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Revision of taxonomic criteria for species demarcation in the family *Geminiviridae*, and an updated list of begomovirus species

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Introduction

Members of the family *Geminiviridae* characteristically have circular single-stranded DNA genomes packaged within twinned (so-called geminate) particles. Geminiviruses are currently divided into four genera on the basis of their genome organizations and biological properties [2, 20]. Those that have a monopartite genome and 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 included in the genus *Curtovirus*, with *Beet curly top virus* as the type species. The genus *Topocuvirus*, recently recognized by the International Committee on Taxonomy of Viruses (ICTV) [18], 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 viruses that are transmitted by the whitefly *Bemisia tabaci* (Gennadius) to dicotyledonous plants, with *Bean golden yellow mosaic virus* (originally *Bean golden mosaic virus – Puerto Rico*) as the type species. Many begomoviruses have bipartite genomes (DNA A and DNA B components), although numerous begomoviruses with a monopartite genome occur in the Old World, and there are some for which a single component is not infectious yet no DNA B component has been found.

Geminiviruses cause significant yield losses to many crop plants throughout the world [5, 7]. Because of their economic importance and the relative ease with which their DNA genomes can be cloned, many geminiviruses have been isolated and characterized. Guidelines for naming geminiviruses have recently been proposed [9] and accepted by the Study Group and the geminivirologist community as a whole. These provide a means of distinguishing viruses that are sufficiently distinct to be classified as distinct species. However, guidelines for determining the taxonomic status of a virus, as outlined in the Seventh Report of the ICTV, are no longer precise enough to demarcate some species, and consequently require urgent revision. The problem is compounded by the recent discovery of a high frequency of recombination between species of geminiviruses [16]. A set of guidelines, which may be to some extent arbitrary, is needed to provide the geminivirologist community with uniform and durable species demarcation criteria. Some of these examples were discussed at the last International Geminivirus Workshop, held at Norwich in July 2001, and a consensus has been reached on the species demarcation guidelines required. We present here a system for demarcating geminivirus species, and provide the list of geminivirus species identified according to these guidelines.

Taxonomic considerations

In 1991, the ICTV agreed to add species to the categories of genus, subfamily, family and order in the universal classification of viruses, and endorsed the following definition of virus species: “A virus species is a polythetic class of viruses that constitutes a replicating lineage and occupies a particular ecological niche” [14, 24]. Inherent in the definition of virus species is the requirement that more than one discriminating character should be considered for distinguishing species, and this has been established for geminiviruses [20]. However this definition does not precisely define the species demarcation criteria for particular families or genera. There is no official definition for a strain, but it is usually considered that strains are viruses belonging to the same species that have distinct but stable and heritable biological, serological, and/or molecular traits. Strain identification could include, but is not restricted to, a particular symptom descriptor, a different host, a different vector or a significant genetic difference such as a deletion, repetition, or recombination. An isolate can be used to refer to any virus isolated that can be classified later as a member of either a strain or a species when sufficient information becomes available.

The list of criteria for demarcating geminivirus species in the Seventh Report of the ICTV may be summarized as follows:

Different numbers of genome components
Different organization of genes in the genome
No transcomplementation of gene products
No pseudorecombination between components
Nucleotide sequence identity ($<$75% for mastreviruses, $<$80% for curtoviruses and $<$90% for begomoviruses)
Virions react differently with key antibodies
$<$90% coat protein gene sequence identity
Different vector species
Different host range/pathogenicity

Comments on criteria for demarcating species of begomoviruses

As the number of characterized begomoviruses increases, it is becoming increasingly clear that most of these established criteria are useful only as a rough guide with which to identify new species due to the growing number of exceptions to these rules. A few examples are as follows:

Different number of genome components. Begomoviruses have either one or two components, although some bipartite viruses [23] have the capacity to infect a plant with only one component, so this criterion may not provide a clear distinction. The fact that some begomoviruses are unable to produce the disease phenotype unless accompanied by a satellite DNA component [4, 22] further complicates the application of this criterion.

Different organization of genes in the genome. Geminiviruses within a particular genus are extremely conserved in their genome composition, both in terms of length and organization. The exception is the different arrangement of genes between begomoviruses from the New World and Old World. This criterion, therefore, has only limited use for virus species determination within this genus.

No trans-*complementation of products.* It is known that viral proteins of one species, for example begomovirus AC2, AC3 and movement proteins [12, 21], can functionally *trans*-complement defects in another. Rep protein interaction with the origin of replication, which is generally highly species-specific, can be altered in response to small changes in the sequence [11], and the propensity of begomoviruses to capture components by origin exchange [23] may also confuse the issue.

No pseudo-recombination between components. This was proposed a few years ago as an important criterion with which to distinguish species. However, there are now examples of pseudo-recombination between components of distinct species [13, 23], reflecting the ability of Rep and movement proteins to *trans*-complement functions between species and even between genera [3].

Nucleotide sequence identity. The gap between species and strains is becoming blurred as increasing numbers of geminivirus sequences become available (www.danforthcenter.org/iltab/geminiviridae), and is further eroded by the frequent recombination events that are known to occur between species.

Virions react differently with key antibodies. Although this is true, this criterion is decreasing in importance as the number of exceptions is growing.

<90% coat protein gene sequence identity. As is the case for overall nucleotide sequence identity, this criterion is becoming less accurate with time as more sequences become available, and may be misleading if recombination has caused coat protein sequences to be exchanged between species [16].

Different vector species. Although this criterion is applicable for leafhopper-transmitted geminiviruses, it is of no use for whitefly-transmitted viruses as they are all transmitted by the same whitefly species, *B. tabaci* (Gennadius) [6]. Although different *B. tabaci* biotypes exist in nature, it has been shown that most can transmit a variety of begomoviruses [1], albeit with differing efficiencies.

Different hosts and symptom phenotype. This is a very useful criterion but it may be difficult to provide a comprehensive assessment. There are examples where different strains of the same species have different host ranges. For example, strains of *Potato yellow mosaic virus* (PYMV) infect potatoes in Venezuela and a range of solanaceous crops in Trinidad where the primary host seems to be tomato. Some strains of *Pepper huasteco yellow vein virus* (PHYVV) are well adapted to tomato but cannot infect pepper, the host from which the virus was first isolated. Some hosts are not diagnostic as they support the replication of a large number of viruses. For example, more than 28 species of geminiviruses have been isolated from tomato and there are probably many more waiting to be found [5, 7, 8, 17]. This does not take into account the many viruses isolated from a range of natural hosts that can infect tomato. In addition, the symptoms induced by different strains of the same species may vary, and so will not provide a reliable species-distinguishing feature.

In summary, because of the large number of begomoviruses that have been isolated, these criteria are becoming less reliable for distinguishing species and strains. The molecular criteria probably have the most practical value. For example, if we consider begomoviruses that have one or two components and are transmitted by whiteflies to tomato, there is essentially only a single criterion, nucleotide sequence identity of the DNA A component or monopartite genome, that can be used to distinguish them. This is equally true for many other begomoviruses that have been isolated from cotton, pepper, cassava and other hosts.

The importance of genome sequence comparisons for geminivirus taxonomy

The viral genome encodes proteins that are necessary for virus particle structure, replication, movement, transmission, tissue tropism and host range and, hence, it is arguable that the sequence contains a wealth of information necessary for virus classification. It is possible to establish and exploit correlations between biological properties and sequences, and to assume that sequence identity can be used as a simple guide to taxonomic relatedness [15, 19]. However, for begomoviruses, the gap between species and strain is becoming less distinct with the increase in the number of sequences available (www.danforthcenter.org/iltab/geminiviridae) and the number of recombination events that have been identified [16]. For this reason, it is necessary to establish a clear set of guidelines that will allow geminivirologists to propose taxonomic status for new viruses in a more uniform manner.

Table 1. Updated list of criteria to be used as a guideline to establish taxonomic status within the genera *Curtovirus*, *Topocuvirus* and *Begomovirus* in the *Geminiviridae* family

- Number of genomic components.
  - Presence or absence of a DNA B component.
- Organization of the genome.
  - Presence or absence of AV2/V2 ORFs.
- DNA A nucleotide sequence identity.
  - Because of the growing number of recognized species, it is likely that derivation of the complete nucleotide sequence of genomic components will be necessary to distinguish species.
  - Full-length nucleotide sequence identity $<89\%$ is generally indicative of a distinct species. However, decisions based on nucleotide sequence comparisons, particularly when close to this value, must take into account the biological properties of the virus.
  - The taxonomic status of a recombinant will depend on relatedness to the parental viruses, the frequency and extent of recombination events, and its biological properties compared with the parental viruses. Information concerning the diversity of related recombinants may be helpful to determine status.
- *Trans*-replication of genomic components.
  - The inability of Rep protein to *trans*-replicate a genomic component suggests a distinct species. However, when considering this as a criterion, it should be kept in mind that small changes in the Rep binding site of otherwise identical viruses may prevent a functional interaction while recombination involving a small part of the genome may confer replication competence on a distinct species.
- Production of viable pseudorecombinants.
  - Account should be taken of the fitness of the pseudorecombinant in the natural host(s) of the parental viruses. It must be ensured that pseudorecombinant viability is not the result of inter-component recombination.
- Coat protein characteristics.
  - Nucleotide sequence identity $<90\%$ and substantial serological differences may be indicative of a distinct species in the first instance, but derivation of the complete nucleotide sequence will be necessary before species status can be established.
- Natural host range and symptom phenotype.
  - These characteristics may relate to a particular species but their commonest use will be to distinguish strains.

Table 2. Revised list of begomovirus species and tentative species. In the following list, species names are italicized and previous names appear in brackets. All viruses have been compared using their complete DNA A component sequences and found to be under the proposed threshold of 89%. Unpublished sequences are available to the Study Group but not yet in the public domain

Species[a]	Accession number	Acronym
Abutilon mosaic virus		AbMV
Abutilon mosaic virus	X15983, X15984	AbMV
Abutilon mosaic virus – HW	U51137, U51138,	AbMV-HW
African cassava mosaic virus		ACMV
(Cassava latent virus)		
African cassava mosaic virus – [Cameroon-DO2]	AF366902, AF112353	ACMV-[CM/DO2]
African cassava mosaic virus – [Cameroon]	AF112352, AF112353	ACMV-[CM]
African cassava mosaic virus – [Ghana]		ACMV-[GH]
African cassava mosaic virus – [Ivory Coast]	AF259894, AF259895	ACMV-[IC]
African cassava mosaic virus – [Kenya]	J02057, J02058	ACMV-[KE]
African cassava mosaic virus – [Nigeria]	X17095, X17096	ACMV-[NG]
African cassava mosaic virus – [Nigeria-Ogo]	AJ427910, AJ427911	ACMV-[Nig-Ogo]
African cassava mosaic virus – [Uganda]	Z83252, Z83253	ACMV-[UG]
African cassava mosaic virus – Uganda Mild	AF126800, AF126801	ACMV-UGMld
African cassava mosaic virus – Uganda Severe	AF126802, AF126803	ACMV-UGSvr
Ageratum enation virus		AEV
Ageratum enation virus	AJ437618	AEV
Ageratum yellow vein China virus		AYVCNV
Ageratum yellow vein China virus – [Hn2]	AJ495813	AYVCNV-[Hn2]
Ageratum yellow vein Sri Lanka virus		AYVSLV
Ageratum yellow vein Sri Lanka virus	AF314144	AYVSLV
Ageratum yellow vein Taiwan virus		AYVTV
Ageratum yellow vein virus – [Taiwan]	AF307861,	AYVTV-[Tai]
Ageratum yellow vein virus – [TaiwanPD]	AF327902	AYVTV-[TaiPD]
Ageratum yellow vein virus		AYVV
Ageratum yellow vein virus	X74516	AYVV
Bean calico mosaic virus		BCaMV
Bean calico mosaic virus	AF110189, AF110190	BCaMV
Bean dwarf mosaic virus		BDMV
Bean dwarf mosaic virus	M88179, M88180	BDMV
Bean golden mosaic virus		BGMV
(Bean golden mosaic virus – Brazil; BGMV-BR)		
Bean golden mosaic virus – [Brazil]	M88686, M88687	BGMV-[BZ]
Bean golden yellow mosaic virus		BGYMV
(Bean golden mosaic virus – Puerto Rico; BGMV-PR)		
Bean golden yellow mosaic virus [Dominican Republic]	L01635, L01636	BGYMV-[DO]
(Bean golden mosaic virus – Puerto Rico [Dominican Republic]; BGMV-PR[DO])		
(Bean golden mosaic virus – Dominican Rep.; BGMV-DO)		
Bean golden yellow mosaic virus – [Guatemala]	M91604, M91605	BGYMV-[GT]

(*continued*)

Table 2 (*continued*)

Species[a]	Accession number	Acronym
(Bean golden mosaic virus – Puerto Rico [Guatemala]; BGMV-PR[GT])		
(Bean golden mosaic virus – Guatemala; BGMV-GT)		
Bean golden yellow mosaic virus – [Mexico]	AF173555, AF173556	BGYMV-[MX]
Bean golden yellow mosaic virus – [Puerto Rico]	M10070, M10080	BGYMV-[PR]
(Bean golden mosaic virus – Puerto Rico; BGMV-[PR])		
Bean golden yellow mosaic virus – [Puerto Rico – Japan]	D00200, D00201	BGYMV-[PR-JP]
Bhendi yellow vein mosaic virus		BYVMV
(Okra yellow vein mosaic virus)		
Bhendi yellow vein mosaic virus – [301]	AJ002453	BYVMV-[301]
Bhendi yellow vein mosaic virus – [Madurai]	AF241479	BYVMV-[Mad]
Cabbage leaf curl virus		CaLCuV
Cabbage leaf curl virus	U65529, U65530	CaLCuV
Chayote yellow mosaic virus		ChaYMV
Chayote yellow mosaic virus	AJ223191	ChaYMV
Chilli leaf curl virus		ChiLCuV
Chilli leaf curl virus – [Multan]	AF336806	ChiLCuV-[Mul]
Chino del tomate virus		CdTV
(Tomato leaf crumple virus; ToLCrV)		
Chino del tomate virus	U57458, AF007823	CdTV
(Tomato leaf crumple virus; ToLCRV)		
Chino del tomate virus – [B52]	AF226666	CdTV-[B52]
Chino del tomate virus – [H6]	AF226665	CdTV-[H6]
Chino del tomate virus – [H8]	AF226664	CdTV-[H8]
Chino del tomate virus – [IC]	AF101476, AF101478	CdTV-[H8]
Cotton leaf crumple virus		CLCrV
Cotton leaf crumple virus	unpublished	CLCrV
Cotton leaf curl Alabad virus		CLCuAV
(Cotton leaf curl virus – Pakistan3; CLCuV-Pk3)		
Cotton leaf curl Alabad virus – [802a]	AJ002455	CLCuAV-[802a]
Cotton leaf curl Alabad virus – [804a]	AJ002452	CLCuAV-[804a]
Cotton leaf curl Gezira virus		ClCuGV
(Okra enation virus; OkEV)		
Cotton leaf curl Gezira virus	AF155064	CLCuGV
Cotton leaf curl Gezira virus – [Cotton]	AF260241	CLCuGV-[Cot]
Cotton leaf curl Gezira virus – [Okra/Egypt]	AY036010	CLCuGV-[Okr/EG]
Cotton leaf curl Gezira virus – [Okra/Gezira]	AY036006	CLCuGV-[Okr/Gez]
Cotton leaf curl Gezira virus – [Sida]	AY036007	CLCuGV-[Sida]
Cotton leaf curl Kokhran virus		CLCuKV
(Cotton leaf curl virus – Pakistan2; CLCuV-Pk2)		
(Pakistani cotton leaf curl virus)		
Cotton leaf curl Kokhran virus – [72b]	AJ002448	CLCuKV-[72b]
Cotton leaf curl Kokhran virus – [806b]	AJ002449	CLCuKV-[806b]
Cotton leaf curl Kokhran virus – [Faisalabad1]	AJ496286	CLCuKV-[Fai1]
(Cotton leaf curl virus – Pakistan2 [Faisalabad1]); CLCuV-PK2[Fai1])		

(*continued*)

Table 2 (*continued*)

Species[a]	Accession number	Acronym
Cotton leaf curl Multan virus		CLCuMV
(Cotton leaf curl virus – Pakistan1; CLCuV-Pk1)		
Cotton leaf curl Multan virus – [26]	AJ002458	CLCuMV-[26]
Cotton leaf curl Multan virus – [62]	AJ002447	CLCuMV-[62]
Cotton leaf curl Multan virus – [Faisalabad1]	X98995	CLCuMV-[Fai1]
(Cotton leaf curl virus – Pakistan1 [Faisalabad1]; CLCuV-PK1[Fai1])		
Cotton leaf curl Multan virus – [Faisalabad2]	AJ496287	CLCuMV-[Fai2]
(Cotton leaf curl virus – Pakistan1 [Faisalabad2]; CLCuV-PK1[Fai2])		
Cotton leaf curl Multan virus – [Faisalabad3]	AJ132430	CLCuMV-[Fai3]
Cotton leaf curl Multan virus – [Multan]	AJ496461	CLCuMV-[Mul]
(Cotton leaf curl virus – Pakistan1 [Multan]; CLCuV-PK1[Mul])		
Cotton leaf curl Multan virus – [Okra]	AJ002459	CLCuMV-[Ok]
(Cotton leaf curl virus – Pakistan1 [Okra]; CLCuV-PK1[Ok])		
Cotton leaf curl Rajasthan virus		CLCuRV
Cotton leaf curl Rajasthan virus	AF363011	CLCuRV
Cowpea golden mosaic virus		CPGMV
Cowpea golden mosaic virus – [Nigeria]	AF029217	CPGMV-[NG]
Cucurbit leaf curl virus		CuLCuV
Cucurbit leaf curl virus	AF224760, AF224761	CuLCuV
Cucurbit leaf curl virus – Arizona	AF256200, AF327559	CuLCuV-AZ
Dicliptera yellow mottle virus		DiYMoV
Dicliptera yellow mottle virus	AF170101, AF139168	DiYMoV
East African cassava mosaic Cameroon virus		EACMCV
East African cassava mosaic Cameroon virus – Cameroon	AF112354, AF112355	EACMCV-CM
East African cassava mosaic Cameroon virus – Cameroon [Ivory Coast]	AF259896, AF259897	EACMCV-CM[CI]
East African cassava mosaic Malawi virus		EACMMV
(East African cassava mosaic virus – Malawi, EACMV-MW)		
East African cassava mosaic Malawi virus – Malawi [K]	AJ006460	EACMMV-MW[K]
East African cassava mosaic Malawi virus – Malawi [MH]	AJ006459	EACMMV-MW[MH]
East African cassava mosaic virus		EACMV
East African cassava mosaic virus – [Kenya – k2B]	Z83258	EACMV-[KE-k2B]
East African cassava mosaic virus – [Tanzania]	Z83256	EACMV-[TZ]
East African cassava mosaic virus – [Uganda1]	AF230375	EACMV-[UG1]
East African cassava mosaic virus – Uganda2	Z83257	EACMV-UG2
(Uganda variant)		
East African cassava mosaic virus – Uganda2 Mild	AF126804	EACMV-UG2Mld
East African cassava mosaic virus – Uganda2 Severe	AF126806	EACMV-UG2Svr
East African cassava mosaic virus – Uganda3 Mild	AF126805	EACMV-UG3Mld
East African cassava mosaic virus – Uganda3 Severe	AF126807	EACMV-UG3Svr

(*continued*)

Table 2 (*continued*)

Species[a]	Accession number	Acronym
East African cassava mosaic Zanzibar virus		EACMZV
East African cassava mosaic Zanzibar virus	AF422174, AF422175	EACMZV
Eupatorium yellow vein virus		EpYVV
Eupatorium yellow vein virus	AB007990	EpYVV
Eupatorium yellow vein virus – [MNS2]	AJ438938	EpYVV-[MNS2]
Eupatorium yellow vein virus – [SOJ3]	AJ438939	EpYVV-[SOJ3]
Eupatorium yellow vein virus – [Tobacco]	E15418	EpYVV-[Tob]
Hollyhock leaf crumple virus		HLCrV
Hollyhock leaf crumple virus – [Cairo] (Hollyhock leaf curl virus; HLCuV)	AY036009	HLCrV-[Cai]
Hollyhock leaf crumple virus – [Giza] (Althea rosea enation virus; AREV)	AF014881	HLCrV-[Giz]
Honeysuckle yellow vein mosaic virus		HYVMV
Honeysuckle yellow vein mosaic virus	AB020781	HYVMV
Indian cassava mosaic virus		ICMV
Indian cassava mosaic virus	Z24758, Z24759	ICMV
Indian cassava mosaic virus – [Maharashtra]	AJ314740, AJ314739	ICMV-[Mah]
Ipomea yellow vein virus		IYVV
Ipomea yellow vein virus (Sweet potato leaf curl virus – [Ipo])	AJ132548	IYVV
Macroptilium mosaic Puerto Rico virus		MaMPRV
Macroptilium mosaic Puerto Rico virus	AY044133, AY044134	MaMPRV
Macroptilium mosaic Puerto Rico virus – [Bean]	AF449192, AF449193	MaMPRV-[Bea]
Macroptilium yellow mosaic Florida virus		MaYMFV
Macroptilium yellow mosaic Florida virus	AY044135, AY044136	MaYMFV
Macroptilium yellow mosaic virus		MaYMV
Macroptilium yellow mosaic virus – [Cuba]	AJ344452	MaYMV-[CU]
Malvastrum yellow vein virus		MYVV
Malvastrum yellow vein virus – [Y47]	AJ457824	MYVV-[Y47]
Melon chlorotic leaf curl virus		MCLCuV
Melon chlorotic leaf curl virus – [Guatemala]	AF325497	MCLCuV-[Gua]
Mungbean yellow mosaic India virus		MYMIV
Mungbean yellow mosaic India virus	AF126406, AF142440	MYMIV
Mungbean yellow mosaic India virus – [Bangladesh]	AF314145	MYMIV-[BG]
Mungbean yellow mosaic India virus – [Cowpea]	AF481865, AF503580	MYMIV-[Cp]
Mungbean yellow mosaic India virus – [Mungbean]	AF416742, AF416741	MYMIV-[Mg]
Mungbean yellow mosaic India virus – [Soybean]	AY049772, AY049771	MYMIV-[Sb]
Mungbean yellow mosaic India virus – [Soybean TN]	AJ416349, AJ420331	MYMIV-[SbTN]
Mungbean yellow mosaic virus		MYMV
Mungbean yellow mosaic virus	D14703, D14704	MYMV
Mungbean yellow mosaic virus – Soybean [Madurai]	AJ421642	MYMV-Sb[Mad]
Mungbean yellow mosaic virus – Thailand	AB017341	MYMV-TH
Mungbean yellow mosaic virus – Vigna	AJ132575, AJ132574	MYMV-Vig
Mungbean yellow mosaic virus – Vigna [Madurai]	AJ439057	MYMV-Vig[Mad]
Mungbean yellow mosaic virus – Vigna [Maharashtra]	AJ314530	MYMV-Vig[Mah]

(*continued*)

Table 2 (*continued*)

Species[a]	Accession number	Acronym
Okra yellow vein mosaic virus		OYVMV
Okra yellow vein mosaic virus – [201]	AJ002451	OYVMV-[201]
Papaya leaf curl virus		PaLCuV
Papaya leaf curl virus	Y15934	PaLCuV
Papaya leaf curl virus – [cotton]	AJ436992	PaLCuV-[Cot]
Pepper golden mosaic virus		PepGMV
(Serrano golden mosaic virus; SGMV)		
(Texas pepper virus; TPV)		
Pepper golden mosaic virus	U57457, AF499442	PepGMV
Pepper golden mosaic virus – [CR]	AF149227	PepGMV-[CR]
Pepper huasteco yellow vein virus		PHYVV
(Pepper huasteco virus; PHV)		
Pepper huasteco yellow vein virus	X70418, X70419	PHYVV
Pepper huasteco yellow vein virus – [Sinaloa]	AY044162, AY044163	PHYVV-[Sin]
Pepper leaf curl Bangladesh virus		PepLCBV
Pepper leaf curl Bangladesh virus	AF314531	PepLCBV
Pepper leaf curl virus		PepLCV
Pepper leaf curl virus	AF134484	PepLCV
Pepper leaf curl virus – [Malaysia]	AF414287	PepLCV-[MY]
Potato yellow mosaic Panama virus		PYMPV
Potato yellow mosaic Panama virus	Y15034, Y15033	PYMPV
(Potato yellow mosaic virus – Panama)		
(Tomato leaf curl virus – Panama; ToLCV-PA)		
Potato yellow mosaic Trinidad virus		PYMTV
Potato yellow mosaic Trinidad virus – Trinidad & Tobago	AF039031, AF039032	PYMTV-TT
Potato yellow mosaic virus		PYMV
Potato yellow mosaic virus – Venezuela	D00940, D00941	PYMV-VE
Potato yellow mosaic virus – [Guadeloupe]	AY120882, AY120883	PYMV-[GP]
Rhynchosia golden mosaic virus		RhGMV
Rhynchosia golden mosaic virus	AF239671	RhGMV
Rhynchosia golden mosaic virus – [Chiapas]	AF408199	RhGMV-[Chi]
Sida golden mosaic Costa Rica virus		SiGMCRV
Sida golden mosaic Costa Rica virus	X99550, X99551	SiGMCRV
Sida golden mosaic Florida virus		SiGMFV
Sida golden mosaic Florida virus – [A1]	U77963, AF039841	SiGMFV-[A1]
Sida golden mosaic Honduras virus		SiGMHV
Sida golden mosaic Honduras virus	Y11097, Y11098	SiGMHV
Sida golden mosaic virus		SiGMV
Sida golden mosaic virus	AF049336, AF039841	SiGMV
Sida golden yellow vein virus		SiGYVV
Sida golden yellow vein virus – [A11]	U77964	SiGYVV-[A11]
(Sida golden mosaic Florida virus – [A11])		
Sida mottle virus		SiMoV
Sida mottle virus – [Brazil]	AY090555	SiMoV-[BZ]

(*continued*)

Table 2 (*continued*)

Species[a]	Accession number	Acronym
Sida yellow mosaic virus		SiYMV
Sida yellow mosaic virus – [Brazil]	AY090558	SiYMV-[BZ]
Sida yellow vein virus		SiYVV
Sida yellow vein virus	Y11099, Y11100, Y11101	SiYVV
(Sida golden mosaic Honduras virus – yellow vein)		
South African cassava mosaic virus		SACMV
South African cassava mosaic virus	AF155807, AF155806	SACMV
South African cassava mosaic virus – [M12]	AJ422132	SACMV-[M12]
Soybean crinkle leaf virus		SbCLV
Soybean crinkle leaf virus – [Japan]	AB050781	SbCLV-[JP]
Squash leaf curl China virus		SLCCNV
Squash leaf curl China virus	AB027465	SLCCNV
Squash leaf curl virus		SLCV
Squash leaf curl virus	M38182, M38183	SLCV
Squash leaf curl Yunnan virus		SLCYV
Squash leaf curl Yunnan virus	AJ420319	SLCYV
Squash mild leaf curl virus		SMLCV
Squash mild leaf curl virus – [Imperial Valley]	AF421552, AF421553	SMLCV-[IV]
(Squash leaf curl virus-R; SLCV-R)		
Squash yellow mild mottle virus		SYMMoV
Squash yellow mild mottle virus – [CR]	AY064391, AF440790	SYMMoV-[CR]
Sri Lankan cassava mosaic virus		SLCMV
Sri Lankan cassava mosaic virus – [Colombo]	AF314738, AF314737	SLCMV-[Col]
Stachytarpheta leaf curl virus		StaLCV
Stachytarpheta leaf curl virus – [Hn5]	AJ495814	StaLCV-[Hn5]
Sweet potato leaf curl Georgia virus		SPLCGV
Sweet potato leaf curl Georgia virus – [16]	AF326775	SPLCGV-[16]
Sweet potato leaf curl virus		SPLCV
Sweet potato leaf curl virus	AF104036	SPLCV
Tobacco curly shoot virus		TbCSV
Tobacco curly shoot virus – [Y1]	AF240675	TbCSV-[Y1]
Tobacco curly shoot virus – [Y35]	AJ420318	TbCSV-[Y35]
Tobacco curly shoot virus – [Y41]	AJ457986	TbCSV-[Y41]
Tobacco leaf curl Japan virus		TbLCJV
(Tobacco leaf curl virus – Japan; TbLCV-JP)		
Tobacco leaf curl Japan virus	AB028604	TbLCJV
Tobacco leaf curl Japan virus – [JP2]	AB055008	TbLCJV-[JP2]
Tobacco leaf curl Kochi virus		TbLCKoV
Tobacco leaf curl Kochi virus – [KK]	AB055009	TbLCKoV-[KK]
Tobacco leaf curl Yunnan virus		TbLCYNV
Tobacco leaf curl Yunnan virus – [Y3]	AF240674	TbLCYNV-[Y3]
Tobacco leaf curl Zimbabwe virus		TbLCZV
Tobacco leaf curl Zimbabwe virus	AF350330	TbLCZV
Tomato chlorotic mottle virus		ToCMoV
Tomato chlorotic mottle virus – [Brazil]	AF490004, AF491306	ToCMoV-[BZ]
Tomato chlorotic mottle virus – Crumple	AY090557	ToCMoV-Cr

(*continued*)

Table 2 (*continued*)

Species[a]	Accession number	Acronym
Tomato golden mosaic virus		TGMV
Tomato golden mosaic virus – Common	M73794	TGMV-Com
Tomato golden mosaic virus – Yellow vein	K02029, K02030	TGMV-YV
Tomato golden mottle virus		ToGMoV
Tomato golden mottle virus – [GT94-R2]	AF132852	ToGMoV-[GT94-R2]
Tomato leaf curl Bangalore virus		ToLCBV
(Tomato leaf curl virus – Bangalore 1; TmLCV-Ban1)		
(Indian tomato leaf curl virus – Bangalore 1; ITmLCV-BanI)		
Tomato leaf curl Bangalore virus	Z48182	ToLCBV
Tomato leaf curl Bangalore virus – [Ban4]	AF165098	ToLCBV-[Ban4]
Tomato leaf curl Bangalore virus – [Ban5]	AF295401	ToLCBV-[Ban5]
Tomato leaf curl Bangalore virus – [Kolar]	AF428255	ToLCBV-[Kol]
Tomato leaf curl Bangladesh virus		ToLCBDV
Tomato leaf curl Bangladesh virus	AF188481	ToLCBDV
Tomato leaf curl Gujarat virus		ToLCGV
Tomato leaf curl Gujarat virus – [Kelloo]	AF449999	ToLCGV-[Kel]
Tomato leaf curl Gujarat virus – [Vadodara]	AF413671	ToLCGV-[Vad]
Tomato leaf curl Gujarat virus – [Varanasi]	unpublished	ToLCGV-[Var]
Tomato leaf curl Karnataka virus		ToLCKV
(Tomato leaf curl virus – Bangalore 2)		
(Indian tomato leaf curl virus – Bangalore II)		
Tomato leaf curl Karnataka virus	U38239	ToLCKV
Tomato leaf curl Laos virus		ToLCLV
Tomato leaf curl Laos virus	AF195782	ToLCLV
Tomato leaf curl Malaysia virus		ToLCMV
Tomato leaf curl Malaysia virus	AF327436	ToLCMV
Tomato leaf curl New Delhi virus		ToLCNDV
(Tomato leaf curl virus – New Delhi; ToLCV-ND)		
(Tomato leaf curl virus – India2, ToLCV-IN2)		
Tomato leaf curl New Delhi virus – [Lucknow]	Y16421, X89653	ToLCNDV-[Luc]
(Tomato leaf curl virus – New Delhi [Lucknow]; ToLCV-ND[Luc])		
Tomato leaf curl New Delhi virus – [Luffa]	AF102276	ToLCNDV-[Luf]
(Tomato leaf curl virus – New Delhi [Luffa]; ToLCV-ND[Luf])		
(Angled luffa leaf curl virus; ALLV)		
Tomato leaf curl New Delhi virus – Mild	U15016	ToLCNDV-Mld
(Tomato leaf curl virus – New Delhi [Mild]; ToLCV-Nde[Mld])		
Tomato leaf curl New Delhi virus [Severe]	U15015, U15017	ToLCNDV-Svr
(Tomato leaf curl virus – New Delhi [Severe]; ToLCV-Nde[Svr])		
Tomato leaf curl New Delhi virus – [Solanum]	unpublished	ToLCNDV-[Sol]
(Solanum yellow leaf curl virus; SYLCV)		

(*continued*)

Table 2 (*continued*)

Species[a]	Accession number	Acronym
Tomato leaf curl Sri Lanka virus		ToLCSLV
Tomato leaf curl Sri Lanka virus	AF274349	ToLCSLV
Tomato leaf curl Taiwan virus		ToLCTWV
(Tomato leaf curl virus – Taiwan; ToLCV-TW)		
Tomato leaf curl Taiwan virus	U88692	ToLCTWV
Tomato leaf curl Vietnam virus		ToLCVV
Tomato leaf curl Vietnam virus	AF264063	ToLCVV
Tomato leaf curl virus		ToLCV
(Tomato leaf curl virus – Australia; ToLCV-AU)		
Tomato leaf curl virus – [AU]	S53251	ToLCV
Tomato leaf curl virus – [Solanum species D1]	AF084006	ToLCV-[SpD1]
Tomato leaf curl virus – [Solanum species D2]	AF084007	ToLCV-[SpD2]
Tomato mosaic Havana virus		ToMHV
(Havana tomato mosaic virus)		
Tomato mosaic Havana virus – [Quivican]	Y14874, Y14875	ToMHV-[Qui]
Tomato mottle Taino virus		ToMoTV
Tomato mottle Taino virus	AF012300, AF012301	ToMoTV
Tomato mottle virus		ToMoV
Tomato mottle virus – [Florida]	L14460, L14461	ToMoV-[FL]
Tomato rugose mosaic virus		ToRMV
Tomato rugose mosaic virus	NC002555, NC002556	ToRMV
Tomato rugose mosaic virus – [Ube]	AF291705, AF291706	ToRMV-[Ube]
Tomato severe leaf curl virus		ToSLCV
Tomato severe leaf curl virus – [Guatemala 96-1]	AF130415	ToSLCV-[GT96-1]
Tomato severe rugose virus		ToSRV
Tomato severe rugose virus	AY029750	ToSRV
Tomato yellow leaf curl China virus		TYLCCNV
(Tomato yellow leaf curl virus – China; TYLCV-CN)		
Tomato yellow leaf curl China virus	AF311734	TYLCCNV
Tomato yellow leaf curl China virus – [Y64]	AJ457823	TYLCCNV-[Y64]
Tomato yellow leaf curl China virus – Tb [Y10]	AJ319675	TYLCCNV-Tb[Y10]
Tomato yellow leaf curl China virus – Tb [Y11]	AJ319676	TYLCCNV-Tb[Y11]
Tomato yellow leaf curl China virus – To [Y25]	AJ457985	TYLCCNV-Tb[Y25]
Tomato yellow leaf curl China virus – Tb [Y36]	AJ420316	TYLCCNV-Tb[Y36]
Tomato yellow leaf curl China virus – Tb [Y38]	AJ420317	TYLCCNV-Tb[Y38]
Tomato yellow leaf curl China virus – Tb [Y5]	AJ319674	TYLCCNV-Tb[Y5]
Tomato yellow leaf curl China virus – Tb [Y8]	AJ319677	TYLCCNV-Tb[Y8]
Tomato yellow leaf curl Gezira virus		TYLCGV
Tomato yellow leaf curl Gezira virus – [1]	AY044137	TYLCGV-[1]
Tomato yellow leaf curl Gezira virus – [2]	AY044138	TYLCGV-[2]
Tomato yellow leaf curl Gezira virus – [Shambat]	AY044139	TYLCGV-[Sha]
Tomato yellow leaf curl Malaga virus		TYLCMalV
Tomato yellow leaf curl Malaga virus	AF271234	TYLCMalV
Tomato yellow leaf curl Sardinia virus		TYLCSV
(Tomato yellow leaf curl virus – Sardinia; TYLCV-Sar)		

(*continued***)**

Table 2 (*continued*)

Species[a]	Accession number	Acronym
Tomato yellow leaf curl Sardinia virus	X61153	TYLCSV
(Tomato yellow leaf curl virus – Sardinia; TYLCV-Sar)		
Tomato yellow leaf curl Sardinia virus – Spain [1]	Z25751	TYLCSV-ES[1]
(Tomato yellow leaf curl virus – Sardinia [Spain1]; TYLCV-Sar[ES1])		
(Tomato yellow leaf curl virus – Spain, TYLCV-Sp)		
Tomato yellow leaf curl Sardinia virus – Spain [2]	L27708	TYLCSV-ES[2]
(Tomato yellow leaf curl virus – Sardinia [Spain2]; TYLCV-Sar[ES2])		
(Tomato yellow leaf curl virus – Almeria, TYLCV-Almeria)		
Tomato yellow leaf curl Sardinia virus – Sicily	Z28390	TYLCSV-Sic
(Tomato yellow leaf curl virus – Sardinia [Sicily]; TYLCV-Sar[Sic])		
(Tomato yellow leaf curl virus – Sicily, TYLCV-SY)		
Tomato yellow leaf curl Thailand virus		TYLCTHV
(Tomato yellow leaf curl virus – Thailand; TYLCV-TH)		
Tomato yellow leaf curl Thailand virus – [1]	X63015, X63016	TYLCTHV-[1]
(Tomato yellow leaf curl virus – Thailand [1]; TYLCV-TH-[1])		
Tomato yellow leaf curl Thailand virus – [2]	AF141922, AF141897	TYLCTHV-[2]
(Tomato yellow leaf curl virus – Thailand – [2]; TYLCV-TH-[2])		
Tomato yellow leaf curl Thailand virus – [Myanmar]	AF206674	TYLCTHV-[MM]
Tomato yellow leaf curl Thailand virus – [Y72]	AJ495812	TYLCTHV-[Y72]
Tomato yellow leaf curl virus		TYLCV
Tomato yellow leaf curl virus	X15656	TYLCV
(Tomato yellow leaf curl virus – Israel; TYLCV-IL)		
Tomato yellow leaf curl virus – [Almeria]	AJ489258	TYLCV-[Alm]
Tomato yellow leaf curl virus – [Aichi]	AB014347	TYLCV-[Aic]
(Tomato yellow leaf curl virus – Israel [Aichi]; TYLCV-IL[Ai])		
Tomato yellow leaf curl virus – [Cuba]	AJ223505	TYLCV-[CU]
(Tomato yellow leaf curl virus – Israel [Cuba]; TYLCV-IL[CU])		
Tomato yellow leaf curl virus – [Dominican Republic]	AF024715	TYLCV-[DO]
(Tomato yellow leaf curl virus – Israel [DO]; TYLCV-IL[DO])		
Tomato yellow leaf curl virus – [Portugal]	AF105975	TYLCV-[PT]
(Tomato yellow leaf curl virus – Israel [Portugal]; TYLCV-IL[PT])		
Tomato yellow leaf curl virus – [Saudi Arabia]		TYLCV-[SA]
(Tomato yellow leaf curl virus – Israel [Saudi Arabia1]; TYLCV-IL[SA1])		
(Tomato yellow leaf curl virus – Northern Saudi Arabia; TYLCV-NSA)		
Tomato yellow leaf curl virus – [Shizuokua]	AB014346	TYLCV-[Shi]

(*continued*)

Table 2 (*continued*)

Species[a]	Accession number	Acronym
(Tomato yellow leaf curl virus – Israel [Shizuokua]; TYLCV-IL[Shi])		
Tomato yellow leaf curl virus – [Spain7297]	AF071228	TYLCV-[ES7297]
(Tomato yellow leaf curl virus – Israel [Spain7297]; TYLCV-IL[ES7297])		
Tomato yellow leaf curl virus – Iran	AJ132711	TYLCV-IR
(Tomato yellow leaf curl virus – Israel [Iran]; TYLCV-IL[IR])		
Tomato yellow leaf curl virus – Mild	X76319	TYLCV-Mld
(Tomato yellow leaf curl virus – Israel [Mild]; TYLCV-IL[Mld])		
Tomato yellow leaf curl virus – Sudan	AY044138	TYLCV-SD
Watermelon chlorotic stunt virus		WmCSV
Watermelon chlorotic stunt virus	AJ012081, AJ012082	WmCSV-[IR]
Watermelon chlorotic stunt virus – [IR]	AJ245652, AJ245653	WmCSV-[IR]
Watermelon chlorotic stunt virus – [SD]	AJ245650, AJ245651	WmCSV-[SD]

Tentative species[b]	Acronym
Acalypha yellow mosaic virus	AYMV
Asystasia golden mosaic virus	AGMV
Cotton yellow mosaic virus	CtYMV
Croton yellow vein mosaic virus	CYVMV
Dolichos yellow mosaic virus	DoYMV
Eclipta yellow vein virus	EYVV
Eggplant yellow mosaic virus	EYMV
Euphorbia mosaic virus	EuMV
Horsegram yellow mosaic virus	HgYMV
Jatropha mosaic virus	JMV
Leonurus mosaic virus	LeMV
Limabean golden mosaic virus	LGMV
Lupin leaf curl virus	LLCuV
Macroptilium golden mosaic virus	MGMV
Macroptilium golden mosaic virus – [Jamaica1]	MGMV-[JM1]
Macroptilium golden mosaic virus – [Jamaica2]	MGMV-[JM2]
Macroptilium golden mosaic virus – [PR]	MGMV-[PR]
Macrotyloma mosaic virus	MaMV
Malvaceous chlorosis virus	MCV
Melon leaf curl virus	MLCuV
Okra leaf curl India virus	OkLCuIV
(Okra leaf curl virus – India; OLCV-IN)	
Okra leaf curl virus	OkLCuV
(Okra leaf curl virus [Ivory Coast]; OLCV-[CI])	
Okra mosaic Mexico virus	OkMMV
Pepper mild tigré virus	PepMTV
Pseuderanthemum yellow vein virus	PYVV
Sida golden mosaic Jamaica virus	SiGMJV
Sida golden mosaic Jamaica virus	SiGMJV

(*continued*)

Table 2 (*continued*)

Tentative species[b]	Acronym
Sida golden mosaic Jamaica virus – [3]	SiGMJV-[3]
Sida golden mosaic Jamaica virus – [Macroptilium 19]	SiGMJV-[Mac19]
Solanum apical leaf curl virus	SALCV
Tobacco apical stunt virus	TbASV
Tomato curly stunt virus	ToCSV
Tomato dwarf leaf curl virus	ToDLCV
Tomato leaf curl India virus	ToLCIV
(Tomato leaf curl virus – India; ToLCV-IN)	
Tomato leaf curl Indonesia virus	ToLCIDV
Tomato leaf curl Nicaragua virus	ToLCNV
Tomato leaf curl Philippines virus	ToLCPV
Tomato leaf curl Senegal virus	
(Tomato leaf curl virus – Senegal; ToLCV-SN)	ToLCSV
Tomato leaf curl Sinaloa virus	ToLCSinV
(Tomato leaf curl virus – Sinaloa; ToLCV-Sin)	
(Sinaloa tomato leaf curl virus, STLCV)	
Tomato leaf curl Tanzania virus	ToLCTZV
(Tomato leaf curl virus – Tanzania; ToLCV-TZ)	
Tomato mosaic Barbados virus	ToMBV
Tomato Uberlandia virus	ToUV
Tomato yellow dwarf virus	ToYDV
Tomato yellow leaf curl Kuwait virus	TYLCKWV
Tomato yellow leaf curl Nigeria virus	TYLCNV
(Tomato yellow leaf curl virus – Nigeria; TYLCV-NG)	
Tomato yellow leaf curl Saudi Arabia virus	TYLCSAV
(Tomato yellow leaf curl virus – Saudi Arabia; TYLCV-SA)	
(Tomato yellow leaf curl virus – Southern Saudi Arabia; TYLCV-SSA)	
Tomato yellow leaf curl Tanzania virus	TYLCTZV
(Tomato yellow leaf curl virus – Tanzania; TYLCV-TZ)	
Tomato yellow leaf curl Yemen virus	TYLCYV
(Tomato yellow leaf curl virus – Yemen; TYLCV-YE)	
Tomato yellow mosaic virus	ToYMV
Tomato yellow mosaic virus – Brazil [1]	ToYMV-BR[1]
Tomato yellow mosaic virus – Brazil [2]	ToYMV-BR[2]
Tomato yellow mottle virus	ToYMoV
Tomato yellow vein streak virus	ToYVSV
(Tomato yellow vein streak virus – Brazil; ToYVSV-BR)	
Watermelon curly mottle virus	WmCMoV
Wissadula golden mosaic virus	WGMV
Zinnia leaf curl virus	ZiLCuV

[a] Species key: ***Bold***: unchanged from the Seventh Report; *Underline*: name change of species appearing in the Seventh Report; *Normal*: new species

[b] Tentative species key: **Bold**: unchanged from the Seventh Report; Underline: downgraded from species in the Seventh Report to tentative species; Normal: new tentative species

Guidelines with which to demarcate begomovirus species

It is proposed to retain biological criteria as possible indicators of taxonomic status although limitations to their predictive value will be made clear (Table 1). Nucleotide sequence comparisons will play a much greater role in determining taxonomic status. Because DNA B components can be exchanged between some begomoviruses, it is proposed that only DNA A components are considered in the first instance. That some viruses have only a DNA A component strengthens this argument. The high recombination frequency that is known to occur between different begomovirus species invalidates the use of small genomic fragments for comparison. Hence, it is proposed that only full-length DNA A sequences are considered for comparative analyses. Analysis of more than 200 such sequences indicates that a figure of 89% sequence identity is the most suitable to distinguish species from strains [10]. However the high frequency of inter-species recombination complicates the partition between strains and species. Currently there is no genetic basis that may be used to assess the contribution of recombination to species demarcation, therefore overall sequence identity will be used in the first instance. Above 89% identity, virus isolates may be considered to belong to the same species. Biological differences may justify strain designation, and the name would then be supplemented with the relevant information. Although this rule is based on the analysis of begomoviruses, it will also be applied to curtoviruses and topocuviruses, which have basically similar genome organizations. Mastreviruses show several fundamental differences in their genome organization and host range characteristics, for which reason the previously established cut-off figure of 75% for species demarcation will be retained.

Updating the list of geminivirus species and tentative species

Taking into account the revised guidelines (Table 1), the entire list of begomovirus DNA A components for which full-length nucleotide sequences are available has been revisited. Begomoviruses that have a pairwise identity value above or below 89% when compared with previously established species have been classified accordingly. Viruses for which there is insufficient information to allow designation as species have been downgraded to the level of tentative species. A revised list of all begomovirus species and tentative species, based on the list of approved viruses appearing in the Seventh Report of the ICTV [20] and updated according to these proposals and the suggested name changes, and including newly described viruses, is provided in Table 2. The lists of curtovirus, topocuvirus and mastrevirus species are unaffected by the proposed changes.

References

1. Bedford ID, Briddon RW, Brown JK, Rosell RC, Markham PG (1994) Geminivirus-transmission and biological characterization of *Bemisia tabaci* (Gennadius) biotypes from different geographic regions. Ann Appl Biol 125: 311–325
2. Briddon RW, Bedford ID, Tsai JH, Markham PG (1996) Analysis of the nucleotide sequence of the treehopper-transmitted geminivirus, tomato pseudo-curly top virus, suggests a recombinant origin. Virology 219: 387–394
3. Briddon RW, Markham PG (2001) Complementation of bipartite begomovirus movement functions by topocuviruses and curtoviruses. Arch Virol 146: 1811–1819
4. Briddon RW, Mansoor S, Bedford ID, Pinner MS, Saunders K, Stanley J, Zafar Y, Malik KA, Markham PG (2001) Identification of DNA components required for induction of cotton leaf curl disease. Virology 285: 234–243
5. Brown JK (1994) The status of *Bemisia tabaci* (Genn.) as a pest and vector in world agroecosystems. FAO Plant Prot Bull 42: 3–32
6. Brown JK (2000) Molecular markers for the identification and global tracking of whitefly vector-begomovirus complexes. Virus Res 71: 233–260
7. Brown JK (2001) The molecular epidemiology of begomoviruses. Pages 279–316 In: Khan JA, Dykstra J, Trends in Plant Virology. Haworth Press, Inc., New York, 537 pp

8. Czosnek H, Laterrot H (1997) A worldwide survey of tomato yellow leaf curl viruses. Arch Virol 142: 1391–1406
9. Fauquet CM, Maxwell DP, Gronenborn B, Stanley J (2000) Revised proposal for naming geminiviruses. Arch Virol 145: 1743–1761
10. Fauquet CM (2002) The best sequence threshold criterion for geminivirus species demarcation. www.danforthcenter.org/iltab/geminiviridae/spdem
11. Fontes EPB, Eagle PA, Sipe PS, Luckow VA, Hanley-Bowdoin L (1994) Interaction between a geminivirus replication protein and origin DNA is essential for viral replication. J Biol Chem 269: 8459–8465
12. Frischmuth T, Roberts S, von Arnim A, Stanley J (1993) Specificity of bipartite geminivirus movement proteins. Virology 196: 666–673
13. Gilbertson RL, Hidayat SH, Paplomatas EJ, Rojas MR, Hou Y-M, Maxwell DP (1993) Pseudorecombination between infectious cloned DNA components of tomato mottle and bean dwarf mosaic geminiviruses. J Gen Virol 74: 23–31
14. Murphy FA, Fauquet CM, Bishop DHL, Ghabrial SA, Jarvis AW, Martelli GP, Mayo MA, Summers MD (eds) (1995) Virus Taxonomy – The Classification and Nomenclature of Viruses: Sixth Report of the International Committee on Taxonomy of Viruses. Springer Wien New York
15. Padidam M, Beachy RN, Fauquet CM (1995) Classification and identification of geminiviruses using sequence comparisons. J Gen Virol 76: 249–263
16. Padidam M, Sawyer S, Fauquet CM (1999) Possible emergence of new geminiviruses by frequent recombination. Virology 265: 218–224
17. Polston JE, Anderson PK (1997) The emergence of whitefly-transmitted geminiviruses in tomato in the western hemisphere. Plant Dis 81: 1358–1369
18. Pringle CR (1999) Virus taxonomy – 1999 – The universal system of virus taxonomy, updated to include the new proposals ratified by the International Committee on Taxonomy of Viruses during 1998. Arch Virol 144: 421–429
19. Rybicki EP (1994) A phylogenetic and evolutionary justification for three genera of *Geminiviridae*. Arch Virol 139: 49–77
20. Rybicki EP, Briddon RW, Brown JE, Fauquet CM, Maxwell DP, Harrison BD, Markham PG, Stanley J (2000) *Geminiviridae*. In: van Regenmortel MHV, Fauquet CM, Bishop DHL, Carstens E, Estes MK, Lemon S, Maniloff J, Mayo MA, McGeoch D, Pringle CR, Wickner RB (eds) Virus Taxonomy. Seventh Report of the International Committee on Taxonomy of Viruses. Academic Press, New York, pp 285–297
21. Saunders K, Stanley J (1995) Complementation of African cassava mosaic virus *AC2* gene function in a mixed bipartite geminivirus infection. J Gen Virol 76: 2287–2292
22. Saunders K, Bedford ID, Briddon RW, Markham PG, Wong SM, Stanley J (2000) A unique virus complex causes *Ageratum* yellow vein disease. Proc Natl Acad Sci USA 97: 6890–6895
23. Saunders K, Salim N, Mali VR, Malathi VG, Briddon R, Markham PG, Stanley J (2002) Characterisation of *Sri Lankan cassava mosaic virus* and *Indian cassava mosaic virus*: evidence for acquisition of a DNA B component by a monopartite begomovirus. Virology 293: 63–74
24. van Regenmortel MHV (1990) Virus species, a much overlooked but essential concept in virus classification. Intervirology 31: 241–254

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