This form should be used for all taxonomic proposals. Please complete all those modules that are applicable (and then delete the unwanted sections). For guidance, see the notes written in blue and the separate document "Help with completing a taxonomic proposal"

Please try to keep related proposals within a single document; you can copy the modules to create more than one genus within a new family, for example.

MODULE 1: TITLE, AUTHORS, etc

Code assigned:	***2016.021a-kP***	(to be completed by ICTV officers)

Short title: Establishment of a family of single-stranded DNA satellites with two genera
(e.g. 6 new species in the genus *Zetavirus*)

Modules attached (modules 1 and 11 are required)	**2** ☐ **3** ☐ **4** ☐ **5** ☐ **6** ☐ **7** ☐ **8** ☐ **9** ☐ **10** ☐

Author(s):

R.W. Briddon, J. Navas-Castillo and E. Fiallo-Olivé on behalf of the *Geminiviridae* SG

Corresponding author with e-mail address:

rob.briddon@gmail.com, jnavas@eelm.csic.es, efiallo@eelm.csic.es

List the ICTV study group(s) that have seen this proposal:

A list of study groups and contacts is provided at http://www.ictvonline.org/subcommittees.asp . If in doubt, contact the appropriate subcommittee chair (fungal, invertebrate, plant, prokaryote or vertebrate viruses)	*Geminiviridae* SG

ICTV Study Group comments (if any) and response of the proposer:

Date first submitted to ICTV: August 2016
Date of this revision (if different to above):

ICTV-EC comments and response of the proposer:

MODULE 2: **NEW SPECIES**

creating and naming one or more new species.

If more than one, they should be a group of related species belonging to the same genus. All new species must be placed in a higher taxon. This is usually a genus although it is also permissible for species to be "unassigned" within a subfamily or family. Wherever possible, provide sequence accession number(s) for **one** isolate of each new species proposed.

Code	***2016.021aP***

(assigned by ICTV officers)

To create 61 new species within:

Genus:	***Betasatellite* (new)**
Subfamily:	
Family:	***Tolecusatellitidae* (new)**
Order:	

Fill in all that apply.

- If the higher taxon has yet to be created (in a later module, below) write "**(new)**" after its proposed name.
- If no genus is specified, enter "**unassigned**" in the genus box.

Name of new species:	**Representative isolate:** (only 1 per species please)	**GenBank sequence accession number(s)**
Ageratum leaf curl Buea betasatellite	ALCuBB-[CM-LIO1-SatB33-09]	FR717140
Ageratum leaf curl Cameroon betasatellite	ALCuCMB-[CM-Man-AMBF-06]	FM164737
Ageratum yellow leaf curl betasatellite	AYLCB-[PK-Fai4-00]	AJ316026
Ageratum yellow vein betasatellite	AYVB-[SG-95]	AJ252072
Ageratum yellow vein India betasatellite	AYVINB-[IN-Mad-03]	AJ557441
Ageratum yellow vein Sri Lanka betasatellite	AYVSLB-[SL-Ag-03]	AJ542498
Alternanthera yellow vein betasatellite	AlYVB-[VN-Hue-05]	DQ641716
Andrographis yellow vein leaf curl betasatellite	AnYVLCuB-[IN-Luc-10]	KC967282
Bhendi yellow vein mosaic betasatellite	BYVB-[IN-Mut-00]	AJ308425
Cardiospermum yellow leaf curl betasatellite	CaYLCuB-[SL-04]	AM933578
Chili leaf curl betasatellite	ChLCuB-[PK-MC-97]	AJ316032
Chili leaf curl Jaunpur betasatellite	ChLCuJB-[IN-Jau-07]	HM007103
Chili leaf curl Sri Lanka betasatellite	ChLCuSLB-[SL-Mih-09]	JN638445
Cotton leaf curl Gezira betasatellite	CLCuGeB-[SD-Dat-06]	DQ644564
Cotton leaf curl Multan betasatellite	CLCuMuB-[PK-Mul-U89-97]	AJ298903
Croton yellow vein mosaic betasatellite	CroYVMB-[PK-Pun-06]	AM410551

Eupatorium yellow vein betasatellite	EpYVB-[JR-MNS2-00]	AJ438938
Eupatorium yellow vein mosaic betasatellite	EpYVV-[JR-Suya-03]	AB300464
French bean leaf curl betasatellite	FBLCuB-[IN-Kan-11]	JQ866298
Hedyotis yellow mosaic betasatellite	HYMB-[VN-BinhDinh-13]	KF641186
Honeysuckle yellow vein betasatellite	HYVB-[UK-Nor1-99]	AJ316040
Honeysuckle yellow vein mosaic betasatellite	HYVMB-[JR-Hy-04]	AB182263
Malvastrum leaf curl betasatellite	MaLCuB-[CN-Gx87-04]	AM072289
Malvastrum leaf curl Guangdong betasatellite	MaLCuGuB-[CN-Gua-11]	KF912951
Momordica yellow mosaic betasatellite	MamYMB-[BJ-57-14-14]	KT454829
Mirabilis leaf curl betasatellite	MiLCuB-[IN-Him-13]	LK054803
Mungbean yellow mosaic betasatellite	MYMB-[IN-Cowpea-12]	JX443646
Okra leaf curl Oman betasatellite	OLCuOMB-[OM-Barka-12]	KF267444
Papaya leaf curl betasatellite	PaLCuB-[IN-ND-03]	AY244706
Papaya leaf curl China betasatellite	PaLCuCNB-[CN-Hainan-14]	KJ642219
Papaya leaf curl India betasatellite	PaLCuINA-[India-Panipat-08]	HM143906
Rose leaf curl betasatellite	RoLCuB-[PK-Fai-06]	GQ478344
Rhynchosia yellow mosaic betasatellite	RhYMB-[IN-Pha-14]	KP752092
Siegesbeckia yellow vein betasatellite	SiYVB-[CN-FZ02-12]	KF499590
Tobacco curly shoot betasatellite	TobCSB-[CN-Yn35-01]	AJ421484
Tobacco leaf curl betasatellite	TobLCuB-[PK-Lah-04]	AM260465
Tobacco leaf curl Patna betasatellite	TobLCuPatB-[IN-Pusa-09]	HQ180394
Tomato leaf curl betasatellite	ToLCB-[PK-RYK-97]	AJ316036
Tomato leaf curl Bangalore betasatellite	ToLCBaB-[IN-Ban-03]	AY428768
Tobacco leaf curl Japan betasatellite	TbLCJRB-[JR-Miy-05]	AB236324
Tomato leaf curl Bangladesh betasatellite	ToLCBDB-[BD-Gaz-01]	AJ542489
Tomato leaf curl China betasatellite	ToLCCNB-[CN-Gx14-02]	AJ704609
Tomato leaf curl Gandhinagar betasatellite	ToLCGanB-[IN-pToGNbH14-12]	KC952006

Tomato leaf curl Java virus betasatellite	ToLCJaB-[NP-R7-Papaya-2010]	KC282642
Tomato leaf curl Joydebpur betasatellite	ToLCJoB-[BD-Gaz-05]	AJ966244
To mato leaf curl Laguna betasatellite	ToLCLaB-[PH-Lag2-06]	AB307732
Tomato leaf curl Laos betasatellite	ToLCLAB-[LA-Sav-01]	AJ542491
Tomato leaf curl Malaysia betasatellite	ToLCMYB-[MY-13]	KM051528
Tomato leaf curl Nepal betasatellite	ToLCNPB-[NP-Jhapa]	AJ542492
Tomato leaf curl Patna betasatellite	ToLCPaB-[IN-Pat-07]	EU862324
Tomato leaf curl Philippine betasatellite	ToLCPHB-[PH-Lag1-06]	AB308071
Tomato leaf curl Sri Lanka betasatellite	ToLCSLB-[SL]	AJ542493
Tomato leaf curl Yemen betasatellite	ToLCYEB-[YE-tob56-89]	JF919717
Tomato yellow leaf curl China betasatellite	TYLCCNB-[CN-Yn45-01]	AJ420313
Tomato yellow leaf curl Rajasthan betasatellite	ToLCRaB-[IN-Raj-03]	AY438558
Tomato yellow leaf curl Shandong betasatellite	ToYLCShB-[CN-SDSG-14]	KP322555
Tomato yellow leaf curl Thailand betasatellite	TYLCTHB-[CN-Yn72-02]	AJ566746
Tomato yellow leaf curl Vietnam betasatellite	TYLCVNB-[VN-Han-05]	DQ641714
Tomato yellow leaf curl Yunnan betasatellite	ToYLCYnB-[CN-tob-]	KF640694
Vernonia yellow vein Fujian betasatellite	VYVFuB-[CN-09]	JF733779
Vernonia yellow vein betasatellite	VYVB-[IN-Mad-09]	FN435836

Reasons to justify the creation and assignment of the new species:

- Explain how the proposed species differ(s) from all existing species.
  - If species demarcation criteria (see module 3) have previously been defined for the genus, **explain how the new species meet these criteria**.
  - If criteria for demarcating species need to be defined (because there will now be more than one species in the genus), please state the proposed criteria.
- Further material in support of this proposal may be presented in the Appendix, Module 11

Due to the rising number of betasatellites being described, owing mainly to the increasing interest in begomovirus-betasatellite complexes, there is an urgent need for a robust and workable system of nomenclature and classification of these components. Since these satellite molecules are not independent entities, relying on a helper virus for their spread, the biological data useful for their classification that can unequivocally be attributed to the satellite molecule are limited and uninformative. It is thus necessary to base a classification system entirely on their nucleotide sequences, which could potentially be adjusted once biological evidence becomes available. Exhaustive pairwise comparisons of the ~1,100 sequences now available in databases resulted in the plot shown in Figure 1. Of the possible percentage cut-off values, only 91% was found to produce an acceptable number of species within the known diversity.

The 61 betasatellite species described here:

1. All have the distinctive organization consisting of an adenine rich (A-rich) region, a single conserved coding sequence (the betaC1 gene) and a sequence well conserved between all betasatellites (the satellite conserved region).
2. All are associated with either a begomovirus or a mastrevirus.

All taxa proposed as new species meet the proposed species demarcation threshold of <91% nucleotide sequence identity based on full-length sequences, when implementing the Muscle alignment method to compute pairwise identity comparisons (one minus Hamming distances of pairwise aligned sequences with pairwise deletion of gaps). This is the approach recently described by the *Geminiviridae* Study Group for the six main genera in the family (Brown *et al.*, 2015; Muhire *et al.*, 2013; Varsani *et al.*, 2014a, b). Previously a manuscript published by the *Geminiviridae* Study Group had proposed a 78% nucleotide sequence cut-off using a ClustalV algorithm (Briddon et al., 2008). The grouping of sequences using the now proposed 91% nucleotide sequence cut-off maintains, for the most part, the species outlined in the earlier publication. The species names established by this earlier publication are now in widespread use in the geminivirus community and every effort has been made to maintain these names.

MODULE 2: **NEW SPECIES**

creating and naming one or more new species.

If more than one, they should be a group of related species belonging to the same genus. All new species must be placed in a higher taxon. This is usually a genus although it is also permissible for species to be "unassigned" within a subfamily or family. Wherever possible, provide sequence accession number(s) for **one** isolate of each new species proposed.

Code	***2016.021bP***	(assigned by ICTV officers)

To create 11 new species within:

Genus:	***Deltasatellite* (new)**
Subfamily:	
Family:	***Tolecusatellitidae* (new)**
Order:	

Fill in all that apply.

- If the higher taxon has yet to be created (in a later module, below) write "**(new)**" after its proposed name.
- If no genus is specified, enter "**unassigned**" in the genus box.

Name of new species:	**Representative isolate:** (only 1 per species please)	**GenBank sequence accession number(s)**
Croton yellow vein deltasatellite	CrYVD-[IN-09]	AJ968684
Malvastrum leaf curl deltasatellite	MaLCuD-[PH-12]	KF433066
Sida golden yellow vein deltasatellite 1	SiGYVD1-[CU-177H1-09]	JN986808
Sida golden yellow vein deltasatellite 2	SiGYVD2-[CU-228H1-09]	JN819490
Sida golden yellow vein deltasatellite 3	SiGYVD3-[CU-412N1-10]	JN819498
Sweet potato leaf curl deltasatellite 1	SPLCD1-[ES-SBG51-02]	FJ914390
Sweet potato leaf curl deltasatellite 2	SPLCD2-[VE-1764E13-09]	KF716173
Sweet potato leaf curl deltasatellite 3	SPLCD3-[PR-T1_1-10]	KT099179
Tomato leaf curl deltasatellite	ToLCD-[AU-96]	U74627
Tomato yellow leaf distortion deltasatellite 1	ToYLDD1-[CU-404N1-10]	JN819495
Tomato yellow leaf distortion deltasatellite 2	ToYLDD2-[CU-603N1-11]	KU232893

Reasons to justify the creation and assignment of the new species:

- Explain how the proposed species differ(s) from all existing species.
  - If species demarcation criteria (see module 3) have previously been defined for the genus, **explain how the new species meet these criteria.**
  - If criteria for demarcating species need to be defined (because there will now be more than one species in the genus), please state the proposed criteria.
- Further material in support of this proposal may be presented in the Appendix, Module 11

Although there are not many sequences of deltasatellites available (142 published and/or submitted to public databases) to determine a robust species demarcation threshold, the use of the 91% threshold of betasatellites yields the range of species that would be expected based on sequence variation, host plant, and geographic location. This is also well supported by phylogenetic analysis. The 91% species demarcation threshold should be considered a temporary value awaiting further information on the diversity of these molecules.

MODULE 3: **NEW GENUS**

creating a new genus

Ideally, a genus should be placed within a higher taxon.

Code	***2016.021cP***	(assigned by ICTV officers)

To create a new genus within:

Subfamily:	
Family:	***Tolecusatellitidae***
Order:	

Fill in all that apply.

- If the higher taxon has yet to be created (in a later module, below) write "**(new)**" after its proposed name.
- If no family is specified, enter "**unassigned**" in the family box

naming a new genus

Code	***2016.021dP***	(assigned by ICTV officers)

To name the new genus: *Betasatellite*

Assigning the type species and other species to a new genus

Code	***2016.021eP***	(assigned by ICTV officers)

To designate the following as the type species of the new genus

Ageratum yellow vein betasatellite	Every genus must have a type species. This should be a well characterized species although not necessarily the first to be discovered

The new genus will also contain any other new species created and assigned to it (Module 2) and any that are being moved from elsewhere (Module 7b). **Please enter here the TOTAL number of species (including the type species) that the genus will contain:**

61 (sixty-one)

Reasons to justify the creation of a new genus:

Additional material in support of this proposal may be presented in the Appendix, Module 11

Betasatellites are important host range and symptom determining molecules (satellites) that associate with either begomoviruses or mastreviruses of the family *Geminiviridae*. They are highly diverse and geographically widespread in the Old World. So far no genus of DNA satellites has been established. To support a rational taxonomy and nomenclature requires the division of satellites into groups (genera).

Origin of the new genus name:

When they were first identified these satellites were referred to as DNA β to distinguish them from the genomic component DNA-B of some begomoviruses (genus *Begomovirus*, family *Geminiviridae*). Only later did it also become apparent that, possibly, betasatellites encode some of the same functions as DNA-B components - specifically that of virus movement in plants. The name later became "betasatellites" to overcome the use of the Greek character β.

Reasons to justify the choice of type species:

Ageratum yellow vein betasatellite was the first betasatellite to be identified and fully characterized. This betasatellite has been shown to be infectious to the host it was isolated from (*Ageratum conyzoides*) in the presence of the begomovirus it was associated with (*Ageratum* *yellow vein virus* [AYVV]). The presence of the betasatellite increases the infectivity of AYVV in *A. conyzoides* and enhances the symptoms induced.

Species demarcation criteria in the new genus:

If there will be more than one species in the new genus, list the criteria being used for species demarcation and explain how the proposed members meet these criteria.

Species demarcation threshold of <91% nucleotide sequence identity when considering full-length sequences.

ODULE 3: **NEW GENUS**

creating a new genus

Ideally, a genus should be placed within a higher taxon.

Code	***2016.021fP***	(assigned by ICTV officers)

To create a new genus within:

Subfamily:	
Family:	***Tolecusatellitidae***
Order:	

Fill in all that apply.

- If the higher taxon has yet to be created (in a later module, below) write "**(new)**" after its proposed name.
- If no family is specified, enter "**unassigned**" in the family box

naming a new genus

Code	***2016.021gP***	(assigned by ICTV officers)

To name the new genus: *Deltasatellite*

Assigning the type species and other species to a new genus

Code	***2016.021hP***	(assigned by ICTV officers)

To designate the following as the type species of the new genus

Tomato leaf curl deltasatellite **(previously known as Tomato leaf curl virus - satellite)**	Every genus must have a type species. This should be a well characterized species although not necessarily the first to be discovered

The new genus will also contain any other new species created and assigned to it (Module 2) and any that are being moved from elsewhere (Module 7b). **Please enter here the TOTAL number of species (including the type species) that the genus will contain:**

11 (eleven)

Reasons to justify the creation of a new genus:

Additional material in support of this proposal may be presented in the Appendix, Module 11

The satellites with similarity to *Tomato leaf curl deltasatellite* (formerly Tomato leaf curl virus - satellite) are distinct from betasatellites. However, deltasatellites are related to betasatellites, most likely having evolved from them. For this reason the deltasatellites are best incorporated in a genus separate from the betasatellites but under the same family, *Tolecusatellitidae.*

Origin of the new genus name:

The satellites contained in the proposed new genus in some respects look like defective betasatellites (betasatellites that lack the betaC1 gene). The deltasatellites encompass an A-rich sequence and a sequence derived from the betasatellite SCR. However, they are distinct from defective betasatellites in that the SCR-like sequence of deltasatellites contains deletions and insertions relative to betasatellites (Lozano et al., 2016). Also, defective betasatellites always occur together with the parental (full-length) betasatellite. Deltasatellites, at least so far, have not been identified in the presence of betasatellites. The Greek letter delta (Δ) is often used in molecular biology to indicate a mutation or deletion - hence deltasatellite.

Reasons to justify the choice of type species:

Tomato leaf curl virus - satellite was the first satellite identified in association with a geminivirus and the first DNA satellite identified. To avoid the use of the term "virus" in a satellite species name, the original name has been shortened to *Tomato leaf curl deltasatellite.*

Species demarcation criteria in the new genus:

If there will be more than one species in the new genus, list the criteria being used for species demarcation and explain how the proposed members meet these criteria.

Species demarcation threshold of <91% nucleotide sequence identity when considering full-length component sequences.

MODULE 5: **NEW FAMILY**

creating and naming a new family

Code	***2016.021iP***	(assigned by ICTV officers)

To create a new family containing the subfamilies and/or genera listed below within the Order: unassigned

If there is no Order, write "**unassigned**" here.
If the Order has yet to be created (in Module 6) please write **"(new)"** after the proposed name.

Code	***2016.021jP***	(assigned by ICTV officers)

To name the new family: *Tolecusatellitidae*

assigning subfamilies, genera and unassigned species to a new family

Code		(assigned by ICTV officers)

To assign the following subfamilies (if any) to the new family:
You may list several subfamilies here. For each subfamily, please state whether it is new or existing.

- If the subfamily is new, it must be created in Module 4
- If the subfamily already exists, please complete Module 7 to 'MOVE' it from its existing family

none

Code	***2016.021kP***	(assigned by ICTV officers)

To assign the following genera to the new family:
You may list several genera here. For each genus, please state whether it is new or existing.

- If the genus is new, it must be created in Module 3
- If the genus already exists, please state whether it is currently unassigned or is to be removed from another family. If the latter, complete Module 7 to 'MOVE' it from that family

Betasatellite

Deltasatellite

The new family will also contain any other new species created and assigned to it (Module 3) and any that are being moved from elsewhere (Module 7). **Please enter here the TOTAL number of unassigned species that the family will contain (those NOT within any of the genera or subfamilies listed above):**

None

Reasons to justify the creation of the new family:
Additional material in support of this proposal may be presented in the Appendix, Module 11

Since the identification of the first satellite associated with a geminivirus, Tomato leaf curl virus - satellite, in 1997 (Dry et al., 1997) it has become increasingly evident that satellites are important additional components of some geminivirus infections. In order to cope with the increasing numbers of satellites identified (which fall into two groups - the betasatellites and the deltasatellites) a rational taxonomy and nomenclature is required to allow researchers to adequately define/describe their satellites. The satellites encompassed by the proposed genera *Betasatellite* and *Deltasatellite* are related, believed to have a common ancestor from which they diverged, and thus can be placed taxonomically in a family which is proposed here.

Origin of the new family name:
The name *Tolecusatellitidae* is based on the first DNA satellite shown to be associated with geminiviruses - Tomato leaf curl virus - satellite

MODULE 11: **APPENDIX**: supporting material

additional material in support of this proposal

References:

Brown, J.K., Zerbini, F.M., Navas-Castillo, J., Moriones, E., Ramos-Sobrinho, R., Silva, J.F., Fiallo-Olivé, E., Briddon, R.W., Hernández-Zepeda, C., Idris, A., Malathi, V.G., Martin, D.P., Rivera-Bustamante, R., Ueda, S., Varsani, A., 2015. Revision of *Begomovirus* taxonomy based on pairwise sequence comparisons. Arch. Virol. 160, 1593-1619.

Dry, I., Krake, L.R., Rigden, J.E., Rezaian, M.A., 1997. A novel subviral agent associated with a geminivirus: the first report of a DNA satellite. Proc. Natl. Acad. Sci. U.S.A. 94, 7088-7093.

Fiallo-Olivé, E., Tovar, R., Navas-Castillo, J., 2016. Deciphering the biology of deltasatellites from the New World: maintenance by New World begomoviruses and whitefly transmission. New Phytol., doi: 10.1111/nph.14071.

Kumar, J., Kumar, J., Singh, S.P., Tuli, R., 2014. Association of satellites with a mastrevirus in natural infection: complexity of *Wheat dwarf India virus* disease. J. Virol. 88, 7093-7104.

Hassan, I., Orílioa, A.F., Fiallo-Olivé, E., Briddon, R.W., Navas-Castillo, J., 2016. Infectivity, effects on helper viruses and whitefly transmission of the deltasatellites associated with sweepoviruses (genus *Begomovirus*, family *Geminiviridae*). Sci. Rep. 6, 30204.

Lozano, G., Trenado, H.P., Fiallo-Olivé, E., Chirinos, D., Geraud-Pouey, F., Briddon, R.W., Navas-Castillo, J., 2016. Characterization of non-coding DNA satellites associated with sweepoviruses (genus *Begomovirus*, *Geminiviridae*) - definition of a distinct class of begomovirus-associated satellites. Front. Microbiol. 7, 162.

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Saunders, K., Bedford, I.D., Briddon, R.W., Markham, P.G., Wong, S.M., Stanley, J., 2000. A unique virus complex causes Ageratum yellow vein disease. Proc. Natl. Acad. Sci. U.S.A. 97, 6890-6895.

Varsani, A., Martin, D.P., Navas-Castillo, J., Moriones, E., Hernández-Zepeda, C., Idris, A., Zerbini, F.M., Brown, J.K., 2014a. Revisiting the classification of curtoviruses based on genome-wide pairwise identity. Arch. Virol. 159, 1873-1882.

Varsani, A., Navas-Castillo, J., Moriones, E., Hernández-Zepeda, C., Idris, A., Brown, J., Zerbini, F.M., Martin, D., 2014b. Establishment of three new genera in the family *Geminiviridae*: *Becurtovirus*, *Eragrovirus* and *Turncurtovirus*. Arch. Virol. 159, 2193-2203.

Zhou, X., 2013. Advances in understanding begomovirus satellites. Ann. Rev. Phytopathol. 51, 357-381.

Annex:

Include as much information as necessary to support the proposal, including diagrams comparing the old and new taxonomic orders. The use of Figures and Tables is strongly recommended but direct pasting of content from publications will require permission from the copyright holder together with appropriate acknowledgement as this proposal will be placed on a public web site. For phylogenetic analysis, try to provide a tree where branch length is related to genetic distance.

A new family is proposed to encompass the true satellites that associate with geminiviruses. Two genera of satellites are recognised, corresponding to the betasatellites and the deltasatellites.

Betasatellites are a highly diverse group of ~1,350 nt ssDNA satellites. They have a highly conserved structure that includes a sequence rich in adenine (A-rich), a sequence well conserved between all betasatellites, known as the satellite conserved region (SCR), and encode a single product (known as betaC1). Although first identified in association with monopartite begomoviruses, it has since become clear that they may also associate with mastreviruses (Kumar et al., 2014) and, on rare occasions, bipartite begomoviruses. Betasatellites are confined to the Old World and have not so far been identified in the Americas. Since they were first identified in 2000, when they were referred to as DNA β (Saunders et al., 2000), more than 1,000 full-length betasatellites have been deposited in the databases demonstrating their importance and pervasive presence. The majority of begomoviruses occurring in the Old World are monopartite and most, but not all, associate with betasatellites. The interactions with betasatellites ranges from fully dependent (the virus cannot infect a particular plant species without the satellite) to facultative (some virus isolates associate with the betasatellites but others do not). The betaC1 protein is a dominant symptom determinant and is involved in overcoming plant host defences by suppressing both post-transcriptional and transcriptional gene silencing (Zhou, 2013).

The first satellite identified with a begomovirus was Tomato leaf curl virus–satellite, which we now recognize as a deltasatellite (Dry et al., 1997; Lozano et al., 2016). Deltasatellites are approx. half the size of betasatellites (~700 nt). In some respects deltasatellites resemble betasatellites, from which they are believed to have evolved. They encompass an A-rich sequence, a sequence derived from the betasatellite SCR, but are non-coding. Although deltasatellites are fully dependent on the begomoviruses, the helper viruses do not seem to depend on them (Fiallo-Olivé et al., 2016; Hassan et al., 2016) which contrasts with the interaction between some begomoviruses and their betasatellites.The precise selective advantage to a helper begomovirus of the presence of a deltasatellite is unclear, although recent evidence suggests that they may act to reduce virus damage and extend the life of the plant, thus allowing a greater period for onward transmission of the virus (Fiallo-Olivé et al., 2016; Hassan et al., 2016). Unlike betasatellites, deltasatellites have been identified, in addition to the Old World, also in the New World. This is likely due to the introduction of infected root crops such as sweet potato (Lozano et al., 2016).

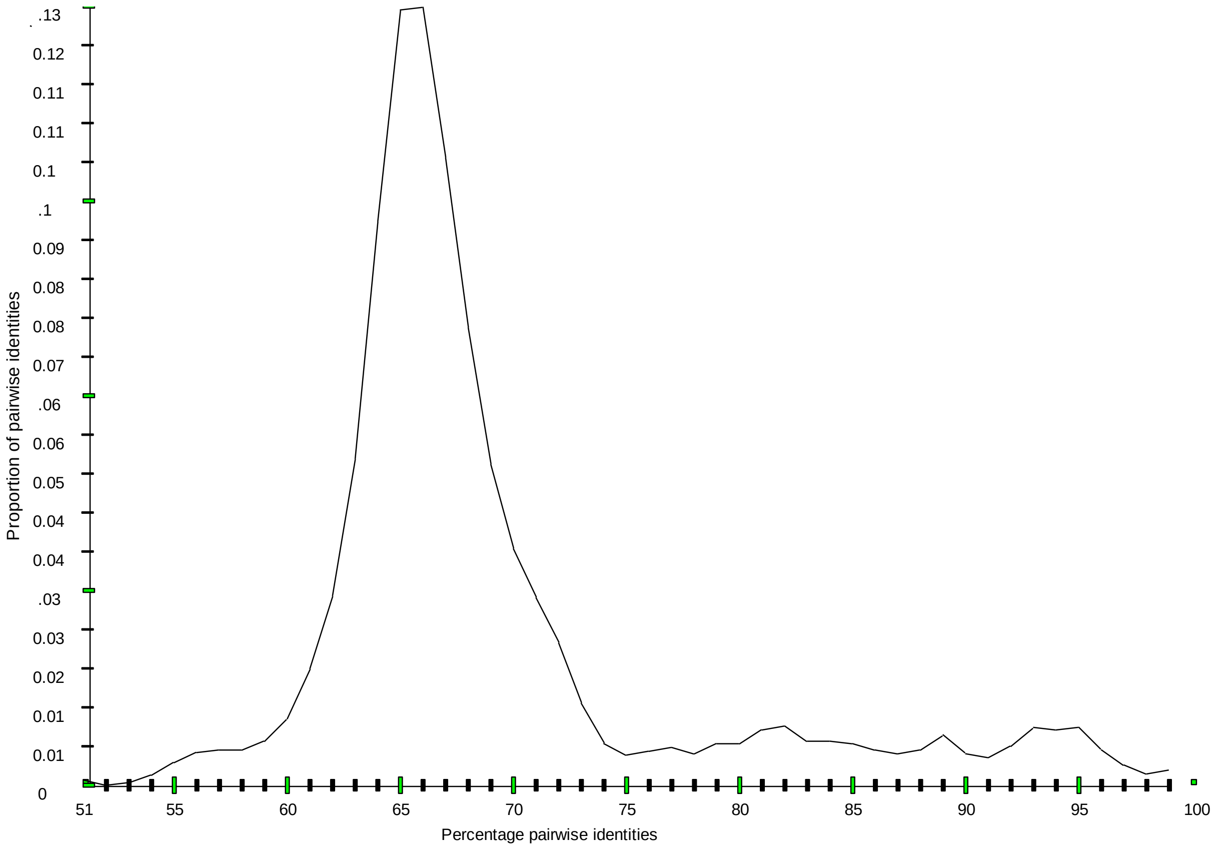

Figure 1. Plot of percentage identity values for pairwise comparisons of 1,116 betasatellite sequences.

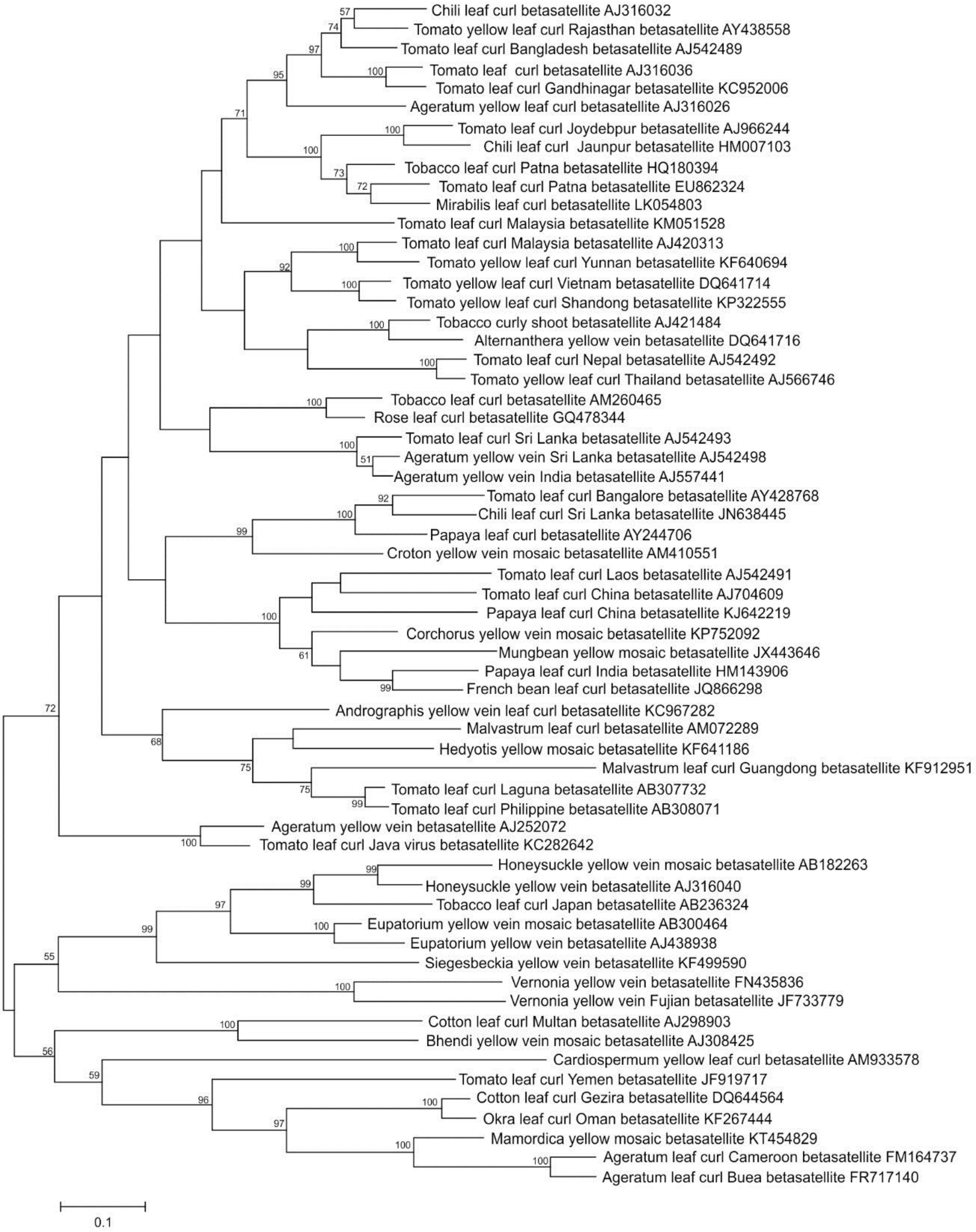

Figure 2. Maximum-likelihood phylogenetic tree based on an alignment of 61 complete betasatellite sequences representative of the newly proposed species. Numbers at nodes are percentage bootstrap values (1,000 repetitions). Only values above 50% are shown.

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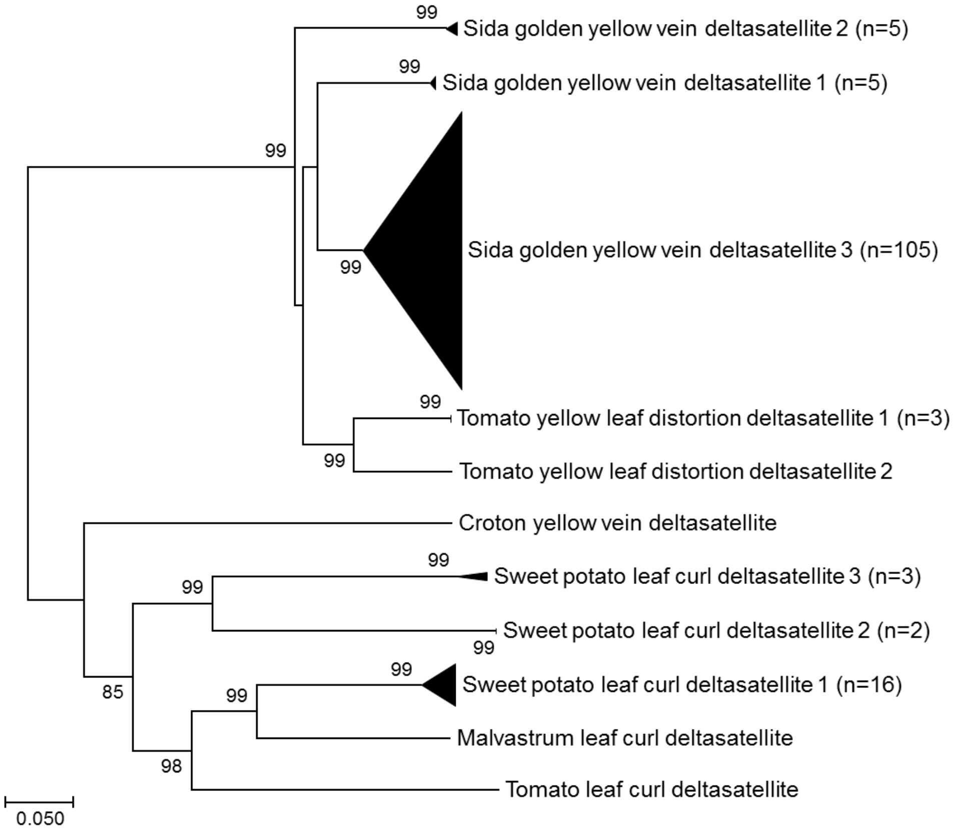

Figure 3. Neighbour-joining phylogenetic tree based on an alignment of 142 complete deltasatellite sequences belonging to the newly proposed species. Subtrees corresponding to the different species are compressed, and the number (n) of sequences included is indicated in parenthesis. Numbers at nodes are percentage bootstrap values (1,000 repetitions). Only values above 70% are shown.