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VIRAL AND VIROID DISEASES

Characterization of novel *French bean leaf curl virus* and betasatellite associated with leaf curl disease of French bean (*Phaseolus vulgaris* L.)

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Abstract

Leaves from French bean plants with severe leaf curl (ten samples) and from asymptomatic plants from 10 fields (FB1–10) in the Western Ghat region of Karnataka, India were collected. Virus isolate FB01 from French bean was shown to be transmitted by whitefly *Bemisia tabaci* cryptic species Asia I. DNA was isolated from the samples (ten field samples and one sample infected with FB01 via whitefly) and subjected to PCR to confirm begomovirus infection using specific primers. All 11 were positive for the expected 1.2-kb amplicon. The sequence analysis of the 1.2-kb amplicon showed that all isolates shared more than 98% nucleotide identity. Further, the complete genome from isolate FB01 was amplified and sequenced and shown to share a maximum nucleotide identity (89.3%) with *Ageratum yellow vein Sri Lanka virus*. As per the ICTV species threshold for begomoviruses, the virus is considered as a new species, with the proposed name *French bean leaf curl virus* (FbLCV). The samples were subjected to PCR using specific primers for DNA B, betasatellite and alphasatellite; only betasatellites were amplified. The detected betasatellite shared maximum nucleotide identity (92.6%) with *Synedrella yellow vein betasatellite*. Recombination analysis indicated that FbLCV and betasatellite were recombinants. The significance of these findings are discussed.

Keywords Begomovirus · Recombination · Phylogenetic analysis · Polymerase chain reaction · Betasatellite

French bean (also called common bean; *Phaseolus vulgaris* L.) is cultivated throughout the world (Pathania et al. 2014), comprising more than 90% of the 50 species of *Phaseolus* crops; 57,496,465 tons of these beans are grown in a total area of about 38,229,984 ha (Arteaga et al. 2019). Brazil leads the world in French bean production. In India, bushy and trailing types of French bean are cultivated commercially. The seeds are a good source of protein (23% [w/w]) and minerals, and the fresh pods are used as a vegetable in India.

Among the numerous pathogens that infect French bean, viral pathogens are major constraints for production. Worldwide, 34 diverse virus species belonging to the genus *Potyvirus*, *Carlavirus*, *Cucumovirus*, *Sobemovirus*, *Endornavirus*, and *Begomovirus* have been reported to infect French bean with huge yield losses (Arli-Sokmen et al. 2016; Mwaipopo et al. 2017). In southern Asia, great losses to grain legume crops are caused by begomoviruses (Ilyas et al. 2009; Qazi et al. 2007). So far, eight distinct begomoviruses associated with grain legumes were reported from different parts of India: *Mungbean yellow mosaic virus* (MYMV), *Mungbean yellow mosaic India virus* (MYMIV) (Capoor and Varma 1950; Nariani 1960; Singh 1979; Williams et al. 1968), *Horsegram yellow mosaic virus* (Muniyappa et al. 1987), *Dolichos yellow mosaic virus* (Maruthi et al. 2006), *Tobacco curly shoot virus* (Venkataravanappa et al. 2012b), *French bean leaf curl virus* (Kamaal et al. 2013), *Tomato leaf curl Gujarat virus* (Kamaal et al. 2014), and *Tomato leaf curl Joydebpur virus* (Ansar et al. 2019).

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During 2017–2018, ten fields in Madikeri District, Karnataka State, India (seven fields at Kushal Nagar, two fields at Gonikoppa and one at Central Horticultural Experiment Station [CHES]) were surveyed for leaf curl disease of French bean. The locations are part of Western Ghats (75.8° E; 12.5° N), which receives an annual rainfall of 1500 mm over more than 100 days with the peak period between July and September. In the surveyed fields, 20–30% of the plants had typical begomovirus-like symptoms such as severe leaf curl and produced very few and nonproductive flowers (Fig. 1). One symptomatic and one asymptomatic leaf sample from French bean plants were collected from each surveyed field. Virus isolates from the symptomatic sample from the ten fields were respectively designated French bean (FB) isolates 1–10.

We tested whitefly *B. tabaci* cryptic species Asia I for the ability to transmit representative isolate FB01 to 7-day-old healthy susceptible French bean plants (cv. Arka Komal), which were raised in pots and maintained in a glasshouse (Venkataravanappa et al. 2012a). Non-viruliferous whiteflies maintained in a glass were given a 24-h acquisition access on symptomatic bean leaves and, then ten of these whiteflies were released on each healthy test plant in a micro-cage for a 24-h inoculation access. Plants were then sprayed with the systemic insecticide Immidachloprid as recommended by the manufacturer, and plants were further to evaluate any symptoms. The results revealed that the white flies transmitted the virus to all tested French bean plants (100/100), which developed symptoms similar to those observed on field-infected plants (Fig. 2).

To confirm the presence of the virus associated with severe leaf curl disease of French bean, we used the CTAB method (Doyle and Doyle 1990) to isolate total DNA from ten symptomatic leaf samples (one from each field), a leaf sample from a symptomatic bean plant after whitefly transmission of FB01 isolate) and asymptomatic leaf samples (from fields and glasshouse), then subjected the DNA samples to PCR using primer pair OY2395F/OY680R specific to begomovirus (Venkataravanappa et al. 2012a). The

Fig. 2 French bean (cv. Arka Komal) plants with leaf curl 16–18 days after inoculation access by whitefly (*Bemisia tabaci*) that fed on symptomatic plants

expected 1.2-kb amplicon, representing the partial genome of begomovirus, was detected in the 11 samples. Then the amplicons for all samples were sequenced. The sequences were found to share more than 98% nucleotide (nt) identity with each other. Comparison of the sequences with the GenBank database revealed that they shared the highest similarity with the monopartite begomovirus *Ageratum yellow vein Sri Lanka virus*. Since the similarity based on the partial genome among the sequences from the samples was very high, representative isolate FB01, that was experimentally transmitted by whitefly to French bean, was selected for complete begomovirus genome (DNA A) amplification using the RCA method described by Venkataravanappa et al. (2016). The amplified RCA product was digested with *Bam*HI to release the 2.7-kb monomeric units of DNA, which were cloned and sequenced in both orientations.

Fig. 1 French bean plant with severe leaf curl after natural field infection

In a test for the DNA B component in symptomatic French bean samples using degenerate universal primers as described by Rojas et al. (1993) and Venkataravanappa et al. (2012a), no DNA B genomic fragment was obtained, indicating the isolate under study is likely a monopartite begomovirus. Some of the old world (OW) begomoviruses are commonly found associated with additional single-stranded DNA molecules known as satellites. To test for any associated DNA satellites, ten French bean samples were subjected to PCR using universal betasatellite-specific primers beta01/beta02 (Briddon et al. 2002) and alphasatellite primers alpha1/alpha2 (Kumar et al. 2010). The expected 1.3-kb amplicon for a betasatellite was detected in all French bean samples, but none were found for an alphasatellite. The 1.3-kb amplicons for betasatellites were cloned and sequenced.

The nucleotide sequences for DNA A component obtained from isolate FB01 were assembled into a circular contig using BioEdit version 7.1, ClustalX2 version 2.1 and SeaView (http://evomics.org/resources/software/bioinformatics-software/seaview/) and deposited in GenBank (accession MK087122). The full-length viral genome (DNA A) is 2738 nt long and displayed a genome organization similar to the OW monopartite begomovirus. DNA A encodes five conserved ORFs: precoat protein (V2, nt 131–478 coding 115 amino acids [aa]), coat protein (V1, nt 291–1061 coding 256 aa) in sense orientation; and replication enhancer protein (C3, nt 1462–1058 coding 134 aa), transcriptional activator protein (C2, nt 1607–1203 coding 134 aa), replication associated protein (C1, nt 2595–1510 coding 361 aa) and C4 (C4 protein, nt 2438–2181 coding 85 aa) in antisense orientation. The sense and antisense ORFs were separated

Table 1 Pairwise percentage of nucleotide identities between the genomic components and amino acid sequence identities of encoded genes from the AYVSLV-French bean with the components and genes of selected other begomoviruses available in the databases

Begomovirus	Accession	Crop	Country	Genome	IR	Gene (percentage amino acid sequence identity)					
						V2	CP (V1)	Rep (C1)	TrAP (C2)	REn (C3)	C4
AYVSLV	AF314144	–	Sri Lanka	89.3	93.2	88.6	97.6	83.1	86.5	92.5	50.5
AEV	JX436472	Tomato	India	87.9	80.7	75.4	93.7	91.6	82.8	85.0	82.3
AEV	JF682242	Amaranthus	India	87.0	77.4	75.4	92.9	91.4	80.5	79.8	81.1
AEV	HE861940	Soybean	India	87.9	80.6	76.2	93.3	91.6	84.3	85.8	84.7
AEV	JQ911765	Poppy	India	86.9	78.4	75.6	91.4	91.4	84.3	85.8	82.3
AEV	JF728866	*Ageratum conyzoides*	India	87.5	80.0	77.3	93.7	91.9	81.3	85.0	83.5
AEV	JF728864	*Ageratum conyzoides*	India	87.2	80.0	77.3	93.7	91.1	81.3	85.0	83.5
AEV	JF728862	*Ageratum conyzoides*	India	87.6	80.0	77.3	93.7	91.9	81.3	85.0	83.5
AEV	AM698011	*Ageratum conyzoides*	India	89.0	82.1	75.6	93.3	97.5	85.0	85.8	91.7
AEV	FJ177031	*Cleome gynandra*	India	88.6	82.5	75.6	93.7	94.1	80.5	79.8	90.5
AEV	GQ268327	Parwal	India	88.4	82.5	76.5	93.3	94.1	81.3	80.5	87.0
AEV	EU867513	*Amaranthus cruentus*	India	88.6	82.5	78.2	93.3	94.1	80.5	79.8	90.5
AEV	AM701770	Turnip	India	88.4	83.3	75.6	93.7	95.0	81.3	82.8	85.8
AEV	FN543099	*Zinnia* sp.	India	87.6	80.3	76.2	93.7	90.8	82.8	87.3	82.3
AEV	AM261836	*Sonchus oleraceus*	Pakistan	89.0	81.3	75.6	91.4	96.3	79.7	85.8	89.4
AEV	KC818421	Tomato	India	88.6	81.1	73.7	93.3	94.7	82.8	85.8	89.4
PaLCuV	JN831446	*Croton bonplandianus*	India	80.4	79.2	69.4	78.9	76.1	81.3	82.8	41.0
PaLCuV	Y15934	Papaya	India	80.9	73.9	72.8	92.5	76.4	81.3	85.0	50.5
TbCSV	JN387045	Tomato	India	81.1	77.1	74.5	92.1	82.5	79.8	81.3	31.4
ToLCBaV-C	AF165098	Tomato	India	79.3	74.0	69.5	84.8	80.0	76.8	79.8	46.3
ChiLCV	JQ654460	*Phaseolus aureus*	India	80.4	77.8	62.7	91.0	80.3	80.5	76.8	42.4
ToLCKaV-Ban	U38239	Tomato	India	84.1	85.2	77.1	92.6	84.4	80.5	84.3	51.5
ToLCKeV	EU910141	Tomato	India	82.6	77.9	77.9	92.9	79.7	82.8	83.5	55.1
FbLCV	JQ866297	French bean	India	87.8	75.9	64.7	89.4	79.3	73.1	73.8	57.0
ToLCV	KF440686	French bean	India	80.3	83.6	76.5	75.7	83.9	79.8	80.5	48.4
TbCSV	JQ733557	French bean	India	83.5	78.5	72.0	91.4	79.5	79.8	82.0	44.3

In each column, the highest value is underlined

AYVSLV *Ageratum yellow vein Sri Lanka virus*, AEV *Ageratum enation virus*, PaLCuV *Papaya leaf curl virus*, TbCSV *Tobacco curly shoot virus*, ToLCBaV *Tomato leaf curl Bangalore virus*, ChiLCV *Chilli leaf curl virus*, ToLCV *Tomato leaf curl virus*, ToLCKaV *Tomato leaf curl Karnataka virus*, ToLCKeV *Tomato leaf curl Kerala virus*, FbLCV *French bean leaf curl virus*

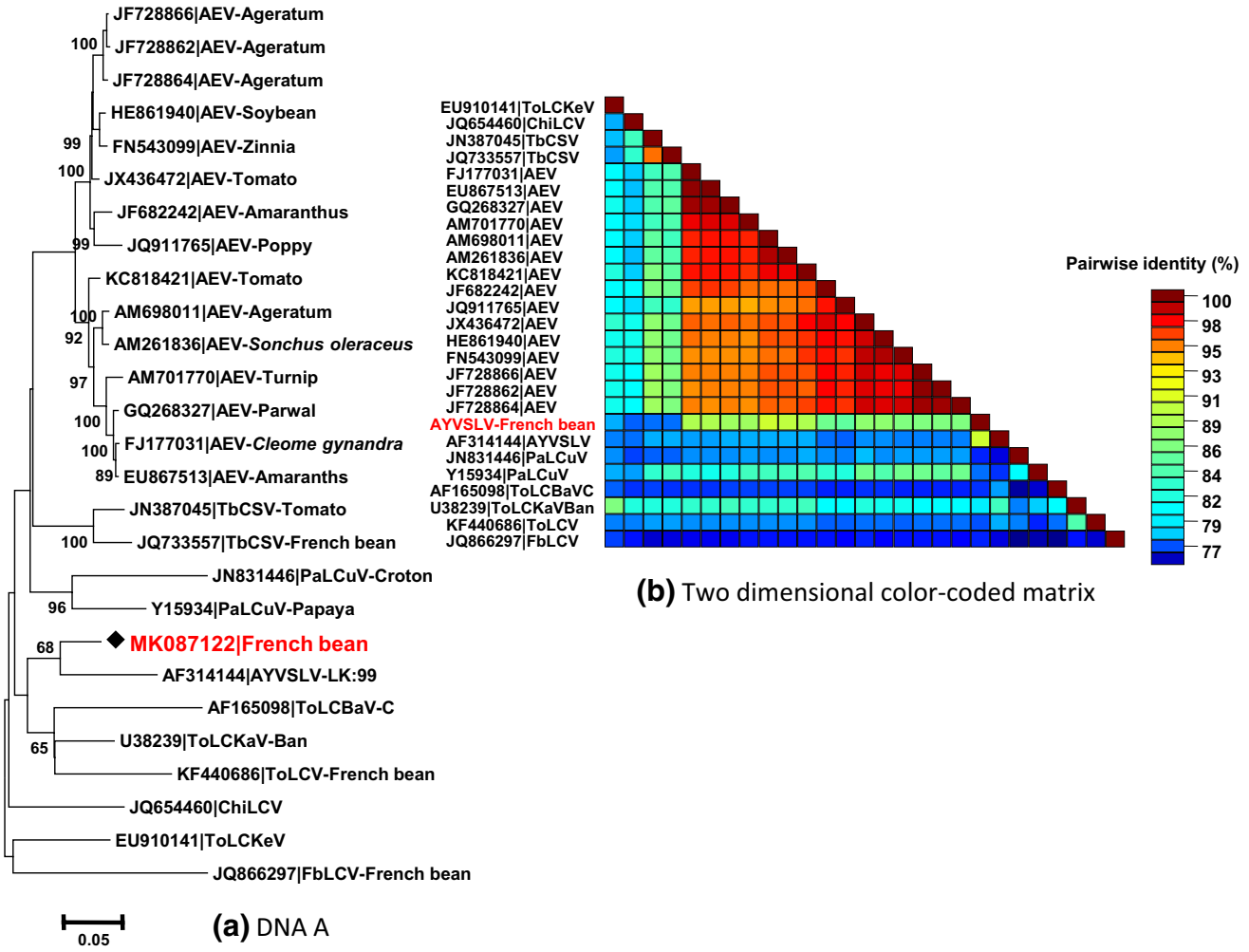

Fig. 3 Phylogenetic trees constructed from aligned complete nucleotide sequences of **a** French bean isolate with other begomoviruses using the maximum likelihood method. Horizontal distances are proportional to sequence distances; vertical distances are arbitrary. The trees are unrooted. Bootstrap analysis with 1000 replicates was performed, and bootstrap percentages greater than 50 are on branches. **b** Two-dimensional color-coded matrix of pairwise identity scores of begomovirus isolate FB01 from French bean were obtained using Species Demarcation Tool (http://web.cbio.uct.ac.za/SDT)

by an untranslated IR (intergenic region) region from nucleotides 2596 to 130, which contained the TATA boxes and contains highly conserved rep gene binding motifs described by Vadivukarasi et al. (2007).

The DNA A component of the begomovirus isolate FB01 was compared with other begomoviruses available in the database, and pairwise identity scores were calculated using the Sequence Demarcation Tool (SDT) (Muhire et al. 2014). The SDT analysis showed that isolate FB01 had maximum nt identity (89.3%) with *Ageratum yellow vein Sri Lanka virus* (AYVSLV) (Table 1). The individual ORFs of FB01 were compared with the ORFs of different begomoviruses. The analysis showed that V1, V2, C2, and C3 shared the highest amino acid identity with AYVSLV from Sri Lanka and that C1 and C4 shared the highest amino acid identity with *Ageratum enation virus* (AEV) from *Ageratum conyzoides* in India (Table 1). The IR had higher identity with the IRs of AYVSLV. The IR comprised 273 nt, similar to the OW begomoviruses reported so far. The IR contained a highly conserved recognition sequence (TAATATTAC) in the loop of the stem loop structure that has been found in all DNA viruses characterized so far. Based on the ICTV threshold of 91% nt identity for classification of begomovirus species (Brown et al. 2015), isolate FB01 infecting French bean should be considered as new species of begomovirus. We thus propose the name *French bean leaf curl virus* (FbLCV) with the additional descriptor (India: Karnataka: French bean: 2018). This new species designation was

Table 2 Percentages of nucleotide or amino acid sequence identities between betasatellite from French bean and betasatellites of other begomoviruses

Betasatellite	Accession	Crop	Country	Complete DNAβ sequence (percentage NSI)	ORF βC1
SYVB	KX363444	*Synedrella nodiflora*	India	<u>92.6</u>	<u>94.9</u>
AYLCB	AJ557441	Ageratum	India	88.6	94.6
CroYVMB	GU111995	Okra	India	70.0	64.1
CroYVMB-Cr2	JN831447	*Croton bonplandianus*	India	69.6	63.8
CroYVMB-Cr1	JQ354987	*Croton bonplandianus*	India	69.2	61.3
CroYVMB	KF964661	*Croton bonplandianus*	India	68.4	61.0
RaLCuB	JN663873	Chilli	India	73.5	76.2
ToLCuB	KU500806	Tomato	India	72.4	66.6
ToLCuB	KJ605115	Tomato	India	73.7	73.1
CLCuMuB	FJ159274	*Hibiscus cannabinus*	India	66.8	55.5
TbCSB	AJ421485	Tobacco	China	70.4	67.6
ToLCJoB	JN663863	Chilli	India	68.5	65.8
ToLCBDB	AY438558	Tomato	India	67.9	65.4
ChLCB	AM279668	Chilli	India	69.2	58.2
ToLCPnB	HQ180393	Tobacco	India	71.3	65.7

In each column, the highest value is underlined

SYVB *Synedrella yellow vein betasatellite*, AYLCB *Ageratum yellow leaf curl betasatellite*, CroYVMB *Croton yellow vein mosaic betasatellite*, RaLCuB *Radish leaf curl betasatellite*, ToLCuB *Tomato leaf curl betasatellite*, CLCuMuB *Cotton leaf curl Multan betasatellite*, TbCSB *Tobacco curly shoot betasatellite*, ToLCJoB *Tomato leaf curl Joydebpur betasatellite*, ToLCBDB *Tomato leaf curl Bangladesh betasatellite*, ChLCB *Chili leaf curl betasatellite*, ToLCPnB *Tomato leaf curl Patna betasatellite*

also supported by a two-dimensional color-coded matrix of pairwise identity scores of the DNA A component of FbLCV generated by SDT (Fig. 3b).

A molecular phylogenetic tree was constructed based on alignment of the DNA A component of FbLCV infecting French bean and selected begomoviruses retrieved from database using the maximum likelihood method (1000 bootstrap replicates) in the MEGA 7 program (Kumar et al. 2016). The analysis revealed that the begomovirus FB01 closely clustered with *Ageratum yellow vein Sri Lanka virus* from Sri Lanka with high bootstrap values (Fig. 3a).

The sequence analysis of the betasatellites from the French bean samples showed that all were identical (sharing > 95% nt identity). Therefore, representative isolate FB01β from the whitefly-transmitted sample was selected for further analysis. Betasatellite FB01β comprised 1357 nt, and the sequence was deposited in GenBank (accession MK087123). Betasatellite FB01β had characteristic features similar to other betasatellite homologs reported from other crops (Briddon et al. 2003) and belongs to the genus *Betasatellite* (family *Tolecusatellitidae*). It shared maximum nucleotide identity (92.6%) with *Synedrella yellow vein betasatellite* (SYVB) (Table 2). This result was also supported by a two-dimensional color-coded matrix of pairwise identity scores for the betasatellite generated by SDT (Fig. 4b). As per the classification of betasatellites, the threshold for species demarcation was set at 78% (Briddon et al. 2008), and betasatellite FB01β was identified as an isolate of SYVB. This result was also supported by a phylogenetic analysis that showed betasatellite FB01β closely clustered with previously reported isolates of SYVB (Fig. 4a).

A recombination breakpoint analysis using six methods (RDP, MAXCHI, CHIMAERA, 3SEQ, GENECONV, and SISCAN) integrated in RDP 4.10 (Martin et al. 2015) with 0.05 *P*-value cut-off throughout and standard Bonferroni correction indicated intraspecific recombination (within the genus/species) in the DNA A component of FbLCV. A recombination breakpoint fragment of 16 nt was found in the DNA A component of FbLCV, with *Papaya leaf curl virus* (JN831446) and *Tomato leaf curl Bangalore virus* (U38239) as the major and minor parents, respectively. At nucleotide coordinates 1064 and 1080, recombinant breakpoints were identified with average *P*-value of 5.876×10^{-5}. Another breakpoint at 1022 nt was identified in DNA A component of FbLCV with major and minor parents resembling *Ageratum yellow vein Sri Lanka virus* (AF314144) and *Ageratum enation virus* (AM698011), respectively. At nucleotide coordinates 1410 and 2432, recombinant breakpoints were predicted with average *P*-value of 2.722×10^{-61}. Similarly, a recombination fragment of 156 nt was detected in DNA A component of FbLCV with the major and minor parent resembling *Tomato leaf curl virus* (KF440686) and *Tomato*

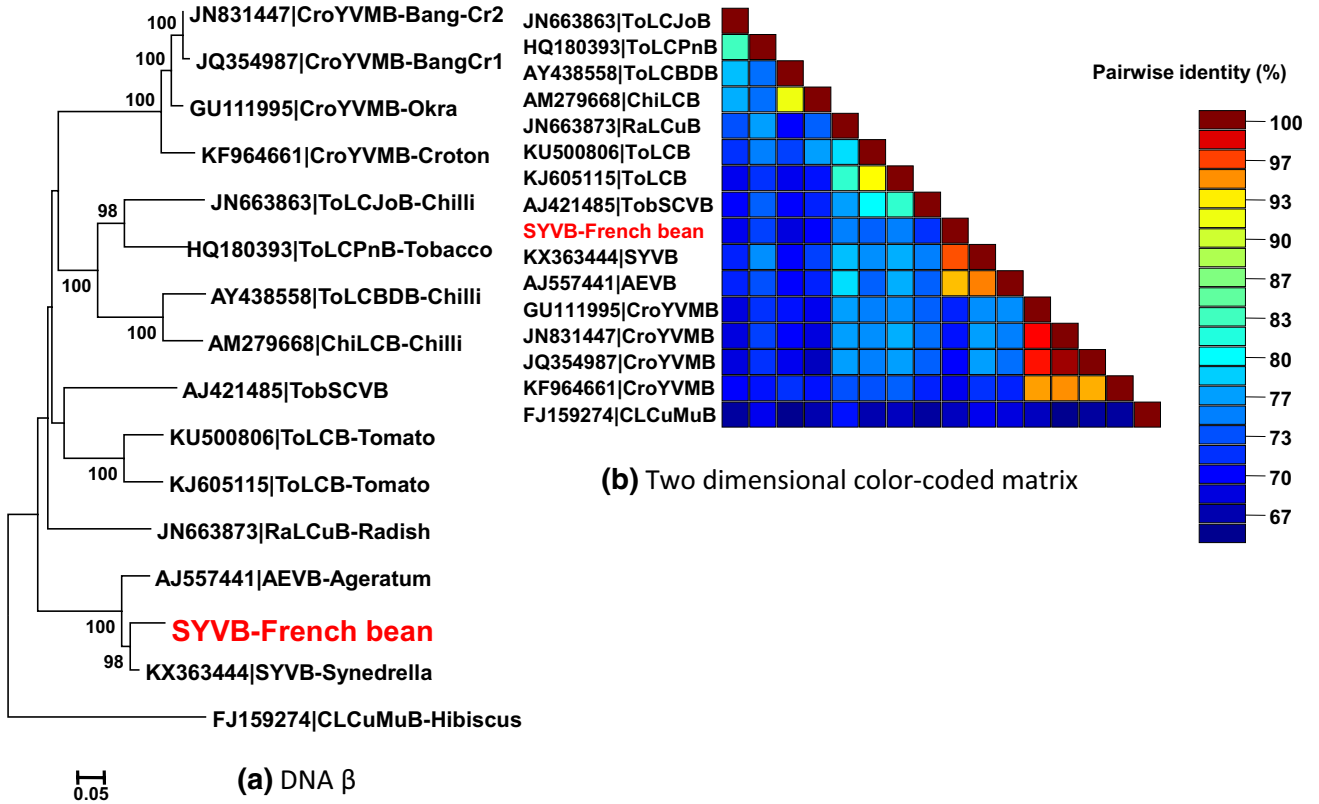

Fig. 4 Phylogenetic trees constructed from aligned complete nucleotide sequences of SYVB betasatellite **a** with other betasatellites retrieved from the database using maximum likelihood method. Horizontal distances are proportional to sequence distances; vertical distances are arbitrary. The trees are unrooted. Bootstrap analysis with 1000 replicates was performed, and bootstrap percentages greater than 50 are on branches. **b** Two-dimensional color-coded matrix of pairwise identity scores of the betasatellite isolate FB01 from French bean were obtained using Species Demarcation Tool (http://web.cbio.uct.ac.za/SDT)

leaf curl Kerala virus (EU910141), respectively. Breakpoints were also predicted at nucleotide coordinates 2274 and 2430 with average *P*-value of 9.36×10^{-2}. In the case of the betasatellite from SYVB, a recombination fragment of 1346 nt was detected in betasatellite of FbLCV, with the major and minor parents resembling *Ageratum yellow leaf curl betasatellite* (AJ557441) and *Croton yellow vein mosaic betasatellite* (KF964661), respectively. At nucleotide positions 20 and 1366, recombinant breakpoints were identified with average *P*-value of 2.787×10^{-23}. A recombinant breakpoint fragment of 308 nt was detected in the betasatellite of AYVSLV, with the major and minor parents resembling the *Croton yellow vein mosaic betasatellite* (KF964661) and *Tomato leaf curl betasatellite* (KJ605115), respectively. Breakpoints were also predicted at nucleotide positions 2274 and 2430 (average $P = 2.005 \times 10^{-5}$).

In the present study, French bean leaves with typical begomovirus symptoms were confirmed by PCR detection and whole-genome sequencing to contain a begomovirus. Insect transmission tests and genome sequence analysis showed that the association of *French bean leaf curl virus* and *Synedrella yellow vein betasatellite* (SYVB) with the symptomatic leaves. SYVB was first identified in a weed species *Synedrella nodiflora* (*Compositae*) in South India (Das et al. 2018). This report is the first of this novel begomovirus, named here as French bean leaf curl virus, in combination with betasatellite from French bean in India.

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Compliance with ethical standards

Conflict of interest All the authors declare that they have no conflict of interests.

Research involving human participants and/or animals This article does not contain any studies with human or animal subjects performed by any of the authors.

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