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Complete sequence of the genomic RNA of the prevalent strain of a potyvirus infecting maize in China*

Brief Report

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Summary. The complete nucleotide sequence of the prevalent strain of a potyvirus isolated from maize in Beijing, China was determined and compared with other closely related potyviruses. The viral genome comprises 9595 nucleotides, excluding the poly (A) tail, and encodes a putative polyprotein of 3063 amino acid residues. Sequence comparison of the coat proteins showed that this isolate was most closely related to most other potyviral isolates infecting maize across China with identities of about 99% and thus represented the prevalent strain. It was also closely related to most isolates of *Sugarcane mosaic virus* (SCMV) infecting maize in Europe with maximum identity of about 95% at the amino acid level. The polyprotein sequence of the Beijing isolate shares identities of 98% with those of two other Chinese maize isolates and shares identity of 69% with *Maize dwarf mosaic virus*-Bulgarian isolate, respectively. Phylogenetic analyses of the sequences indicated that the Beijing isolate can be tentatively referred to as a prevalent strain of SCMV.

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Among the nearly 200 definitive and tentative species in the genus *Potyvirus* with a positive-sense ssRNA genome encoding a single polyprotein, only a few species infect monocots [18, 19]. Four distinct potyviruses have been known to infect maize and sorghum: *Sugarcane mosaic virus* (SCMV), *Maize dwarf mosaic virus* (MDMV), *Sorghum mosaic virus* (SrMV), *Johnsongrass mosaic virus* (JGMV) forming the SCMV subgroup in the genus *Potyvirus* [18], and the newly identified

*The GenBank accession number for the sequence in this paper reported is AY042184.

Table 1. Sources and sequence accession numbers of viruses used in sequence alignments or comparisons in this paper

Virus	Source (country)	Accession number (genomic region)	Reference
JGMV-JG	johnsongrass (Australia)	Z26920 (genomic)	Gough and Shukla [7]
MDMV-A	maize (USA)	U07216 (CP)	direct submission
MDMV-BG	maize (Bulgaria)	AJ001691 (genomic)	Kong and Steinbiss [10]
SCMV-A	sugarcane (USA)	U57354 (CP)	Yang and Mirkov [21]
SCMV-BG	maize (Bulgaria)	AJ006201 (CP)	direct submission
SCMV-BJ	maize (China)	AY042184 (genomic)	This paper
SCMV-BJS	maize (China)	S77088 (CP)	Sai et al. [15]
SCMV-BOR	maize (Germany)	X98167 (CP)	Oertel et al. [12]
SCMV-GD	maize (China)	AJ310105 (genomic)	Chen et al. [1]
SCMV-HN	maize (China)	AF494510 (genomic)	direct submission
SCMV-HZ	maize (China)	AJ297628 (genomic)	Chen et al. [1]
SCMV-HOE	maize (Germany)	X98169 (CP)	Oertel et al. [12]
SCMV-LP	sugarcane (China)	AJ310102 (genomic)	Chen et al. [1]
SCMV-MDB	maize (USA)	D00947 (CP)	Frenkel et al. [5]
SCMV-SC	sugarcane (Australia)	D00948 (CP)	Frenkel et al. [5]
SrMV-YH	sugarcane (China)	AJ310198 (genomic)	Chen et al. [1]
SrMV-SCH	sugarcane (USA)	U07219 (CP)	direct submission
ZeMV	maize (Israel)	AF228693 (CP)	Seifers et al. [16]
PVY-N	potato (France)	X12465 (genomic)	Robaglia et al. [14]

Note: The abbreviations of virus names used in this table stand for *Johnsongrass mosaic virus* (JGMV), *Maize dwarf mosaic virus* (MDMV), *Sugarcane mosaic virus* (SCMV), *Sorghum mosaic virus* (SrMV), Zea mosaic virus (ZeMV), and *Potato virus Y* (PVY), the type member of the genus *Potyvirus*; and the letter(s) following a virus name represents an isolate or a strain of that particular virus

Zea mosaic virus (ZeMV) should also belong to this subgroup [16]. All the references to the various viruses, strains and isolates compared or used in this paper are given in Table 1.

Maize stripe mosaic and sorghum red-stripe diseases have been reported in many regions across China and have caused tremendous economic losses since their first epidemics in late 1960s in North China [1, 4, 15, 17]. An isolate of the causative agent from sorghum and maize plants showing chlorotic stripe, mosaic and dwarfing in Beijing was initially designated as MDMV-B (now referred to as SCMV-MDB) based on its biological properties [4, 17] and most isolates from maize and sorghum in many provinces and regions across China had been identified as the same virus ever since [1, 4, 15, 17, and unpublished results]. The coat protein (CP) genes for about 20 other isolates from maize across China have been cloned [1, 15 and unpublished results] and sequence analysis showed that most of these isolates were very closely related and should be assigned as the prevalent strain. This virus isolate did not infect sugarcane and both its complete genomic sequence and the N-terminal sequence of its CP were significantly

different from those of all known SCMV isolates from sugarcane, nevertheless it is referred to as SCMV-BJ herein since it is most closely related to SCMV among all the potyviruses identified so far.

The isolate SCMV-BJ was collected from diseased maize plants in northern suburbs of Beijing, China (Table 1) and maintained in its perennial host sorghum (*Sorghum bicolor*) by aphid transfer in an insect-proofing greenhouse. For the purification of virus particles and isolation of RNA, the virus isolate was transmitted by aphids (*Myzus persicae*) to 10 to 14 day-old seedlings of maize (*Zea mays*) cv. Mo 107. Virus purification was conducted according to a method described previously with some modifications [4]. Viral RNA was extracted from the purified virus particles by the phenol method, and total RNA was extracted from 0.1 g of an infected maize leaf using Tri-Reagent (Sigma) procedures as recommended by the manufacturer.

The oligonucleotides used for RT-PCR were designed based on conserved regions of the sequences previously determined for other related potyviruses or by previous sequencing results for the Beijing isolate. Both viral RNA extracted from purified virions and total RNA from diseased maize leaves were used as template and oligo (dT) as the primer for reverse transcription. The avian myeloblastosis virus reverse transcriptase and *Taq* and *Pfu* DNA polymerases (Promega) were used for RT-PCR according to the supplier's recommendations. Reverse transcription and PCR were performed in a Hybaid Sprint thermal cycler programmed to give one cycle at 42 °C (60 min); one cycle at 94 °C (3 min), two cycles at 94 °C (1 min), 37 °C (3 min) and 72 °C (1 to 3 min); 35 cycles at 94 °C (30 sec), 64 °C (30 sec) and 72 °C (1 to 3 min); and a final cycle at 72 °C (7 min) for amplifying most parts of the viral genome. The RT-PCR products were analyzed by electrophoresis in a 1% agarose gel. Reaction products of the expected sizes were excised from the gel and eluted using a Geneclean II kit (Bio 101). The PCR product for the CP gene was ligated to the plasmid vector pUC18 after double digestion of both the insert and vector DNA by restriction endonucleases *Sal* I and *Bam*HI, or ligated directly to the vector pGEM-T (Promega), and transformed into *E. coli* DH5*α* cells. Plasmid DNA was isolated from overnight cultures by alkaline lysis. Both strands of at least two independently amplified and cloned PCR products were sequenced using either M13 forward or reverse primers or internal oligonucleotides based on previously determined sequences, with the Thermo Sequenase dye terminator cycle sequencing kit (Amersham). Sequencing reactions were analyzed with an automated ABI Prism 3700 DNA sequencer (PE Applied Biosystems). The 5′-terminal nontranslated region (5′-NTR) and P1 sequences was cloned with the 5′RACE (rapid amplification of cDNA ends) reagent kit (TaKaRa) according to the manufacturer's instructions. The software DNAMAN (Lynnon BioSoft, ver. 4.0) was used to analyse the nucleotide and amino acid sequences.

The viral genome of SCMV-BJ (accession number AY042184) was composed of 9595 nucleotides (nt), excluding the poly (A) tail. The genome of SCMV-BJ has a 148 nt 5′-NTR and a 255 nt 3′-NTR. There were three in-frame AUG codons within the first 500 nts of the long single open reading frame (ORF). Since only the

first AUG situated in the context CGAGAUGGC which conforms roughly with the consensus sequence proposed for plant mRNAs (AACAAUGGC) [11], it was most likely the initiation codon of the polyprotein. The large ORF starts with AUG at nucleotide 149 and ends with a UAG stop codon at nucleotide 9340, and encodes a putative polyprotein of 3063 amino acids (aa) with a calculated Mr of 345,706. The 5′-NTR contained many CAA nucleotide motifs described for the TMV 5′ leader sequence associated with translation enhancement [6], and contained a 12 nt "box a" (14)UCAACACAACAC and 8 nt "box b" (38)CCAAGCAA [18].

Nine putative protease cleavage sites were identified by comparing the putative coding region of SCMV-BJ with the consensus protease recognition motifs in other potyviruses [18] (Table 2). Hence, the polyprotein is likely to be processed into 10 smaller proteins by the 3 viral-encoded proteases P1, HC-Pro and NIa-Pro [3, 18]. This was supported by the presence of conserved motifs which are required for the proteolytic process of potyviral polyprotein in this sequence, such as the serine-type protease domain H_{153}-X_8-D_{162}-X_{31}-G_{194}-X-S_{196}-G_{197} and the proteolytic domain F_{207}IVRGR_{212} in P1, C_{579}-X_{72}-H_{652} in HC-Pro, and H_{2033}-X_{34}-D_{2068}-X_{69}-C_{2138} in NIa-Pro [3]. Among the 9 putative cleavage sites, the HC-Pro/P3 junction (G_{693}-G_{694}) for the Beijing isolate is identical to those of other potyviruses sequenced to date, whereas the NIa/NIb junction (Q_{2229}-C_{2230}) is distinct from those of other potyviruses except for that of the SCMV isolates infecting sugarcane and maize [1, 8]. The conserved sequence motifs K_{287}ITC_{290}P$_{545}$TK_{547} in HC-Pro and D_{2755}AG_{2757} in the CP are believed to be essential in the transmission of the virus by aphids [2, 13] and the motifs C_{527}CCVT_{531} in HC-Pro and R_{2952}-X_{43}-D_{2996} in the CP are presumably involved in long-distance movement of SCMV-BJ as other potyviruses [2, 13]. A nucleotide-binding site (G_{1195}AVGSGKST_{1203}) and the RNA helicase motif D_{1284}-E-X-H_{1287} were found in the CI protein; while a putative RNA-dependent RNA polymerase motif (C_{2475}DADGS$_{2480}$ and S_{2540}-G-X_3-T_{2545}-X_3-N_{2549}-T-X_{30}-G_{2581}-D-D_{2583}) was found in the large nuclear inclusion protein (NIb).

The current potyviral species demarcating criteria as to the genome sequence relatedness are: complete nucleotide sequence identity less than 85%; CP amino acid sequence identity less than about 80%; 3′-NTR sequence identity less than 75% and different polyprotein cleavage sites [19]. The complete sequence of SCMV-BJ and that of MDMV-Bulgarian isolate (MDMV-BG) [10] shares identities of 69% and 74% at the nucleotide and amino acid levels, respectively. The first five of the nine potential protease cleavage sites were the same for SCMV-BJ and MDMV-BG, while the last four were different (Table 2). The numbers of amino acid residues for the putative mature proteins of MDMV-BG and SCMV-BJ were the same except for the CP. The CP of MDMV-BG and MDMV-A both consists of 291 aa, their homology to the Beijing isolate was about 73%. Thus SCMV-BJ and MDMV definitely belong to different virus species according to the current criteria [18, 19]; and the phylogenetic and homology trees indicated that both SCMV-BJ and MDMV-BG are distantly related to monocots-infecting potyvirus JGMV and comparatively closely related to SrMV (Table 3; Figs. 1 and 2).

Table 2. Alignment of putative cleavage sites and the adjacent amino acid sequences in the polyprotein of monocots-infecting sugarcane mosaic virus (SCMV) subgroup of potyviruses and PVY, the type member of the genus *Potyvirus*

Potyvirus	P1/HC	HC/P3	P3/6K1	6K1/CI	CI/6K2	6K2/VPg	VPg/NIa	NIa/NIb	NIb/CP
JGMV-JG	KQICHY/S	KEYIVG/G	TEVEHE/R	QEVKHE/G	QTVIHE/N	TEVEHE/G	PEVEHE/G	ERISNE/S	VDVEHQ/S
MDMV-BG	QEIEHY/A	REYAVG/G	VGVIHE/G	SQVTHQ/S	VTVIHQ/G	TDVKHE/A	VEVEHE/A	FDVTEQ/G	IDVKHQ/A
SCMV-BJ	**MEIEHY/A**	**REYIVG/G**	**TGVIHE/G**	**PPVTQQ/S**	**NTVIHQ/G**	**TEVSHQ/G**	**AGVAHE/S**	**MSVEEQ/C**	**EDVFHQ/S**
SCMV-GD	LDIEHY/A	ibid	ibid	ibid	ibid	TNVAHQ/G	ibid	ibid	ibid
SCMV-LP	FDIEHY/A	ibid	ibid	PPVVQQ/S	ibid	TNVSHQ/G	TGVAHE/S	ibid	ibid
SrMV-YH	NEIDHF/S	REYVVG/G	TGVIHE/A	TQVTHQ/S	TTVIHQ/G	TKVCHQ/G	VEVEHE/S	CEVTEQ/G	IDVFHQ/A
PVY-N	NSMIQF/S	KHYRVG/G	DVRHQ/R	YEVRHQ/S	QFVHHQ/A	ETVSHQ/G	QEVEHE/A	DVVVEQ/A	YEVHHQ/A

Note: SCMV-HZ and -HN share identical putative cleavage sites and the adjacent amino acid sequences in the polyprotein with SCMV-BJ, while SCMV-GD and -LP share identical putative cleavage sites, but the adjacent amino acid sequences are somewhat different from those of SCMV-BJ. The abbreviations of virus names used in this table stand for *Johnsongrass mosaic virus* (JGMV), *Maize dwarf mosaic virus* (MDMV), *Sugarcane mosaic virus* (SCMV), *Sorghum mosaic virus* (SrMV), Zea mosaic virus (ZeMV), and *Potato virus Y* (PVY)

Table 3. Homology matrix of the percent identities of the complete nucleotide sequences (bottom left, in bold face) and amino acids in the polyproteins (top right) of viruses in the sugarcane mosaic virus (SCMV) subgroup of potyviruses

	SrMV-YH	MDMV-BG	SCMV-BJ	SCMV-HZ	SCMV-HN	SCMV-GD	SCMV-LP	JGMV-JG
SrMV-YH		78.5	77.1	76.9	77.2	76.5	76.3	50.4
MDMV-BG	**71.6**		75.3	75.0	75.5	74.6	74.7	49.9
SCMV-BJ	**69.9**	**69.1**		98.7	98.5	91.3	90.6	49.9
SCMV-HZ	**69.9**	**69.3**	**96.9**		98.3	91.3	90.5	50.0
SCMV-HN	**70.2**	**69.1**	**95.1**	**94.2**		91.5	90.7	50.0
SCMV-GD	**69.9**	**69.4**	**81.0**	**80.9**	**81.6**		93.6	49.8
SCMV-LP	**69.4**	**69.0**	**79.8**	**79.7**	**80.0**	**83.0**		49.8
JGMV-JG	**55.6**	**54.9**	**55.5**	**55.5**	**55.5**	**55.3**	**55.1**	

Note: The homology matrix was derived from multiple alignment of the complete genomic nucleotide sequences and that of the deduced amino acid sequences of polyproteins illustrating the percent identities of MDMV-Bulgarian isolate, JGMV-JG, one SrMV isolate infecting sugarcane (SrMV-YH) and five SCMV isolates from China–four isolates infecting maize (SCMV-BJ, -HZ, -HN and -GD) and one isolate infecting sugarcane (SCMV-LP). The 3 isolates of SCMV-BJ, -HN and -HZ share the identities high enough (figures underlined) that they form one virus species. The abbreviations of virus names used in this table stand for *Johnsongrass mosaic virus* (JGMV), *Maize dwarf mosaic virus* (MDMV), *Sugarcane mosaic virus* (SCMV), and *Sorghum mosaic virus* (SrMV)

Three more complete sequences of SCMV infecting maize in China have been determined so far: SCMV-HZ (accession no. AJ297628) from Hangzhou, Zhejiang Province in eastern China, SCMV-GD (accession no. AJ310105) from Guangdong Province, southern China [1] and SCMV-HN (accession no. AF494510) from Henan Province, north-central China [Liu X, Wang X, Zhao Y, and Zhou G, unpublished] (Table 1). The complete nucleotide sequence alignments showed that SCMV-BJ shared identities of 96.9% and 95.1% with SCMV-HZ and SCMV-HN, respectively; but only shared identities of 81.0% with SCMV-GD (Table 3). The CP sequence encodes 313 aa, the same as the previously published one of an isolate from Beijing (accession no. S77088) [15], but 3 aa are different from the latter (not shown). The amino acid at position 5 is an Asp residue in the newly determined CP sequence, hence the DAG motif was present at the N-terminus. The CP sequence of SCMV-BJ and those of all (20) SCMV isolates but one (SCMV-GD) infecting maize from 10 provinces across China share identities of 97–99.5% and 98–100% at the nucleotide and amino acid levels, respectively (not shown) [1, 15 and unpublished data]. Therefore, SCMV-BJ from northern China represented the prevalent strain of SCMV (including SCMV-HZ and SCMV-HN) infecting maize in China, while SCMV-GD may represent another strain (or even virus).

A number of potyviral isolates from maize in several countries have been classified as SCMV due to their 3′-terminal sequence homologies [1, 5, 12] (Table 1). All the CP sequences of SCMV strains/isolates from both sugarcane and maize that were aligned and compared in this paper grouped together with their sequence identities ranging from 87% to 100% (not shown), but those from sugarcane (SCMV-A, -SC and -LP) do not mingle with those from maize

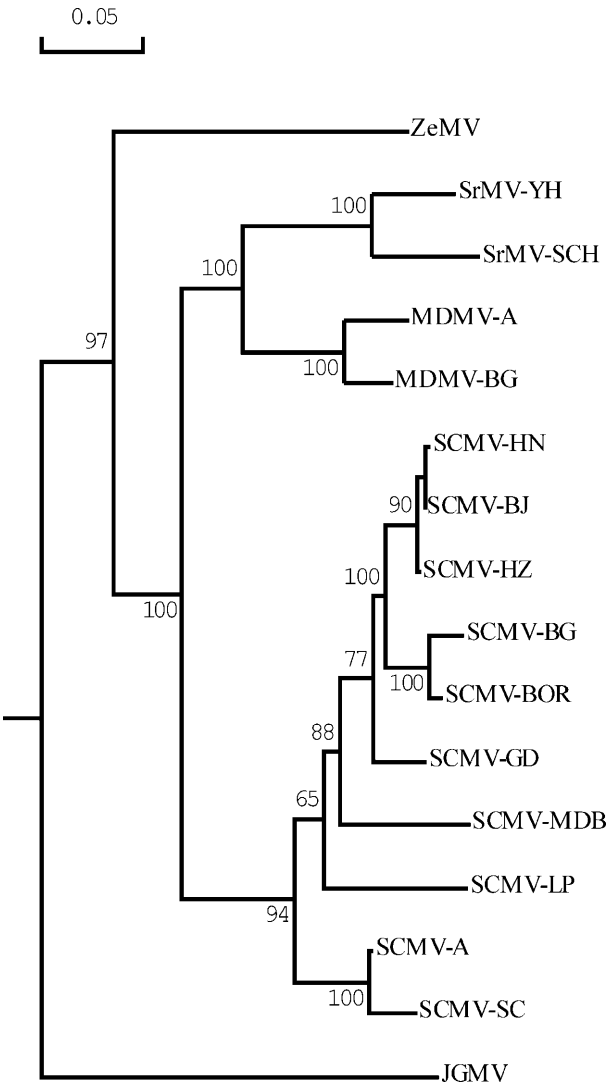

Fig. 1. Phylogenetic tree illustrating the position of the Beijing isolate of SCMV (SCMV-BJ) among the members of the SCMV subgroup of potyviruses. The tree was constructed from multiple sequence alignment of capsid proteins using DNAMAN 4.0. The percentage of bootstrap replicates in each node is noted. The scale bar represents, for the horizontal branch lengths, a genetic distance of 0.05. The abbreviations of virus names used in this figure stand for *Johnsongrass mosaic virus* (JGMV), *Maize dwarf mosaic virus* (MDMV), *Sugarcane mosaic virus* (SCMV), *Sorghum mosaic virus* (SrMV), and Zea mosaic virus (ZeMV)

(Fig. 1), and the N-terminal sequences of the CPs were remarkably variable, which might be partly responsible for the difference in their host ranges [20]. From a GenBank/EMBL search using BLAST, it was revealed that the SCMV-BJ CP sequence was very closely related to those of some European isolates of SCMV from maize [12]. They share the same number of amino acid residues (i.e. 313 aa) and their sequence identity was ca. 95%, therefore they definitely belong to one virus species.

Though most potyviral isolates (include the Beijing one) from maize in China was initially described as MDMV-B (SCMV-MDB), they are significantly different in the N-terminal CP sequences. SCMV-MDB originated in maize and does not infect sugarcane, and the CP sequence is significantly different from any other strains of SCMV. Thus it was suggested that the strain MDB should be separated

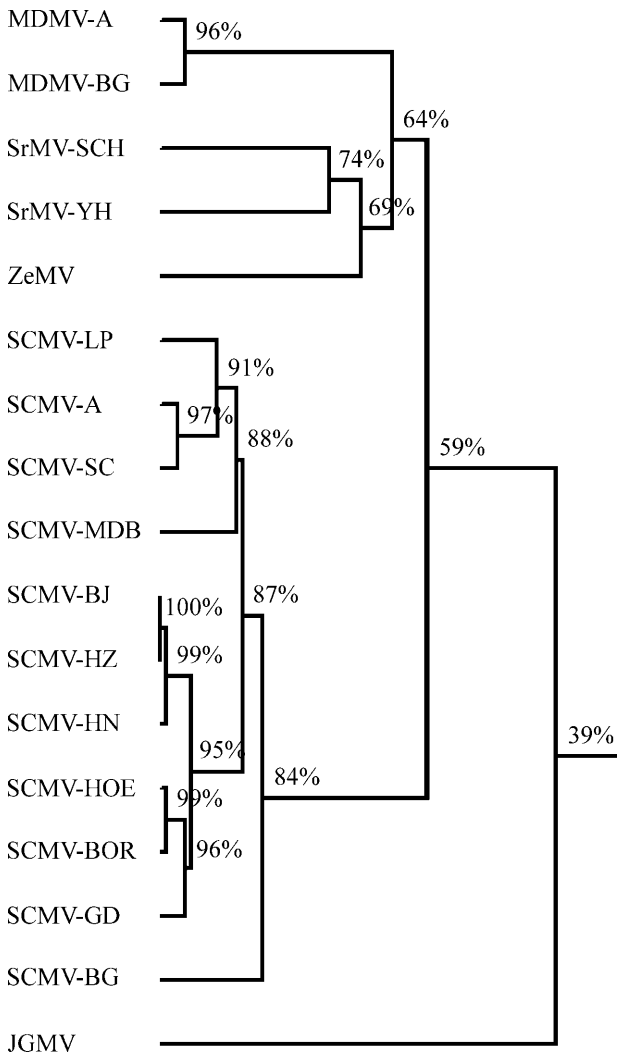

Fig. 2. Homology tree derived from the multiple alignment of the 3′-NTR illustrating the relationships of isolates and strains of ZeMV, MDMV, SCMV, SrMV. Among the five SCMV isolates from China, four isolates were isolated from maize (SCMV-BJ, -HZ, -HN and -GD), and one from sugarcane (SCMV-LP). All the SCMV strains and isolates from sugarcane and maize should belong to one virus species according to the current potyvirus species-demarcating criteria. The abbreviations of virus names used in this figure stand for *Johnsongrass mosaic virus* (JGMV), *Maize dwarf mosaic virus* (MDMV), *Sugarcane mosaic virus* (SCMV), *Sorghum mosaic virus* (SrMV), and Zea mosaic virus (ZeMV)

from SCMV and established as a distinct virus species [9, 21]. Actually, all of the SCMV maize isolates from China were more distantly related to SCMV sugarcane isolates than SCMV-MDB was (Figs. 1 and 2).The homology tree derived from the multiple alignment of the 3′-NTR indicated that the relationships of most isolates and strains of the viruses revealed corresponded well with those from the phylogenetic tree of CP sequences (Figs. 1 and 2). Therefore, all the SCMV

strains and isolates from sugarcane and maize could be classified into one virus species if the results from the complete nucleotide sequences comparisons were not taken into account. Otherwise the Chinese SCMV maize isolates are more qualified to be recognized as a distinct virus than SCMV-MDB.

GenBank/EMBL search using BLAST and phylogenetic analyses were done separately for the nucleotide sequences of each part of the genome (5′- and 3′-UTRs and the coding sequences for the putative ten polypeptides). The sequences of SCMV-BJ and other viruses and isolates grouped consistently in these analyses and there was therefore no evidence that RNA recombination had occurred. The classification of the SCMV subgroup of viruses used to be rather confused and some more complete nucleotide sequences of SCMV from other countries would be of help to clarify the positions of the Chinese maize isolates.

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