



Taxonomy update for the family *Alphasatellitidae*: new subfamily, genera, and species

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Abstract

Alphasatellites (family *Alphasatellitidae*) are circular, single-stranded DNA molecules (~1–1.4 kb) that encode a replication-associated protein and have commonly been associated with some members of the families *Geminiviridae*, *Nanoviridae*, and *Metaxyviridae* (recently established). Here, we provide a taxonomy update for the family *Alphasatellitidae* following the International Committee on Taxonomy of Viruses (ICTV) Ratification Vote held in March 2021. The taxonomic update includes the establishment of the new subfamily *Petromoaalphasatellitinae*. This new subfamily includes three new genera as well as the genus *Babusatellite*, which previously belonged to the subfamily *Nanoalphasatellitinae*. Additionally, three new genera and 14 new species have been established in the subfamily *Geminialphasatellitinae*, as well as five new species in the subfamily *Nanoalphasatellitinae*.

Introduction

Alphasatellitidae is a family of replication-associated protein (Rep)-expressing circular, single-stranded DNA molecules (~1–1.4 kb) that have commonly been found in association with some members of the families *Geminiviridae* (viruses in the genera *Begomovirus* and *Mastrevirus*) [14] and

Nanoviridae [12]. Similar molecules have also been found associated with coconut foliar decay virus [4] (family *Metaxyviridae*, genus *Cofodevirus*) [13]. Alphasatellites are unable to trans-replicate the *bona fide* genome components of these ‘helper viruses’ or vice versa, but they do rely on them for encapsidation, movement, and vector transmission [1].

Since the establishment of the family *Alphasatellitidae* in 2018 [1], various new alphasatellites have been identified,

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and here, we provide a taxonomic update. The update includes: (1) the establishment of a new subfamily, *Petromoalphasatellitinae*; (2) reassignment of existing family members and assignment of new members to the subfamily *Petromoalphasatellitinae*; (3) the establishment of three new genera and 14 new species in the subfamily *Geminalphasatellitinae*; and (4) the establishment of five new species in the subfamily *Nanoalphasatellitinae*.

Geminalphasatellitinae

A genus demarcation threshold of 70% and a species demarcation threshold of 88% based on genome-wide pairwise identity values were recommended by Briddon et al. [1] (Fig. 1). Accordingly, the members were classified into four genera (*Ageyisatellite*, *Clecrusatellite*, *Colecusatellite*, and *Gosmusatellite*) and a total of 41 species. In the last couple of years, various geminalphasatellites have been identified, and using the taxonomic guidelines outlined by Briddon et al. [1], we established three new genera (*Draftysatellite*, *Somasatellite*, and *Whiflysatellite*) to accommodate the two previously unassigned species (*Dragonfly associated alphasatellite* and *Whitefly associated Guatemala alphasatellite 1*) and one new species (*Sorghum mastrevirus associated alphasatellite*). In addition to these, we established 12 new species in the genera *Clecrusatellite* ($n = 7$), *Colecusatellite* ($n = 2$), and *Gosmusatellite* ($n = 3$). The details of the new taxa are provided in Table 1. With all the new geminalphasatellites being identified, we reanalysed the distribution of pairwise identity values for 960 complete sequences with intact Rep open reading frames using SDT v1.2 [7] and determined that the 88% species demarcation threshold is still a valid criterion for their classification (Fig. 1).

Nanoalphasatellitinae

A genus demarcation threshold of 67% and a species demarcation threshold of 80% based on genome-wide pairwise identity values were recommended previously by Briddon et al. [1]. This resulted in the original creation of 19 species, which were assigned to seven genera (*Babusatellite*, *Clostunsatellite*, *Fabenesatellite*, *Milvetsatellite*, *Mivedwarsatellite*, *Sophoyesatellite*, and *Subclovsatellite*). The major change in this subfamily is the reassignment of the genus *Babusatellite* to the subfamily *Petromoalphasatellitinae*. We also established five new species in the genera *Mivedwarsatellite* ($n = 3$), *Sophoyesatellite* ($n = 1$), and *Subclovsatellite* ($n = 1$). To verify that, with the reassignment of *Babusatellite* to the subfamily *Petromoalphasatellitinae*, the species demarcation threshold of 80% is still valid, we reanalysed the distribution of pairwise identity values for 104 complete nanoalphasatellite sequences with intact Rep open reading

frames using SDT v1.2 [7] and confirmed the species demarcation threshold (Fig. 1).

Petromoalphasatellitinae

In 2018, novel types of single-stranded DNA molecules comprising the genome of coconut foliar decay virus [4] (family *Metaxyviridae*) were identified. The virus was found to affect only coconut palm (*Cocos nucifera*) and is restricted to the Vanuatu Archipelago [8, 9]. Nine different alphasatellites are associated with coconut foliar decay virus. Our analysis of these alphasatellites revealed that, based on a species demarcation threshold of 81% sequence identity, they can be classified in several distinct species (Fig. 1). Applying a genus demarcation threshold of 68% sequence identity among members, three new genera, *Cocosatellite* (*Coco* for coconut), *Coprasatellite* (*Copra* for coconut meat), and *Kobbarisatellite* (*Kobbari* is an Indian dish from coconut meat) were established. Five of the seven alphasatellite species were assigned to the genus *Cocosatellite*, one to the genus *Coprasatellite*, and one to the genus *Kobbarisatellite* (Table 1).

In addition to the creation of these three genera, we reassigned the genus *Babusatellite* to the new subfamily *Petromoalphasatellitinae*, as these alphasatellites collectively associate with viruses that infect perennial tropical monocotyledonous plants. Moreover, their respective size range is between those of the members of the subfamilies *Geminalphasatellitinae* and *Nanoalphasatellitinae*. Finally, phylogenetic analysis clearly supports inclusion of the species of the genus *Babusatellite* in the same subfamily along with the species of the newly established genera *Cocosatellite*, *Coprasatellite*, and *Kobbarisatellite* (Fig. 2). The distribution of the pairwise identity values for the 28 petromoalphasatellites is shown in Fig. 1.

Based on the phylogenetic analysis coupled with pairwise comparisons, we moved three species (*Banana bunchy top alphasatellite 2*, *Banana bunchy top alphasatellite 3*, and *Cardamom bushy dwarf alphasatellite*) from the genus *Babusatellite* to a new genus, *Muscarsatellite* (*Muscar* from *Musa* and *Elettaria cardamomum*). A summary of the genera and species is provided in Table 1.

For the classification of new petromoalphasatellites, we recommend similar steps to those outlined by Briddon et al. [1]. To resolve conflict in cases where (1) a complete petromoalphasatellite sequence shares $\geq 81\%$ pairwise identity with sequences of members of two different species or (2) a complete petromoalphasatellite sequence shares $\geq 81\%$ pairwise identity with sequences of one or more members of a particular species while sharing $< 81\%$ identity with the sequences of the majority of the members of that particular species:

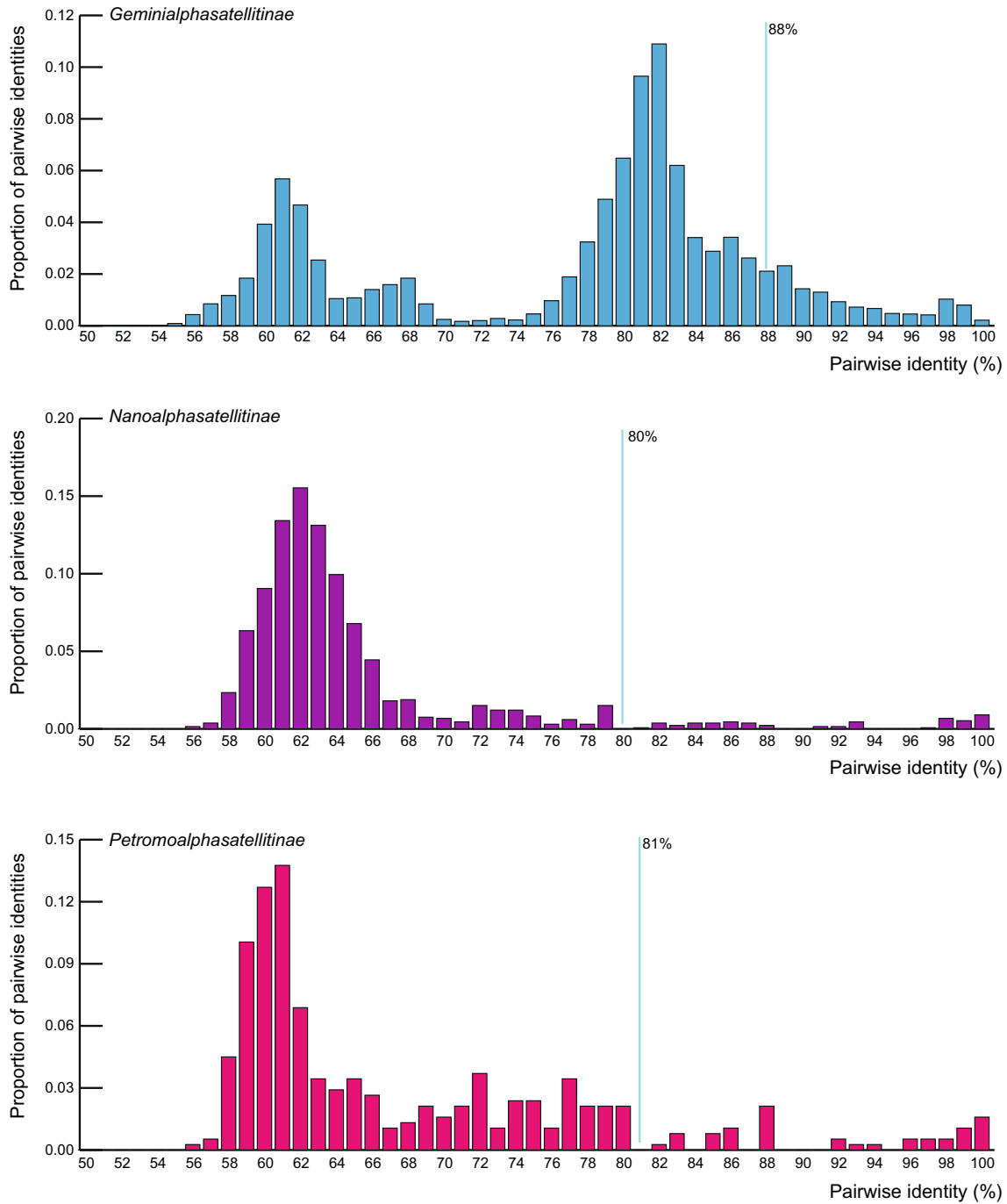


Fig. 1 Distribution of pairwise identity values of complete sequences with intact Rep ORFs of members of the subfamilies *Geminalphasatellitinae* ($n = 960$), *Nanoalphasatellitinae* ($n = 104$), and *Petromoalphasatellitinae* ($n = 28$), determined using SDT v1.2 [7]

- (1) The new petromoalphasatellite should be assigned to the species whose members share with it the highest pairwise sequence identity.
- (2) The petromoalphasatellite should be classified as belonging to any species in which it shares $\geq 81\%$ pair-

wise sequence identity with any existing member of that species, even if it has $< 81\%$ pairwise sequence identity to other members of that species.

Table 1 Summary of the genera and species in the subfamilies *Geminalphasatellitinae*, *Nanoalphasatellitinae*, and *Petromopalphasatellitinae*

Subfamily	Genus	Species	Alphasatellite name	Isolate	Accession no.
<i>Geminalphasatellitinae</i>	<i>Ageyesisatellite</i>	<i>Ageratum yellow vein Singapore alphasatellite</i>	ageratum yellow vein Singapore alphasatellite	SG-98	AJ416153
		<i>Cotton leaf curl Saudi Arabia alphasatellite</i>	cotton leaf curl Saudi Arabia alphasatellite	SA-Jazan-13	HG530543
	<i>Clecrusatellite</i>	◇ <i>Ash gourd yellow vein mosaic alphasatellite</i>	ash gourd yellow vein mosaic alphasatellite	IN-UdA-15	KX363561
		◇ <i>Capsicum India alphasatellite</i>	begomovirus-associated alphasatellite sp.	IN-PJ-Cap-15	KU923759
		◇ <i>Chiapas weed alphasatellite</i>	begomovirus-associated alphasatellite	MX-UHAsV-1-CD-W-2014	MN203219
		<i>Cleome leaf crumple alphasatellite</i>	cleome leaf crumple alphasatellite	BR-Mato Grosso do Sul-07	FN436007
		<i>Croton yellow vein mosaic alphasatellite</i>	croton yellow vein mosaic alphasatellite	IN-Haryana-Acalypha-07	FN658711
		<i>Euphorbia yellow mosaic alphasatellite</i>	euphorbia yellow mosaic alphasatellite	BR-Mato grosso do sul-1-07	FN436008
		<i>Melon chlorotic mosaic alphasatellite</i>	melon chlorotic mosaic alphasatellite	VE-2009_02_04_0-09	HM163578
		<i>Sida Cuba alphasatellite</i>	sida Cuba alphasatellite	CU-Trinidad-07	HE806451
		◇ <i>Tomato leaf curl Anand alphasatellite</i>	tomato leaf curl Anand alphasatellite	IN-Anand-2016	MH577036
		◇ <i>Tomato leaf curl New Delhi alphasatellite</i>	tomato leaf curl New Delhi alphasatellite	IN-VNS_SP4-Luf-15	MH550542
		◇ <i>Tomato leaf curl Virudhunagar alphasatellite</i>	tomato leaf curl Virudhunagar alphasatellite	IN-sev-Mom-16	KY848691
		<i>Tomato yellow spot alphasatellite</i>	tomato yellow spot alphasatellite	BR-Dou1095.1-11	KX348228
		◇ <i>Tomato yellow spot alphasatellite 2</i>	tomato yellow spot alphasatellite 2	AR-Jujuy-Yuto-Leonurus417-2008	MN518743
		<i>Whitefly associated Guatemala alphasatellite 2</i>	whitefly associated Puerto Rico alphasatellite 2	GT-GfTo2-1-10	KT099170
	<i>Whitefly associated Puerto Rico alphasatellite 1</i>	whitefly associated Puerto Rico alphasatellite 1	PR-PR3-6-10	KT099173	
	<i>Colecusatellite</i>	<i>Ageratum enation alphasatellite</i>	ageratum enation alphasatellite	IN-Luc-12	JX913532
		<i>Ageratum yellow vein alphasatellite</i>	ageratum yellow vein alphasatellite	SG-98	AJ238493
		<i>Ageratum yellow vein China alphasatellite</i>	ageratum yellow vein China alphasatellite	PH-Davao-SN3-Syn-edrella nodiflora-12	KF785752
		<i>Ageratum yellow vein India alphasatellite</i>	ageratum yellow vein India alphasatellite	IN-Luc-parthenium-12	JX570736
		<i>Bhendi yellow vein alphasatellite</i>	bhendi yellow vein alphasatellite	IN-Har-07	FN658716

Table 1 (continued)

Subfamily	Genus	Species	Alphasatellite name	Isolate	Accession no.
		<i>Cassava mosaic</i>	cassava mosaic	MG-Diana-635A1-11	HE984148
		<i>Madagascar alphasatellite</i>	Madagascar alphasatellite		
		<i>Chilli leaf curl alphasatellite</i>	chilli leaf curl alphasatellite	IN-273-06	KF471043
		<i>Cotton leaf curl Egypt alphasatellite</i>	cotton leaf curl Egypt alphasatellite	EG-SB45-95	AJ512960
		<i>Cotton leaf curl Gezira alphasatellite</i>	cotton leaf curl Gezira alphasatellite	ML-Bamako-okra-06	EU589450
		<i>Cotton leaf curl Lucknow alphasatellite</i>	cotton leaf curl Lucknow alphasatellite	IN-Luc-10	HQ343234
		<i>Cotton leaf curl Multan alphasatellite</i>	cotton leaf curl Multan colecusatellite	PK-Fai01-98	AJ132344
		<i>Gossypium darwinii symptomless alphasatellite</i>	Gossypium darwinii symptomless alphasatellite	PK-Mul-Dav7C-06	EU384623
		<i>Malvastrum yellow mosaic alphasatellite</i>	malvastrum yellow mosaic alphasatellite	CN-Hn39	AM236765
		<i>Malvastrum yellow mosaic Cameroon alphasatellite</i>	malvastrum yellow mosaic Cameroon satellite	CM-Mundemba-UMU1D1-08	FN675297
		<i>Pedilanthus leaf curl alphasatellite</i>	pedilanthus leaf curl alphasatellite	IN-carrot	KX168428
		<i>Sida leaf curl alphasatellite</i>	sida leaf curl alphasatellite	PK-Lahore-Alcea rosea-06	FR772088
◇		<i>Sida leaf curl alphasatellite 2</i>	sida leaf curl alphasatellite	IN-Gandhinagar-Sida-2016	KX513861
		<i>Sida yellow vein Vietnam alphasatellite</i>	sida yellow vein Vietnam alphasatellite	VN-Han-05	DQ641718
		<i>Sunflower leaf curl Karnataka alphasatellite</i>	sunflower leaf curl Karnataka alphasatellite	IN-tomato-11	JX569789
		<i>Synedrella leaf curl alphasatellite</i>	synedrella leaf curl alphasatellite	IN-Por-synf_1-09	KJ939346
		<i>Tobacco curly shoot alphasatellite</i>	tobacco curly shoot alphasatellite	IN-WSF1-Helianthus-10	HQ407396
		<i>Tomato leaf curl Buea alphasatellite</i>	tomato leaf curl Buea alphasatellite	CM-Buea-TOS2D1-07	FN675299
		<i>Tomato leaf curl Cameroon alphasatellite</i>	tomato leaf curl Cameroon alphasatellite	CM-Buea-OMHD3-08	FN675296
◇		<i>Tomato leaf curl Pakistan alphasatellite</i>	tomato leaf curl alphasatellite	PK-SZ_258-Gos-15	KY420167
		<i>Tomato yellow leaf curl China alphasatellite</i>	tomato yellow leaf curl China alphasatellite	PK-Fai-09	AM749493
		<i>Tomato yellow leaf curl Thailand alphasatellite</i>	tomato yellow leaf curl Thailand alphasatellite	TH-Y70-03	AJ579359
		<i>Tomato yellow leaf curl Yunnan alphasatellite</i>	tomato yellow leaf curl Yunnan alphasatellite	CN-YN4368_69-14	KX759649

Table 1 (continued)

Subfamily	Genus	Species	Alphasatellite name	Isolate	Accession no.	
Nanoalphasatellitinae	▶ <i>Draftysatellite</i>	◇ <i>Dragonfly associated alphasatellite</i>	dragonfly associated alphasatellite	PR-09	JX458742	
	<i>Gosmusatellite</i>	◇ <i>Cotton leaf curl Cameroon alphasatellite</i>	cotton leaf curl Gezira alphasatellite 3	CM-OBKG-Okra-2007	MN614472	
		◇ <i>Eclipta yellow vein alphasatellite</i>	eclipta yellow vein alphasatellite	PK-AIYVA-S3-13	KX938425	
		<i>Gossypium mustelinum symptomless alphasatellite</i>	Gossypium mustelinum symptomless alphasatellite	PK-Mul-2-06	EU384656	
		<i>Hollyhock yellow vein alphasatellite</i>	hollyhock yellow vein alphasatellite	PK-Lahor-17_5-06	FR772086	
		<i>Mesta yellow vein mosaic alphasatellite</i>	mesta yellow vein mosaic alphasatellite	IN-Ludhiana-Okra-10	JX183090	
		<i>Okra enation leaf curl alphasatellite</i>	okra enation leaf curl alphasatellite	IN-Surat-11	HF546575	
		<i>Okra yellow crinkle Cameroon alphasatellite</i>	okra yellow crinkle Cameroon alphasatellite	CM-Lys1sp3-08	FN675285	
		<i>Vernonia yellow vein Fujian alphasatellite</i>	vernonia yellow vein Fujian alphasatellite	IN-Vamban-blackgram-12	KC959931	
	▶ <i>Somasatellite</i>	◇ <i>Sorghum mastrevirus associated alphasatellite</i>	sorghum mastrevirus associated alphasatellite	RE-Bassin plat-Sorghum arundinaceum-RE180_a-2017	MN901968	
	▶ <i>Whiftysatellite</i>	◇ <i>Whitefly associated Guatemala alphasatellite 1</i>	whitefly associated Guatemala alphasatellite 1	WfaGA-[GT-GtTo2_2-12]	KT099172	
		<i>Clostunsatellite</i>	<i>Milk vetch dwarf alphasatellite 2</i>	milk vetch dwarf alphasatellite 2	MVDC3A-JR-C3-96	AB000922
			<i>Pea necrotic yellow dwarf alphasatellite 2</i>	pea necrotic yellow dwarf alphasatellite 2	PNYD3A-AT-Gross_Enzersdorf_1-10	KC979052
			<i>Sophora yellow stunt alphasatellite 4</i>	sophora yellow stunt alphasatellite 4	SYS9A-IR-Kerman-Ta1-14	KX534409
			<i>Sophora yellow stunt alphasatellite 5</i>	sophora yellow stunt alphasatellite 5	SYS8A-IR-Kerman-Ta1-14	KX534398
			<i>Subterranean clover stunt alphasatellite 2</i>	subterranean clover stunt alphasatellite 2	SCSC6A-[AU-C6-93]	U16735
		<i>Fabenesatellite</i>	<i>Faba bean necrotic yellows alphasatellite 2</i>	faba bean necrotic yellows alphasatellite 2	FBNYC9A-SY-C9-93	AJ005966
		<i>Milvetsatellite</i>	<i>Milk vetch dwarf alphasatellite 3</i>	milk vetch dwarf alphasatellite 3	MVDC10A-JR-C10-97	AB009047
		<i>Mivedwarsatellite</i>	<i>Faba bean necrotic stunt alphasatellite</i>	faba bean necrotic stunt alphasatellite	AZ-12b-10	KC978990
			<i>Milk vetch dwarf alphasatellite 1</i>	milk vetch dwarf alphasatellite 1	MVDC1A-JR-C1-96	AB000920
	◇	<i>Milk vetch dwarf China alphasatellite</i>	milk vetch dwarf C1 alphasatellite	CN-G48-2017	MN059431	
	◇	<i>Parsley severe stunt alphasatellite 3</i>	parsley severe stunt alphasatellite 3	DE-Pa21-2017	MK039141	

Table 1 (continued)

Subfamily	Genus	Species	Alphasatellite name	Isolate	Accession no.
		◇ <i>Parsley severe stunt alphasatellite 4</i>	parsley severe stunt alphasatellite 4	DE-Pa21-2017	MK039142
		<i>Pea necrotic yellow dwarf alphasatellite 1</i>	pea necrotic yellow dwarf alphasatellite 1	PNYD1A-AT-Gross_Enzersdorf_1-10	KC979051
		<i>Sophora yellow stunt alphasatellite 2</i>	sophora yellow stunt alphasatellite 2	SYS4A-IR-Kerman-Ta1-14	KX534408
	<i>Sophoyesatellite</i>	◇ <i>Cow vetch latent alphasatellite</i>	cow vetch latent virus alphasatellite	FR-VcLV_Sambuc-10	MF535455
		<i>Sophora yellow stunt alphasatellite 3</i>	sophora yellow stunt alphasatellite 3	SYS7A-IR-Kerman-Ta1-14	KX534400
	<i>Subclovsatellite</i>	<i>Faba bean necrotic yellows alphasatellite 1</i>	fabo bean necrotic yellows alphasatellite 1	FBNYC1A-SY-C1-88	X80879
		◇ <i>Faba bean necrotic yellows alphasatellite 3</i>	fabo bean necrotic yellows virus associated alphasatellite 1	TN-Tuf9_1-15	MF510471
		<i>Sophora yellow stunt alphasatellite 1</i>	sophora yellow stunt alphasatellite 1	SYSA1-[IR-Kerman-Ta1-14]	KX534399
		<i>Subterranean clover stunt alphasatellite 1</i>	subterranean clover stunt alphasatellite 1	SCSC2A-AU-C2-93	U16731
● <i>Petromalphasatellitinae</i>	<i>Babusatellite</i>	<i>Banana bunchy top alphasatellite 1</i>	banana bunchy top alphasatellite 1	BBTS2A-93	L32167
	▶ <i>Cocosatellite</i>	◇ <i>Coconut foliar decay alphasatellite 1</i>	coconut foliar decay alphasatellite 1	VU-85	M29963
		◇ <i>Coconut foliar decay alphasatellite 2</i>	coconut foliar decay alphasatellite 2	VU-89	MF926426
		◇ <i>Coconut foliar decay alphasatellite 4</i>	coconut foliar decay alphasatellite 4	VU-89	MF926429
		◇ <i>Coconut foliar decay alphasatellite 5</i>	coconut foliar decay alphasatellite 5	VU-89	MF926430
	▶ <i>Coprasatellite</i>	◇ <i>Coconut foliar decay alphasatellite 7</i>	coconut foliar decay alphasatellite 7	VU-89	MF926432
	▶ <i>Kobbarisatellite</i>	◇ <i>Coconut foliar decay alphasatellite 3</i>	coconut foliar decay alphasatellite 3	VU-89	MF926427
	▶ <i>Muscarsatellite</i>	◇ <i>Banana bunchy top alphasatellite 2</i>	banana bunchy top alphasatellite 2	BBTS3A-VN-VB-sat3-00	AF416471
		◇ <i>Banana bunchy top alphasatellite 3</i>	banana bunchy top alphasatellite 3	BBTHA-CN-Haikou-10	HQ616080
		◇ <i>Cardamom bushy dwarf alphasatellite</i>	cardamom bushy dwarf alphasatellite	IN-Kalimpong-07	KF435148

The symbol “●” indicates a new subfamily, the symbol “▶” indicates a new genus, and the symbol “◇” indicates a new species

Concluding remarks

As more sequence data become available, more changes to *Alphasatellitidae* taxonomy will certainly occur. We would also like to inform the *Alphasatellitidae* research community that a standardized binomial species nomenclature, consisting of the genus name and a free-form species epithet, has been ratified by the International

Committee on Taxonomy of Viruses (ICTV) [10]. This needs to be adopted for currently established species in the family *Alphasatellitidae* by the year 2023. Thus, we encourage the community to engage with the ICTV *Geminiviridae* and *Tolecusatellitidae* Study Group and the *Nanoviridae* Study Group to determine the binomial names for current and new species in the family *Alphasatellitidae*.

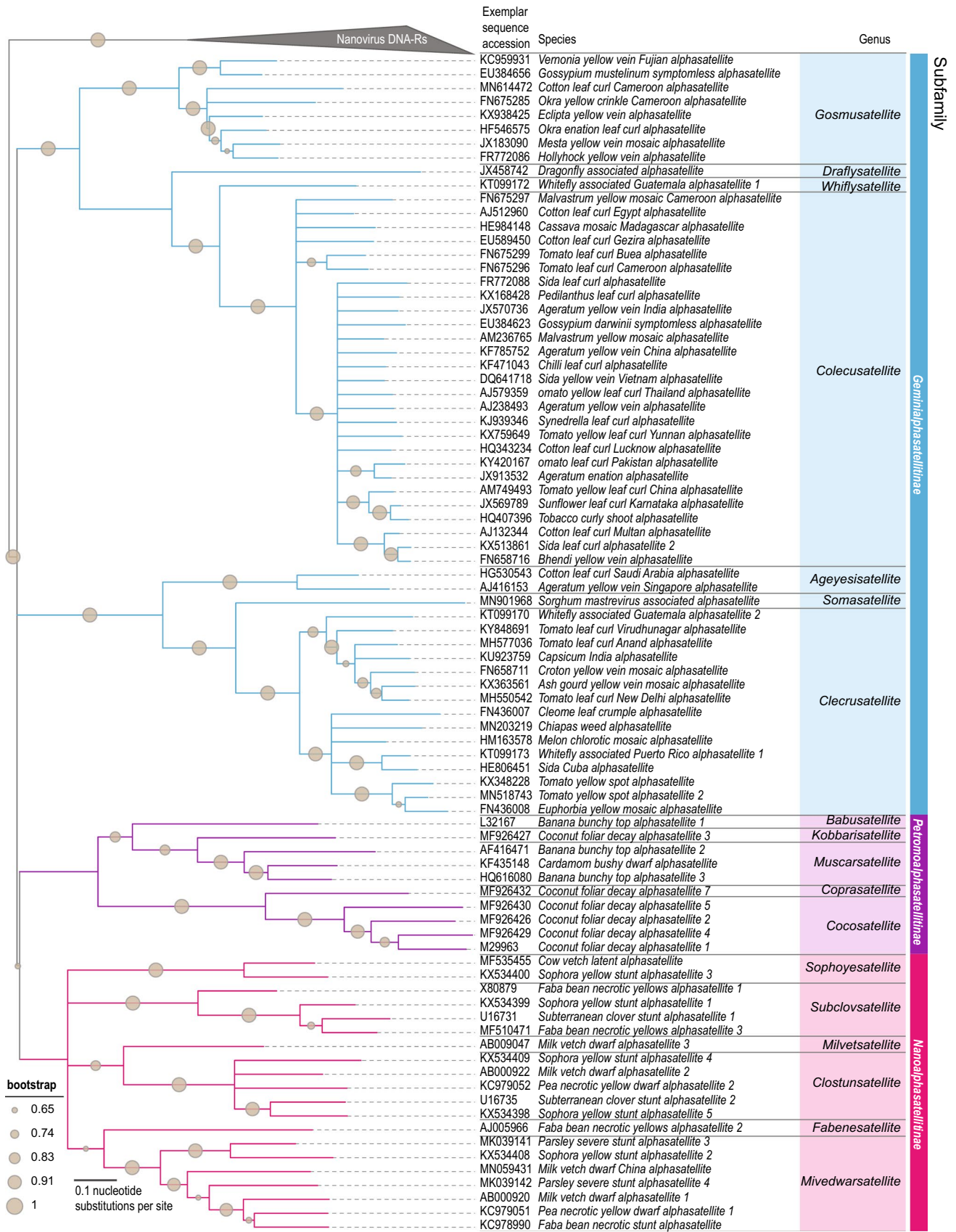


Fig. 2 Maximum-likelihood phylogenetic tree constructed from a MUSCLE [3] sequence alignment of representative alphasatellites using PHYML [5] with the GTR+I+G4 nucleotide substitution model (determined to be the best-fitting model by jModelTest [2]). The tree shows support for the proposed establishment of the new subfamily *Petromalphasatellitinae* as well as support for the reassignment of the viruses in the genus *Babuvirus*. Branches with less than 60% bootstrap support have been collapsed using TreeGraph2 [11]. The tree was visualized in iTOL v6 [6].

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Declarations

Conflict of interest The authors declare no conflicts of interest.

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