

Recommendations for the classification and nomenclature of the DNA- β satellites of begomoviruses

R. W. Briddon · J. K. Brown · E. Moriones ·
J. Stanley · M. Zerbini · X. Zhou · C. M. Fauquet

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Abstract The symptom-modulating, single-stranded DNA satellites (known as DNA- β) associated with begomoviruses (family *Geminiviridae*) have proven to be widespread and important components of a large number of plant diseases across the Old World. Since they were first identified in 2000, over 260 full-length sequences ($\sim 1,360$ nucleotides) have been deposited with databases, and this number increases daily. This has highlighted the need for a standardised, concise and unambiguous nomenclature for these components, as well as a meaningful and robust classification system. Pairwise comparisons of all available

full-length DNA- β sequences indicate that the minimum numbers of pairs occur at a sequence identity of 78%, which we propose as the species demarcation threshold for a distinct DNA- β . This threshold value divides the presently known DNA- β sequences into 51 distinct satellite species. In addition, we propose a naming convention for the satellites that is based upon the system already in use for geminiviruses. This maintains, whenever possible, the association with the helper begomovirus, the disease symptoms and the host plant and provides a logical and consistent system for referring to already recognised and newly identified satellites.

R. W. Briddon
National Institute for Biotechnology and Genetic Engineering,
Jhang Road, P.O. Box 577, Faisalabad, Pakistan

J. K. Brown
Department of Plant Sciences, University of Arizona,
Tucson, AZ 85721, USA

E. Moriones
Estación Experimental “La Mayora”, Consejo Superior de
Investigaciones Científicas, 29750 Algarrobo-Costa, Málaga,
Spain

J. Stanley
John Innes Centre, Colney Lane, NR4 7UH Norwich, UK

M. Zerbini
Departamento de Fitopatologia, Universidade Federal de Viçosa,
Viçosa MG 36570-000, Brazil

X. Zhou
Institute of Biotechnology, Zhejiang University,
310029 Hangzhou, China

C. M. Fauquet (✉)
ILTAB/Danforth Plant Science Center,
975 N. Warson Rd, St Louis, MO 63132, USA
e-mail: iltab@danforthcenter.org

Introduction

Viruses of the family *Geminiviridae* are distinct in having genomes of circular, single-stranded (ss) DNA that are packaged within twinned quasi-isometric (“geminata”) virions. Geminiviruses are divided into four genera based on genome organisation and biological properties, most important of which are the type of insect vector (either whitefly, leafhopper or treehopper) and host range (either mono- or dicotyledonous hosts) [12]. Those having monopartite genomes that are transmitted by leafhopper vectors, primarily to monocotyledonous plants, are included in the genus *Mastrevirus*, of which *Maize streak virus* is the type species. Viruses that have monopartite genomes distinct from those of the mastreviruses and that are transmitted by leafhopper vectors to dicotyledonous plants are placed in the genus *Curtovirus*, with *Beet curly top virus* as the type species. The genus *Topocuvirus*, the most recently established genus, has only one member (also the type species), *Tomato pseudo-curly top virus*, which has a

monopartite genome and is transmitted by a treehopper vector to dicotyledonous plants. The genus *Begomovirus* contains the majority of the identified geminivirus species and these are transmitted exclusively by the whitefly *Bemisia tabaci* (Gennadius) to dicotyledonous plants, with *Bean golden yellow mosaic virus* (originally considered an isolate of *Bean golden mosaic virus*) as the type species. Many begomoviruses have bipartite genomes (known as the DNA-A and DNA-B components), although numerous begomoviruses with monopartite genomes occur in the Old World. Recently, the monopartite begomovirus tomato yellow leaf curl virus has been inadvertently introduced to the New World from the Middle East/Mediterranean region [21, 22], and the New World virus, squash leaf curl virus from the southwestern U.S.A., has been introduced into the Middle East [2, 14], most likely due to the global trade in agricultural products.

A somewhat unexpected development occurred in 1999–2000, when additional components were shown to be associated with some begomoviruses. The first indication of this came with the report by Dry et al. [9] of a ssDNA satellite associated with tomato leaf curl virus (ToLCV) occurring in Australia. Later, this molecule was shown to be a defective (truncated) version of a much larger group of subviral components associated with begomoviruses.

A number of the apparently monopartite begomoviruses were shown to be incapable of inducing *bona fide* disease symptoms when introduced as infectious clones to the host species from which they were isolated. These included *Ageratum yellow vein virus* (AYVV) [31] and cotton leaf curl Multan virus (CLCuMV). Clones of these viruses were either not infectious or poorly infectious to the hosts in which they occur naturally; *Ageratum conyzoides* and *Gossypium hirsutum* (cotton), respectively [4, 26]. Upon closer inspection, plants naturally infected with AYVV and CLCuMV were shown to include additional ssDNA components. The first, now known as DNA-1, was interesting because it has similarity to, and likely evolved from, components of another group of ssDNA viruses; the nanoviruses [18, 25]. DNA-1, however, was shown to play no part in symptom induction or infectivity of its helper virus, and its function remains unclear.

The second group of components, collectively known as DNA- β , were shown to be approximately half the size of a begomovirus component ($\sim 1,360$ nucleotides) and required for efficient infection of some hosts [5, 26]. Since they were first recognized, DNA- β components have been shown to be associated with an increasing number of diseases caused by begomoviruses, including many of the most significant, economically damaging diseases occurring in the Old World. Probably the most important of these is cotton leaf curl disease (CLCuD). CLCuD was epidemic during the 1990s across Pakistan and continues to

be so in northern India. During 2002, a second epidemic of a resistance-breaking strain of the virus initiated in central Pakistan and is threatening major yield losses for future cotton harvests [17]. The disease is caused by a complex consisting of multiple begomoviruses and a specific DNA- β component. Members of at least seven distinct begomovirus species, but only one type of DNA- β component, were shown to have caused the disease epidemic which occurred during the 1990s [19]. DNA- β has also been associated with the earliest written description of a plant virus disease [29].

Satellites are defined as subviral agents composed of nucleic acid that depend on co-infection with a helper virus for their productive multiplication. Satellite nucleic acids have substantially distinct nucleotide sequences from those of the genomes of their helper viruses. RNAs satellites that are associated with many RNA-containing viruses vary greatly in size, from less than 200 nucleotides to greater than 1,500 nucleotides. Although the larger satellites may encode functional open reading frames, the smaller satellites do not but are highly structured. Despite their small size and the apparent absence of potential gene products, satellites may have a dramatic effect on the symptoms induced by their helper viruses [7, 30]. These effects range from amelioration to severe exacerbation of symptoms, which vary with the helper virus, host plant and satellite combination.

At this time, plant virus-associated satellites are not classified by the International Committee on Taxonomy of Viruses (ICTV). They are grouped under the term “subviral agents” and divided into satellite viruses (those satellites that encode their own coat protein) and satellite nucleic acids, and subsequently according to the type of nucleic acid (either DNA or RNA) [12].

DNA- β satellites associated with begomoviruses

In the short time since they were first identified, over 260 full-length DNA- β sequences have been deposited in the databases. This number is in no small part due to the relative ease, with modern PCR-based cloning and automated sequencing procedures, with which these components can be isolated and characterised. However, it is also an indication of the importance and widespread nature of these components, at least in the Old World. Although we far from fully understand the functions that they provide to their helper begomoviruses, it is clear that a large number of viruses are associated with DNA- β components and that, at least in Asia, the DNA- β -requiring begomoviruses likely outnumber the bipartite and truly monopartite begomoviruses. This explosion in available DNA- β sequences has highlighted the need for a clear set of guidelines for naming

and classifying newly characterised DNA- β components using a standardised approach.

The DNA- β satellites are typically half the length of their helper begomoviruses ($\sim 1,360$ nucleotides) and share no significant sequence homology with their helper viruses other than the presence of a potential stem-loop structure containing the ubiquitous nonanucleotide sequence TAATATTAC that marks, for geminiviruses, the origin of virion-strand DNA replication. They have a highly conserved structure consisting of a sequence of approx. 100 nucleotides conserved between all DNA- β s [known as the satellite conserved region (SCR)], a region of sequence rich in adenine (A-rich) and encode a single gene, the product of which known as β C1 [20]. β C1 is a pathogenicity determinant, a suppressor of post-transcriptional gene silencing, up-regulates viral DNA levels *in planta*, binds DNA and may be involved in virus movement [5, 8, 23, 24, 26, 32]. DNA- β satellites depend upon their helper viruses for replication, movement in plants and transmission between plants, presumably by *trans*-encapsulation in the helper virus' coat protein. DNA- β components have been cloned from a diverse range of hosts, and DNA sequence comparison shows them to be highly diverse [3, 6, 32].

The nature of begomoviruses associated with DNA- β

AYVV was the first begomovirus shown to be associated with a DNA- β component [26]. Its peculiar behaviour, in comparison to begomoviruses identified prior to this, in being poorly infectious to the host from which it was isolated (*A. conyzoides*) and inducing atypical symptoms, initiated the search for additional components. This is a common property of the majority of begomoviruses which associate with a DNA- β component, as is the observation that the virus usually does not naturally infect plants in the absence of the satellite. This includes viruses such as those associated with cotton leaf curl disease [19] and bhendi yellow vein mosaic disease [15].

More recently, some begomoviruses have been identified which have a facultative association with their DNA- β component. A recent study [16] has shown that some isolates of *Tobacco curly shoot virus* are associated with a satellite, whereas others are not. Viruses cloned from these isolates were shown to behave similarly, each being able to associate with DNA- β (yielding a more severe infection but not elevated viral DNA levels) as well as inducing asymptomatic infection in the absence of the satellite. It is possible that tobacco curly shoot virus (TbCSV) represents an evolutionary intermediate, although it is unclear whether it is evolving to gain or lose the requirement for a DNA- β component.

Phylogenetic comparisons show that begomoviruses associated with a DNA- β component are not monophyletic, thus are not likely to have a single recent common progenitor. This suggests that begomoviruses not associated with a DNA- β component (either monopartite or bipartite) may subsequently become associated with one or that begomoviruses may lose their DNA- β component, becoming monopartite or bipartite if associated with a DNA-B component. There is evidence to support all of these possibilities. The absence of both DNA- β and DNA-1 components in the New World is strong circumstantial evidence supporting the evolution of the DNA- β complex after the divergence of Old and New World begomoviruses [20]. The half unit-length DNA- β component associated with ToLCV in Australia is evidence for a begomovirus which has dispensed with the need for a symptom-modulating satellite [9], although it retains the ability to interact with an intact DNA- β component [1, 23]. Sri Lankan cassava mosaic virus may have been a satellite-requiring begomovirus which has exchanged the satellite for a DNA-B component, most likely captured from Indian cassava mosaic virus [28], but nevertheless is able to productively interact with DNA- β . The range of begomoviruses (seven species identified to date) associated with CLCuD on the Indian subcontinent [19], all associated with a single DNA- β component, indicates that the satellites can be highly promiscuous.

Proposed nomenclature for DNA- β satellites

Virus nomenclature is important for researchers since it provides labels with which to identify viruses in a concise and unambiguous manner. To be practical, however, any system of nomenclature requires uniformity based on a simple set of rules that everybody can apply in a similar manner. The explosion in the number of available DNA- β sequences during the last few years has highlighted the need for such a standardised nomenclature for begomovirus satellites. For geminiviruses, the ICTV has accepted that English vernacular names will be used to describe begomovirus species with, if necessary, a geographical descriptor. Thus, species names take the form “host-disease symptom-[origin]-virus”, such as *Cotton leaf curl Multan virus*, although a few historical names, such as *African cassava mosaic virus*, are maintained [11]. The use of such descriptive names for the DNA- β satellites is desirable, as is both the maintenance of the association with the virus and the disease symptoms, since most DNA- β satellites play a major role in symptom determination. It is thus a simple process to use the virus name to derive the satellite name. For example, the DNA- β component associated with Cotton leaf curl Multan virus would become

Cotton leaf curl Multan beta (CLCuMB) (the ICTV requirement that only ASCII characters be used in virus names entails the use of the term “beta” rather than the Greek character “ β ”). Further details, including strain and isolate descriptors, are appended with geminivirus species names [13] which can similarly be applied to DNA- β . Thus, the DNA- β component associated with the first description of CLCuMV infectivity becomes *Cotton leaf curl Multan beta*-[Pakistan:Faisalabad1:1996], which is abbreviated to CLCuMB-[PK:Fai1:96]. However, it should be noted that, just because a virus belongs to a particular species, it does not necessarily follow that the associated DNA- β component will belong solely to that species or that members of that species will necessarily be associated only with the same DNA- β component. Thus, although the isolate information for a DNA- β component should mirror that of the helper virus, the strain information may not (different strains/isolate of a single virus species being able to interact with different strains/isolates of a DNA- β).

Clearly the diversity of the satellites and the complexity of their interactions means that the simple association between disease symptoms, host plant, virus name and corresponding DNA- β names will not necessarily be maintained in all cases. As with the naming of new begomovirus species, the naming of new satellites should follow the “grandfather principle”, with the name given at first description being adopted.

Proposed taxonomy for DNA- β satellites

Sequence data are now the major criterion for assigning geminiviruses to species, although biological characteristics are used in some cases to distinguish strains. The threshold cut-off value for distinguishing species from strains (89% for begomoviruses) was determined by Pairwise sequence comparisons [10]. This criterion for species demarcation is proving very robust, although some begomovirus species are beginning to overlap as more sequences become available, necessitating merging/synonymization of these taxa.

A study of 261 full-length DNA- β sequences available in the databases as of August 2007 (Table 1) was conducted. Nine recombinant DNA- β components, in which the SCR has been replaced by the origin of replication of the helper begomovirus, were not included in the analysis; plants infected with such recombinant components have been shown to accumulate reduced viral DNA levels, and the recombinants will probably not be maintained in nature, being at a selective disadvantage with respect to intact DNA- β [27]. An exhaustive pairwise comparison of the DNA- β sequences showed a multimodal distribution (Fig. 1) consisting of three major peaks between 25 and

78% identity made up of recombinant DNA- β components, a major peak between 33 and 61%, and a succession of smaller peaks above this.

Of these DNA- β components, 44 are associated with begomoviruses for which full-length DNA sequences are available (Table 2). Separate pairwise nucleotide sequence comparison studies were conducted for each. The correlation between these two studies is highly significant ($R^2 = 0.72$), indicating a direct evolutionary relationship (co-evolution) between a helper begomovirus and its associated DNA- β component (Fig. 2). Since *trans*-replication of these satellites is not confined to a single virus and they can infect diverse hosts, it might be anticipated that frequent exchanges between distinct helper begomoviruses should have resulted in their independent evolution from the latter, in which case such a strong correlation would not be expected. However, DNA- β satellites depend on the begomovirus for their replication, movement in plants and insect transmission between plants. In turn, the helper begomovirus depends on DNA- β for efficient infection of hosts, possibly by β C1-mediated post-transcriptional gene silencing suppression of a host defense response [8]. These findings suggest that the association between the begomovirus and its cognate DNA- β satellite is subject to subtle interactions that confer a selective advantage, and that component exchange is (or at least has been) relatively infrequent. Consequently, evolutionary pressures have acted on the disease complex as a whole rather than on each component of the complex independently. This means that, for taxonomic purposes, we can deal with the complex as whole and derive a “species” demarcation value for DNA- β from that determined for the helper begomoviruses. The demarcation threshold for distinguishing begomovirus species from isolates currently is set at 89% nucleotide sequence identity for full-length genomic (DNA-A component) sequences [12]. This corresponds to 77% nucleotide sequence identity for DNA- β components (Fig. 2). However, if the available 261 full-length DNA- β sequences are considered, the percentage identity having the minimum number of pairs is 78% (Fig. 1). There is a very high correlation between the distribution of full-length DNA- β component sequences and the nucleotide sequences of the β C1 gene (91%). However, the use of full-length sequences for species demarcation is more meaningful, since it corresponds to a biological entity and eliminates recombinant DNA- β components containing helper virus sequences. Consequently this proposal favours the 78% demarcation threshold provided by analysis of full-length sequences, in line with the recommendations used for geminivirus species demarcation, and avoids the complexity of variation in the coding capacity (length) of β C1, which could create confusion.

Table 1 List of DNA- β components for which full-length sequences are available in the databases grouped according to species using the criteria detailed in the text

<i>Species</i>	Betasatellite name	Accession #	Beta abbreviation
<i>Ageratum yellow leaf curl betasatellite</i>	Ageratum yellow leaf curl betasatellite [Pakistan: Bahawalpur:1997]	AJ316031	AYLCB-[PK:BAH:97]
<i>Ageratum yellow leaf curl betasatellite</i>	Ageratum yellow leaf curl betasatellite [Pakistan: Faisalabad 1:1994]	AJ316028	AYLCB-[PK:Fai1:94]
<i>Ageratum yellow leaf curl betasatellite</i>	Ageratum yellow leaf curl betasatellite [Pakistan: Faisalabad 2:1994]	AJ316041	AYLCB-[PK:Fai2:94]
<i>Ageratum yellow leaf curl betasatellite</i>	Ageratum yellow leaf curl betasatellite [Pakistan: Faisalabad 3:1994]	AJ316027	AYLCB-[PK:Fai3:94]
<i>Ageratum yellow leaf curl betasatellite</i>	Ageratum yellow leaf curl betasatellite [Pakistan: Faisalabad 4:2000]	AJ316026	AYLCB-[PK:Fai4:00]
<i>Ageratum yellow leaf curl betasatellite</i>	Ageratum yellow leaf curl betasatellite [Pakistan: Lahore:2006]	AM698010	AYLCB-[PK:Fai4:00]
<i>Ageratum yellow vein betasatellite</i>	Ageratum yellow vein betasatellite [China: Fuzhou: Tomato:2006]	AM691551	AYVB-[CN:Fuz:Tom:06]
<i>Ageratum yellow vein betasatellite</i>	Ageratum yellow vein betasatellite [China: Fuzhou 2: Tomato:2006]	EF527824	AYVB-[CN:Fuz2:Tom:06]
<i>Ageratum yellow vein betasatellite</i>	Ageratum yellow vein betasatellite [China: Guangxi 66:2003]	AJ971257	AYVB-[CN:Gx66:03]
<i>Ageratum yellow vein betasatellite</i>	Ageratum yellow vein betasatellite [China: Guangxi 69:2003]	AJ971258	AYVB-[CN:Gx69:03]
<i>Ageratum yellow vein betasatellite</i>	Ageratum yellow vein betasatellite [China: Guangxi 86:2004]	AJ971259	AYVB-[CN:Gx86:04]
<i>Ageratum yellow vein betasatellite</i>	Ageratum yellow vein betasatellite [China: Guangxi 95:2004]	AJ971260	AYVB-[CN:Gx95:04]
<i>Ageratum yellow vein betasatellite</i>	Ageratum yellow vein betasatellite [China: Guangxi 96:2004]	AJ971261	AYVB-[CN:Gx96:04]
<i>Ageratum yellow vein betasatellite</i>	Ageratum yellow vein betasatellite [China: Guangxi 98:2004]	AJ971262	AYVB-[CN:Gx98:04]
<i>Ageratum yellow vein betasatellite</i>	Ageratum yellow vein betasatellite [China: Hainan 12:2004]	AM048836	AYVB-[CN:Hn12:04]
<i>Ageratum yellow vein betasatellite</i>	Ageratum yellow vein betasatellite [China: Hainan 2:2001]	AM048834	AYVB-[CN:Hn2:01]
<i>Ageratum yellow vein betasatellite</i>	Ageratum yellow vein betasatellite [China: Hainan 9:2004]	AM048835	AYVB-[CN:Hn9:04]
<i>Ageratum yellow vein betasatellite</i>	Ageratum yellow vein betasatellite [Malaysia: Klang:2002]	AJ542497	AYVB-[MY:Kla:02]
<i>Ageratum yellow vein betasatellite</i>	Ageratum yellow vein betasatellite [Singapore::1992]	AJ252072	AYVB-[SG::92]
<i>Ageratum yellow vein betasatellite</i>	Ageratum yellow vein betasatellite [Taiwan: Chang-Hua:2002]	AJ542495	AYVB-[TW:CHu:02]
<i>Ageratum yellow vein betasatellite</i>	Ageratum yellow vein betasatellite [Vietnam: Hatay: Tobacco:05]	DQ641709	AYVB-[VN:Hat:Tb:05]
<i>Ageratum yellow vein Sri Lanka betasatellite</i>	Ageratum yellow vein Sri Lanka betasatellite [India: Madurai:2003]	AJ557441	AYVSLB-[IN:Mad:03]
<i>Ageratum yellow vein Sri Lanka betasatellite</i>	Ageratum yellow vein Sri Lanka betasatellite [Sri Lanka: Ageratum:2003]	AJ542498	AYVSLB-[SL:Ag:03]
<i>Ageratum yellow vein Sri Lanka betasatellite</i>	Ageratum yellow vein Sri Lanka betasatellite [Sri Lanka: Tomato:2003]	AJ542493	AYVSLB-[SL:To:03]
<i>Alternanthera yellow vein betasatellite</i>	Alternanthera yellow vein betasatellite [Vietnam: Hue:2005]	DQ641716	AIYVB-[VN:Hue:05]
<i>Bean leaf curl China betasatellite</i>	Bean leaf curl China betasatellite [China: Yuanmou:2004]	DQ256459	BLCCNB-[CN:Yua:04]

Table 1 continued

<i>Species</i>	Betasatellite name	Accession #	Beta abbreviation
<i>Bean leaf curl China betasatellite</i>	Bean leaf curl China betasatellite [China:Yunnan 295:2004]	AM260730	BLCCNB-[CN:Yn295:02]
<i>Bean leaf curl China betasatellite</i>	Bean leaf curl China betasatellite [China:Yunnan 296:2004]	AM260731	BLCCNB-[CN:Yn296:02]
<i>Bean leaf curl China betasatellite</i>	Bean leaf curl China betasatellite [China:Yunnan 297:2004]	AM260732	BLCCNB-[CN:Yn297:02]
<i>Bean leaf curl China betasatellite</i>	Bean leaf curl China betasatellite [China:Yunnan 298:2004]	AM260733	BLCCNB-[CN:Yn298:02]
<i>Bean leaf curl China betasatellite</i>	Bean leaf curl China betasatellite [China:Yunnan 72:2006]	EF011560	BLCCNB-[CN:Yn72:06]
<i>Bhendi yellow vein betasatellite</i>	Bhendi yellow vein betasatellite [India:Barrackpore:2006]	EF417919	BYVB-[IN:Bar:06]
<i>Bhendi yellow vein betasatellite</i>	Bhendi yellow vein betasatellite [India:Muthuppatti:2000]	AJ308425	BYVB-[IN:Mut:00]
<i>Bhendi yellow vein betasatellite</i>	Bhendi yellow vein betasatellite [Pakistan:Bahawalpur:1997]	AJ316030	BYVB-[PK:Bah:97]
<i>Chilli leaf curl betasatellite</i>	Chilli leaf curl betasatellite [Pakistan:Multan55:2004]	AM279671	ChLCB-[PK:Mu55:04]
<i>Chilli leaf curl betasatellite</i>	Chilli leaf curl betasatellite [Pakistan:Gujranwala23:2004]	AM279664	ChLCB-[PK:Guj23:04]
<i>Chilli leaf curl betasatellite</i>	Chilli leaf curl betasatellite [Pakistan:Faisalabad62:2004]	AM279672	ChLCB-[PK:Fai62:04]
<i>Chilli leaf curl betasatellite</i>	Chilli leaf curl betasatellite [Pakistan:Lahore2:2004]	AM258978	ChLCB-[PK:LAH2:04]
<i>Chilli leaf curl betasatellite</i>	Chilli leaf curl betasatellite [Pakistan:Lahore1:2004]	AM260466	ChLCB-[PK:LAH1:04]
<i>Chilli leaf curl betasatellite</i>	Chilli leaf curl betasatellite [Pakistan:Sialkot21:2004]	AM279663	ChLCB-[PK:Sia21:04]
<i>Chilli leaf curl betasatellite</i>	Chilli leaf curl betasatellite [Pakistan:Multan52:2004]	AM279670	ChLCB-[PK:Mu52:04]
<i>Chilli leaf curl betasatellite</i>	Chilli leaf curl betasatellite [Pakistan:Nowshera44:2004]	AM279668	ChLCB-[PK:Now44:04]
<i>Chilli leaf curl betasatellite</i>	Chilli leaf curl betasatellite [Pakistan:Mian Channu:1997]	AJ316032	ChLCB-[PK:MC:97]
<i>Cotton leaf curl Gezira betasatellite</i>	Cotton leaf curl Gezira betasatellite []	AY044143	CLCuGB-[]
<i>Cotton leaf curl Gezira betasatellite</i>	Cotton leaf curl Gezira betasatellite [Egypt:Fayourn:1996]	AJ316039	CLCuGB-[EG:Fay:96]
<i>Cotton leaf curl Gezira betasatellite</i>	Cotton leaf curl Gezira betasatellite [Egypt:Okra 10:2000]	AF397215	CLCuGB-[EG:Ok10:00]
<i>Cotton leaf curl Gezira betasatellite</i>	Cotton leaf curl Gezira betasatellite [Egypt:Okra 3:2000]	AF397217	CLCuGB-[EG:Ok3:00]
<i>Cotton leaf curl Gezira betasatellite</i>	Cotton leaf curl Gezira betasatellite [Mali:Tomato:2005]	DQ136001	CLCuGB-[ML:To:05]
<i>Cotton leaf curl Gezira betasatellite</i>	Cotton leaf curl Gezira betasatellite [Mali:Bamako01:Tomato:2006]	EU241121	CLCuGB-[ML:Bam01:To:06]
<i>Cotton leaf curl Gezira betasatellite</i>	Cotton leaf curl Gezira betasatellite [Mali:Bamako02:Tomato:2006]	EU241122	CLCuGB-[ML:Bam02:To:06]
<i>Cotton leaf curl Gezira betasatellite</i>	Cotton leaf curl Gezira betasatellite [Sudan:??:]	AY044140	CLCuGB-[SD:??]
<i>Cotton leaf curl Gezira betasatellite</i>	Cotton leaf curl Gezira betasatellite [Sudan:Cotton 46:1996]	AY669328	CLCuGB-[SD:Cot46:96]
<i>Cotton leaf curl Gezira betasatellite</i>	Cotton leaf curl Gezira betasatellite [Sudan:Cotton 55:1996]	AY077797	CLCuGB-[SD:Cot55:96]

Table 1 continued

<i>Species</i>	Betasatellite name	Accession #	Beta abbreviation
<i>Cotton leaf curl Gezira betasatellite</i>	Cotton leaf curl Gezira betasatellite [Sudan:Okra 43:1996]	AY044141	CLCuGB-[SD:Ok43:96]
<i>Cotton leaf curl Gezira betasatellite</i>	Cotton leaf curl Gezira betasatellite [Sudan:Okra 44-1:1996]	AY077799	CLCuGB-[SD:Ok44-1:96]
<i>Cotton leaf curl Gezira betasatellite</i>	Cotton leaf curl Gezira betasatellite [Sudan:Okra 44-2:96]	AY044142	CLCuGB-[SD:Ok44-2:96]
<i>Cotton leaf curl Gezira betasatellite</i>	Cotton leaf curl Gezira betasatellite [Sudan:Sida 32:1996]	AY077798	CLCuGB-[SD:Si32:96]
<i>Cotton leaf curl Multan betasatellite</i>	Cotton leaf curl Multan betasatellite [China:Guandong 6:2006]	EF465536	CLCuMB-[CN:Gd6:06]
<i>Cotton leaf curl Multan betasatellite</i>	Cotton leaf curl Multan betasatellite [India:Basirhat:Hibiscus:2005]	DQ298137	CLCuMB-[IN:Bas:Hib:05]
<i>Cotton leaf curl Multan betasatellite</i>	Cotton leaf curl Multan betasatellite [India:Bhatinda:2005]	DQ191161	CLCuMB-[IN:Bha:05]
<i>Cotton leaf curl Multan betasatellite</i>	Cotton leaf curl Multan betasatellite [India:Dabwali 1:1995]	AJ316037	CLCuMB-[IN:Dab1:95]
<i>Cotton leaf curl Multan betasatellite</i>	Cotton leaf curl Multan betasatellite [India:Dabwali 2:1995]	AJ316038	CLCuMB-[IN:Dab2:95]
<i>Cotton leaf curl Multan betasatellite</i>	Cotton leaf curl Multan betasatellite [India:Dabwali 3:1995]	AJ291601	CLCuMB-[IN:Dab3:95]
<i>Cotton leaf curl Multan betasatellite</i>	Cotton leaf curl Multan betasatellite [India:Hisar:2002]r	AY763123	CLCuMB-[IN:His:02]r
<i>Cotton leaf curl Multan betasatellite</i>	Cotton leaf curl Multan betasatellite [India:Hisar2:2002]	DQ364230	CLCuMB-[IN:His2:02]
<i>Cotton leaf curl Multan betasatellite</i>	Cotton leaf curl Multan betasatellite [India:Hisar3:2004]	AY795608	CLCuMB-[IN:His3:04]
<i>Cotton leaf curl Multan betasatellite</i>	Cotton leaf curl Multan betasatellite [India:New Delhi 1:2003]	AY438562	CLCuMB-[IN:ND1:03]
<i>Cotton leaf curl Multan betasatellite</i>	Cotton leaf curl Multan betasatellite [India:New Delhi 2:2004]	AY795604	CLCuMB-[IN:ND2:04]
<i>Cotton leaf curl Multan betasatellite</i>	Cotton leaf curl Multan betasatellite [India:Sirsa:2004]	AY744380	CLCuMB-[IN:Sir:04]
<i>Cotton leaf curl Multan betasatellite</i>	Cotton leaf curl Multan betasatellite [India:Sri Ganganagar:2002]	AY083590	CLCuMB-[IN:Sri:02]
<i>Cotton leaf curl Multan betasatellite</i>	Cotton leaf curl Multan betasatellite [Pakistan:Burewala 1:2002]	AM084379	CLCuMB-[PK:Bur1:02]
<i>Cotton leaf curl Multan betasatellite</i>	Cotton leaf curl Multan betasatellite [Pakistan:Burewala 2:2002]	AM084380	CLCuMB-[PK:Bur2:02]
<i>Cotton leaf curl Multan betasatellite</i>	Cotton leaf curl Multan betasatellite [Pakistan:Faisalabad 1:1996]	AJ298903	CLCuMB-[PK:Fai1:96]
<i>Cotton leaf curl Multan betasatellite</i>	Cotton leaf curl Multan betasatellite [Pakistan:Faisalabad 2:1996]	AJ299443	CLCuMB-[PK:Fai2:96]
<i>Cotton leaf curl Multan betasatellite</i>	Cotton leaf curl Multan betasatellite [Pakistan:Faisalabad 3:1996]	AJ292769	CLCuMB-[PK:Fai3:96]
<i>Cotton leaf curl Multan betasatellite</i>	Cotton leaf curl Multan betasatellite [Pakistan:Faisalabad:Hibiscus:1996]	AJ297908	CLCuMB-[PK:Fai:Hib:96]
<i>Cotton leaf curl Multan betasatellite</i>	Cotton leaf curl Multan betasatellite [Pakistan:Okara:Tomato:1999]	AJ316035	CLCuMB-[PK:Oka:To:99]
<i>Cotton leaf curl Multan betasatellite</i>	Cotton leaf curl Multan betasatellite [India:Bongaon:Kenaf:2006]	EF614158	CLCuMB-[IN:Har05:Ken:06]
<i>Cotton leaf curl Multan betasatellite</i>	Cotton leaf curl Multan betasatellite [India:Haringhata 19:Kenaf:2006]	EF614159	CLCuMB-[IN:Har05:Ken:06]
<i>Cotton leaf curl Multan betasatellite</i>	Cotton leaf curl Multan betasatellite [India:Haringhata 05:Kenaf:2006]	EF620565	CLCuMB-[IN:Har05:Ken:06]

Table 1 continued

<i>Species</i>	Betasatellite name	Accession #	Beta abbreviation
<i>Cotton leaf curl Multan betasatellite</i>	Cotton leaf curl Multan betasatellite [India:Barrackpore 01:Kenaf:2006]	EF620564	CLCuMB-[IN:Nar01:Ken:06]
<i>Croton yellow vein mosaic betasatellite</i>	Croton yellow vein mosaic betasatellite [Pakistan:Punjab:2006]	AM410551	CroYVMB-[PK:Pun:06]
<i>Croton yellow vein mosaic betasatellite</i>	Croton yellow vein mosaic betasatellite [India:Barrackpore:2006]	EF597245	CroYVMB-[IN:Bar:06]
<i>Erectites yellow mosaic betasatellite</i>	Erectites yellow mosaic betasatellite [Vietnam:Hoabinh:2005]	DQ641713	ErYMB-[VN:Hoa:05]
<i>Eupatorium yellow vein betasatellite</i>	Eupatorium yellow vein betasatellite [Japan:MNS2:2000]	AJ438938	EpYVB-[JR:MNS2:00]
<i>Eupatorium yellow vein betasatellite</i>	Eupatorium yellow vein betasatellite [Japan:SOJ1:2000]	AJ438939	EpYVB-[JR:SOJ1:00]
<i>Honeysuckle yellow vein betasatellite</i>	Honeysuckle yellow vein betasatellite [Japan:Fukua:2005]	AB236322	HYVB-[JR:Fuk:05]
<i>Honeysuckle yellow vein betasatellite</i>	Honeysuckle yellow vein betasatellite [Japan:Kumamoto:2005]	AB236327	HYVB-[JR:Kum:05]
<i>Honeysuckle yellow vein betasatellite</i>	Honeysuckle yellow vein betasatellite [United Kingdom:Norwich 1:1999]	AJ316040	HYVB-[UK:Nor1:99]
<i>Honeysuckle yellow vein betasatellite</i>	Honeysuckle yellow vein betasatellite [United Kingdom:Norwich 2:1999]	AJ543430	HYVB-[UK:Nor2:99]
<i>Honeysuckle yellow vein Kobe betasatellite</i>	Honeysuckle yellow vein Kobe betasatellite [Japan:Hyogo:2004]	AB182263	HYVKB-[JR:Hy:04]
<i>Honeysuckle yellow vein Japan betasatellite</i>	Honeysuckle yellow vein Japan betasatellite [Japan:Miyizaki:2005]	AB236324	HYVJB-[JR:Miy:05]
<i>Honeysuckle yellow vein mosaic betasatellite</i>	Honeysuckle yellow vein mosaic betasatellite [Japan:Ibaraki:2006]	AB287442	HYVMB-[JR:Iba:06]
<i>Honeysuckle yellow vein Nara betasatellite</i>	Honeysuckle yellow vein Nara betasatellite [Japan:Nara:2006]	AB287443	HYVNB-[JR:Nar:06]
<i>Kenaf leaf curl betasatellite</i>	Kenaf leaf curl betasatellite [India:Bangalore:Barbadense:2004]	AY705381	KLCuB-[IN:Ban:Bar:04]
<i>Kenaf leaf curl betasatellite</i>	Kenaf leaf curl betasatellite [India:Bhraich 03:2006]	EF620566	KLCuB-[IN:Bah03:06]
<i>Ludwigia leaf distortion betasatellite</i>	Ludwigia leaf distortion betasatellite [India:Luffa:2004]	AY728262	LuLDB-[IN:Lu:04]
<i>Ludwigia leaf distortion betasatellite</i>	Ludwigia leaf distortion betasatellite [India:Luffa2:2004]	DQ020491	LuLDB-[IN:Lu2:04]
<i>Ludwigia leaf distortion betasatellite</i>	Ludwigia leaf distortion betasatellite [India:Bitter Gourd:2004]	AY817151	LuLDB-[IN:BG:04]
<i>Ludwigia leaf distortion betasatellite</i>	Ludwigia leaf distortion betasatellite [India:Bhangha:2006]	EF614161	LuLDB-[IN:Bha:06]
<i>Ludwigia leaf distortion betasatellite</i>	Ludwigia leaf distortion betasatellite [India:Kaisarganj:2006]	EF614162	LuLDB-[IN:Kai:06]
<i>Mesta yellow mosaic betasatellite</i>	Mesta yellow mosaic betasatellite [India:Bhraich:2006]	EF614160	MeYMB-[IN:Bah:06]
<i>Lindernia anagallis yellow vein betasatellite</i>	Lindernia anagallis yellow vein betasatellite [Vietnam:Hanoi:2005]	DQ641715	LaYVB-[VN:Hoa:05]
<i>Ludwigia yellow vein betasatellite</i>	Ludwigia yellow vein betasatellite [China:Guangxi 37:2004]	AJ965541	LuYVB-[CN:Gx37:04]
<i>Malvastrum leaf curl betasatellite</i>	Malvastrum leaf curl betasatellite [China:Guangxi 87:2004]	AM072289	MaLCuB-[CN:Gx87:04]
<i>Malvastrum leaf curl betasatellite</i>	Malvastrum leaf curl betasatellite [China:Guangxi 87:]def	AJ971264	MaLCuB-[CN:Gx87:04]def
<i>Malvastrum yellow vein betasatellite</i>	Malvastrum yellow vein betasatellite [China:Yunnan 189:2003]	AJ971459	MaYVB-[CN:Yn189:03]

Table 1 continued

<i>Species</i>	Betasatellite name	Accession #	Beta abbreviation
<i>Malvastrum yellow vein betasatellite</i>	Malvastrum yellow vein betasatellite [China:Yunnan 190:2003]	AJ971460	MaYVB-[CN:Yn190:03]
<i>Malvastrum yellow vein betasatellite</i>	Malvastrum yellow vein betasatellite [China:Yunnan 193:2003]	AJ971461	MaYVB-[CN:Yn193:03]
<i>Malvastrum yellow vein betasatellite</i>	Malvastrum yellow vein betasatellite [China:Yunnan 194:2003]	AJ971462	MaYVB-[CN:Yn194:03]
<i>Malvastrum yellow vein betasatellite</i>	Malvastrum yellow vein betasatellite [China:Yunnan 195:2003]	AJ971463	MaYVB-[CN:Yn195:03]
<i>Malvastrum yellow vein betasatellite</i>	Malvastrum yellow vein betasatellite [China:Yunnan 197:2003]	AJ971695	MaYVB-[CN:Yn197:03]
<i>Malvastrum yellow vein betasatellite</i>	Malvastrum yellow vein betasatellite [China:Yunnan 198:2003]	AJ971696	MaYVB-[CN:Yn198:03]
<i>Malvastrum yellow vein betasatellite</i>	Malvastrum yellow vein betasatellite [China:Yunnan 200:2003]	AJ971697	MaYVB-[CN:Yn200:03]
<i>Malvastrum yellow vein betasatellite</i>	Malvastrum yellow vein betasatellite [China:Yunnan 205:2003]	AJ971698	MaYVB-[CN:Yn205:03]
<i>Malvastrum yellow vein betasatellite</i>	Malvastrum yellow vein betasatellite [China:Yunnan 206:2003]	AJ744882	MaYVB-[CN:Yn206:03]
<i>Malvastrum yellow vein betasatellite</i>	Malvastrum yellow vein betasatellite [China:Yunnan 216:2003]	AJ971699	MaYVB-[CN:Yn216:03]
<i>Malvastrum yellow vein betasatellite</i>	Malvastrum yellow vein betasatellite [China:Yunnan 217:2003]	AJ971700	MaYVB-[CN:Yn217:03]
<i>Malvastrum yellow vein betasatellite</i>	Malvastrum yellow vein betasatellite [China:Yunnan 249:2004]	AJ971703	MaYVB-[CN:Yn249:04]
<i>Malvastrum yellow vein betasatellite</i>	Malvastrum yellow vein betasatellite [China:Yunnan 250:2004]	AJ971704	MaYVB-[CN:Yn250:04]
<i>Malvastrum yellow vein betasatellite</i>	Malvastrum yellow vein betasatellite [China:Yunnan 251:2004]	AJ971705	MaYVB-[CN:Yn251:04]
<i>Malvastrum yellow vein betasatellite</i>	Malvastrum yellow vein betasatellite [China:Yunnan 252:2004]	AJ971706	MaYVB-[CN:Yn252:04]
<i>Malvastrum yellow vein betasatellite</i>	Malvastrum yellow vein betasatellite [China:Yunnan 292:2004]	AJ971702	MaYVB-[CN:Yn292:04]
<i>Malvastrum yellow vein betasatellite</i>	Malvastrum yellow vein betasatellite [China:Yunnan 300:2004]	AJ971707	MaYVB-[CN:Yn300:04]
<i>Malvastrum yellow vein betasatellite</i>	Malvastrum yellow vein betasatellite [China:Yunnan 301:2004]	AJ971708	MaYVB-[CN:Yn302:04]
<i>Malvastrum yellow vein betasatellite</i>	Malvastrum yellow vein betasatellite [China:Yunnan 302:2004]	AJ971709	MaYVB-[CN:Yn302:04]
<i>Malvastrum yellow vein betasatellite</i>	Malvastrum yellow vein betasatellite [China:Yunnan 303:2004]	AJ971710	MaYVB-[CN:Yn303:04]
<i>Malvastrum yellow vein betasatellite</i>	Malvastrum yellow vein betasatellite [China:Yunnan 47:2001]	AJ421482	MaYVB-[CN:Yn47:01]
<i>Malvastrum yellow vein Yunan betasatellite</i>	Malvastrum yellow vein Yunan betasatellite [China:Yunnan 278:2003]	AJ971701	MaYVYnB-[CN:Yn278:03]
<i>Malvastrum yellow vein Yunan betasatellite</i>	Malvastrum yellow vein Yunan betasatellite [China:Yunnan 160:2003]	AJ786712	MaYVYnB-[CN:Yn160:03]
<i>Malvastrum yellow vein Yunan betasatellite</i>	Malvastrum yellow vein Yunan betasatellite [China:Yunnan 304:2003]	AM236776	MaYVYnB-[CN:Yn304:03]
<i>Malvastrum yellow vein Yunan betasatellite</i>	Malvastrum yellow vein Yunan betasatellite [China:Yunnan 307:2003]	AM236777	MaYVYnB-[CN:Yn307:03]
<i>Malvastrum yellow vein Yunan betasatellite</i>	Malvastrum yellow vein Yunan betasatellite [China:Yunnan 308:2003]	AM236778	MaYVYnB-[CN:Yn308:03]
<i>Okra leaf curl betasatellite</i>	Okra leaf curl betasatellite [Pakistan:Gojra:1997]	AJ316029	OLCuB-[PK:Goj:97]

Table 1 continued

<i>Species</i>	Betasatellite name	Accession #	Beta abbreviation
<i>Papaya leaf curl betasatellite</i>	Papaya leaf curl betasatellite [India:Chinthapalli:2005]	DQ118862	PaLCuB-[IN:Chi:05]
<i>Papaya leaf curl betasatellite</i>	Papaya leaf curl betasatellite [India:Jabalpur:2003]	AY230138	PaLCuB-[IN:Jab:03]
<i>Papaya leaf curl betasatellite</i>	Papaya leaf curl betasatellite [India:Mungbean:2003]	AY438557	PaLCuB-[IN:Mb:05]
<i>Papaya leaf curl betasatellite</i>	Papaya leaf curl betasatellite [India:New Delhi:2003]	AY244706	PaLCuB-[IN:ND:03]
<i>Papaya leaf curl betasatellite</i>	Papaya leaf curl betasatellite [India:Meerut:2006]	EF053234	PaLCuB-[IN:Mee:06]
<i>Sida leaf curl betasatellite</i>	Sida leaf curl betasatellite [China:Hainan 57:2004]	AM050732	SiLCuB-[CN:Hn57:04]
<i>Sida leaf curl betasatellite</i>	Sida leaf curl betasatellite [China:Hainan 60:2004]	AM050733	SiLCuB-[CN:Hn60:04]
<i>Sida leaf curl betasatellite</i>	Sida leaf curl betasatellite [Vietnam:Thanhhoa:2005]	DQ641711	SiLCuB-[VN:Tha:05]
<i>Sida yellow mosaic China betasatellite</i>	Sida yellow mosaic China betasatellite [China:Hainan 40:2004]	AJ810094	SiYMCNB-[CN:Hn40:04]
<i>Sida yellow mosaic China betasatellite</i>	Sida yellow mosaic China betasatellite [China:Hainan 41:2004]	AJ810095	SiYMCNB-[CN:Hn41:04]
<i>Sida yellow mosaic China betasatellite</i>	Sida yellow mosaic China betasatellite [China:Hainan 7:2003]	AM048833	SiYMCNB-[CN:Hn7:03]
<i>Sida yellow mosaic China betasatellite</i>	Sida yellow mosaic China betasatellite [China:Hainan 8:2003]	AJ810093	SiYMCNB-[CN:Hn8:03]
<i>Sida yellow mosaic China betasatellite</i>	Sida yellow mosaic China betasatellite [China:Yunnan 36r:2004]r	AM236768	SiYMCNB-[CN:Yn36r:04]r
<i>Sida yellow mosaic China betasatellite</i>	Sida yellow mosaic China betasatellite [China:Yunnan 37:2004]	AM236761	SiYMCNB-[CN:Yn37:04]
<i>Sida yellow mosaic China betasatellite</i>	Sida yellow mosaic China betasatellite [China:Yunnan 38:2004]	AM236762	SiYMCNB-[CN:Yn38:04]
<i>Sida yellow mosaic China betasatellite</i>	Sida yellow mosaic China betasatellite [China:Yunnan 38r:2004]r	AM236769	SiYMCNB-[CN:Yn38r:04]r
<i>Sida yellow mosaic China betasatellite</i>	Sida yellow mosaic China betasatellite [China:Yunnan 44r:2004]r	AM236770	SiYMCNB-[CN:Yn44r:04]r
<i>Sida yellow vein betasatellite</i>	Sida yellow vein betasatellite [India:Madurai:2005]	AJ967003	SiYVB-[IN:Mad:05]
<i>Sida yellow vein Vietnam betasatellite</i>	Sida yellow vein Vietnam betasatellite [Vietnam:Hanoi:2005]	DQ641712	SiYVNB-[VN:Han:05]
<i>Sigesbeckia yellow vein betasatellite</i>	Sigesbeckia yellow vein betasatellite [China:Guandong 13:2004]	AM230643	SibYVB-[CN:Gd13:04]
<i>Sigesbeckia yellow vein betasatellite</i>	Sigesbeckia yellow vein betasatellite [China:Guandong 24:2004]	AM230644	SibYVB-[CN:Gd24:04]
<i>Sigesbeckia yellow vein betasatellite</i>	Sigesbeckia yellow vein betasatellite [China:Guandong 27:2004]	AM230645	SibYVB-[CN:Gd27:04]
<i>Sigesbeckia yellow vein Guangxi betasatellite</i>	Sigesbeckia yellow vein Guangxi betasatellite [China:Guangxi 13:2005]	AM238695	SibYVGxB-[CN:Gx111:05]
<i>Tobacco curly shoot betasatellite</i>	Tobacco curly shoot betasatellite [China:Yunnan 115:2002]	AJ457822	TbCSB-[CN:Yn115:02]
<i>Tobacco curly shoot betasatellite</i>	Tobacco curly shoot betasatellite [China:Yunnan 2:1999]	AJ421485	TbCSB-[CN:Yn2:99]
<i>Tobacco curly shoot betasatellite</i>	Tobacco curly shoot betasatellite [China:Yunnan 35:2001]	AJ421484	TbCSB-[CN:Yn35:01]
<i>Tobacco curly shoot betasatellite</i>	Tobacco curly shoot betasatellite [China:Yunnan 98:2002]	AJ457821	TbCSB-[CN:Yn98:02]

Table 1 continued

<i>Species</i>	Betasatellite name	Accession #	Beta abbreviation
<i>Tobacco curly shoot betasatellite</i>	Tobacco curly shoot betasatellite [China:Yunnan 317:2004]	AM260736	TbCSB-[CN:Yn317:04]
<i>Tobacco curly shoot betasatellite</i>	Tobacco curly shoot betasatellite [China:Yunnan 291:2004]	AM260735	TbCSB-[CN:Yn291:04]
<i>Tobacco curly shoot betasatellite</i>	Tobacco curly shoot betasatellite [China:Yunnan 289:2004]	AM260734	TbCSB-[CN:Yn289:04]
<i>Tobacco leaf curl betasatellite</i>	Tobacco leaf curl betasatellite [Pakistan:Bahawalpur:1999]	AJ316034	TbLCB-[PK:Bah:99]
<i>Tobacco leaf curl betasatellite</i>	Tobacco leaf curl betasatellite [Pakistan:Lahore:2004]	AM260465	TbLCB-[PK:Lah:04]
<i>Tobacco leaf curl betasatellite</i>	Tobacco leaf curl betasatellite [Pakistan:Rahim Yar Khan:1998]	AJ316033	TbLCB-[PK:RYK:98]
<i>Tomato leaf curl Bangalore betasatellite</i>	Tomato leaf curl Bangalore betasatellite [India:Bangalore:2003]	AY428768	ToLCBB-[IN:Ban:03]
<i>Tomato leaf curl Bangalore betasatellite</i>	Tomato leaf curl Bangalore betasatellite [India:Coimbatore:2003]	AY438560	ToLCBB-[IN:Coi:03]
<i>Tomato leaf curl Bangladesh betasatellite</i>	Tomato leaf curl Bangladesh betasatellite [Bangladesh:Gazipur:2001]	AJ542489	ToLCBDB-[BD:Gaz:01]
<i>Tomato leaf curl Bangladesh betasatellite</i>	Tomato leaf curl Bangladesh betasatellite [India:Rajasthan:2003]	AY438558	ToLCBDB-[IN:Raj:03]
<i>Tomato leaf curl Bangladesh betasatellite</i>	Tomato leaf curl Bangladesh betasatellite [India:Lucknow:2005]	DQ343289	ToLCBDB-[IN:Luk:05]
<i>Tomato leaf curl Bangladesh betasatellite</i>	Tomato leaf curl Bangladesh betasatellite [India:Varanasi:2006]	EF190215	ToLCBDB-[IN:Var:06]
<i>Tobacco leaf curl Japan betasatellite</i>	Tobacco leaf curl Japan betasatellite [Japan:Masuda:2005]	AB236326	TbLCJB-[JR:Mas:05]
<i>Tomato leaf curl betasatellite</i>	Tomato leaf curl betasatellite [Pakistan:Rahim Yar Khan:1997]	AJ316036	ToLCB-[PK:RYK:97]
<i>Tomato leaf curl betasatellite</i>	Tomato leaf curl betasatellite [India:Cowpea:2004]	AY728263	ToLCB-[IN:CP:04]
<i>Tomato leaf curl betasatellite</i>	Tomato leaf curl betasatellite [India:New Delhi:2002]	AJ542490	ToLCB-[IN:ND:02]
<i>Tomato leaf curl betasatellite</i>	Tomato leaf curl betasatellite [India:Ludhiana:2004]	AY765255	ToLCB-[IN:Lud:04]
<i>Tomato leaf curl China betasatellite</i>	Tomato leaf curl China betasatellite [China:Guangxi 14:2002]	AJ704609	ToLCCNB-[CN:Gx14:02]
<i>Tomato leaf curl China betasatellite</i>	Tomato leaf curl China betasatellite [China:Guangxi 16:2002]	AJ704610	ToLCCNB-[CN:Gx16:02]
<i>Tomato leaf curl China betasatellite</i>	Tomato leaf curl China betasatellite [China:Guangxi 17:2002]	AJ704611	ToLCCNB-[CN:Gx17:02]
<i>Tomato leaf curl China betasatellite</i>	Tomato leaf curl China betasatellite [China:Guangxi 18:2002]	AJ704612	ToLCCNB-[CN:Gx18:02]
<i>Tomato leaf curl China betasatellite</i>	Tomato leaf curl China betasatellite [China:Guangxi 22:2002]	AJ704613	ToLCCNB-[CN:Gx22:02]
<i>Tomato leaf curl China betasatellite</i>	Tomato leaf curl China betasatellite [China:Guangxi 55:2003]	AJ704614	ToLCCNB-[CN:Gx55:03]
<i>Tomato leaf curl China betasatellite</i>	Tomato leaf curl China betasatellite [China:Guangxi 60:2003]	AJ704615	ToLCCNB-[CN:Gx60:03]
<i>Tomato leaf curl China betasatellite</i>	Tomato leaf curl China betasatellite [China:Guangxi 61:2003]	AJ704616	ToLCCNB-[CN:Gx61:03]
<i>Tomato leaf curl China betasatellite</i>	Tomato leaf curl China betasatellite [China:Guangxi 65:2003]	AJ704617	ToLCCNB-[CN:Gx65:03]
<i>Tomato leaf curl China betasatellite</i>	Tomato leaf curl China betasatellite [China:Guangxi 7:2002]	AJ704618	ToLCCNB-[CN:Gx7:02]

Table 1 continued

<i>Species</i>	Betasatellite name	Accession #	Beta abbreviation
<i>Tomato leaf curl Java betasatellite</i>	Tomato leaf curl Java betasatellite [Indonesia:Indonesia 1:2003]	AB100306	ToLCJB-[ID:ID1:03]
<i>Tomato leaf curl Java betasatellite</i>	Tomato leaf curl Java betasatellite [Indonesia:Indonesia 2:2003]	AB113651	ToLCJB-[ID:ID2:03]
<i>Tomato leaf curl Java betasatellite</i>	Tomato leaf curl Java betasatellite [Indonesia:Indonesia 3:2004]	AB162142	ToLCJB-[ID:ID3:04]
<i>Tomato leaf curl Joydebpur betasatellite</i>	Tomato leaf curl Joydebpur betasatellite [Bangladesh:Gazipur:2005]	AJ966244	ToLCJoB-[BD:Gaz:05]
<i>Tomato leaf curl Karnataka betasatellite</i>	Tomato leaf curl Karnataka betasatellite [India:Janti:2004]	AY754813	ToLCKB-[IN:Jan:04]
<i>Tomato leaf curl Laos betasatellite</i>	Tomato leaf curl Laos betasatellite [Laos:Savannakhet:2001]	AJ542491	ToLCLB-[LA:Sav:01]
<i>Tomato leaf curl Laos betasatellite</i>	Tomato leaf curl Laos betasatellite [Vietnam:Binhduong:Mimosa:2005]	DQ641710	ToLCLB-[VN:Bin:Mi:05]
<i>Tomato leaf curl Maharashtra betasatellite</i>	Tomato leaf curl Maharashtra betasatellite [India:Pune:2004]	AY838894	ToLCMaB-[IN:Pun:04]
<i>Tomato leaf curl Maharashtra betasatellite</i>	Tomato leaf curl Maharashtra betasatellite [India:Pune:2006]	AY754815	ToLCMaB-[IN:Pun:06]
<i>Tomato leaf curl Philippines betasatellite</i>	Tomato leaf curl Philippines betasatellite [Philippines:Labuna1:2006]	AB308071	ToLCPHB-[PH:Lag1:06]
<i>Tomato leaf curl Philippines betasatellite</i>	Tomato leaf curl Philippines betasatellite [Philippines:Labuna2:2006]	AB307732	ToLCPHB-[PH:Lag2:06]
<i>Tomato yellow leaf curl China betasatellite</i>	Tomato yellow leaf curl China betasatellite [China:Guangxi 102:2004]	AM050556	TYLCCNB-[CN:Gx102:04]
<i>Tomato yellow leaf curl China betasatellite</i>	Tomato yellow leaf curl China betasatellite [China:Guangxi 103:2004]	AM050557	TYLCCNB-[CN:Gx103:04]
<i>Tomato yellow leaf curl China betasatellite</i>	Tomato yellow leaf curl China betasatellite [China:Guangxi 30:2002]	AJ704606	TYLCCNB-[CN:Gx30:02]
<i>Tomato yellow leaf curl China betasatellite</i>	Tomato yellow leaf curl China betasatellite [China:Guangxi 32:2002]	AJ704607	TYLCCNB-[CN:Gx32:02]
<i>Tomato yellow leaf curl China betasatellite</i>	Tomato yellow leaf curl China betasatellite [China:Guangxi 33:2002]	AJ704608	TYLCCNB-[CN:Gx33:02]
<i>Tomato yellow leaf curl China betasatellite</i>	Tomato yellow leaf curl China betasatellite [China:Guangxi 35:2002]	AJ704605	TYLCCNB-[CN:Gx35:02]
<i>Tomato yellow leaf curl China betasatellite</i>	Tomato yellow leaf curl China betasatellite [China:Guangxi 36T-1:2003]	AJ704578	TYLCCNB-[CN:Gx36T-1:03]
<i>Tomato yellow leaf curl China betasatellite</i>	Tomato yellow leaf curl China betasatellite [China:Guangxi 36T-2:2003]	AJ704579	TYLCCNB-[CN:Gx36T-2:03]
<i>Tomato yellow leaf curl China betasatellite</i>	Tomato yellow leaf curl China betasatellite [China:Yunnan 10:2000]	AJ421621	TYLCCNB-[CN:Yn10:00]
<i>Tomato yellow leaf curl China betasatellite</i>	Tomato yellow leaf curl China betasatellite [China:Yunnan 10-10:1999]r	AJ781300	TYLCCNB-[CN:Yn10-10:99]r
<i>Tomato yellow leaf curl China betasatellite</i>	Tomato yellow leaf curl China betasatellite [China:Yunnan 10-4:1999]r	AJ781297	TYLCCNB-[CN:Yn10-4:99]r
<i>Tomato yellow leaf curl China betasatellite</i>	Tomato yellow leaf curl China betasatellite [China:Yunnan 10-6:1999]r	AJ781298	TYLCCNB-[CN:Yn10-6:99]r
<i>Tomato yellow leaf curl China betasatellite</i>	Tomato yellow leaf curl China betasatellite [China:Yunnan 10-9:1999]r	AJ781299	TYLCCNB-[CN:Yn10-9:99]r

Table 1 continued

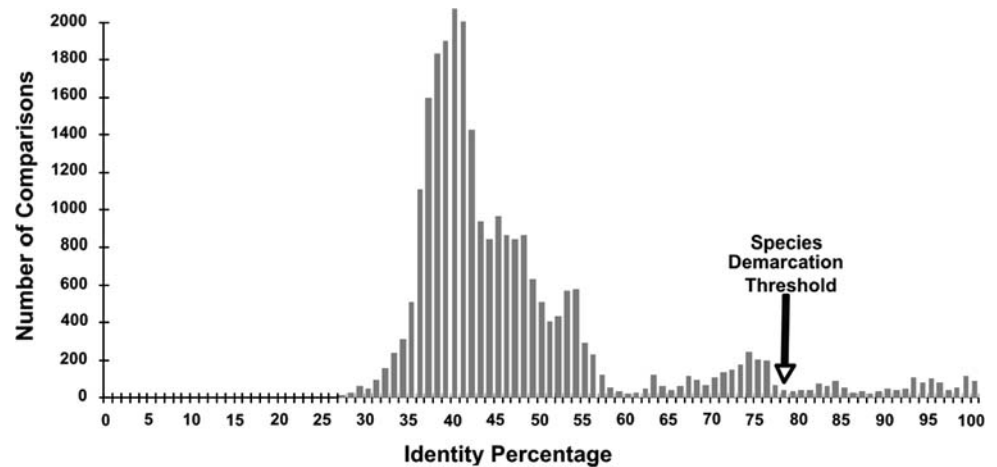
<i>Species</i>	Betasatellite name	Accession #	Beta abbreviation
<i>Tomato yellow leaf curl China betasatellite</i>	Tomato yellow leaf curl China betasatellite [China:Yunnan 136-2:2002]	AJ536626	TYLCCNB-[CN:Yn136-2:02]
<i>Tomato yellow leaf curl China betasatellite</i>	Tomato yellow leaf curl China betasatellite [China:Yunnan 143-22:2002]	AJ536624	TYLCCNB-[CN:Yn143-22:02]
<i>Tomato yellow leaf curl China betasatellite</i>	Tomato yellow leaf curl China betasatellite [China:Yunnan 143-30:2002]	AJ536625	TYLCCNB-[CN:Yn143-30:02]
<i>Tomato yellow leaf curl China betasatellite</i>	Tomato yellow leaf curl China betasatellite [China:Yunnan 143-5:2002]	AJ536627	TYLCCNB-[CN:Yn143-5:02]
<i>Tomato yellow leaf curl China betasatellite</i>	Tomato yellow leaf curl China betasatellite [China:Yunnan 231:2004]	AM260714	TYLCCNB-[CN:Yn231:02]
<i>Tomato yellow leaf curl China betasatellite</i>	Tomato yellow leaf curl China betasatellite [China:Yunnan 238:2004]	AM260715	TYLCCNB-[CN:Yn238:02]
<i>Tomato yellow leaf curl China betasatellite</i>	Tomato yellow leaf curl China betasatellite [China:Yunnan 241:2004]	AM260716	TYLCCNB-[CN:Yn241:02]
<i>Tomato yellow leaf curl China betasatellite</i>	Tomato yellow leaf curl China betasatellite [China:Yunnan 244:2004]	AM260717	TYLCCNB-[CN:Yn244:02]
<i>Tomato yellow leaf curl China betasatellite</i>	Tomato yellow leaf curl China betasatellite [China:Yunnan 248:2004]	AM260718	TYLCCNB-[CN:Yn248:02]
<i>Tomato yellow leaf curl China betasatellite</i>	Tomato yellow leaf curl China betasatellite [China:Yunnan 25:2000]	AJ421619	TYLCCNB-[CN:Yn25:04]
<i>Tomato yellow leaf curl China betasatellite</i>	Tomato yellow leaf curl China betasatellite [China:Yunnan 253:2004]	AJ971331	TYLCCNB-[CN:Yn253:04]
<i>Tomato yellow leaf curl China betasatellite</i>	Tomato yellow leaf curl China betasatellite [China:Yunnan 254:2004]	AJ971332	TYLCCNB-[CN:Yn254:04]
<i>Tomato yellow leaf curl China betasatellite</i>	Tomato yellow leaf curl China betasatellite [China:Yunnan 255:2004]	AJ971333	TYLCCNB-[CN:Yn255:04]
<i>Tomato yellow leaf curl China betasatellite</i>	Tomato yellow leaf curl China betasatellite [China:Yunnan 318:2004]	AM260725	TYLCCNB-[CN:Yn318:02]
<i>Tomato yellow leaf curl China betasatellite</i>	Tomato yellow leaf curl China betasatellite [China:Yunnan 319:2004]	AM260726	TYLCCNB-[CN:Yn319:02]
<i>Tomato yellow leaf curl China betasatellite</i>	Tomato yellow leaf curl China betasatellite [China:Yunnan 321:2004]	AM260728	TYLCCNB-[CN:Yn321:02]
<i>Tomato yellow leaf curl China betasatellite</i>	Tomato yellow leaf curl China betasatellite [China:Yunnan 322:2005]	AM181684	TYLCCNB-[CN:Yn322:05]
<i>Tomato yellow leaf curl China betasatellite</i>	Tomato yellow leaf curl China betasatellite [China:Yunnan 323:2004]	AM260729	TYLCCNB-[CN:Yn323:02]
<i>Tomato yellow leaf curl China betasatellite</i>	Tomato yellow leaf curl China betasatellite [China:Yunnan 330:2004]	AM260727	TYLCCNB-[CN:Yn330:02]
<i>Tomato yellow leaf curl China betasatellite</i>	Tomato yellow leaf curl China betasatellite [China:Yunnan 36:2001]	AJ506791	TYLCCNB-[CN:Yn36:01]
<i>Tomato yellow leaf curl China betasatellite</i>	Tomato yellow leaf curl China betasatellite [China:Yunnan 38:2001]	AJ420315	TYLCCNB-[CN:Yn38:01]
<i>Tomato yellow leaf curl China betasatellite</i>	Tomato yellow leaf curl China betasatellite [China:Yunnan 43:2001]	AJ420314	TYLCCNB-[CN:Yn43:01]
<i>Tomato yellow leaf curl China betasatellite</i>	Tomato yellow leaf curl China betasatellite [China:Yunnan 43-8:2003]r	AJ781301	TYLCCNB-[CN:Yn43-8:03]r
<i>Tomato yellow leaf curl China betasatellite</i>	Tomato yellow leaf curl China betasatellite [China:Yunnan 45:2001]	AJ420313	TYLCCNB-[CN:Yn45:01]
<i>Tomato yellow leaf curl China betasatellite</i>	Tomato yellow leaf curl China betasatellite [China:Yunnan 5:1999]	AJ421623	TYLCCNB-[CN:Yn5:99]

Table 1 continued

<i>Species</i>	Betasatellite name	Accession #	Beta abbreviation
<i>Tomato yellow leaf curl China betasatellite</i>	Tomato yellow leaf curl China betasatellite [China:Yunnan 64:2001]	AJ421483	TYLCCNB-[CN:Yn64:01]
<i>Tomato yellow leaf curl China betasatellite</i>	Tomato yellow leaf curl China betasatellite [China:Yunnan 8:1999]	AJ421622	TYLCCNB-[CN:Yn8:99]
<i>Tomato yellow leaf curl Thailand betasatellite</i>	Tomato yellow leaf curl Thailand betasatellite [China:Thailand 136:2002]	AJ536621	TYLCTHB-[CN:Yn136:02]
<i>Tomato yellow leaf curl Thailand betasatellite</i>	Tomato yellow leaf curl Thailand betasatellite [China:Thailand 143:2002]	AJ536622	TYLCTHB-[CN:Yn143:02]
<i>Tomato yellow leaf curl Thailand betasatellite</i>	Tomato yellow leaf curl Thailand betasatellite [China:Thailand 72:2002]	AJ566746	TYLCTHB-[CN:Yn72:02]
<i>Tomato yellow leaf curl Thailand betasatellite</i>	Tomato yellow leaf curl Thailand betasatellite [China:Thailand 77:2002]	AJ566747	TYLCTHB-[CN:Yn77:02]
<i>Tomato yellow leaf curl Thailand betasatellite</i>	Tomato yellow leaf curl Thailand betasatellite [China:Thailand 79:2002]	AJ566748	TYLCTHB-[CN:Yn79:02]
<i>Tomato yellow leaf curl Thailand betasatellite</i>	Tomato yellow leaf curl Thailand betasatellite [India:Aurangabad:2006]	EF095958	TYLCTHB-[IN:Aur:06]
<i>Tomato yellow leaf curl Vietnam betasatellite</i>	Tomato yellow leaf curl Vietnam betasatellite [Vietnam:Hanoi:2005]	DQ641714	TYLCVNB-[VN:Han:05]
<i>Tomato yellow leaf curl Yunan betasatellite</i>	Tomato yellow leaf curl Yunan betasatellite [China:Yunnan 11:2000]	AJ421620	TYLCYnB-[CN:Yn11:00]
<i>Tomato yellow leaf curl Yunan betasatellite</i>	Tomato yellow leaf curl Yunan betasatellite [China:Yunnan 136:2002]	AJ536623	TYLCYnB-[CN:Yn136:02]
<i>Tomato yellow leaf curl Yunan betasatellite</i>	Tomato yellow leaf curl Yunan betasatellite [China:Yunnan 261:2004]	AM260719	TYLCYnB-[CN:Yn261:02]
<i>Tomato yellow leaf curl Yunan betasatellite</i>	Tomato yellow leaf curl Yunan betasatellite [China:Yunnan 262:2004]	AM260720	TYLCYnB-[CN:Yn262:02]
<i>Tomato yellow leaf curl Yunan betasatellite</i>	Tomato yellow leaf curl Yunan betasatellite [China:Yunnan 263:2004]	AM260721	TYLCYnB-[CN:Yn263:02]
<i>Tomato yellow leaf curl Yunan betasatellite</i>	Tomato yellow leaf curl Yunan betasatellite [China:Yunnan 264:2004]	AM260722	TYLCYnB-[CN:Yn264:02]
<i>Tomato yellow leaf curl Yunan betasatellite</i>	Tomato yellow leaf curl Yunan betasatellite [China:Yunnan 265:2004]	AM260723	TYLCYnB-[CN:Yn265:02]
<i>Tomato yellow leaf curl Yunan betasatellite</i>	Tomato yellow leaf curl Yunan betasatellite [China:Yunnan 268:2004]	AM260724	TYLCYnB-[CN:Yn268:02]
<i>Tomato yellow leaf curl Yunan betasatellite</i>	Tomato yellow leaf curl Yunan betasatellite [China:Yunnan 284:2004]	AJ971334	TYLCYnB-[CN:Yn284:04]
<i>Tomato yellow leaf curl Yunan betasatellite</i>	Tomato yellow leaf curl Yunan betasatellite [China:Yunnan 285:2004]	AJ971335	TYLCYnB-[CN:Yn285:04]
<i>Tomato yellow leaf curl Yunan betasatellite</i>	Tomato yellow leaf curl Yunan betasatellite [China:Yunnan 286:2004]	AJ971336	TYLCYnB-[CN:Yn286:04]
<i>Tomato yellow leaf curl Yunan betasatellite</i>	Tomato yellow leaf curl Yunan betasatellite [China:Yunnan 73:2002]	AJ566749	TYLCYnB-[CN:Yn73:02]
<i>Tomato yellow leaf curl Yunan betasatellite</i>	Tomato yellow leaf curl Yunan betasatellite [China:Yunnan 87:2002]	AJ457818	TYLCYnB-[CN:Yn87:02]
<i>Tomato yellow leaf curl Yunan betasatellite</i>	Tomato yellow leaf curl Yunan betasatellite [China:Yunnan 88:2002]	AJ457819	TYLCYnB-[CN:Yn88:02]
<i>Tomato yellow leaf curl Yunan betasatellite</i>	Tomato yellow leaf curl Yunan betasatellite [China:Yunnan 92:2002]	AJ457820	TYLCYnB-[CN:Yn92:02]
<i>Zinnia leaf curl betasatellite</i>	Zinnia leaf curl betasatellite [Thailand:Pattaya:2002]	AJ542499	ZLCuB-[TH:PAT:02]

The recombinant betasatellites are marked with a lower cap “r”

Fig. 1 Distribution of pairwise nucleotide sequence identities of 202 DNA- β full-length sequences (listed in Table 1)



Application of the DNA- β species demarcation criteria

Application of the 78% nucleotide sequence identity demarcation threshold to the 261 available sequences leads to their division into 51 distinct DNA- β satellite species. These are indicated in Table 1 using the proposed nomenclature for DNA- β components.

Conclusions

Due to the rapidly increasing number of recognised DNA- β satellites, there is an urgent need for a robust and workable system of nomenclature and classification of these components. Since these satellites are not independent entities, relying on a helper virus for their replication and spread, the biological data useful for their classification that can unequivocally be attributed to the satellite are limited at this time. It is thus not unreasonable to base the classification system entirely on their nucleotide sequence. It is possible that in future we will recognize distinct satellite strains, based on sequence differences or distinct biological properties, and will want to classify them below the family level into distinct genera.

Whenever possible, the proposed satellite naming system correlates with the original helper virus and host. Although it can accommodate an unlimited number of new satellite isolates, this system currently predicts a manageable number of satellite species. It provides guidelines for assigning future isolates and an accepted system of nomenclature covering species and isolates that will greatly benefit the research community investigating the diversity and function of these widespread and economically important subviral components.

The following criteria should be used as guidelines to establish taxonomic status of a DNA- β component.

1. Species status should only be conferred once a full-length sequence is available (this is in line with the established convention for geminiviruses). Comparison of component parts of the satellite (SCR, β C1 coding sequence and A-rich sequence) broadly yields the same result as analysis of the full-length sequence. Nevertheless, their propensity for recombination means that species status may only be bestowed when the entire sequence has been established.
2. Pairwise nucleotide sequence identity comparisons between 261 full-length DNA- β components indicate that a value of 78% nucleotide sequence identity is appropriate for distinguishing species from isolates. Application of this criterion to 261 full-length sequences currently available in the databases leads to 51 species.

The naming of satellite species follows the convention set down for geminiviruses and, wherever possible, mirrors that of the helper begomovirus. For example, the two satellites associated with cotton leaf curl disease are called *Cotton leaf curl Multan beta* and *Cotton leaf curl Gezira beta*, indicating their association with cotton leaf curl disease but also their association with helper viruses belonging to the species *Cotton leaf curl Multan virus* and *Cotton leaf curl Gezira virus*, respectively. Isolate names similarly follow the convention set down for geminiviruses. These indicate country of origin, isolate descriptor [preferably place (town/region) of origin] and year of isolation. For example, *Cotton leaf curl Multan beta*-[India:Dabwali1:1995] originates from India, in the vicinity of the city of Dabwali, and was collected from the field in 1995. The number 1 indicates that this is the first isolate from this region (if more than one isolate was collected). This name is abbreviated to CLCuMB-[IN:Dab1:95].

Table 2 List of cognate begomovirus-DNA- β pairs for which full-length sequences are available

Virus name	Accession number	Virus abbreviation	DNA- β name	Accession number	DNA- β abbreviation
Ageratum yellow vein China virus [China:Hainan2:2001]	AJ495813	AYVCNV-[CN:Hn2:01]	Ageratum yellow vein beta [China:Hainan2:2001]	AM048834	AYVB-[CN:Hn2:01]
Ageratum yellow vein virus [Singapore:1992]	X74516	AYVV-[SG:92]	Ageratum yellow vein beta [Singapore:1992]	AJ252072	AYVB-[SG:92]
Bhendi yellow vein mosaic virus [India:Madurai:1999]	AF241479	BYVMV-[IN:Mad:99]	Bhendi yellow vein beta [India:Muthupatti:2000]	AJ308425	BYVB-[IN:Mut:00]
Cotton leaf curl Gezira virus [Egypt:Cairo:Okra:2000]	AY036010	CLCuGV-[EG:Cai:Ok:00]	Cotton leaf curl Gezira beta [Egypt:okra3:2000]	AF397217	CLCuGB-[EG:ok3:00]
Cotton leaf curl Gezira virus [Sudan:Gezira:Sida]	AY036007	CLCuGV-[SD:Gez:Si]	Cotton leaf curl Gezira beta [Sudan:sida32:1996]	AY077798	CLCuGB-[SD:si32:96]
Cotton leaf curl Gezira virus [Sudan:Gezira]	AF260241	CLCuGV-[SD:Gez]	Cotton leaf curl Gezira beta [Sudan:okra44-1:1996]	AY077799	CLCuGB-[SD:ok44-1:96]
Cotton leaf curl Multan virus [Pakistan:Faisalabad 1:1996]	X98995	CLCuMV-[PK:Fai:1:96]	Cotton leaf curl Multan beta [Pakistan:Faisalabad:Hibiscus:1996]	AJ297908	CLCuMB-[PK:Fai:Hib:96]
Cotton leaf curl Multan virus [Pakistan:Faisalabad 3:1996]	AJ132430	CLCuMV-[PK:Fai3:96]	Cotton leaf curl Multan beta [Pakistan:Faisalabad1:1996]	AJ298903	CLCuMB-[PK:Fai:1:96]
Cotton leaf curl Rajasthan virus [India:SriGanganagar:1994]	AF363011	CLCuRV-[IN:Sri:94]	Cotton leaf curl Multan beta [India:Sri Ganganagar:2002]	AY083590	CLCuMB-[IN:Sri:02]
Eupatorium yellow vein mosaic virus [Japan:SOJ3:2000]	AJ438937	EpYVMV-[JR:SOJ3:00]	Eupatorium yellow vein beta [Japan:SOJ1:2000]	AJ438939	EpYVB-[JR:SOJ1:00]
Eupatorium yellow vein virus [Japan:MNS2:2000]	AJ438936	EpYVV-[JR:MNS2:00]	Eupatorium yellow vein beta [Japan:MNS2:2000]	AJ438938	EpYVB-[JR:MNS2:00]
Honeysuckle yellow vein virus [UK:Norwich 1:1999]	AJ542540	HYVV-[UK:Nor1:99]	Honeysuckle yellow vein beta [United Kingdom:Norwich1:1999]	AJ316040	HYVB-[UK:Nor1:99]
Honeysuckle yellow vein virus [UK:Norwich 2:1999]	AJ543429	HYVV-[UK:Nor2:99]	Honeysuckle yellow vein beta [United Kingdom:Norwich2:1999]	AJ543430	HYVB-[UK:Nor2:99]
Ludwigia yellow vein virus [China:Guangxi 37:2003]	AJ965539	LuYVV-[CN:Gx37:03]	Ludwigia yellow vein beta [China:Guangxi37:2004]	AJ965541	LuYVB-[CN:Gx37:04]
Malvastrum leaf curl virus [China:Guangxi 87:2004]	AJ971263	MaLCV-[CN:Gx87:04]	Malvastrum leaf curl beta [China:Guangxi 87:2004]	AJ971264	MaLCuB-[CN:Gx87:04]
Malvastrum yellow mosaic virus [China:Hainan 36:2004]	AM236755	MaYMV-[CN:Hn36:04]	Malvastrum yellow mosaic beta [China:Yunnan 36r:2004]	AM236768	MaYMB-[CN:Yn36r:04]
Malvastrum yellow mosaic virus [China:Hainan 37:2004]	AM236756	MaYMV-[CN:Hn37:04]	Sida yellow mosaic beta [China:Yunnan37:2004]	AM236761	SiYMB-[CN:Yn37:04]
Malvastrum yellow vein virus [China:Yunnan 47:2001]	AJ457824	MaYVV-[CN:Yn47:01]	Malvastrum yellow vein beta [China:Yunnan 47:2001]	AJ421482	MaYVB-[CN:Yn47:01]
Malvastrum yellow vein virus [China:Yunnan 206:Age:2003]	AJ744881	MaYVV-[CN:Yn206:Age:03]	Malvastrum yellow vein beta [China:Yunnan 206:2003]	AJ744882	MaYVB-[CN:Yn206:03]

Table 2 continued

Virus name	Accession number	Virus abbreviation	DNA- β name	Accession number	DNA- β abbreviation
Malvastrum yellow vein Yunnan virus [China:Yunnan160:2003]	AJ786711	MaYVYV-[CN:Yn160:03]	Malvastrum yellow vein Yunnan beta [China:Yunnan160:2003]	AJ786712	MaYVYnB-[CN:Yn160:03]
Sida leaf curl virus [China:Hainan 57:2004]	AM050730	SiLCuV-[CN:Hn57:04]	Sida yellow mosaic Hainan beta [China:Hainan57:2004]	AM050732	SiYMHnB-[CN:Hn57:04]
Sida yellow mosaic China virus [China:Hainan 8:2003]	AJ810096	SiYMCNV-[CN:Hn8:03]	Sida yellow mosaic beta [China:Hainan8:2003]	AJ810093	SiYMB-[CN:Hn8:03]
Siegesbeckia yellow vein virus [China:Guangdong 13:2004]	AM183224	SbYVV-[CN:Gd13:04]	Siegesbeckia yellow vein beta [China:Guangdong 13:2004]	AM183224	SbYVB-[CN:Gd13:04]
Siegesbeckia yellow vein virus [China:Guangdong 24:2004]	AM230634	SbYVV-[CN:Gd24:04]	Siegesbeckia yellow vein beta [China:Guangdong 24:2004]	AM230634	SbYVB-[CN:Gd24:04]
Siegesbeckia yellow vein virus [China:Guangdong 27:2004]	AM230635	SbYVV-[CN:Gd27:04]	Siegesbeckia yellow vein beta [China:Guangdong 27:2004]	AM230635	SbYVB-[CN:Gd27:04]
Siegesbeckia yellow vein virus [China:Guangxi 111:2005]	AM238692	SbYVGxV-[CN:Gx111:05]	Siegesbeckia yellow vein Guangxi beta [China:Guangxi 111:2005]	AM238695	SbYVGxB-[CN:Gx111:05]
Tobacco curly shoot virus [China:Yunnan 35:2001]	AJ420318	TbCSV-[CN:Y35:01]	Tobacco curly shoot beta [China:Yunnan35:2001]	AJ421484	TbCSB-[CN:Yn35:01]
Tobacco leaf curl Yunnan virus [China:Yunnan 136:2002]	AJ512761	TbLCYnV-[CN:Yn136:02]	Tobacco leaf curl Yunnan beta [China:Yunnan136:2002]	AJ536621	TbLCYnB-[CN:Yn136:02]
Tobacco leaf curl Yunnan virus [China:Yunnan 143:2002]	AJ512762	TbLCYnV-[CN:Yn143:02]	Tobacco leaf curl Yunnan beta [China:Yunnan143:2002]	AJ536622	TbLCYnB-[CN:Yn143:02]
Tomato leaf curl China virus [China:Guangxi 16:2002]	AJ704602	ToLCCNV-[CN:Gx16:02]	Tomato leaf curl China beta [China:Guangxi 16:2002]	AJ704610	ToLCCNB-[CN:Gx16:02]
Tomato leaf curl China virus [China:Guangxi 18:2002]	AJ558119	ToLCCNV-[CN:Gx18:02]	Tomato leaf curl China beta [China:Guangxi 18:2002]	AJ704612	ToLCCNB-[CN:Gx18:02]
Tomato leaf curl Joydebpur virus [Bangladesh]	AJ875159	ToLJoV-[BD]	Tomato leaf curl Joydebpur beta [Bangladesh:Gazipur:2005]	AJ966244	ToLJoB-[BD:Gaz:05]
Tomato yellow leaf curl China virus [China:Yunnan 10:Tobacco:2000]	AJ319675	TYLCCNV-[CN:Yn10:Tob:00]	Tobacco leaf curl China beta [China:Yunnan10:2000]	AJ421621	TbLCCNB-[CN:Yn10:00]
Tomato yellow leaf curl China virus [China:Yunnan 11:Tobacco:2000]	AJ319676	TYLCCNV-[CN:Yn11:Tob:00]	Tomato yellow leaf curl China beta [China:Yunnan11:2000]	AJ421620	TYLCCNB-[CN:Yn11:00]
Tomato yellow leaf curl China virus [China:Yunnan 25:Tomato:2000]	AJ457985	TYLCCNV-[CN:Yn25:Tom:00]	Tobacco leaf curl China beta [China:Yunnan25:2000]	AJ421619	TbLCCNB-[CN:Yn25:00]
Tomato yellow leaf curl China virus [China:Yunnan 322:Solanum:2005]	AM181683	TYLCCNV-[CN:Yn322:Sol:05]	Tobacco leaf curl China beta [China:Yunnan322:2005]	AM181684	TbLCCNB-[CN:Yn322:05]
Tomato yellow leaf curl China virus [China:Yunnan 36:Tobacco:2001]	AJ420316	TYLCCNV-[CN:Yn36:Tob:01]	Tobacco leaf curl China beta [China:Yunnan36:2001]	AJ506791	TbLCCNB-[CN:Yn36:01]
Tomato yellow leaf curl China virus [China:Yunnan 38:Tobacco:2001]	AJ420317	TYLCCNV-[CN:Yn38:Tob:01]	Tobacco leaf curl China beta [China:Yunnan38:2001]	AJ420315	TbLCCNB-[CN:Yn38:01]

Table 2 continued

Virus name	Accession number	Virus abbreviation	DNA- β name	Accession number	DNA- β abbreviation
Tomato yellow leaf curl China virus [China:Yunnan 43:Tobacco:2001]	AJ781302	TYLCCNV- [CN:Yn43:Tob:01]	Tobacco leaf curl China beta [China:Yunnan43:2001]	AJ420314	TbLCCNB- [CN:Yn43:01]
Tomato yellow leaf curl China virus [China:Yunnan 5:Tobacco:1999]	AJ319674	TYLCCNV- [CN:Yn5:Tob:99]	Tobacco leaf curl China beta [China:Yunnan5:1999]	AJ421623	TbLCCNB- [CN:Yn5:99]
Tomato yellow leaf curl China virus [China:Yunnan 64:Siegesbeckia:2001]	AJ457823	TYLCCNV- [CN:Yn64:Sie:01]	Tobacco leaf curl China beta [China:Yunnan64:2001]	AJ421483	TbLCCNB- [CN:Yn64:01]
Tomato yellow leaf curl China virus [China:Yunnan 8:Tobacco:1999]	AJ319677	TYLCCNV- [CN:Yn8:Tob:99]	Tobacco leaf curl China beta [China:Yunnan8:1999]	AJ421622	TbLCCNB- [CN:Yn8:99]
Tomato yellow leaf curl China virus [China:Yunnan:Beam:2004]	DQ256460	TYLCCNV- [CN:Yn:Bea:04]	Bean leaf curl China beta [China:Yunnan:2004]	DQ256459	BLCuCNB- [CN:Yua:04]
Tomato yellow leaf curl Thailand virus [China:Yunnan 72:2002]	AJ495812	TYLCTHV- [CN:Yn72:02]	Tobacco leaf curl Yunnan beta [China:Yunnan72:2002]	AJ566746	TbLCYnB- [CN:Yn72:02]

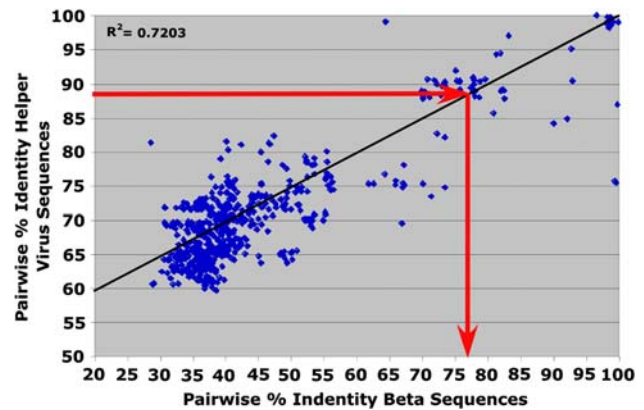


Fig. 2 Correlation between pairwise nucleotide sequence comparison identities of the complete genome sequences of 44 begomoviruses (listed in Table 2) and their cognate DNA- β satellites. The species demarcation threshold defined by the co-evolution study is indicated by the red arrows

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