscript.

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ABSTRACT

Durian is one of the important fruit crops in Southeast Asia with its unique flavor and important economic benefits. Breeding programs have produced hundreds of different cultivars of durian. These cultivars are classified mainly by fruit and flower characteristics, which cannot be observed at the vegetative stage. Therefore, molecular biology is a powerful tool to approach and explore the genetic characteristics of durians. Many studies based on barcoded DNA and molecular markers have been conducted and valuable data have been exploited. Thanks to the advancement of sequencing technology, the plastid genome and the whole genome were sequenced in some durian cultivars. The data revealed reliable data on the structure and function of several genes. This review

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[++] Graduate Student Course 28;
**Corresponding author: E-mail: tghuy@ctu.edu.vn;*

aims to update recent studies on the durian genome attributes and potential applications in the conservation of germplasm, authentication, and exploration of the gene structure and function of this specialty plant.

Keywords: Durian; genome analysis; molecular marker; plastid genome; whole genome sequencing.

1. INTRODUCTION

Durian is a woody and flowering plant belonging to the family Malvaceae. This is one of the most important tropical fruits, which is considered “the King of fruits”. Such fruit tree was cultivated ubiquitously in Southeast Asia countries such as Malaysia, Indonesia, Thailand, and Viet Nam. Durian fruit has a special taste and aroma, so its price is much higher than the others, bringing farmers a valuable income. In agriculture, durian fruit is a valuable commodity for both domestic consumption and global export [1]. The presence of fat, sugar, and volatile compounds such as esters and sulfur-containing substances such as thioacetals, thioesters, and thiolanes, as well as alcoholic compounds, contribute to the unique taste and aroma of durian. In addition, durian is also a rich source of bioactive compounds like flavonoids (i.e., flavonols, anthocyanins), ascorbic acid, and carotenoids [2-4]. In 2019, China imported fresh durian imported was worth ¥1.66 billion RMB, with a significant increase of 47 % every year, and durian occupied about 16.8 % of the total imported fruit market [5].

“The genus *Durio* has approximately 28 species including 8 edible species, namely, *Durio testudinarius* Becc., *Durio graveolens* Becc., *Durio grandiflorus* Kosterm. & Soegeng, *Durio dulcis* Becc., *Durio oxleyanus* Griff., *Durio kutejensis* Hassk. & Becc., and *Durio lowianus* Scort. ex King and also *D. zibethinus* Murr.” [6,7]. *D. zibethinus* is the most popular and economical species due to its fruit quality and yield. During the last 50 years, more than 100 cultivars of *D. zibethinus* are developed [8]. Initially, farmers and plant breeders use seedlings from seeds harvested from their farms or use clonal material from hybridization and selection programs. Durian breeding involves a strategy of selecting and cloning trees based on existing variations found in natural populations or through hybridization. The initial step is to identify and choose superior trees, then evaluate them over time and in different locations to determine their adaptability and fruit production. Using this selection approach has resulted in the development of several cultivars. There are more than 300 registered durian cultivars in Thailand and 127 registered durian varieties in Malaysia 126 durian types have been registered based on phenotyping [9]. Such cultivars were characterized in terms of fruit shape, size, smell, flesh color, texture, taste, and tree growth habit [7,10]. There are three major limitations of identification, hybridization by morphological and agronomic criteria. Firstly, quantitative traits are influenced by abiotic and biotic factors of the environment such as cultivation conditions. Secondly, cultivar-specific traits have not yet appeared at the vegetative stage, so it is unavailable to observe them in seedlings or young trees (2) and the life cycle of fruit trees is much longer than that of food crops such as rice and maize (3). As a result, the breeding of fruit trees is difficult by their long generation time, large plant size, long juvenile phase, and the necessity to wait for the physiological maturity of the plant to assess the edible product.

In order to surpass the limitations of morphological classification, it is necessary to conduct genetic characterization of the different types of durian. DNA sequence approaches are an accurate and reliable solution because the stability of DNA molecules is independent of environmental fluctuations. So far, studies focus on molecular markers and DNA barcodes for genetic characterization [11,12]. However, new cultivars are under species level, involving the more powerful molecular tools not only for identification but also discover specific genes, especially for metabolic pathways fruit quality, and resistance in durians. The rapid development of next-generation sequencing opened a new for cultivar authentication and genome selection [13-15]. The objective of this review is to update and summarized the advancements in molecular biology and genomic publications for durian cultivars, which contribute to improved knowledge in fruit tree genetics and genomics.

2. MOLECULAR MARKERS

2.1 Random Amplified Polymorphic DNA (RAPD)

The RAPD is a dominant marker involving arbitrary oligonucleotide primers with short

lengths, usually 8 to 15 nucleotides, these primers randomly hybridize with DNA template [16]. RAPD marker was applied to estimate the genetic diversity of local durian cultivars in Indonesian regions. In South Kalimantan's province by RAPD markers. Eleven local durian samples were collected and analyzed with five RAPD primers consisting of OPA-01, OPA-02, OPA-07, OPA-16, OPA-18, and OPA-19 [17]. The outputs illustrated the genetic richness of durian cultivars in this province, indicated by a polymorphism degree of 82.17%, and the samples were classified into six. The result also determined the close genetic relatedness of three local cultivars, namely 'Likol', 'Sipisang', and 'Sihabuk', which showed 95% similarity, while the 'Enam Hapat' cultivar was grouped into another cluster by higher genetic distance. Moreover, fifty durian trees from Nias Island were analyzed by five RAPD markers. All amplicons were polymorphic and the primer OPA-3 was considered as a highly informative marker. Based on Principal Coordinate Analysis (PCoA) and UPGMA dendrogram, such durian accessions included five main groups [18]. In West Halmahera, one of the origins of durian cultivation. Five RAPD primers were selected for the polymorphism when analyzing 37 indigenous durians. With 100% amplicons polymorphic, the study revealed the genetic diversity among local cultivars in this region [19]. RAPD marker was applied to examine the genetic relationship between hybrids and their parents. The molecular analysis of 32 durian F1 hybrids, resulted from the crossing of the Arp 8990 (female parent) and 'Otong' (male parent). From the results, 114 scoring bands were amplified with 112 (98.2%) of them polymorphic, with 4 to 11 bands amplified per primer. From the gel pattern, It was visualized that some hybrids contained different compared to their parents; this feature indicated the allele combinations from both the parents by cross-breeding. This result implied that RAPD is a useful molecular tool to evaluate durian hybrids [20].

2.2 Inter Simple Sequence Repeat (ISSR)

The ISSR marker is a dominant marker that focuses to repeat sequences in genomic DNA. Primers bind on the microsatellites repeat sequences that are oppositely oriented and amplify the region between them. Based on the high percentage of plant genomes being repeat sequences, ISSR is a powerful marker for genotyping [12,21]. "Ten ISSR primers were utilized to study the genetic diversity of six endangered durian *D. tanjungpurensis* populations with 60 individuals. An analysis of molecular variance (AMOVA) clarified that the genetic diversity within and between populations was 65% and 35%, respectively. UPGMA clustering and principal coordinate analysis, based on the DICE similarity matrix, were used to classify the populations into three groups: 1) Hutan Rejunak and Tembaga, 2) Bukit Merindang, and 3) Hutan Rawak, Bukit Sagu 1, and Bukit Sagu 2. However, further analysis by STRUCTURE software has merged groups 2 and 3 as one group. It was proposed that there was a high level of genetic diversity in the Durian Tengkurak was revealed utilizing the ISSR markers employed in the dataset" [22]. The genetic diversity of 58 durian trees belonging to three species (*D. zibethinus*, *D. kutejensis*, and *D. tanjungpurensis*) was elucidated by ten ISSR primers. The result found 13 species-specific loci amplified by 7 ISSR primers, such specific bands were able to authenticate Indonesian durians [23]. "In Viet Nam, Ri6 and Monthong are the two most popular cultivars grown in many provinces. Thirteen ISSR primers that showed high polymorphic levels were found when analyzing these two cultivars. The polymorphism information content (PIC) was calculated up to 0.82, reflecting the genetic variation of such durians. The dendrograms generated by clustering and PCoA analysis were able to distinguish the accessions genetically. The obtained results provide molecular biological information for classification, identification of plant origins, breeding, and conservation programs; furthermore, utilization of molecular marker analysis could provide new insights to breeders for the molecular-assisted selection of durian" [24]. Twenty-five Brongkol individuals, which is a superior durian in Indonesia, showed low genetic similarity despite of they were the same cultivar by analysis of 7 ISSR markers. Besides that, two specific amplicons were detected in varieties B5 (1,200 bp) and B16 (1,500 bp) [25]. The recent studies based on DNA molecular markers were summarized in Table 1. Although genetic diversity is important for conservation and evolution study; however, in terms of application, species- or cultivar-specific amplicons were also crucial results, which triggered further investigations for plant authentication. For instance, such bands could be applied to develop sequence characterized amplified region (SCAR) markers, the reliable marker to discriminate plant cultivars [26,27]. Main information such as sample size, markers, software, etc., was summarized in Table 1.

Table 1. Main information from molecular marker-based studies in durian cultivars

Marker	No. samples	No. primers	Scored bands	Data analysis	Software	Country	Ref.
RAPD	32	14	114	UPGMA, PCA	NTSYSpc.	Indonesia	[20]
RAPD	37	10	41	UPGMA	Multivariate Statistical Package program	North Maluku, Indonesia	[19]
RAPD	50	6	66	UPGMA, PCA	POPGENE, NTSYSpc.	Nias island, Indonesia	[18]
RAPD	10	6	112	UPGMA	NTSYSpc.	Nias island, Indonesia	[28]
ISSR	22	25	175	UPGMA, PCA	NTSYSpc.	Viet Nam	[24]
ISSR	25	7	36	UPGMA	NTSYSpc	Semarang, Indonesia	[25]
ISSR	58	10	164	UPGMA	GenAlEx,	West Kalimantan, Indonesia	[23]
ISSR	60	10	148	UPGMA	AMOVA, NTSYSpc, STRUCTURE	West Kalimantan, Indonesia	[22]
ISSR	16	13	181	UPGMA	STATISTICA	Viet Nam	[29]
SSR	27	7	19	Probability of identity (PI)	GenAlEx	Malaysia	[9]
SSR	30	4	NA	UPGMA	NTSYSpc	Nias island, Indonesia	[31]

2.3 Simple Sequence Repeat (SSR)

"SSRs are the codominant markers, they belong to microsatellite DNA sequences. Other classes of microsatellites include simple sequences that arrange in short tandem repeats and polymorphic microsatellite length variations. Of these classes of microsatellites, SSRs show a small number of repetitions per locus but express higher polymorphic levels" [30]. "Genetic variation in 27 durian types from the germplasm collection of University Putra Malaysia. Unique DNA fingerprints were generated for 21 out of 27 durian types using five polymorphic SSR markers while the other two SSR markers were monomorphic. Further DNA assays by the utility of these markers by evaluating the clonal status of shared durian types from different germplasm collection sites, and found that some were not clones, ''varieties'', or ''cultivars''. Such matters have a direct impact on the regulation and management of durian genetic resources in the region" [9]. "Genetic similarity of 3 durian populations [Nias Kota (NK), Nias Induk (NI), and Nias Barat (NB)] had been evaluated based on Simple Sequence Repeat (SSR) markers. There were 30 durian genotypes were analyzed using 4 primers (DzMTb021, Dz621, Dz535, and Dz504). All of the loci had 100% of polymorphism except Dz621 with 33.33% polymorphism. The result showed that the ten samples were not clustered within their populations. The genetic similarity of 30 durians from three populations was 63%, and the genetic similarity of durian within the NK, NI, and NB population was 72, 74, and 59% respectively. The similarity of NK and NI populations was the highest when compared to NB" [31].

"The population genetics of durians in China were elucidated by analyzing 32 genotypes in durian plantation sites in Hainan. Based on whole genome sequencing through restriction site-associated DNA sequencing, the population was grouped into two clusters. Seven genotypes, namely D24, D101, MSW, JH, D163, HFH, and NLX-5 were the core durian germplasm in Hainan. In addition, 79,178 SSR markers were developed, which bring the foundation for molecular breeding via marker-assisted selection, quantitative trait loci targeting, and gene positions" [32].

3. DNA BARCODES

DNA barcodes are also an accurate method for genetic diversity and species discrimination [33]. These standardized sequences were utilized widely for fruit tree identification such as dragon fruits [34], star apple [35], Burmese grape [36], and mango [37]. In durians, DNA barcodes from both the nucleus and plastid were studied to seek a potential sequence with high discrimination power. Sequence candidates included ITS in the nucleus and *mat*K, *rbc*L and *trn*L intron. ITSwas proposed as a reliable barcode for durian following these parameters; sequencing success, number of variable and parsimony informative sites, effectiveness for BLASTN search, and phylogeny construction. Moreover, this noncoding sequence also reached the highest distribution of intraspecific K2P distance (> 0.02), so it was used as a marker to discriminate the durian. In contrast, *mat*K showed the lowest sequencing success due to variables on primer binding sites but was more effective for species resolution than *trn*L [38]. It was reported that the plastid gene *rbc*L primer showed a high efficiency of amplification while *mat*K primer generated a smeared amplicon [39]. "Sequence analysis showed no variation of *rbc*L sequence in the examined genotypes. A similar result was also observed on *D. zibethinus* and *D. graveolent*. Overall, both genes were not able to describe the genetic relationship among the evaluated durians, and they were grouped in the same branch in phylogenetics" [39].

The *rbc*L gene showed 23 variable sites for the durian germplasm in Kalimantan, Indonesia has a low genetic diversity (π%=0.24). "Based on the phylogenetic and principal component analyses, 29 durians showed a close relationship, and the farthest was shown by Durian Burung (*D. acutifolius*) and Kalih Haliyang (*D. kutejensis*) as well as Pampaken Burung Kecil (*D. kutejensis*) and Durian Burung (*D. acutifolius*) with a divergence coefficient of 0.011. The Pearson correlation analysis confirms that 20 pairs of individual durians have a strong relatedness, indicated by, e.g., Maharawin Hamak and Durian Burung as well as Mantuala Batu Hayam and Durian Burung Besar" [40]. A short matK gene sequence with only 245 bp was amplified for the identification of 15 local durians [41]. Although this short sequence was successfully amplified, the low sequencing success (71.3%) and the miss identification by BLAST results were observed. It could be concluded that the matK gene with the short sequence is not suitable for durian identification [41]. The recent DNA barcode studies were listed in Table 2.

Table 2. DNA barcode studies on durian cultivars

No. of samples	DNA sequences	Data analysis	Software	Country	Ref.
36	*mat*K, ITS, *trn*L	Homology, K2P distance	BLAST, MEGA 5	North Maluku, Indonesia	[38]
3	*mat*K, *rbc*L	UPGMA	Genestudio, MEGA X	Indonesia	[39]
15	ITS, *mat*K, *rpo*C1	Alignment, homology	BLAST, Bioedit, MEGAX	Viet Nam	[42]
15	*mat*K	Homology	ABI sequence scanner v.10, BLAST	Ternate island, Indonesia	[41]
29	*rbc*L	Alignment, PCA, Pearson correlation	MEGA X, AMOVA, MVSP	Kalimantan, Indonesia	[40]
27	ITS	UPGMA, Maximum Likelihood	BLAST, MultAlin, MEGA X	Indonesia	[43]

Another comparative study also confirmed the high variable of ITS region in the durian genome. A dataset was constructed from 16 ITS sequences from Genbank and analyzed using bioinformatic tools such as BLAST, MultAlin, and MEGA-X software. ITS region of durians was 702 bp in length and contained several variable sites; SNPs and indel mutations. "At the nucleotide level, this germplasm shows a relatively high diversity of 0.065. The cluster analyses (UPGMA and Maximum Likelihood) can separate this germplasm into four clusters and five main clades, respectively. In this study, *D. zibethinus*, the most popular species in the *Durio* genus, is closely related to *D. lowianus* and far from *D. griffithii*." [43]. It was also concluded that ITS is an informative barcode sequence, which can identify some of the durian cultivars in Viet Nam [42].

4. CHLOROPLAST GENOME

The complete plastome of *D. zibethinus* L. (Malvaceae) is published with the accession number MG138151 [8]. This was the first reported sequence from the subfamily Helicteroideae of Malvaceae. The chloroplast sequence size of the *D. zibethinus* Monthong cultivar is 163,974 bp in length and it comprises a pair of 23,679 bp inverted repeat regions separated by large and small single-copy regions of 95,704 bp and 20,912 bp, respectively (Table 3). The gene order and structure of *D. zibethinus* are similar to those of the typical plastome of land plants, genes in chloroplast border regions were described in Fig. 1 [44]. There were 113 genes, consisting of 79 protein-coding genes, 30 tRNA genes, and four rRNA genes. Fifteen genes contained one intron and two genes with two introns. Moreover, 144 chloroplast SSRs (cpSSR) were identified, which was useful for marker development, cpSSRs were higher polymorphism levels and thus make the marker accuracy for genotype determination and population genetic studies [12]. From phylogenetic analysis with 100% bootstrap, the data revealed that *D. zibethinus* (Helicteroideae) is the sister group of Tilia (Tilioideae) [8].

Another chloroplast genome of the Monthong cultivar was also sequenced by utilizing long read technology from Pacbio. The chloroplast genome assembled into a single 143 kb cyclic contig that contained 111 genes. There were 46 short direct repeats (45 to 586 bp) and five short inverted repeats (63 to 169 bp). An interesting feature was found that this plastome lacked the large inverted repeat, which is a common component in chloroplast genomes. An additional 24 durian varieties were sequenced and compared to the assembly and found to also lack the large inverted repeat. There were nine SNPs among the varieties [45]. The underutilized durian, *D. oxleyanus* (Griff) of Malvaceae is considered an endangered plant in Malaysia, which lead to the requirement for conservation. Despite durian being a commercially valuable fruit, the growth of this species is uncommon, leading to a decrease in the population of this species. *D. oxleyanus* had a 164,831 bp genome size and 135 genes were predicted, which consisted of 90 protein-coding, 37 tRNA, and eight rRNA genes. The phylogenetic analysis based on the maximum-likelihood and Bayesian inference methods revealed that *D. oxleyanus* is closely related to *D. zibethinus* [46]. Recently, the chloroplast genome of D. dulcis was also sequenced, the size of this genome was similar compared to that of *D. zibethinus* MT321069. Thus, there was a fluctuation in size among durian chloroplast genomes, reflecting the evolutionary events.

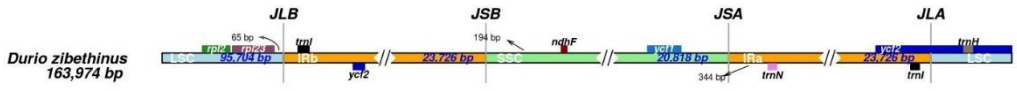

Fig. 1. Border regions of *D. zibethinus* chloroplast genome (generated by IRscope program)

Table 3. Chloroplast genome of four durian species

Species	*D. zibethinus*	*D. zibethinus*	*D. oxeylanus*	*D. dulcis*
Accession number	MG138151	MT321069	ON653424	OQ439952
Genome size (bp)	163,974	142,733	164,831	141,676
Country	Korea	Thailand	Malaysia	Indonesia
Sequencing platform	Illumina HiSeq 2000	Long PacBio reads	Illumina Novaseq	Illumina

5. WHOLE GENOME SEQUENCING

Sequencing of the whole genome contributes a huge amount of data for many further investigations such as involution, breeding, gene expression, and metabolite pathways. The draft genome of *D. zibethinus* Musang King cultivar was first reported in 2017 [47]. The data showed that repeat sequences occupied 54.8% of the assembly genome (Table 4). The two regions called LTR/*Gypsy* and LTR/*Copia* elements showed a high proportion of repeat nucleotide with 26.2% and 3.2% of the genome, respectively. The results also revealed that the durian genome is highly heterozygous, resulting from various breeding programs. Transcriptomic analysis showed upregulation of sulfur-, ethylene-, and lipid-related pathways in durian fruits, corresponding to the special flavor and aroma of durian. In terms of evolution, the paleo-polyploidization means that the whole genome duplication events shared by durian and cotton and durian-specific gene expansions in MGL (methionine g-lyase), are associated with the production of volatile sulfur compounds (VSCs). MGL and the ethylene-related gene ACS (aminocyclopropane-1-carboxylic acid synthase) were upregulated in fruits concomitantly with their downstream metabolites (VSCs and ethylene), suggesting a potential association between ethylene biosynthesis and methionine regeneration via the Yang cycle [47].

Based on the reference genome of the Musang King cultivar [47]. Three genomes of Thailand durians such as Kradumthong (KD), Monthong (MT), and Puangmanee (PM) were sequenced by Illumina HiSeq X Ten system. KD, MT, and PM genome assemblies were 832.7, 762.6, and 821.6 Mb [48]. In terms of genome size, such genomes were relatively larger than the Musang king cultivar's genome. The previous genome was sequenced by a combination of a long read (PacBio RSII platform) and a short read (Illumina HiSeq 2500) technology. Due to the high proportion of repetitive regions in the plant genome [49,50], so different sequencing platforms influenced the final assembly genome. This study found that Thai durian cultivars were distinct compared to the Musang King cultivar based on phylogenetic relatedness, copy number variations (CNVs), and presence/absence variations (PAVs) analysis. Interestingly, the Monthong cultivar showed unique PAV and CNV profiles for resistant genes and the regulation of genes involved in flowering and fruit ripening. Such genome assemblies and their downstream analysis provide valuable molecular data to gain advanced knowledge of genomic variation, which could be useful for future breeding strategies [48].

The whole genome sequences provided a molecular basis for further publications in gene expression and transcriptomics. Furthermore, transcriptomic analysis was performed to analyze the dynamic changes in sugar metabolism, glycolysis, TCA cycle, and amino acid pathways to identify essential candidate genes [51]. Furthermore, researchers have discovered the metabolic pathway for taste-related characteristics, which can aid in the development of markers for cultivar selection and breeding. A gene family called ERF (Ethylene Response Factor) has also been identified in durians, which plays a crucial role in ethylene biosynthesis and other physiological processes [52,53]. 34 ERFs in the durian genome exhibited ripening-associated expression patterns during fruit ripening. Such ERFs were classified into three clades, among which, clade I consisted of repressors and clade III were activators ripening stages. During the fruit maturation, transcriptome analysis proposed that most genes with upregulation at the ripening stage were prioritized and involved in pathways of cofactors and vitamins, nucleotide metabolism, and carbohydrate metabolism. The transcriptome data generated an in-depth understanding of durian fruit development-specific genes and could be powerful in fruit trait improvement [54]. By analysis of the reference genome, 2586 resistance genome analogs (RGAs) were identified, and characterized their structural features. The study informed the understanding of the response of durian to insect pests and pathogenic microorganisms [55].

Table 4. Genome statistics of four durian cultivars

Features	Musang King	Kradumthong	Puangmanee	Monthong
Estimated genome size (Mb)	738	839.66	821.59	762.61
Predicted gene models	45,335	47,980	44,814	45,705
Average of exons/genes	5.8	5.285	5.333	5.274
Repeats (%)	54.8	62.27	60.27	61.27
LTR/*Gypsy*	26.2	33.30	30.56	30.29

6. CONCLUSION

This review highlighted the recent advancements in durians, focusing on DNA-based studies. Thanks to advancements in sequencing technology, it is now possible to generate a high-resolution map of an organism's entire genetic material through whole genome sequencing. Data from the genome provide a molecular basis for scientists to discover new genes and their variants, which control essential traits such as fruit quality, flavor, and aroma pathway, pathogen resistance. Moreover, useful markers were able to discover for cultivar authentication and breeding programs. Last but not least, the sequencing of other durian cultivars should be investigated for the construction of the durian pan-genome.

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COMPETING INTERESTS

Authors have declared that no competing interests exist.

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