

A critical review on cytogenetics of Cucurbitaceae with updates on Indian taxa

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Abstract

The cytogenetic relationships in the species of Cucurbitaceae are becoming immensely important to answer questions pertaining to genome evolution. Here, a simplified and updated data resource on cytogenetics of Cucurbitaceae is presented on the basis of foundational parameters (basic, zygotic and gametic chromosome numbers, ploidy, genome size, karyotype) and molecular cytogenetics. We have revised and collated our own findings on seven agriculturally important Indian cucurbit species in a comparative account with the globally published reports. Chromosome count (of around 19% species) shows nearly three-fold differences while genome size (of nearly 5% species) shows 5.84-fold differences across the species. There is no significant correlation between chromosome numbers and nuclear genome sizes. The possible trend of evolution is discussed here based on molecular cytogenetics data, especially the types and distribution of nucleolus organizer regions (NORs). The review supersedes the scopes of general chromosome databases and invites scopes for continuous updates. The offline resource serves as an exclusive toolkit for research and breeding communities across the globe and also opens scope for future establishment of web-database on Cucurbitaceae cytogenetics.

Keywords

chromosome, genome size, karyotype, NORs, ploidy

Introduction

The family Cucurbitaceae contains an extensive range of diversity consisting of about 1000 species spread over 96 genera (Renner and Schaefer 2017). The diversity of plant families is associated with variation in genome sizes and chromosome numbers as a result of enormous adaptive radiation (Soltis et al. 2004; Lysák and Schubert 2013). The viewpoint of evolution has been changed with the understanding of whole genome duplication (WGD) (Soltis et al. 2014) followed by core-eudicot hexaploidy (Wang et al. 2018). A cytogenetic database is essential to gain insights into evolution by supplementing phylogeny trees with chromosome number information (Mota et al. 2016) to upgrade knowledge on plant systematics (Soltis et al. 2014; Viruel et al. 2021). Cucurbitaceae, being the fourth most important and one of the earliest consumed vegetables yielding family, has coped with extreme climates, extensive human intervention and a huge domestication syndrome (Chomicki et al. 2020). Considerable advances have been made in molecular phylogeny (Renner and Schaefer 2016; Bellot et al. 2020; Chomicki et al. 2020; Guo et al. 2020) and genomics (CuGenDB, <http://cucurbitgenomics.org>) (Zheng et al. 2019). We had previously discussed about the gaps in cytogenetic studies (Bhowmick and Jha 2015b) which has been surmounted with the advent of molecular cytogenetics.

Currently, we have collated the cytogenetic reports of Cucurbitaceae globally and integrated our own findings for a collective interpretation. The review attempts to address i) the trend of chromosome evolution in specific tribes and species based on available information, ii) correlation between chromosome numbers and ploidy or genome size in the studied taxa and iii) the requirement of an exclusive cytogenetic catalogue for genome researchers, taxonomists and breeders working on Cucurbitaceae.

Methodological approaches

Data compilation









The data have been collated as per Schaefer and Renner (2011) after consultation of books, Chromosome atlases, research articles and public resources like Chromosome Counts Database (CCDB; <http://ccdb.tau.ac.il/>) (Rice et al. 2015), The Index to Plant Chromosome Numbers (IPCN, <http://legacy.tropicos.org/Project/IPCN>) (Goldblatt and Lowry 2011) and The Plant DNA C-values database (Pellicer and Leitch 2020) (<https://cvalues.science.kew.org/>).

Chromosome analysis in the Cucurbit species occurring in India

Presently an enzymatic maceration and air drying (EMA) method followed by fluoro-chrome banding has been employed as per our previous protocols (Bhowmick et al. 2012, 2016; Bhowmick and Jha 2015a, 2019, 2021) to represent fresh karyotypes of seven agriculturally important cucurbit species (Table 1) belonging to Benincaseae and

Sicyoeae. Fresh and healthy roots were used from different sources (like germinating seeds, seedlings and underground root stocks). Roots were pretreated with 0.002 M hydroxyquinoline and fixed in 1:3 aceto-methanol solution. The standardization of EMA- fluorescence banding was conducted for the different species. In brief, fixed roots were digested in enzyme mixture [1% Cellulase (Onozuka RS), 0.75% Macerozyme (R-10), 0.15% Pectolyase (Y-23), 1 mM EDTA] for 40–45 min at 37 °C, macerated on slides, air-dried, stained with 2% Giemsa solution (Merck, Germany) and plates selected for karyotyping. After de-staining, slides were kept in McIlvaine buffer, stained with 0.1 µg mL⁻¹ DAPI for 15–20 min in darkness. For CMA staining, slides were incubated in 0.1 mg mL⁻¹ CMA for 15–25 min in darkness. For meiotic chromosomes, fixed anthers were digested in enzyme mixture for 5–8 min, macerated on slides and DAPI staining protocol was followed with minor modifications. All slides

Table 1. Chromosome numbers and nature of fluorescent bands in some cucurbit species occurring in India.

Tribes	Species (common name, status of cultivation/ wild)	Collection site, Latitude/ Longitude	Fruit image	2n	CMA bands		DAPI bands (Non-nucleolar)
					Nucleolar	Non-nucleolar	
Sicyoeae	<i>Luffa acutangula</i> Linnaeus, 1753 (ridged gourd, cultivated)	Bhubaneswar, Odisha, 20.2960°N, 85.8245°E		26	11 th , 12 th , 13 th	12 th (centromeric)	1 st to 13 th (distal)
	<i>Luffa cylindrica aegyptiaca</i> Miller, 1768 (sponge gourd, cultivated)	Imphal, Manipur, 24.6637°N, 93.906°E		26	12 th , 13 th	1 st , 2 nd (distal)	0
	<i>Luffa echinata</i> Roxburgh, 1814 (wild)	Pantnagar, Uttarakhand, 30.0667°N, 79.019°E		26	11 th , 12 th , 13 th	0	1 st to 13 th (distal)
	<i>Trichosanthes cucumerina</i> Linnaeus, 1753 (wild)	NBPGR, Thrisur, Kerala, 10.5276°N, 76.2144°E		22	10 th , 11 th	0	1 st to 11 th (distal)
	<i>Trichosanthes cucumerina</i> ssp. <i>cucumerina</i> Anguina (snake gourd, cultivated)	Bengaluru, 12.9716°N, 77.5946°E		22	10 th , 11 th	2 nd (distal)	0
	<i>Trichosanthes dioica</i> Roxburgh, 1832 (pointed gourd, cultivated)	Bhagalpur, Bihar, 25.2414°N, 86.9924°E		22 (female) 22 (male)	0 0	7 th , 8 th , 10 th (distal) 0	1 st to 11 th 1 st to 11 th
	Benincaseae	<i>Benincasa hispida</i> Thunberg, 1784 (ash gourd, cultivated)	Imphal, Manipur 24.6637°N, 93.906°E		24	12 th	9 th (distal)
<i>Coccinia grandis</i> Linnaeus, 1767 (ivy gourd, restricted cultivation)		Nagpur, Maharashtra, 21.1458°N, 79.0881°E		24 (female) 24 (male)	8 th , 12 th * 8 th , 12 th *	1 st to 5 th , 8 th to 12 th (centromeric) 1 st to 5 th , 8 th , 10 th to 12 th (centromeric)	0 0

were mounted in non-fluorescent glycerol and chromosome plates were observed under a Zeiss Axioscop 2 fluorescence microscope (using UV and BV filter cassettes for DAPI and CMA stains, respectively). Images were captured using the attached ProgRes MFscan Jenoptik D07739 camera and ProgRes CapturePro 2.8.8 software.

Statistical analyses

Statistical analysis involving foundational cytogenetic parameters have been demonstrated to imply significant knowledge on chromosomal evolution within a group (Winterfeld et al. 2020). Considering the lack of hypotheses, we have tested for correlation between the dependent variables (2C genome size, MCL and HCL) and predictor variables [chromosome number (2n) and ploidy level (p)] and also calculated linear models for regression analysis using IBM SPSS (v23, free).

The modern cytogenetic catalogue of cucurbitaceae

Along with the global review, fresh EMA based somatic plates and idiograms (Figs 1–3) of Indian species are presented here. We retain the previous designation of 10 tribes as ‘understudied’ (Bhowmick and Jha 2015b), excluding Indofevilleae, having no cytological reports.

Chromosome numbers

Currently, chromosome counts are available for 188 species (~19%) belonging to about 44 genera (~46%) of the 15 tribes, including the less attended ‘understudied tribes’. Within the ‘understudied tribes’, chromosome counts are available for only 42 species (out of almost 310) belonging to 17 genera (out of nearly 44). The basal number ranges from $x/n = 5$ (*Thladiantha* Bunge, 1833) to $x/n = 15$ (*Zanonia* Linnaeus, 1753) in these tribes (Table 2). Polyploidy has been abundantly reported in Gomphogyneae. Momordiceae have almost 60 species (Schaefer and Renner 2011) of which reports are known in nearly 11 species. The dibasic condition is noticed in *Momordica* Linnaeus, 1753 ($x = 11$ and 14) (Table 3) while polyploidy is detected in *M. charantia* Linnaeus, 1753 and *M. dioica* Willdenow, 1805 ($2n = 56$). *M. cymbalaria* Hooker, 1871, has the lowest count ($2n = 18$). In Bryonieae the X-Y sex determination system has been analysed in *Bryonia* Linnaeus, 1753 as the model along with *Ecballium* Richard, 1824 (Bhowmick and Jha 2015a). Chromosome counts are reported so far in 10 species of *Bryonia* ($x = 10$) and its sister genus *Ecballium* ($x = 12$ or $x = 9$, Table 4). Polyploidy is frequent in *Bryonia*. Sicyoeae is largest in terms of species (~264–266 species) (Schaefer and Renner 2011) of which cytological reports are known in around 14% species belonging to 9 genera (Table 5). Sicyoeae species range from $x = 8$ to $x = 14$ (Table 5). *Trichosanthes* Linnaeus, 1753 and *Luffa* Miller, 1754 have $x = 11$ and $x = 13$, respectively (Table 1). The less prevalent numbers include $x = 12$, $x = 8$ and $x = 9$ (Table 5). The possibility of multiple base number is noted in *Frantzia* Pittier, 1910 ($x = 12/14$) and *Sicyos* Lin-

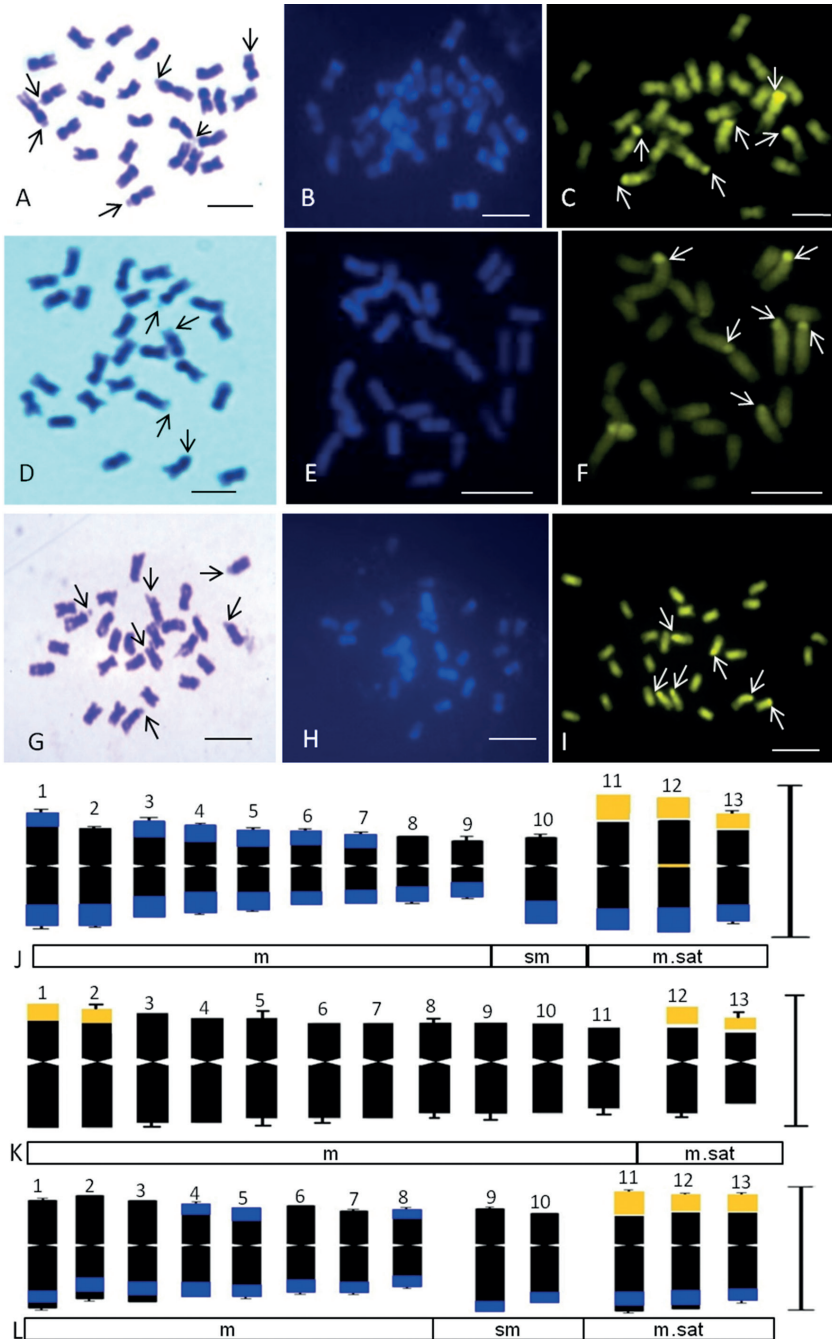


Figure 1. Somatic metaphase chromosomes and idiograms of *Luffa* species ($2n = 26$) stained with Giemsa (A, D, G), DAPI (B, E, H) and CMA3 (C, F, I) A–C *L. acutangula* D–F *L. aegyptiaca cylindrica* G–I *L. echinata*. Arrows indicate satellited chromosomes in Giemsa plates and CMA⁺ signals in C, F, I. Corresponding somatic idiograms (haploid set) of: J *L. acutangula* K *L. aegyptiaca* L *L. echinata*, showing DAPI⁺ (blue) and CMA⁺ (golden yellow) bands. Scale Bars: 5 μm

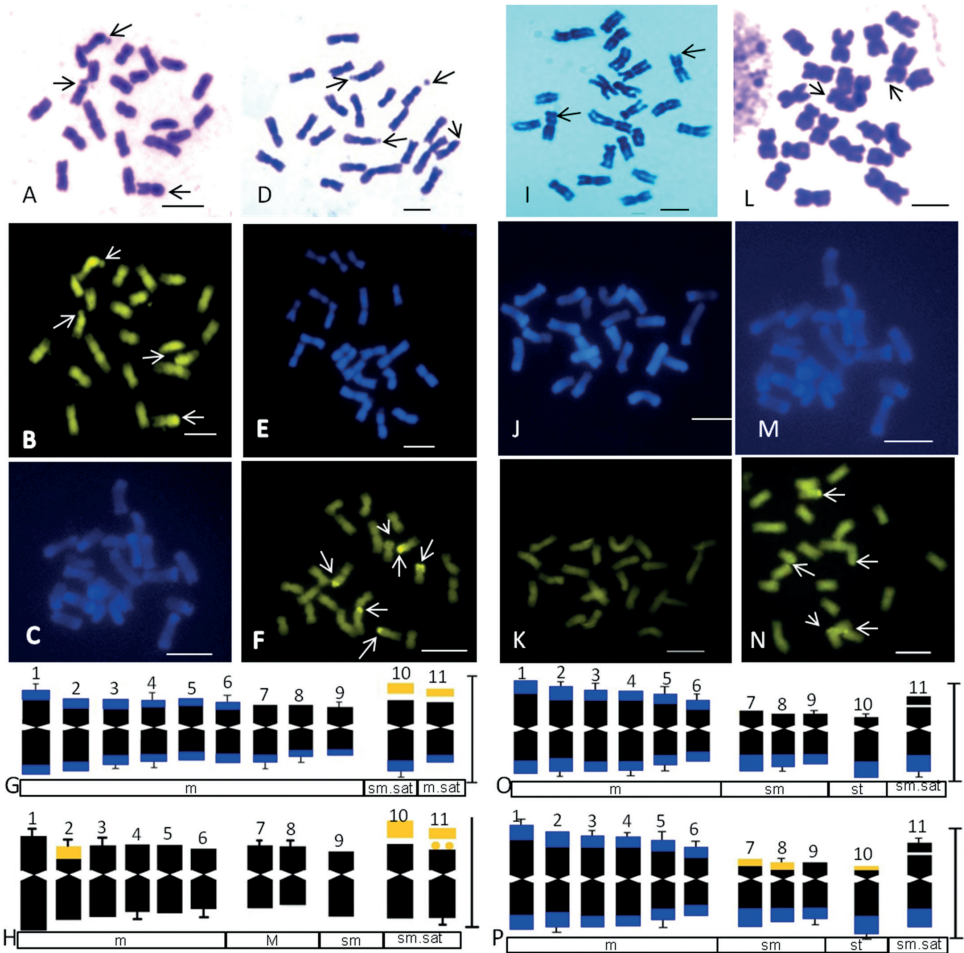


Figure 2. Somatic metaphase chromosomes and idiograms of *Trichosanthes* species stained with Giemsa (**A, D, I, L**), DAPI (**C, E, J, M**) and CMA3 (**B, F, K, N**) **A–C** *T. cucumerina* ssp. *cucumerina* ($2n = 22$), **D–F** *Trichosanthes cucumerina* ssp. *cucumerina* ‘Anguina’ ($2n = 22$) **I–K** *T. dioica* (male, $2n = 22$) **L–N** *T. dioica* (female, $2n = 22$). Arrows indicate satellited chromosomes in Giemsa plates and CMA⁺ signals in **B, F, K, N**. Corresponding somatic idiograms (haploid set) of: **G** *T. cucumerina* ssp. *cucumerina* **H** *Trichosanthes cucumerina* ssp. *cucumerina* ‘Anguina’ **O** *T. dioica* male plant **P** *T. dioica* female plant. Blue and golden yellow bands in idiograms indicate DAPI⁺ and CMA⁺ signals, respectively. Scale Bars: 5 μ m

naeus, 1753 ($x = 12/13/14$). Natural tetraploids are known in two species of *Trichosanthes* while the majority are diploids. Benincaseae is the second largest tribe comprising of 204–214 species in 24 genera (Schaefer and Renner 2011). Cytological reports are known in around 35% species (76 species of which 41 belong to *Cucumis* Linnaeus, 1753) of 12 genera (Tables 6, 7). $x = 12$ is the prevalent condition in Benincaseae (Tables 1, 6, 7). Dual base numbers are noted in the widely studied *Cucumis* ($x = 7, 12$). *Coccinia* Wight et Arnott, 1834 ($x = 12$) may also possess dual base numbers ($x = 10$ in *C. trilobata* Cogniaux, 1895). Molecular cytogenetics of *Cucumis sativus* Linnaeus, 1753

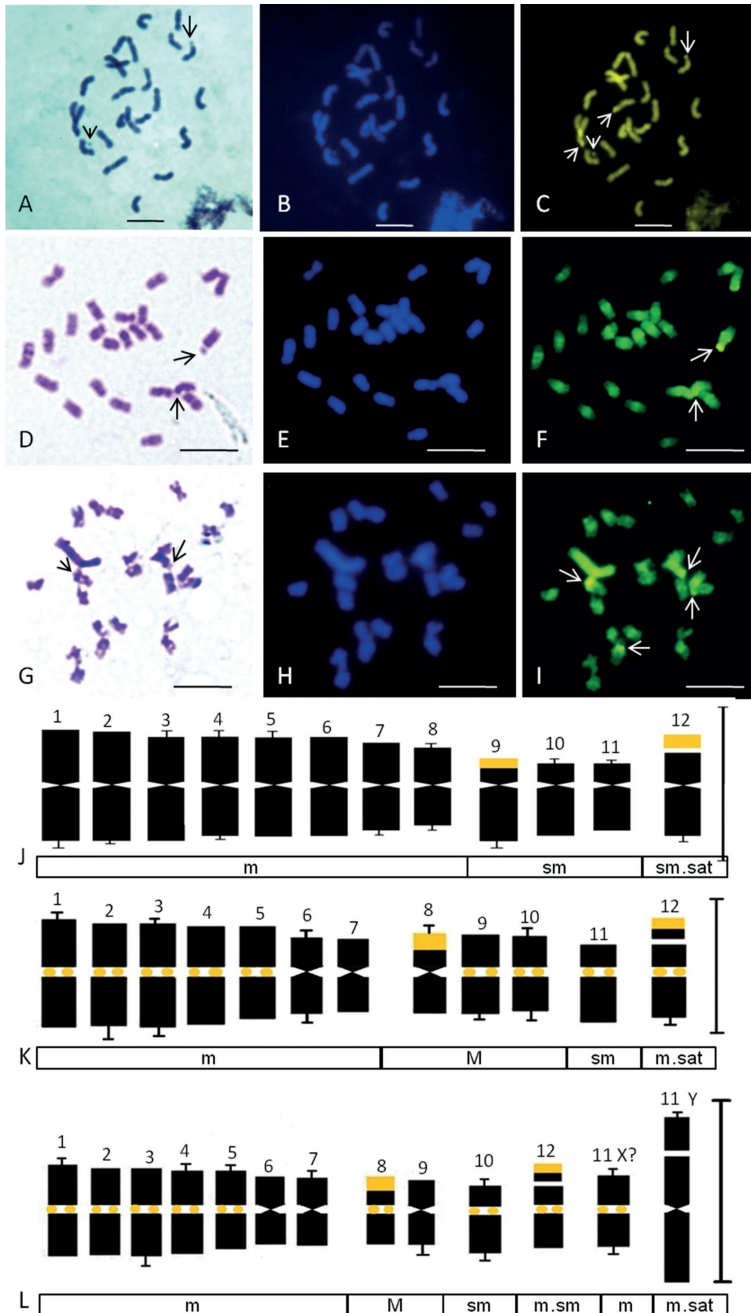


Figure 3. Somatic metaphase chromosomes and idiograms of two Benincaseae species ($2n = 24$) stained with Giemsa (**A, D, G**), DAPI (**B, E, H**) and CMA3 (**C, F, I**) **A–C** *Benincasa hispida* **D–F** *Coccinia grandis* (female plant) **G–I** *Coccinia grandis* (male plant). Arrows indicate satellited chromosomes in Giemsa plates and distal CMA⁺ve signals in **C, F, I**. Note the longest Y chromosome without any CMA band in **G–I** and centromeric CMA⁺ve signals in **F, I**. Corresponding somatic idiograms (haploid set) of: **J** *Benincasa hispida* **K** *Coccinia grandis* (female plant) **L** *Coccinia grandis* (male plant) with CMA⁺ve (golden yellow) bands. Note the X chromosome remaining indistinguishable in **L**. Scale Bars: 5 μ m

Table 2. Cytogenetic reports in the understudied tribes of Cucurbitaceae #.

Tribe and Genera	Species studied	Chromosome no.			Ploidy, Genome size, Chromosome features	References
		x	2n	n		
Gomphogyneae <i>Gomphogyne</i> Griffith, 1845	<i>G. cissiformis</i> Griffith, 1837		32 ^a	16 ^b	Tetraploid ^d ; autopolyploid ^d ; 10 secondary constrictions, one pair satellited ^d ; II, III, IV in meiosis ^f	CCDB ^b ; Kumar and Subramaniam (1987) ^a , Singh (1990) ^{a,d} , Roy et al. (1991) ^{a,c,e,f}
<i>Hemsleya</i> F.B. Forbes et Hemsley, 1888	<i>H. amabilis</i> Diels, 1912, <i>H. carnosiflora</i> Wu et Chen, 1985, <i>H. chinensis</i> Forbes et Hemsley, 1888, <i>H. emeiensis</i> Shen et Chang, 1983, <i>H. graciliflora</i> Cogniaux, 1916, <i>H. heterosperma</i> Wallich, 1831, <i>H. macrocarpa</i> Cogniaux, 1916, <i>H. panacis-scandens</i> Wu et Chen, 1985, <i>H. sphaerocarpa</i> Kuang et Lu, 1982	7 ^a	28 ^b , 22 ^c , 24 ^d , 26 ^e , 32 ^f , 40 ^g , 42 ^h	14 ^b	Tetraploid ⁱ , aneuploid ^j	Samuel et al. (1995) ^{a,j} , Anmin et al. (2011) ^{b,h}
<i>Gymostemma</i> Blume, 1825	<i>G. cardiospermum</i> Oliver, 1892	11 ^a	66 ^b		Hexaploid ^d	IPCN ^{a,c}
	<i>G. guangxiense</i> Chen et Qin, 1988		22 ^a		Diploid ^b	IPCN ^{a,b}
	<i>G. laxiflorum</i> Wu et Chen, 1983		22 ^a		Diploid ^b	IPCN ^{a,b}
	<i>G. longipes</i> Wu et Chen, 1983		22 ^a , 44 ^b		Polyplod ^d	IPCN ^{a,c}
	<i>G. microspermum</i> Wu et Chen, 1983		22 ^a		Diploid ^b	IPCN ^{a,b}
	<i>G. pedatum</i> Blume, 1825	12 ^a	24 ^b		Diploid ^c	Roy et al. (1991) ^{a,b,c}
	<i>G. pentagynum</i> Wang, 1989		22 ^a		Diploid ^b	IPCN ^{a,b}
	<i>G. pentaphyllum</i> Thunberg, 1784		22 ^a , 24 ^b , 64 ^c , 66 ^d		Diploid ^d ; triploid ^d ; hexaploid ^d ; 2C (flow cytometry): 3.62pg ^b ; 17M+14sm+2sr ^c ; CSR: 2.16–4.09 μm ³ 5S (8), 45S (10) rDNA and telomeric signals ^k	IPCN ^{a,b,c,e,f} , Zhang et al. (2013) ^b , Pellerin et al. (2018) ^{d,g,i,j,k}
	<i>G. pentaphyllum</i> var. <i>dasy carpum</i> Wu, 1983		22 ^a , 33 ^b , 44 ^c		Polyplod ^d	IPCN ^{a,d}
	<i>G. pentaphyllum</i> var. <i>pentaphyllum</i> Thunberg, 1784		22 ^a , 44 ^b , 66 ^c , 88 ^d		Polyplod ^d	IPCN ^{a,c}
	<i>G. yixingense</i> Wang et Xie, 1981		88 ^a		Polyplod ^b	IPCN ^{a,b}
Triceratiaceae		8 ^a			-	Roy et al. (1991) ^a
<i>Fevillea</i> Linnaeus, 1753						
Zanonieae <i>Zanonia</i> Linnaeus, 1753	<i>Z. indica</i> Linnaeus, 1759	15 ^a	30 ^b	15 ^c	Autoploid ^d ; Metacentric chromosomes ^e ; CSR: 1.10–1.98 μm ^f	Lekhak et al. (2018) ^{a,f}
Actinostemmateae	<i>A. lobatum</i> (Maxim.) Maxim. ex Franch. & Sav.		16 ^a		-	IPCN ^a
<i>Actinostemma</i> Griffith, 1841	<i>A. tenerum</i> Griffith, 1837		16 ^a		Diploid ^b ; 7M + 1sm ^c ; CSR: 2.88–4.02 μm ³ ; 45S (1) rDNA and 45S+5S (1) rDNA adjacent signal ^d ; telomeric repeat signals ^e	Pellerin et al. (2018) ^{a,f}
Thladiantheae	<i>T. calcarata</i> Clarke, 1876, <i>T. cordifolia</i> Blume, 1826 <i>T. davidii</i> Franchet, 1886, <i>T. dentata</i> Cogniaux, 1916, <i>T. lijiangensis</i> Lu et Zhang, 1981, <i>T. nudiflora</i> Hemsley, 1887, <i>T. pustulata</i> Léveillé, 1916	3 ^a , 5 ^b , 9 ^c	18 ^d	5 ^e , 9 ^f	Diploid ^g	Darlington and Janaki Ammal (1945) ^g ; Roy et al. (1991) ^{h,i,d,e,g} , IPCN ^{d,f}
	<i>T. dubia</i> Bunge, 1833		18 ^a , 22 ^b		Diploid ^d ; 7M+1sm+1st ^d ; CSR: 2.60–4.10 μm ³ ; 45S (4) and co-localized 45S+5S (1) rDNA signals ^e ; telomeric repeat signals ^g	Samuel et al. (1995) ^h , Pellerin et al. (2018) ^{a,c,d,e,f,g}
<i>Baijiana</i> Lu et Li, 1993	<i>B. yunnanensis</i> Lu et Zhang, 1984		32 ^a		-	IPCN ^a
Siraitieae <i>Siraitia</i> Merrill, 1934	<i>S. grosvenorii</i> Swingle, 1941		28 ^a		45S (6) and 5S (2) rDNA signals ^b	IPCN ^a , Li et al. (2007) ^b
Joliffieae <i>Telfairia</i> Hooker, 1827	<i>T. occidentalis</i> Hooker, 1871		22 ^a , 33 ^b , 44 ^c		Diploid ^d , aneuploid ^d , triploid ^d , Tetraploid ^e ; 1 B ^b	Uguru and Onovo (2011) ^{a,b}
	<i>T. pedata</i> Sims, 1826		22 ^a		-	Bhowmick and Jha (2015) ^a

Tribe and Genera	Species studied	Chromosome no.			Ploidy, Genome size, Chromosome features	References
		x	2n	n		
Schizopeoneae <i>Herpetospermum</i> Hooker, 1867	<i>H. pedunculosum</i> Seringe, 1828			11 ^a	45S (14), 5S (2) rDNA signals ^b	Xie et al. (2019a) ^{ab}
<i>Schizopepon</i> Maximowicz, 1859	<i>S. bryoniifolius</i> Maximowicz, 1859	10 ^a	20 ^b		-	Roy et al. (1991) ^a , IPCN ^b
Coniandreae <i>Apodanthera</i> Arnott, 1841	<i>A. undulata</i> Gray, 1853	14 ^a			-	IPCN ^a
<i>Conalocarpus</i> Bentham et Hooker, 1867	<i>C. epigaeus</i> Rottler, 1803		26 ^a	13 ^b	-	Beevy and Kuriachan (1996) ^{ab}
	<i>C. welwitschii</i> Naudin, 1863		72 ^a		-	Singh (1990) ^a
<i>Ibervillea</i> Greene, 1895		11 ^a , 12 ^b			-	Darlington and Janaki Ammal (1945) ^{ab}
<i>Kedrostis</i> Medikus, 1791	<i>K. africana</i> Linnaeus, 1753		40 ^a		2C (feulgen densitometry): 0.8 pg ^b ; 2C (flow cytometry): 1674 Mbp ^c	Bennet et al. (1982) ^{ab} , Plant C DNA Values Database ^c
	<i>K. foetidissima</i> Jacquin, 1788		26 ^a	13 ^b		Beevy and Kuriachan (1996) ^{ab}
	<i>K. rostrata</i> Rottler, 1803	13 ^a	26 ^b	13 ^c	-	IPCN ^{a-c}
<i>Seyrigia</i> Keraudren, 1960				13 ^a	-	IPCN ^a

x: base number; 2n: zygotic number; n: gametic number; CSR: chromosome size range; B: B chromosome; II: bivalents, III: trivalent, IV: tetraivalent; superscripts correspond to references.

has demonstrated the evolution of x = 7 from x = 12 in Benincaseae. x = 11 has been confirmed in *Citrullus* Schrader, 1836 and *Lagenaria*. The base number of *Melothria* Linnaeus, 1753, *Solena* Loureiro, 1790 and *Zehneria* Endlicher, 1833 can be x = 11 or x = 12 or both (Table 6). Cases of natural polyploidy are noted only in four species of *Cucumis* (Table 7). Cytogenetic information is available for 17 species in three genera of Cucurbitaceae with x = 10 and many polyploids (Table 8). The zygotic chromosome numbers of *Luffa*, *Trichosanthes*, *Benincasa* Savi, 1818 and *Coccinia*, corroborate the previous reports (Figs 1–3, Table 1).

Nuclear genome contents

Nuclear genome sizes are reported in 49 species (~5% of total species) belonging to 15 genera (~16% of total genera) of Cucurbitaceae. Among the understudied tribes, 2C genome content is known for one species each from Gomphogyneae and Coniandreae (Table 2). Within the Momordiceae species of India, significant interspecific genome size differences have been reported (Ghosh et al. 2021). The species differed 5.19-fold in their genome sizes (2C = 0.72–3.74 pg) (Table 3) (Ghosh et al. 2021). Interestingly, the species with lowest chromosome number (*M. cymbalaria*, 2n = 18) contained highest nuclear DNA content among the four *Momordica* species (Table 3). In Bryonieae, flow cytometric genome size of *Bryonia* shows a 2.2-fold increase than *Ecballium* (Table 4). In case of Sicyoeae, flow cytometric 2C DNA content ranges from 1.49–2.32 pg/2C, indicating 1.55-fold differences in genome size. *Echinocystis lobata* Michaux, 1803, in spite of tetraploid condition, shows lowest genome size (Table 5). There is no significant difference in genome size between the genders of *Trichosanthes dioica* Roxburgh, 1832

Table 3. Cytogenetic information in *Momordica* (Momordiceae)#.

Species	Chromosome no.		Ploidy, Genome size, Chromosome features	References
	2n	n		
<i>M. balsamina</i> Linnaeus, 1753	22 ^a		Diploid ^b ; two chromosomes with double constrictions; CSR:0.65–1.98µm ³ ; MCL:1.30µm ³ ; TCL: 28.6µm ³	Bharathi et al. (2011) ^{a,f}
<i>M. charantia</i>	22 ^a	11 ^b	Diploid ^c ; 2C (Feulgen densitometry): 4.10pg ³ ; 2C (flow cytometry): 1.43pg ³ ; chromosomes mostly metacentric, few submetacentric and subtelocentric ^c ; 2 chromosomes with satellites ^c ; CSR: 1.26–1.81µm ³ ; 45S (4) and 5S (2) rDNA signals ^k	Plant DNA C-Values Database ³ ; Bharathi et al. (2011) ^{a,f} ; Barow and Meister (2003) ^g ; Lombello and Pinto-Maglio (2007) ^{h,i,j} ; Bharathi et al. (2011); Waminal and Kim (2012) ^{j,k,l,m,n} ; Kausar et al. (2015) ^h ; Kido et al. (2016) ^{h,i}
<i>M. charantia</i> var. <i>charantia</i>	22 ^a	11 ^b	Diploid ^c ; 2C (flow cytometry): 0.72pg ³ ; NORs: 4 ^c ; nucleolar and centromeric CMA ^a bands ^c ; CSR: 1.27–3.07µm ³ ; MCL: 1.97µm ³ ; HCL: 21.77µm ³	Ghosh et al. (2018) ^{h,i} ; Ghosh et al. (2021) ^{j,k,l,m,n}
<i>M. charantia</i> var. <i>nuricata</i> Chakravarty, 1982	22 ^a	11 ^b	Diploid ^c ; 2C (flow cytometry): 1.16pg ³ ; NORs: 6 ^c ; nucleolar and centromeric CMA ^a bands ^c ; CSR: 1.64–3.13µm ³ ; MCL: 2.19µm ³ ; HCL: 24.19µm ³	Ghosh et al. (2018) ^{h,i} ; Ghosh et al. (2021) ^{j,k,l,m,n}
<i>M. cochinchinensis</i> Lourreiro, 1790	28 ^a	14 ^b	Diploid ^c ; 2C (flow cytometry): 2.64pg ³ ; 6 ^c chromosomes with secondary constrictions; CSR:1.16–2.03µm ³ /1.71–3.17µm ³ ; MCL: 2.27µm ³ ; HCL: 31.86µm ³ ; 45S (8) and 5S (2) rDNA signals ^k	IPCN ^h ; Xie et al. (2019a) ^{h,i} ; Bharathi et al. (2011) ^{j,k,l} ; Ghosh et al. (2021) ^{j,k,l,m,n}
<i>M. cymbalaria</i>	18 ^a	8 ^b ; 9 ^c ; 11 ^d	Diploid ^c ; 2C (flow cytometry): 3.74 pg ³ ; 2 ^{a–d} chromosomes with secondary constrictions; CSR: 2.71–4.57µm ³ ; MCL:3.75µm ³ ; HCL: 33.79µm ³	IPCN ^h ; CCDB ^{h,i} ; Bharathi et al. (2011) ^{j,k,l,m,n} ; Ghosh et al. (2021) ^{j,k,l,m,n}
<i>M. denudata</i> Clarke, 1879		14 ^a	-	IPCN ^h
<i>M. dioica</i> Willdenow, 1805	28 ^a ; 56 ^b		Diploid ^c ; 2C (flow cytometry): 3.36 pg ³ ; 2 ^{a–12^c} chromosomes with secondary constrictions; CSR: 2.04–3.58µm ³ ; MCL: 2.75µm ³ ; HCL: 77.10µm ³ ; 45S (4) and 5S (2) rDNA signals ^k	Bharathi et al. (2011) ^{j,k,l} ; Xie et al. (2019a) ^{h,i} ; Ghosh et al. (2021) ^{j,k,l,m,n}
<i>M. foetida</i> Schumacher, 1827	44 ^a		-	Behera et al. (2011) ^a
<i>M. rostrata</i> Zimmermann, 1922	22 ^a		-	Behera et al. (2011) ^a
<i>M. subyadriza</i> Kattukunnel et Antony, 2007	28 ^a		2 chromosomes with secondary constrictions ^b ; CSR: 0.73–1.83µm ³ ; TCL: 37.53µm ³ ; MCL: 1.34µm ³	Behera et al. (2011) ^a
<i>M. subangulata</i> Blume, 1826	56 ^a		2C (flow cytometry): 3.06pg ³ ; 8 chromosomes with secondary constrictions; CSR: 1.52–3.1µm ³ ; HCL: 60.30µm ³	Behera et al. (2011) ^a
<i>M. subangulata</i> subsp. <i>renigera</i> Don, 1834	56 ^a		4 chromosomes with secondary constrictions ^b ; CSR: 0.52–1.26µm ³ ; MCL: 0.93µm ³ ; TCL 51.88µm ³	Ghosh et al. (2021) ^{j,k}
<i>M. tuberosa</i> Miquel, 1855	22 ^a	11 ^b	-	Bharathi et al. (2011) ^{j,k}

2n: Zygotic chromosome number; n: gametic chromosome number; I: univalent; II: bivalent; III: trivalent; CSR: chromosome size range; MCL: mean chromosome length; HCL: total length of haploid set of chromosomes; TCL: total length of diploid set of chromosomes; NOR: nucleolar organizing region, superscripts correspond to references.

IPCN^h, CCDB^{h,i}

Table 4. Chromosome number and genome size in Bryoniae#.

Genera	Species studied	Chromosome no.			Genome size	References
		x	2n	n		
<i>Bryonia</i>		10 ^a				Darlington and Janaki Ammal (1945) ^a
	<i>B. alba</i> Linnaeus, 1753	10 ^a	20 ^b	10 ^c	2C (flow cytometry): 5827Mbp ^d	CCDB ^d , Volz and Renner (2008) ^{abc}
	<i>B. aspera</i> Ledebour, 1843	10 ^a	40 ^b , 60 ^c	20 ^d , 10 ^e	-	Kumar and Subramaniam (1987) ^e , Volz and Renner (2008) ^{abd,c}
	<i>B. cretica</i> Linnaeus, 1753	10 ^a	60 ^b	30 ^c	-	Volz and Renner (2008) ^{abc}
	<i>B. dioica</i> Jacquin, 1774	10 ^a	20 ^b	10 ^c	2C (microdensitometry): 4.01pg ^d ; 2C (flow cytometry): 5522Mbp ^e	CCDB ^{d,e} , Volz and Renner (2008) ^{abc}
	<i>B. macrostylis</i> Heilbronn et Bilge, 1954			10 ^a	-	IPCN ^a
	<i>B. marmorata</i> Petit, 1889		40 ^a	20 ^b	-	Volz and Renner (2008) ^{ab}
	<i>B. monoica</i> Aitchison et Hemsley, 1886	10 ^a	20 ^b		-	Volz and Renner (2008) ^{ab}
	<i>B. multiflora</i> Boissier et Heldreich, 1849	10 ^a			-	Volz and Renner (2008) ^a
	<i>B. syriaca</i> Boissier, 1856	10 ^a	20 ^b		-	Volz and Renner (2008) ^{ab}
	<i>B. verrucosa</i> Aiton, 1789	10 ^a	20 ^b	10 ^c	2C (flow cytometry): 2.09pg ^d ; 4504Mbp ^e	CCDB ^{d,e} , Volz and Renner (2008) ^{abc}
<i>Ecballium</i>		12 ^a				Darlington and Janaki Ammal (1945) ^a
	<i>E. elaterium</i> Linnaeus, 1753		18 ^a	12 ^b	2C (flow cytometry): 2442Mbp ^c	Vesely (2012) ^c , Volz and Renner (2008) ^b
	<i>E. elaterium</i> subsp. <i>dioicum</i> Battandier, 1989		18 ^a , 24 ^b	9 ^c , 12 ^d	-	Volz and Renner (2008) ^{ad}
	<i>E. elaterium</i> Linnaeus, 1753 subsp. <i>elaterium</i>		18 ^a	9 ^b	-	Volz and Renner (2008) ^{ab}

2n: Zygotic chromosome number; n: gametic chromosome number.

(Table 5). Genome size estimates are known from 24 Benincaseae species of which 17 species belong to *Cucumis* (Tables 6, 7). Highest 2C nuclear genome is known in *Benincasa hispida* Thunberg, 1784 (1.97 pg) (Bhowmick and Jha 2015a) while the lowest is known in *Cucumis melo* var. *inodorus* Harz, 1885 (0.64 pg) (Karimzadeh et al. 2010). In case of *Cucumis*, there is yet no consensus on whether the taxa with different base numbers (x = 7, 12) have correspondingly dissimilar genome sizes since the researchers depended on diverse methods of genome size estimation. Lower 2C genome size was reported in *C. Coccinia grandis* Linnaeus, 1767 (2n = 24) while *C. trilobata* (2n = 20) had higher 2C DNA content (Table 6). The divergence in genome size between genders was found to be highest in dioecious *C. grandis* (Table 6), a sharp contrast to dioecious *Trichosanthes dioica* (Table 5). Benincaseae shows a 3.07-fold overall difference in genome size. Genome sizes are known in eight species of *Cucurbita* Jussieu, 1789. Flow cytometric genome size ranges from 0.686–0.933 pg/2C, indicating a 1.36-fold variation (Table 8). Despite polypoidy, the nuclear DNA content of *Cucurbita* species is comparable to many diploids.

Karyotypes, chromosome banding and molecular cytogenetics

Among the understudied tribes, information on chromosome morphology, size and karyotype are reported in very few taxa (Table 2). In *Gynostemma pentaphyllum* Thunberg, 1784, the number of rDNA loci was suggested to reduce during polyploidization (Pellerin et al. 2018). The *Actinostemma tenerum* Griffith, 1837, genome contained in-

Table 5. Cytogenetic information in Sicyoeae#.

Genera studied	Species studied	Chromosome no.		Ploidy, Genome size, Chromosome features	References
		x	2n		
<i>Cyclanthera</i> Lilja, 1870	<i>C. pedata</i> (L.) Schrader, 1831	8 ^a	16 ^a , 32 ^b	8 ^a	Darlington and Janaki Ammal (1945) ^a Roy et al. (1991) ^{a,c} , Samuel et al. (1995) ^b
		8 ^a	16 ^a , 32 ^b	16 ^b	Bhowmick and Jha (2015b) ^b , Darlington and Janaki Ammal (1945) ^a IPCN ^b , Plant DNA C-Values Database ^{c,d}
<i>Echinocystis</i> Tourneay et Gray, 1840	<i>E. lobata</i> Michaux, 1803 <i>E. macrocarpa</i> Greene, 1885 <i>E. wrightii</i> Gray, 1853	32 ^a	-	Tetraploid ^d ; 2C (flow cytometry): 1.49pg ^d	Whitaker (1950) ^a IPCN ^a , CCDB ^a
		12 ^a	-	-	Schaefer and Renner (2011) ^{a,b}
<i>Hodgsonia</i> Persson, 1953	<i>H. macrocarpa</i> var. <i>capnicarpa</i> Ridley, 1920	12 ^a , 14 ^b	-	-	IPCN ^a , CCDB ^a
		18 ^a	-	-	IPCN ^a , CCDB ^a
<i>Luffa</i>	<i>L. acutangula</i> <i>L. acutangula</i> var. <i>acutangula</i> <i>L. acutangula</i> var. <i>amara</i> Clarke, 1879 <i>L. aegyptiaca</i> (syn. <i>L. cylindrica</i>) Roemer, 1846	13 ^a	26 ^a	Diploid ^d ; CSR: 1.39–3.20µm ² ; 18m+2sm+6m.st ^d ; NORs: 6 ^d ; distal DAPI and nucleolar CMA signals ^b	Darlington and Janaki Ammal (1945) ^a Kumar and Subramaniam (1987) ^{a,b} , IPCN ^a , Bhowmick and Jha (2021) ^b
		13 ^a	13 ^a	-	Beegy and Kuriachan (1996) ^a Beegy and Kuriachan (1996) ^a
<i>Sicyos</i> (75, includes <i>Sechium</i> , <i>Microsechium</i>)	<i>S. acuminata</i> <i>S. graveolens</i> Roxburgh, 1832 <i>S. hermaphrodita</i> Singh et Bhandari, 1963 <i>S. operculata</i> Linnaeus, 1759	13 ^a	26 ^a	Diploid ^d , 2C (flow cytometry): 1.56 pg; 2C (Feulgen densitometry): 1.7pg ^d ; CSR: 1.60–2.06µm ² ; 24M+1sm ^b ; 22m+ 4m.st ^d ; nucleolar and distal CMA signals ^d ; 45S (10) and 5S (2) rDNA signals ^d	Bennet et al. (1982) ^{b,c,d} , Kumar and Subramaniam (1987) ^{a,b} , Waminal and Kim (2012) ^{b,d,e,f,h} , Bhowmick and Jha (2015a) ^{b,c,d,e,h,k}
		13 ^a	26 ^a , 39 ^b , 52 ^c	Diploid ^d ; CSR 2.44–3.96 µm ² ; 16m+4sm+6m.st ^d ; NORs: 6 ^d ; Distal and intercalary DAPI and nucleolar CMA signals ^d	Kumar and Subramaniam (1987) ^{a,c} , Bhowmick and Jha (2021) ^{b,c,e,i}
<i>Sicyos</i> (75, includes <i>Sechium</i> , <i>Microsechium</i>)	<i>S. angulatus</i> <i>S. australis</i> Erdllicher, 1833 <i>S. edulis</i> Jacquin, 1760 (syn of <i>Sechium edule</i>) <i>S. nbaucensis</i> St. John, 1970	13 ^a	13 ^a	-	Kumar and Subramaniam (1987) ^a IPCN ^a
		13 ^a	26 ^a	-	Kumar and Subramaniam (1987) ^{a,b} , IPCN ^a
<i>Sicyos</i> (75, includes <i>Sechium</i> , <i>Microsechium</i>)	<i>S. angulatus</i> <i>S. australis</i> Erdllicher, 1833 <i>S. edulis</i> Jacquin, 1760 (syn of <i>Sechium edule</i>) <i>S. nbaucensis</i> St. John, 1970	12 ^a	24 ^b	-	Darlington and Janaki Ammal (1945) ^{a,b}
		12 ^a	24 ^b	-	Waminal and Kim (2015) ^{a,c} ; IPCN ^b
<i>Sicyos</i> (75, includes <i>Sechium</i> , <i>Microsechium</i>)	<i>S. edulis</i> Jacquin, 1760 (syn of <i>Sechium edule</i>) <i>S. nbaucensis</i> St. John, 1970	13 ^a	26 ^a , 28 ^a	Diploid ^d ; CSR: 1.9-4.6µm ² ; 4 adjacent 45S+5S rDNA signals ^d 12H ^d , 1.3H ^d	IPCN ^a , CCDB ^{a,d}
		13 ^a	26 ^a , 28 ^a	Diploid ^d ; metacentric and submetacentric chromosomes ^d ; CSR: 2.69–5.38µm ² ; 45S (6), 5S (2) rDNA and telomeric repeat signals (28)	Beegy and Kuriachan (1996) ^{a,b,c} , Pellerin et al. (2018) ^{e,f,g,h} , Ting et al. (2019) ⁱ ; IPCN ^a , CCDB ^a
<i>Sicyos</i> (75, includes <i>Sechium</i> , <i>Microsechium</i>)	<i>S. nbaucensis</i> St. John, 1970 <i>Sechium compositum</i> Smith, 1903 (syn. <i>Microsechium compositum</i>) <i>S. hintonii</i> Wilson, 1958 (syn. <i>Microsechium hintonii</i>)	12 ^a	14 ^b	-	IPCN ^a , CCDB ^a
		14 ^a	14 ^b	-	IPCN ^a , CCDB ^a

Genera studied	Species studied	Chromosome no.		Ploidy, Genome size, Chromosome features	References	
		x	2n			
<i>Trichosanthes</i> (100)	<i>T. amaindaciensis</i> Beddome, 1864	11 ^a	22 ^b	11 ^b	-	Darlington and Janaki Ammal (1945) ^a
	<i>T. boninensis</i> Nakai et Tuiyama, 1928	22 ^a	22 ^a	-	-	Bevy and Kuriachan (1996) ^{ab}
	<i>T. bracteata</i> Lamarck, 1797	11 ^a	22 ^b , 44 ^c , 66 ^d	-	-	IPCN ^b Kumar and Subramaniam (1987) ^{ab} , Roy et al. (1991) ^{c,d}
	<i>T. bracteata</i> var. <i>bracteata</i>			11 ^a , 22 ^b	-	Bevy and Kuriachan (1996) ^{ab}
	<i>T. chingiana</i> Handel-Mazzetti, 1936	22 ^a	22 ^a	-	-	IPCN ^b
	<i>T. costata</i> Blume, 1826 (syn <i>Gymnopetalum chinense</i> Loureiro, 1790)	22 ^a	22 ^a	Diploid ^d ; 45S (6) and 5S (4) rDNA signals ^e	-	Kumar and Subramaniam (1987) ^a ; Xie et al. (2019a) ^{bc}
	<i>T. cucumerina</i>	22 ^a	22 ^a	Diploid ^d ; 12m+4M+2sm+4sm.sr ^d ; CSR: 2.26–4.99µm ³ ; 6 chromosomes with double constrictions; NORs: 4 ^d ; nucleolar CMA and distal DAPI bands ^b	-	Bhowmick and Jha (2019) ^{ab}
	<i>T. cucumerina</i> sp. <i>cucumerina</i> Anguina	11 ^a	22 ^b	11 ^a , 22 ^d , 32 ^e , 33 ^f	Diploid ^d ; 2C (Feulgen densitometry): 2.2pg; CSR: 2.77–5.01µm ³ ; 12m+4M+2sm+4sm.sr ^d ; 6 chromosomes with double constrictions; NORs: 4 ^d ; nucleolar and distal CMA bands ^d ; 45S (6) and 5S (2) rDNA signals ^d	Kumar and Subramaniam (1987) ^a ; Bhowmick and Jha (2019) ^{bc,de,gh,ik} , Xie et al. (2019a) ^{hi} , IPCN ^{e,f}
	<i>T. dioica</i>	11 ^a	22 ^b	11 ^c	Diploid ^d ; 2C (flow cytometry): male-2.27pg, female-2.32pg; 12m+6Sm+2St+25m.r ^d ; distal DAPI bands ^d ; distal CMA bands in females ^d ; 1 rod bivalent in meiosis ^d	Kumar and Subramaniam (1987) ^a ; Guha et al. (2004) ^{h,kl} , Bhowmick and Jha (2015a) ^{h,de,ef,gh,il}
	<i>T. dianniana</i> Léveillé, 1911	22 ^a	22 ^a	11 ^a	Diploid ^d ; 45S (6) and 5S (2) rDNA signals ^e	Xie et al. (2019a) ^{bc}
	<i>T. himalensis</i> Clarke, 1879	22 ^a	22 ^a	-	-	Roy et al. (1991) ^a
	<i>T. hupchensis</i> Cheng et Yueh, 1974	22 ^a	22 ^a	-	-	IPCN ^b , CCDB ^a
	<i>T. kirilouii</i> Maximowicz, 1859	66 ^a , 88 ^b , 110 ^d	60 ^a	Hexa-, octa-, decaploid ^d ; CSR: 2.3-3.5µm ³ ; 45S (4), 5S (4) and 45S + 5S (6) adjacent rDNA signals ^e	-	IPCN ^b , CCDB ^a ; Waminal and Kim (2015) ^{bc,de,fg}
	<i>T. kirilouii</i> var. <i>japonica</i>	11 ^a	11 ^a	-	-	Roy and Saran (1990) ^b
	<i>T. leptanana</i> Naudin, 1868	44 ^a	44 ^a	11 ^b	11 ^b	Roy et al. (1991) ^{b,c} ; IPCN ^b , CCDB ^a
<i>T. lobata</i> Roxburgh, 1832	11 ^a	11 ^a	-	-	Kumar and Subramaniam (1987) ^a ; Bevy and Kuriachan (1996) ^b	
<i>T. miayungensis</i> Yueh et. Liao, 1992	88 ^a	88 ^a	-	-	IPCN ^b , CCDB ^a	
<i>T. nerifolia</i> Linnaeus, 1753	11 ^a	11 ^a	-	-	Bevy and Kuriachan (1996) ^a	
<i>T. origena</i> Blume, 1826	22 ^a	22 ^a	Diploid ^d ; 45S (10) and 5S (2) rDNA signals ^e	-	Xie et al. (2019a) ^{bc}	
<i>T. palmata</i> Linnaeus, 1759	22 ^a , 44 ^b , 11 ^d , 66 ^e	22 ^a	11 ^d	-	IPCN ^d	
<i>T. pedata</i> Merrill et Chun, 1934	22 ^a	22 ^a	-	-	IPCN ^b , CCDB ^a	
<i>T. truncata</i> Clarke, 1879	22 ^a	22 ^a	-	-	IPCN ^b , CCDB ^a	
<i>T. uallichiana</i> Wright, 1840	11 ^a	11 ^a	-	-	Kumar and Subramaniam (1987) ^{ab}	

#x: base number; 2n: zygotic number; n: gametic number; NOR: nucleolar organizing region; B: B chromosome; II: bivalents; superscripts correspond to references.

Table 6. Cytogenetic information on Benicaseae#.

Genera studied	Species studied	Chromosome no.		Ploidy, Genome size, Chromosome features	References
		x	2n		
Benicasea	<i>B. farulosa</i>	12 ^a	24 ^a	Diploid ^b ; 45S (4) and 5S (4) signals ^b	Li et al. (2016) ^{abc}
	<i>B. hispida</i>	12 ^a	24 ^b	Diploid ^d ; 2C (flow cytometry): 1.97pg; 2C (feulgen densitometry): 2.1pg; CSR 2.54-4.59µm ² ; 16m+6Sm+2Sm.t ⁴ ; NORs2; distal CMA signals ⁴ ; 45S (2) and 45S+5S (2) adjacent rDNA signals ⁴	Plant DNA C-Values Database ⁴ , Waminal et al. (2011) ^{bdeh} , Bhowmick and Jha (2015a) ^{bcd,efgh} , Darlington and Janaki Ammal (1945) ^a
Cirmalus	<i>C. amarus</i> (syn. <i>C. lanatus</i> var. <i>citroides</i>)	11 ^a	22 ^b	Diploid ^c ; CSR: 3.1–4.7µm ² ; 45S (2) and 5S (4) rDNA signals ^c	Reddy et al. (2013) ^{bc} , Waminal and Kim (2015) ^{ac} , Renner et al. (2017) ^b
	<i>C. eobryanthis</i>	11 ^a	22 ^a	Diploid ^d ; 45S (2) and 45S+5S (2) adjacent rDNA signals ^d	Beey and Kuriachan (1996) ^b , Reddy et al. (2013) ^{bc,d} , Li et al. (2016) ^{pc,d}
	<i>C. ectrhosus</i>	22 ^a	11 ^b	Diploid ^c ; 2 satellites detected in meiosis ^c ; 45S (2) and 5S (4) rDNA signals ^c ; regular meiosis ^c	Li et al. (2016) ^{bc,e} , Renner et al. (2017) ^{abcd}
	<i>C. lanatus</i>	22 ^a	11 ^b	Diploid ^c ; CSR: 1.09µm-1.72µm ² ; 14m+8sm; 45S (2) and 45S+5S (2) adjacent rDNA signals ^c ; linkage groups hybridized to chromosomes ^{ef}	Beey and Kuriachan (1996) ^b , Waminal et al. (2011) ^{cd,ef} , Ren et al. (2012) ^{efg}
	<i>C. lanatus</i> subsp. <i>lanatus</i>	22 ^a	22 ^a	Diploid ^d ; 45S (2) and 5S (4) rDNA signals ^c	Li et al. (2016) ^{bc}
	<i>C. lanatus</i> subsp. <i>nucospermus</i> Fursa, 1972	22 ^a	22 ^a	Diploid ^d ; 45S (2) and 45S+5S (2) adjacent rDNA signals ^c	Li et al. (2016) ^{bc}
	<i>C. lanatus</i> subsp. <i>vilgeris</i> Schradler, 1836	22 ^a	22 ^a	Diploid ^d ; 45S (2) and 45S+5S (2) adjacent rDNA signals ^c	Li et al. (2016) ^{bc}
	<i>C. lanatus</i> var. <i>lanatus</i>	22 ^a	22 ^a	Diploid ^d ; 45S (2) and 45S+5S (2) adjacent rDNA signals ^c	Reddy et al. (2013) ^{bc}
	<i>C. naudinianus</i> (syn. <i>Aanthoicyos naudinianus</i>)	24 ^a	24 ^a	Diploid ^d ; 45S (2) and co-localized 45S+5S (2) rDNA signals ^c	Li et al. (2016) ^{abc}
	<i>C. rehmsii</i>	22 ^a	22 ^a , 44 ^b	Diploid ^d ; 45S (2) and 5S (2) rDNA signals ^c	Reddy et al. (2013) ^{bc} , Li et al. (2016) ^{bc}
<i>Coccinia</i> (30)	<i>C. vilgeris</i> Schradler, 1836	12 ^a	22 ^a , 44 ^b	Diploid ^d ; 45S (2) and 5S (2) rDNA signals ^c	IPCN ^{cd} , Arumuganathan and Earle (1991) ^e
	<i>C. abyssinica</i> Lamarck, 1753	12 ^a	24 ^b	Diploid ^d ; 2C: 0.88/0.90pg ^c	Darlington and Janaki Ammal (1945) ^a
	<i>C. grandis</i>	12 ^a	24 ^b	Diploid ^d ; 45S (2) and 5S (2) rDNA signals ^c	Kumar and Subramaniam (1987) ^a , Roy et al. (1991) ^b
<i>Genolepis</i> Hooker, 1867	<i>C. hirtella</i> Cogniaux, 1896	24 ^a	24 ^b	Diploid ^d , 2C (Flow cytometry): male- 0.943/0.92 ¹ pg and female- 0.849/ 0.73 ¹ pg; CSR: 1.33-4.71µm (male) and 1.35-2.26µm (female); 15m+4M+2sm+2msm+1ms.t (Y) in male and 14m+6M+2sm+2ms.t in female; NORs-2 ¹ ; chromosomal C bands ¹ ; centromeric, nucleolar CMA bands ² ; 45S (4) ¹ rDNA signals, 2 signals adjacent to 5S ¹ ; GISH performed ¹ ; repetitive, organellar DNA hybridized ¹ ; centromere immunofluorescence ¹ ; heteromorphic sex chromosomes (largest Y); X-Y bivalent (meiosis) ¹	Bhowmick et al. (2012) ^{b,cd,h,ms,t} , (2016) ^{bd,h,kl,ms} , Sousa et al. (2013) ^{b,de,g,kl,ms,t,r} , Sousa et al. (2017) ^{b,kl,ms,pq,r} , Xie et al. (2019a) ^{h,ko}
	<i>C. sessifolia</i> Sonder, 1881	24 ^a	24 ^a	Diploid ^d , 2C (flow cytometry): male-0.988pg; 45S (4) and 45S+5S (2) adjacent rDNA signals ^d , repetitive and organellar DNA hybridized ^d ; centromere immunofluorescence performed ^d	Sousa et al. (2017) ^{ef}
	<i>C. tribolata</i>	20 ^a	20 ^a	Diploid ^d ; 2C (flow cytometry): male- 1.2,63pg ¹ ; 45S (2) and 45S+5S (2) adjacent rDNA signals ^d , repetitive, organellar DNA sequence hybridized ^d	Li et al. (2016) ^{abcd} , Sousa et al. (2017) ^{bc}
	<i>C. garcinii</i> Burman, 1768	24 ^a	24 ^a	Diploid ^d ; 2C (flow cytometry): male-1.2,63pg ¹ ; 45S (2) and 45S+5S (2) adjacent rDNA signals ^d , repetitive, organellar DNA sequence hybridized ^d	Sousa et al. (2017) ^{bc}

Kumar and Subramaniam (1987)^a, Beey and Kuriachan (1996)^b

Genera studied	Species studied	Chromosome no.		Ploidy, Genome size, Chromosome features	References
		x	2n		
<i>Diplocyclos</i> Endlicher, 1833	<i>D. palmatus</i>		24 ^a	Diploid ^b ; 45S (4) and 45S+5S (2) adjacent rDNA signals ^c	Li et al. (2016) ^{c,e}
	<i>L. tucanatha</i> Rusby, 1896	11 ^b	22 ^a	-	IPCN ^{b,h} , CCDB ^{b,h}
<i>Lagenaria</i> Seringe, 1825	<i>L. tucanatha</i> var. <i>clavata</i> Makino, 1940		22 ^a	-	CCDB ^b
	<i>L. siceraria</i>	11 ^a	22 ^b	Diploid ^d , 2C (flow cytometry); 0.734pg; 2C (Feulgen densitometry); 1.4pg; CSR: 0.56–1.06µm ² ; metacentric and few sub-metacentric chromosomes ^b ; 45S (2) and 45S+5S (2) adjacent rDNA signals ^c	Darlington and Janaki Ammal (1945) ^b ; Plant DNA C-Values Database ^c ; Beevy and Kuriachan (1996) ^e ; Achigan-Dako et al. (2008) ^{d,e} ; Waminal and Kim (2012) ^{b,d,g,h,i} ; Li et al. (2016) ^{b,d,i} ; Xie et al. (2019a) ^{b,i}
<i>Melobria</i>	<i>L. siceraria</i> var. <i>macrocarpa</i>		22 ^a	-	CCDB ^b
	<i>L. vulgaris</i> Seringe, 1825	11 ^a , 12 ^b	22 ^a	Diploid ^d ; 2C (Feulgen densitometry); 1.40pg ^d	Bennet et al. (1982) ^{b,h,e} Darlington and Janaki Ammal (1945) ^{b,h}
	<i>M. pendula</i> Linnaeus, 1753		24 ^a	Diploid ^d ; 45S (2) and 45S+5S (2) adjacent rDNA signals ^c	Li et al. (2016) ^{c,e} Kumar and Subramaniam (1987) ^a
<i>Peponium</i> Engler, 1897	<i>M. perpusilla</i> Blume, 1826		48 ^a	-	CCDB ^b
	<i>M. scabra</i> Naudin, 1866		24 ^a	-	CCDB ^b
<i>Selena</i>	<i>P. bresiliense</i> Keraudren, 1960		24 ^a	-	CCDB ^b
	<i>S. amplicaxianalis</i> Lamarck, 1785 (syn. <i>S. heterophylla</i> , <i>Melobria heterophylla</i> , <i>Zehneria umbellata</i>)	22 ^a , 24 ^b , 26 ^c , 36 ^d , 48 ^e	11 ^f ; 12 ^g , 24 ^h	2-4 B ⁱ	Kumar and Subramaniam (1987) ^{b,h,c,e} ; Roy et al. (1991) ^{d,i} ; Beevy and Kuriachan (1996) ^{b,g,e,h} ; IPCN ^{b,d,e,f,g,h}
<i>Zehneria</i>	<i>Z. capillacea</i> Jeffrey, 1962 (syn. <i>Melobria capillacea</i>)	22 ^a		-	CCDB ^b
	<i>Z. indica</i> Loureiro, 1790 (syn. <i>Melobria japonica</i>)	11 ^a	22 ^b	Diploid ^d ; 45S (2) and 45S+5S (2) adjacent rDNA signals ^c	Waminal and Kim (2015) ^{b,h,d,e}
	<i>Z. marlabhii</i> Cogniaux, 1962		24 ^a	Diploid ^d ; 45S (2) and 45S+5S (2) adjacent rDNA signals ^c	Li et al. (2016) ^{b,h,e}
	<i>Z. mayranis</i> Wright et Arnott, 1834		48 ^a	45S (2) and 5S (2) signals ^c	Beevy and Kuriachan (1996) ^{b,h} ; Xie et al. (2019a) ^{c,e}
	<i>Z. macronata</i> Blume, 1856 (syn. <i>Melobria macronata</i>)		22 ^a	-	Darlington et al. (1956) ^a , CCDB ^b
	<i>Z. scabra</i> Sonder, 1862 (syn. <i>Melobria punctata</i>)		24 ^a , 48 ^b	-	CCDB ^b , Kumar and Subramaniam (1987) ^b
	<i>Z. thwaitesii</i> Schweinfurth, 1868		44 ^a	-	CCDB ^b

genera included other than *Cucumis*; x: base number; 2n: zygotic number; n: gametic number; NOR: nucleolar organizing region; B: B chromosome; II: bivalents; IPCN: Index to Plant Chromosome Number Reports; CCDB: Chromosome Counts Database; superscripts correspond to references.

Table 7. Cytogenetic features of *Cucumis* (Benincaseae) #.

Species with subspecies/ varieties	Chromosome no.		Ploidy, Genome size, Chromosome features	References
	x	2n		
<i>C. aculeatus</i> Cogniaux, 1895	48 ^a		Allotetraploid ^b ; 24II ^c	IPCN ^{b,c} , CCDB ^c
<i>C. africanus</i> Linnaeus, 1782	12 ^a , 24 ^a , 48 ^a	12 ^d	Diploid ^d ; 2C (Feulgen microdensitometry); 1.782pg; 4 satellited chromosomes ^e ; 45S (4I/6) rDNA signals, 2 co-localized 45S+5S signals ^f	IPCN ^{b,c} , Yadava et al. (1984) ^d , Ramachandran and Narayan (1985) ^{b,e,f} , Yagi et al. (2015) ^{b,g,h,i} , Zhang et al. (2016) ^{b,h,i}
<i>C. angolanis</i> Cogniaux, 1881.	24 ^f			IPCN ^b
<i>C. anguria</i> Linnaeus, 1753	24 ^f		Diploid ^g ; majorly submetacentric and few nearly metacentric chromosomes ^g ; 1 pair satellited ^g ; 45S (2) and co-localized 45S+5S (2) rDNA signals ^g ; SegCP enables chromosome identification ^g ; GISH reveals cross species relationships ^g	Singh and Roy (1974) ^d , Zhang et al. (2015) ^{h,i} , (2016) ^{b,c} , Li et al. (2018) ^{a,f}
<i>C. anguria</i> var. <i>anguria</i>	12 ^a	12 ^c	Diploid ^d ; 4 satellited chromosomes ^g ; 45S (2) and co-localized 45S+5S (2) rDNA signals ^f	Yadava et al. (1984) ^{b,c} , Yagi et al. (2015) ^{a,d,e,f}
<i>C. anguria</i> var. <i>longipes</i>	24 ^a	12 ^b	Diploid ^d ; 2C (Feulgen microdensitometry); 1.587pg ^d	Yadava et al. (1984) ^b , Ramachandran and Narayan (1985) ^{a,d}
<i>C. anguria</i> var. <i>longicaule</i>	12 ^a	12 ^c	Diploid ^d ; 4 satellited chromosomes ^g ; 45S (2) and co-localized 45S+5S (2) rDNA signals ^e	Yagi et al. (2015) ^{a,c}
<i>C. asper</i> Cogniaux, 1901	24 ^f		Diploid ^g ; 45S (4) and 5S (2) signals detected ^g	IPCN ^g ; Zhang et al. (2016) ^{b,c}
<i>C. callosus</i> Rottler, 1803	14 ^f , 24 ^b	12 ^c	Diploid ^d ; 2C (Feulgen microdensitometry); 1.590pg ^g ; 11m+1sm (haploid) ^f	Ramachandran and Narayan (1985) ^{b,d,e} , Rajkumari et al. (2013) ^{b,c} , (2015) ^{a,c,f}
<i>C. cinereus</i> Cogniaux, 1901 (syn. <i>Cucumella citrera</i>)	48 ^a		2C (Feulgen microdensitometry); 0.5pg ^g	Bennet et al. (1982) ^g
<i>C. dinitae</i> Raamsdonk et Visser, 1992	24 ^f			IPCN ^b
<i>C. dinteri</i> Cogniaux, 1901	24 ^f		Diploid ^g ; 2C (Feulgen microdensitometry); 2.167pg ^g	IPCN ^g , Ramachandran and Narayan (1985) ^{a,c}
<i>C. dipsacens</i> Spach, 1838	24 ^f	12 ^b	Diploid ^d ; 2C (Feulgen microdensitometry); 2.448pg ^g ; 2m+8sm+2sr (haploid) ^g ; 45S (2) and co-localized 45S+5S (2) rDNA signals ^f	Yadava et al. (1984) ^b , Ramachandran and Narayan (1985) ^{b,d} , Rajkumari et al. (2015) ^{a,c,e} , Zhang et al. (2016) ^{a,c,f}
<i>C. ficifolius</i> Richard, 1847	24 ^a , 48 ^b	12 ^c	Diploid ^d ; 2C (Feulgen microdensitometry); 1.373pg ^g ; 45S (2) and co-localized 45S+5S (2) rDNA signals ^f	Yadava et al. (1984) ^{b,c} , Ramachandran and Narayan (1985) ^{b,d,e} , Zhang et al. (2016) ^{b,f}
<i>C. figerei</i> Naudin, 1859	48 ^a , 72 ^b		Autoallopolyploid ^d ; 2C (Feulgen microdensitometry); 3.886pg ^g ; 36II ^f	IPCN ^{a,f} , Ramachandran and Narayan (1985) ^{a,c,e}
<i>C. leptodactylis</i> Naudin, 1859	48 ^a , 24 ^f , 52 ^d		Autotetraploid ^d ; 2C (Feulgen microdensitometry); 2.225pg ^g ; 8 satellited chromosomes ^g ; 45S (8) rDNA signals ^h of which 4 co-localized to 5S signals ^g or separate 5S (4) rDNA signals ^g ; 10IV+4II ^g ; irregular meiosis ^g	IPCN ^{a,f} , Ramachandran and Narayan (1985) ^{a,c,e}
<i>C. hookeri</i> Naudin, 1870	24 ^f	12 ^b	Diploid ^d	Yadava et al. (1984) ^{b,h}
<i>C. luniffractus</i> Stent, 1927	24 ^f		Diploid ^d ; 2C (Feulgen microdensitometry); 2.455 pg ^g	Ramachandran and Narayan (1985) ^{b,h}
<i>C. hyarix</i> Chakravarty, 1952	12 ^a	24 ^b	Diploid ^d ; 2m+10sm (haploid) ^g ; 45S (4) and co-localized 45S+5S (2) rDNA signals ^g ; FISH with bulked oligo probe from cucumber chromosome C7 ^g ; GISH reveals cross species relationships ^g	Rajkumari et al. (2015) ^{b,c,d} , Han et al. (2015) ^g , Zhang et al. (2015) ^{b,g} , (2016) ^{b,h,c}
<i>C. indicus</i> Ghebretinsae et Thulin, 2007	20 ^a		Diploid ^d ; 4m+ 6sm (haploid) ^e	Rajkumari et al. (2015) ^{a,c}

Species with subspecies/ varieties	Chromosome no.		Ploidy, Genome size, Chromosome features	References
	x	2n n		
<i>C. jamaicensis</i> Miquel, 1856 (syn. <i>Melobhria asanatica</i>)	12 ^a	24 ^b , 48 ^c	-	Kumar and Subramaniam (1987) ^a , CCDB ^{b,c}
<i>C. leioepermus</i> Wright et Arnott, 1834 (syn. <i>Melobhria leioepermus</i>)	24 ^b	24 ^b	-	CCDB ^b
<i>C. lepodermis</i> : Schwieckendrt, 1933	24 ^b	12 ^b	-	Yadava et al. (1984) ^{ab}
<i>C. longipes</i> Hooker, 1871	24 ^b	24 ^b	-	IPCN ^b
<i>C. meerasi</i> Jeffrey, 1965	48 ^b	22 ^a , 24 ^d	Tetraploid ^d ; 2C- 3.203pg (Feulgen microdensitometry) ^d ; 45S (6) and co-localized 45S+5S (2) rDNA signals ^f	Yadava et al. (1984) ^{b,e,d} , Ramachandran and Narayan (1985) ^{b,e,f} , Zhang et al. (2016) ^{b,g}
<i>C. melo</i> Linnaeus, 1753	12 ^a	20 ^b , 22 ^c , 24 ^d	Diploid ^d ; 2C (Feulgen photometry): 0.94-1.04pg ^g ; 1.90pg ^g ; 2C (Flow cytometry): 1.05pg ^g ; 14m+ 10st (2SAT) ^h ; 7m+5sm (haploid) ^h ; 4 satellites ^h or 2 satelites ^h ; CSR1.0-2.1µm ^h ; CMA bands detected ^h ; 45S (2) and co-localized 45S+5S (2) rDNA signals ^h ; centromeric, telomeric, nucleolar and SSR probe hybridization reveals chromosomal relation ^h ; SegCP applied for comparative chromosome rearrangement study with <i>C. sativus</i> ^h ; FISH with bulked oligo probe from cucumber chromosome C7 ^h ; novel centromeric satellite DNA hybridized on chromosomes; GISH reveals cross species relationships ^h ; infraspetic positional differences in 45S (terminal and interstitial) -5S (terminal, subterminal and interstitial) rDNA signals ^h	Yadava et al. (1984) ^{b,e,d} , Ramachandran and Narayan (1985) ^{b,e,f} , Zhang et al. (2016) ^{b,g} , Earle (1991) ^h , Maie and Brown (1993) ^h , Zhang (2005) ^{h,i,j,k} , Song and Kim (2008) ^{h,i,m} , Han et al. (2009) ^{h,i,n} , (2015) ^h , Liu et al. (2010) ^h , Hoshi et al. (2013) ^{h,i,j,k,m,n,p} , Lou et al. (2014) ^h , Rajkumari et al. (2013) ^h , (2015) ^{h,k} , Setiawan et al. (2018) ^{h,k} , (2020) ^h
<i>C. melo</i> subsp. <i>melo</i>	12 ^a	24 ^b	Diploid; 45S (4) and 5S (2) rDNA signals ^g	Zhang et al. (2016) ^h
<i>C. melo</i> subsp. <i>agrestis</i> Naudin, 1859	12 ^a	24 ^b	Diploid; 45S (4) and 5S (2) rDNA signals ^g	Zhang et al. (2016) ^h
<i>C. melo</i> var. <i>agrestis</i>	12 ^a	24 ^b	Diploid ^d ; 2C (Feulgen microdensitometry): 2.483pg ^g ; 10m+2sm (haploid) ^g ; 1 pair satellited ^g rDNA signals ^g	Singh and Roy (1974) ^{h,i,g} , Yadava et al. (1984) ^h , Ramachandran and Narayan (1985) ^{h,k,e} , Beey and Kuriachan (1996) ^h , Rajkumari et al. (2015) ^{h,d} , Zhang et al. (2005) ^h , Rajkumari et al. (2015) ^h
<i>C. melo</i> var. <i>conomon</i> Thunberg, 1780	24 ^b	24 ^b	Diploid ^b ; 7m+3sm+2st (haploid) ^c	IPCN ^b
<i>C. melo</i> var. <i>flexuosus</i> Linnaeus, 1763	24 ^b	24 ^b	Diploid ^b ; 2C (flow cytometry): 0.64pg ^g	Karimzadeh et al. (2010) ^h
<i>C. melo</i> var. <i>indonesiacquin</i> , 1832	24 ^b	24 ^b	Diploid ^d ; 4m+8sm (haploid) ^d	Beey and Kuriachan (1996) ^h , Rajkumari et al. (2015) ^h
<i>C. melo</i> var. <i>melo</i>	24 ^b	12 ^b	Diploid ^d ; 2C (Feulgen microdensitometry): 2.291pg ^g ; 6m+5sm+1st (haploid) ^g	Yadava et al. (1984) ^h , Ramachandran and Narayan (1985) ^h , Rajkumari et al. (2015) ^h
<i>C. melo</i> var. <i>monandica</i> : Roxburgh, 1832	24 ^b	24 ^b	Diploid ^d ; 2C (Feulgen densitometry): 2.358 pg ^d	Yadava et al. (1984) ^h
<i>C. melo</i> var. <i>muskmelon</i>	24 ^b	12 ^b	Diploid ^d ; 2C (Feulgen densitometry): 2.358 pg ^d	Yadava et al. (1984) ^h , Ramachandran and Narayan (1985) ^h
<i>C. melo</i> var. <i>utilissimus</i> Roxburgh, 1832	24 ^b	12 ^b	Diploid ^d ; 2C (Feulgen densitometry): 2.358 pg ^d	Yadava et al. (1984) ^h
<i>C. membranifolius</i> Hooker, 1871	48 ^c	24 ^b	-	Yadava et al. (1984) ^h

Species with subspecies/ varieties	Chromosome no.		Ploidy, Genome size, Chromosome features	References
	x	2n		
<i>C. metulifer</i> Naudin, 1859 (syn. <i>C. metuliferus</i>)	2 ^f	12 ^b	Diploid ^g ; 2C (Feulgen microdensitometry): 2.391 pg ^g ; metacentric, submetacentric, subtelocentric chromosomes ^g ; CSR: 0.9–2.0 μm ^h ; 4 satellites ^g ; nucleolar and centromeric CMA-DAPI bands ^g ; 45S (2) and co-localized 45S+5S (2) rDNA signals ^g , satellite sequences ^g and telomeric DNA ^g hybridized on chromosomes; SegCP applied for comparative chromosome rearrangement study with <i>C. sativus</i> ^g ; GISH reveals cross species relationships ^g Diploid ^g ; 45S (2 ^h /4 ^h) and co-localized 45S+5S (2) ^g rDNA signal ^g	Yadava et al. (1984) ^{abc} , Ramachandran and Narayan (1985) ^{bcg} , Ramachandran and Narayan (1990) ^{cd} , Hoshi et al. (2013) ^{bcdefgh} , Lou et al. (2014) ^g , Yagi et al. (2014) ^g , Yagi et al. (2016) ^{acd} , Zhang et al. (2015) ^{am} , (2016) ^{acd} , CCDB ^g ; Zhang et al. (2016) ^{abcd} , Yagi et al. (2015) ^{ef}
<i>C. myriocarpus</i>	2 ^f	12 ^b	Diploid ^g ; 4 satellited chromosomes ^g ; 45S (3 ^g ; 2 ^g) and co-localized 45S+5S (2 ^g) rDNA signals	Yagi et al. (2015) ^{efg}
<i>C. myriocarpus</i> subsp. <i>leptodermis</i> Schweickert, 1933	2 ^f	24 ^b	Diploid ^g ; 4 satellited chromosomes ^g ; 45S (3 ^g ; 2 ^g) and co-localized 45S+5S (2 ^g) rDNA signals	Yagi et al. (2015) ^{efg}
<i>C. myriocarpus</i> var. <i>myriocarpus</i>	12 ^a	48 ^b	Tetraploid ^g ; 8 satellited chromosomes ^g ; 45S (4) and co-localized 45S+5S (4) rDNA signals ^g	Yagi et al. (2015) ^{efg}
<i>C. prophanetarium</i> Linnaeus, 1755	2 ^f	12 ^b	Diploid ^g ; 2C (Feulgen Microdensitometry): 1.656 pg ^g 5m+7sm (haploid) ^g	Ramachandran and Narayan (1985) ^{bc} , Rajkumari et al. (2013) ^{ab} , (2015) ^{ace} IPCN ^b
<i>C. prophanetarium</i> subsp. <i>zeyheri</i> Sonder, 1862	4 ⁸	48 ^b	-	IPCN ^b ; Beevy and Kuriachan (1996) ^b
<i>C. pubescens</i> Willdenow, 1805	2 ^f	12 ^b	-	Yadava et al. (1984) ^{ac} , Han et al. (2015) ^f , Zhang et al. (2016) ^{bd}
<i>C. pustulatus</i> Hooker, 1871	48 ^a , 72 ^b	24 ^c	Hexaploid ^g ; 45S (8) and co-localized 45S+5S (2) rDNA signals ^g ; FISH with bulked oligo probe from cucumber chromosome C7 ^g Diploid ^h ; 8m+4sm (haploid) ^c	Rajkumari et al. (2015) ^{abc}
<i>C. ritchei</i> Clarke, 1879	2 ^f	12 ^b	Diploid ^g ; 2C (Feulgen microdensitometry): 1.571 pg ^g	Yadava et al. (1984) ^{ab} , Ramachandran and Narayan (1985) ^{acd}
<i>C. sagittatus</i> Peyritsch, 1860	2 ^f	12 ^b	Diploid ^g ; 2C (Feulgen microdensitometry): 1.571 pg ^g	Yadava et al. (1984) ^{ab} , Ramachandran and Narayan (1985) ^{acd}
<i>C. sativus</i> Linnaeus, 1753	7 ⁱ	14 ^b	Diploid ^g ; 2C (flow cytometry): 1.03pg ^g /1.77pg ^g ; 12 metacentric and 2 sub-metacentric chromosomes ^g ; CSR: 0.83–1.0 μm ^h , chromosomal C-bands ^g ; centromeric 45S (10) and distal 5S (2) rDNA signals ^g ; FISH with centromeric and telomeric ^g and SSR probe reveals chromosome evolution ^g ; high resolution molecular cytogenetic map ^g ; SegCP applied for cross species chromosome rearrangement study ^g ; FISH with bulked oligo probe from cucumber chromosome C7 ^g in comparison with 5 <i>Cucumis</i> species ^g ; GISH reveals cross species relationships ^g	Kumar and Subramanian (1987) ^{bc} , Marie and Brown (1993) ^f , Beevy and Kuriachan (1996) ^{bc} , Hoshi et al. (2008) ^{bd} , Barow and Meister (2003) ^{bc} , Han et al. (2011) ^{bd} , Liu et al. (2010) ^{bd} , Waminal and Kim (2012) ^{bd} , Rajkumari et al. (2013) ^{bc} , Sun et al. (2013) ^{bm} , Lou et al. (2014) ^{bn} , Han et al. (2015) ^b , Zhang et al. (2015) ^{bp} , Li et al. (2016) ^{bd}
<i>C. sativus</i> var. <i>Hokutosei</i>	7 ⁱ	14 ^b	Diploid ^g ; 12 metacentric, 2 sub-metacentric chromosomes ^g ; centromeric and telomeric signals ^g	Zhang et al. (2012) ^{bc}
<i>C. sativus</i> var. <i>hardwickii</i> Royle, 1835	7 ⁱ	14 ^b	Diploid ^g ; 2C (Feulgen Microdensitometry): 1.798pg ^g ; 6m+1sm (haploid) ^g ; centromeric 45S (6) and intercalary 5S (2) rDNA signals ^g ; centromeric, telomeric and SSR probe hybridizations ^g ; molecular cytogenetic map ^g	Ramachandran and Narayan (1985) ^{bd} , Zhao et al. (2011) ^{bc} , Yang et al. (2012) ^{bc} , Rajkumari et al. (2015) ^{bc} , Zhang et al. (2016) ^{abcd}
<i>C. sativus</i> var. Long green	7 ⁱ	14 ^b	Diploid ^g ; 12 metacentric, 2 sub-metacentric chromosomes ^g ; centromeric and telomeric sequence signals ^g	Zhang et al. (2012) ^{bc}
<i>C. sativus</i> var. <i>sativus</i> (CSS)	7 ⁱ	14 ^b	Diploid ^g ; centromeric 45S (10) and intercalary 5S (2) rDNA signals ^g ; centromeric and distal repetitive sequence probes ^g ; molecular cytogenetic map ^g	Zhao et al. (2011) ^{bc} , Yang et al. (2012) ^{bc} , Zhang et al. (2016) ^{cd}

Species with subspecies/ varieties	Chromosome no.			Ploidy, Genome size, Chromosome features	References
	x	2n	n		
<i>C. sativus</i> cv. Winter Long	14 ^a	14 ^b	7 ^b	Diploid ^d , C-banding ^d , DAPI banding ^d ; 45S (6) and 5S (2) rDNA signals ^d , repetitive sequence based molecular karyotype in somatic and pachytene chromosomes ^g	Koo et al. (2002) ^{a,f} , (2005) ^{a,g}
<i>C. sativus</i> var. <i>xishuangbunnensis</i> Qi et Yuan Zhenzhen, 1983	7 ^a	14 ^b	-	Diploid ^d ; centromeric-45S (2) rDNA signals ^d ; centromeric and telomeric signals ^e	Zhao et al. (2011) ^{b,c,e} , Zhang et al. (2016) ^d
<i>C. setosus</i> Cogniaux, 1881	24 ^a	24 ^b	12 ^b	Diploid ^d ; 4m+5sm+3st (haploid) ^d	Rajkumari et al. (2013) ^{c,e} , (2015) ^{b,c,d}
<i>C. silentalleyii</i> Manilal et Sabu et Mathew, 1985	24 ^a	24 ^b	12 ^b	-	Rajkumari et al. (2013) ^{ab}
<i>C. trigonus</i> Roxb.	24 ^a	24 ^b	12 ^b	-	Rajkumari et al. (2013) ^{ab}
<i>C. zambianus</i> Widdr., J.H.Kirkbr., Ghebret, and K.R.Reitsma	12 ^a	24 ^b	-	Diploid ^d ; 45S (2) and co-localized 45S+5S (2) signals ^d	Zhang et al. (2016) ^d
<i>C. zeyheri</i> Sond.	24 ^a , 48 ^b	-	-	Diploid ^d ; Allotetraploid ^d ; 2C (Feulgen densitometry): 1.682/2.846 pg; 4 satellites ^g ; 45S (2) and co-localized 45S+5S (2) rDNA signals ^d ; FISH with bulked oligo probe from cucumber chromosome C7 ^g ; 24II ^g , 12II ^g , 11II+2I ^g	IPCN ^{a,b,d,i,j} , Ramachandran and Narayan (1985) ^{a,f} , Han et al. (2015) ^g ; Yagi et al. (2015) ^{a,c,g,h}
<i>Cucumella cinerea</i> (Cogn.) C.Jeffrey	24 ^b	24 ^b	11 ^a , 12 ^d	2C (Feulgen Microdensitometry): 0.50pg ^a	Bennet et al. (1982) ^a CCDB ^{b,c} , Rajkumari et al. (2015) ^{b,d}
<i>Mukia madenspatana</i> (L.) M.Roem. (syn. <i>Cucumis madenspatanus</i> and <i>Melothria madenspatana</i>)	12 ^a	48 ^b	-	Tetraploid ^d ; co-localized 45S and 5S rDNA signals (2) ^d ; FISH with bulked oligo probe from cucumber chromosome C7 ^e	Han et al. (2015) ^e , Zhang et al. (2016) ^d

#x: base number; 2n: zygotic number; n: gametic number; NOR: nucleolar organizing region; SAT: satellite chromosome; SegCP: Single-copy gene-based chromosome painting (Lou et al. 2014); I: univalent, II: bivalent, IV: tetravalent; CCDB: Chromosome Counts Database; superscripts correspond to reference.

Table 8. Cytogenetic information in Cucurbiteae #.

Genera studied	Species studied	Chromosome no.			Ploidy, Genome size, Chromosome features	References
		x	2n	n		
<i>Cayaponia</i> Silva Manso, 1836	<i>C. laciniata</i> Linnaeus, 1753		24 ^a		-	Kumar and Subramaniam (1987) ^a
<i>Cucurbita</i>		10 ^a , 12 ^b			-	Darlington and Janaki Ammal (1945) ^{a,b}
	<i>C. andreana</i> Naudin, 1896		40 ^a			CCDB ^a
	<i>C. argyrosperma</i> Huber, 1867 (syn. <i>C. mixta</i> Pangalo, 1930)		40 ^a		2C (flow cytometry): 0.748 pg ^b	Sisko et al. (2003) ^{a,b}
	<i>C. cylindrata</i> Bailey, 1943		40 ^a	20 ^b	-	CCDB ^{a,b}
	<i>C. digitata</i> Gray, 1853	10 ^a , 12 ^b	40 ^c	20 ^d	-	Darlington and Janaki Ammal (1945) ^{a,b} , CCDB ^{c,d}
	<i>C. ecuadorensis</i> Cutler et Whitaker, 1969				2C: 0.72pg ^e	Plant DNA C Value database ^e
	<i>C. ficifolia</i> Bouché, 1837 (syn. <i>C. melanosperma</i> Gasparrini, 1847)		40 ^a		2C (flow cytometry): 0.933pg ^b	Plant DNA C- Values Database ^{a,b}
	<i>C. foetidissima</i> Kunth, 1817	10 ^a , 12 ^b	40 ^c , 42 ^d		2C (flow cytometry): 0.686pg ^e	Darlington and Janaki Ammal (1945) ^{a,b} , Plant DNA C- Values Database ^{c,e} , CCDB ^{c,d}
	<i>C. indica</i> (unresolved)		40 ^a		-	IPCN ^a
	<i>C. hundelliana</i> Bailey, 1943			20 ^a	2C (flow cytometry): 0.72pg ^b	CCDB ^a , Plant DNA C Value database ^b
	<i>C. maxima</i> Duchesne, 1786	20 ^a	24 ^b , 40 ^c , 44 ^d , 48 ^e	20 ^f		Kumar and Subramaniam (1987) ^{a,c,d,e} , Beevy and Kuriachan (1996) ^f , CCDB ^{c-f}
	<i>C. moschata</i> Duchesne, 1786	10 ^a , 12 ^b	24 ^c , 40 ^d , 44 ^e , 48 ^f		Diploid ^g ; 2C (Feulgen microdensitometry): 0.90pg ^g ; 2C (flow cytometry): 0.708/0.97pg ^g ; 36 metacentric and 4 sub-metacentric chromosomes ^g ; CSR: 1.05-1.78µm ¹ , 45S (10) and 5S (4) rDNA signals ^m	CCDB ^g , Plant DNA C- Values Database ^{h,i} , Kumar and Subramaniam (1987) ^{a-f} , Barrow and Meister (2003) ^j , Xu et al. (2007) ^{d,m} , Waminal et al. (2011) ^{e,d,k,l,m}
	<i>C. okeechobeensis</i> ssp. <i>martinezii</i> Bailey, 1943		40 ^a		2C (flow cytometry): 0.74pg ^b	Plant DNA C- Values Database ^{a,b}
	<i>C. palmata</i> Watson, 1876	10 ^a , 12 ^b	40 ^c , 42 ^d	20 ^e	-	Kumar and Subramaniam (1987) ^{a,b} , CCDB ^{c,d,e}
	<i>C. pedatifolia</i> Bailey, 1943		40 ^a		-	CCDB ^a
	<i>C. pepo</i> Linnaeus, 1753	10 ^a , 12 ^b	22 ^c , 24 ^d , 28 ^e , 40 ^f , 42 ^g , 44 ^h , 46 ⁱ , 80 ^j	20 ^k	2C (flow cytometry): 0.74pg ^l ; 0.864 ^m ; 1.109 pg-1.064 pg ^g ; 1.18pg ^g ; 45S (10) and 5S (4) rDNA signals ^p	Kumar and Subramaniam (1987) ^{a-l} , CCDB ^k , Marie and Brown (1993) ^j , Barrow and Meister (2003) ^o , Rayburn (2008) ⁿ , Plant DNA C- Values Database ^m , Xie et al. (2019b) ^{f,p}
<i>Sicana</i> Naudin, 1862	<i>S. odorifera</i> Vellozo, 1831		40 ^a	20 ^b	-	IPCN ^{a,b}

x: base number; 2n: zygotic number; n: gametic number; CCDB: Chromosome Counts Database; superscripts correspond to references.

terstitial telomeric repeats which were suggested to be the result of chromosome fusion from ancestral genome. The co-localization of 45S and 5S rDNA loci in *A. tenerum* and *Thladiantha dubia* Bunge, 1833, have been thought to imply regional synteny and shared ancestral traits (Xie et al. 2019b). In the tribe Cucurbiteae, detailed karyotype analysis is known only in *Cucurbita moschata* Duchesne, 1786 and *C. pepo* Linnaeus, 1753, showing conserved 45S and 5S rDNA signals (non-co-localized) in independent analyses (Table 8).

Karyotypes and chromosome sizes are reported in ten species of Momordiceae (Table 3). Interspecific differences have been observed and found to correlate with phylogenetic

relationship within *Momordica* (Ghosh et al. 2021). Intraspecific delimitation of Indian *M. charantia* varieties was based on fluorochrome banding pattern and genome size divergence (Table 3), corresponding to intraspecific distinction reported in the Japanese bitter gourd cultivars (Kido et al. 2016). FISH in three *Momordica* species revealed 45S and 5S rDNA sites to be localised on different chromosomes (Table 3). In context of the genome sequence of bitter gourds (Matsumura et al. 2020), further scopes for cytogenetic and genomic investigation remain open.

Karyotype and chromosome size is reported in eight species of Sicyoeae (Table 5). Fluorochrome banding pattern has facilitated comparative analysis in *Luffa* species occurring in India (Tables 1, 5) (Bhowmick and Jha 2015a, 2021). The cultivated ridged gourd (*L. acutangula* Linnaeus, 1753) showed three CMA⁺ satellite bearing pairs (Fig. 1A–C, J) as in the wild *L. echinata* Roxburgh, 1814 (Fig. 1G–I, L), while the sponge gourd (*L. aegyptiaca* Miller, 1768) has two satellited pairs (Fig. 1D–F, K). *Luffa acutangula* and *L. echinata* also showed up distal DAPI bands (Fig. 1J, L), absent in *L. aegyptiaca* (Fig. 1K). *Trichosanthes* species (2n = 22) have inter-specific differences (Fig. 2) as well as intraspecific distinction (*T. cucumerina* Linnaeus, 1753) in fluorochrome banding pattern (Tables 1, 5, Fig. 2A–H). The male and female plants of *T. dioica* show similar chromosome number, morphology and genome size but show differences in fluorochrome banding pattern (Fig. 2I–P, Table 5). The 11th, 12th and 13th pairs (CMA⁺) are marker chromosomes in *Luffa* (Fig. 1, Table 1) while the 10th and 11th pairs are conserved CMA⁺ satellited pairs in *Trichosanthes* (Fig. 2, Table 1). Eight species of Sicyoeae have been subjected to FISH (Table 5). The polyploid and diploid species have differences in the number of rDNA loci, showing separate localization of the 45S and 5S rDNA signals except *Sicyos angulatus* Linnaeus, 1753 and *Trichosanthes kirilowii* Maximowicz, 1859 (Table 5).

Benincaseae generally reveal two distal 45S rDNA loci of which at least one locus is either adjacent to 5S rDNA locus (Table 6) or co-localized in the same chromosome as in most of the *Cucumis* species (Table 7). Exceptionally, a wild species of *Benincasa* (*B. fistulosa* Stocks, 1851) has non-adjacent 45S and 5S signals (Li et al. 2016). GC rich satellites were observed in the 12th pair of chromosomes showing CMA⁺ bands in cultivated Indian ashgourd (*B. hispida*) (Fig. 3 A–C, J, Tables 1, 6). *Lagenaria siceraria* Molina, 1782 and *Cucumis melo* Linnaeus, 1753 are the other two genera having similarity in rDNA hybridization profile, agreeing with phylogenetic affinity (Li et al. 2016).

Citrullus colocynthis Linnaeus, 1753 and *C. lanatus* Thunberg, 1794 may share a common ancestor both having two 45S rDNA loci and one 5S locus. Loss of one 45S rDNA locus has given way to *C. rehmii* De Winter, 1990 while gain of one 5S rDNA locus has been proposed to lead to *C. ecirrhosus* Cogniaux, 1888 and *C. lanatus* var. *citroides* Bailey, 1930 (presently *C. amarus* Schrader, 1836) (Reddy et al. 2013; Li et al. 2016). GISH using *C. lanatus* var. *citroides* genome has revealed divergence from *C. lanatus* var. *lanatus* (Reddy et al. 2013).

The genus *Cucumis* is the largest in Benincaseae with 65 species of which 39 have been studied (Table 7). Among the *Cucumis* species with x = 12, co-localization rDNA loci (45S and 5S rDNA) have been documented in 14 species, including *C. melo* (Table 7). However, the number of 45S sites is generally four, which may be six or eight in some

cases (Table 7). rDNA hybridization data strongly corroborated with the ‘fusion’ theory for derivation of $x = 7$ (*C. sativus*) from $x = 12$ (*C. melo*) (Waminal and Kim 2012) which is substantiated by genomic studies (Li et al. 2011). There are ten pericentromeric/ centromeric 45S and two distal 5S rDNA sites in *C. sativus* while six 45S rDNA sites were reported in *C. sativus* var. *hardwickii* Royle, 1835 (Koo et al. 2005; Zhang et al. 2012). Comparative chromosome painting (Lou et al. 2014) and GISH (Zhang et al. 2015) proved high colinearity between cucumber and melon. Based on chloroplast and nuclear DNA (ITS) phylogeny, *C. melo* (melon) has been found to be sister to a clade comprising *C. sativus* and related genera (*Dicaelospermum* Clarke, 1879 and *Mukia* Arnot, 1840) (Renner et al. 2007). rDNA site co-localization was found to coincide with geographical origin of 12 *Cucumis* species (Zhang et al. 2016). The chromosomal affinity between *C. metuliferus* Schrader, 1838, *C. anguira* Linnaeus, 1753, *C. zeyheri* Sonder, 1862, *C. myriocarpus* Naudin, 1859 and polyploid *C. heptadactylis* Naudin, 1859 (dioecious) (Yagi et al. 2015) can be substantiated by their phylogenetic proximity based on chloroplast and nuclear DNA (ITS) sequences (Renner et al. 2007). rDNA distribution of *C. metuliferus* was also the reason to consider proximity with *Citrullus naudinianus* Sonder, 1862, (previously *Acanthosicyos naudinianus* Sonder, 1862) (Reddy et al. 2013). Intraspecific differences were documented in *Cucumis melo* on the basis of 45S- 5S rDNA signals (linked or separated) which also possessed unique centromeric satellites (Setiawan et al. 2018, 2020). Moreover, chromosome painting method elucidated chromosomal rearrangement in some *Cucumis* species (Lou et al. 2014; Li et al. 2018).

The dramatic evolution of Y chromosome was validated in karyotypes (Fig. 3 D–I, K–L) of *Coccinia grandis* (Table 6). The 45S rDNA sites enabled confirmation of NORs in the 8th and 12th pair containing distal GC rich CMA⁺ signals in *C. grandis* (Fig. 3 D–I, K–L, Tables 1, 6). 45S and 5S rDNA hybridization pattern was similar in three other *Coccinia* species and *Diplocyclos palmatus* Linnaeus, 1753 (Table 6). The three closely related dioecious species of *Coccinia* accumulated Y chromosome repeats and displayed sex chromosome turnover (Sousa et al. 2017). Strong centromeric CMA bands (Fig. 3 D–I, K–L, Table 1) were observed in *C. grandis* except Y chromosome (Fig. 3 I, L), presenting a possibility that *CgCent* (CL1) is a feature of centromeres of dioecious *Coccinia* species (Sousa et al. 2017). In addition, non-nucleolar CMA⁺ heterochromatin might be associated with sexual differentiation of autosomes in dioecious *C. grandis* (Fig. 3) which is also a marker in *Trichosanthes dioica* (Fig. 2, Table 1), opening good scope for further study.

Distinct 45S rDNA sites are higher in number than 5S rDNA sites in Cucurbitaceae (Fig. 4) (Waminal and Kim 2012). The distal 45S rDNA loci are conserved genomic landmarks (Fig. 4) while 5S rDNA loci are relatively diverse (Fig. 4). Based on the literature reports, some NORs (Type I) included chromosomes showing non-colocalized 45S and 5S rDNA sites in seven species of Benincaseae, one species each from Cucurbitaceae and Momordiceae and two species of Sicyoeae. The rearrangement of 45S rDNA site in *Cucumis sativus*, probes for chromosome number reduction which may be a consequence of diploidization. The second type (Type II) shows colocalised 45S and 5S rDNA loci, either adjacent or distant, but always on the same chromosome and found in one species each of Benincaseae, Sicyoeae and Actinostemmateae. The third type (Type III) was characterized by chromosomes with non-colocalized and

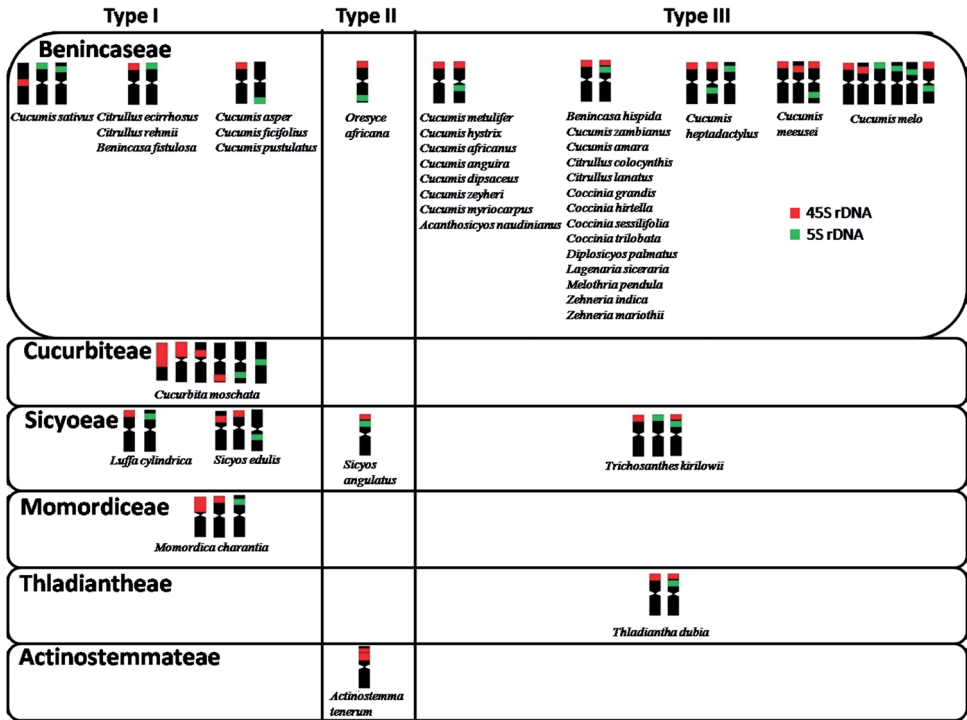


Figure 4. Types of chromosomes bearing the NORs as per available reports of rDNA hybridization in Cucurbitaceae. Type I: Chromosomes with only non-colocalised 45S and 5S rDNA sites, Type II: Chromosomes with colocalised 45S and 5S rDNA sites, Type III: Chromosomes with both non- colocalised and colocalised 45S and 5S rDNA sites. See text for explanation.

colocalised 45S and 5S rDNA loci, as in 14 species of Benincaseae and one species each of Sicyoeae and Thladiantheae. The rDNA sites of majority of *Cucumis* species were of non-adjacent type. Hence, type III NORs in majority of Benincaseae genera advocates conservation of the marker chromosomes having distal NOR (45S rDNA). *Gynostemma pentaphyllum* and some polyploid *Cucumis* reveal rDNA loci reduction after polyploidization (Zhang et al. 2016; Pellerin et al. 2018).

Correlation between parameters

Chromosome numbers in Cucurbitaceae range from x = 5 to x = 16. The most prevalent number x = 12 (Fig. 5) is considered ancestral (Xie et al. 2019b), followed by x = 11, 13, 14 and 10 (Fig. 5). The present regression analyses for 41 taxa (including 16 Indian taxa) (Table 9) revealed significant linear correlation between 2n and HCL, between ploidy and genome size and between ploidy and HCL (Fig. 6). Therefore, an increase in ploidy/ 2n number is linked with increase in HCL. There was no significant correlation between 2C genome size and chromosome numbers. Cytogenetic parameters may not reflect residual evidence of CCT in Cucurbitaceae at present, as reasoned by Alix et al. (2017).

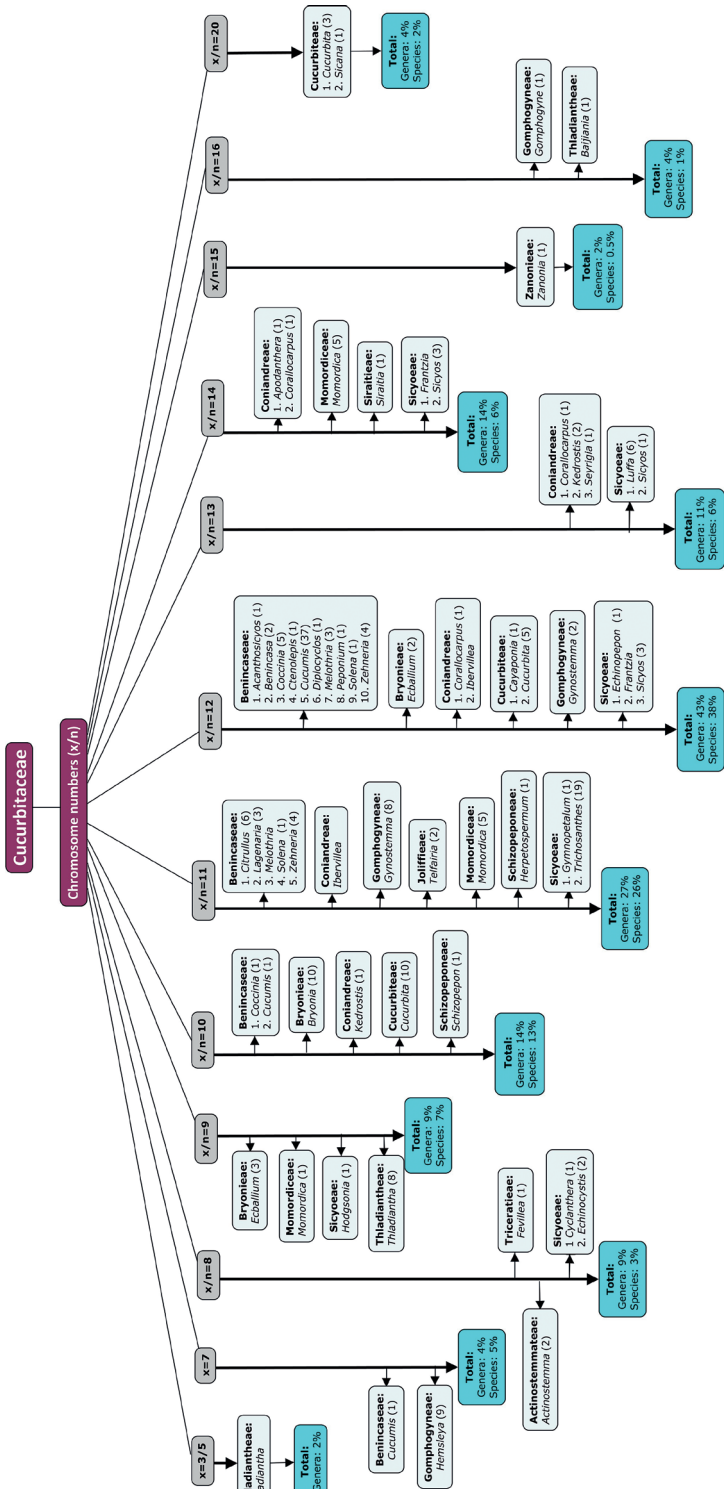


Figure 5. The types of different base numbers (x, based on published reports) or possible base numbers (x/n, based on reported haploid counts) in Cucurbitaceae. The numbers in brackets beside names of genera signify the number of species whose chromosome counts are reported. The % of genera and species with a particular chromosome number, is indicated at the end arrow (out of a total of 44 genera and 188 species with chromosome counts).

Table 9. Data on fundamental cytogenetic parameters utilized for statistical analysis.

Species	2n Chromosome no.	Ploidy	2C genome size (pg)	MCL (µm)	HCL (µm)	References
<i>Gynostemma pentaphyllum</i>	66	6	3.62			Zhang et al. (2013), Pellerin et al. (2018)
<i>Zanonia indica</i>	30	2		1.47	22.12	Lekhak et al. (2018)
<i>Momordica balsamina</i>	22	2		1.30	14.3#	Bharathi et al. (2011)
<i>Momordica charantia</i> var. <i>charantia</i>	22	2	0.72	1.97	21.77	Ghosh et al. (2018)
<i>Momordica charantia</i> var. <i>muricata</i>	22	2	1.16	2.19	24.19	Ghosh et al. (2018)
<i>Momordica cochinchinensis</i>	28	2	2.64	2.27	31.86	Ghosh et al. (2021)
<i>Momordica cymbalaria</i>	18	2	3.74	3.75	33.79	Ghosh et al. (2021)
<i>Momordica dioica</i>	56	4	3.36	2.75	77.1	Ghosh et al. (2021)
<i>Momordica sahyadrica</i>	28	2		1.34	18.76	Bharathi et al. (2011)
<i>Momordica subangulata</i>	56	4	3.06	2.15	60.3	Ghosh et al. (2021)
<i>Luffa acutangula</i>	26	2		2.20	28.63	this study
<i>Luffa cylindrica</i>	26	2	1.56	2.98	38.77	Bhowmick and Jha (2015a), this study
<i>Luffa echinata</i>	26	2		3.17	41.26	this study
<i>Trichosanthes cucumerina</i>	22	2		3.47	37.855	Bhowmick and Jha (2019), this study
<i>Trichosanthes cucumerina</i> subsp. <i>cucumerina</i> Anguina	22	2		3.43	37.74	Bhowmick and Jha (2019), this study
<i>Trichosanthes dioica</i> Male	22	2	2.27	3.71	40.82	Bhowmick and Jha (2015a), this study
<i>Trichosanthes dioica</i> Female	22	2	2.32	3.71	40.82	Bhowmick and Jha (2015a), this study
<i>Benincasa hispida</i>	24	2	1.97	3.17	38.08	Bhowmick and Jha (2015a), this study
<i>Citrullus lanatus</i>	22	2		1.33#	14.67	Waminal et al. (2011)
<i>Coccinia grandis</i> male	24	2	0.92	1.80	20.32	Bhowmick et al. (2012, 2016), this study
<i>Coccinia grandis</i> female	24	2	0.73	1.86	19.85	Bhowmick et al. (2012, 2016), this study
<i>Coccinia hirtella</i>	24	2	0.988			Sousa et al. (2017)
<i>Coccinia sessilifolia</i> Male	24	2	0.984			Sousa et al. (2017)
<i>Coccinia sessilifolia</i> Female	24	2	0.998			Sousa et al. (2017)
<i>Coccinia trilobata</i>	20	2	1.263			Sousa et al. (2017)
<i>Lagenaria siceraria</i>	22	2	0.734	1.79	20.06	Achigan-Dako et al. (2008)
<i>Cucumis africanus</i>	24	2		2.08	25.045	Yagi et al. (2015)
<i>Cucumis anguria</i> var. <i>anguria</i>	24	2		2.13	25.6	Yagi et al. (2015)
<i>Cucumis anguria</i> var. <i>longaculeatus</i>	24	2		2.10	25.195	Yagi et al. (2015)
<i>Cucumis heptadactylus</i>	48	4		2.09	50.225	Yagi et al. (2015)
<i>Cucumis melo</i>	24	2	1.05	1.50	17.8#	Marie and Brown (1993), Hoshi et al. (2013)
<i>Cucumis melo</i> var. <i>inodorus</i>	24	2	0.64			Karimzadeh et al. (2010)
<i>Cucumis myriocarpus</i> var. <i>leptodermis</i>	24	2		1.93	23.19	Yagi et al. (2015)
<i>Cucumis myriocarpus</i> var. <i>myriocarpus</i>	48	4		2.25	53.985	Yagi et al. (2015)
<i>Cucumis zeyheri</i>	24	2		2.30	27.56	Yagi et al. (2015)
<i>Cucumis sativus</i>	14	2	1.03, 1.77##	2.07#	14.50	Barow and Meister (2003), Marie and Brown (1993), Waminal and Kim (2012)
<i>Cucurbita argyrosperma</i>	40		0.748			Roy et al. (1991), Sisko et al. (2003)
<i>Cucurbita ecuadorensis</i>	40		0.933			Sisko et al. (2003)
<i>Cucurbita foetidissima</i>	40		0.686			Sisko et al. (2003)
<i>Cucurbita moschata</i>	40	2	0.708, 0.97##	1.26#	25.19	Sisko et al. (2003), Barrow and Meister (2003), Waminal et al. (2011)
<i>Cucurbita okeechobeensis</i> ssp. <i>martinezii</i>	40		0.74			Sisko et al. (2003)

calculated from chromosome measurements reported in publications, ## different entries for same taxa were taken from different reports

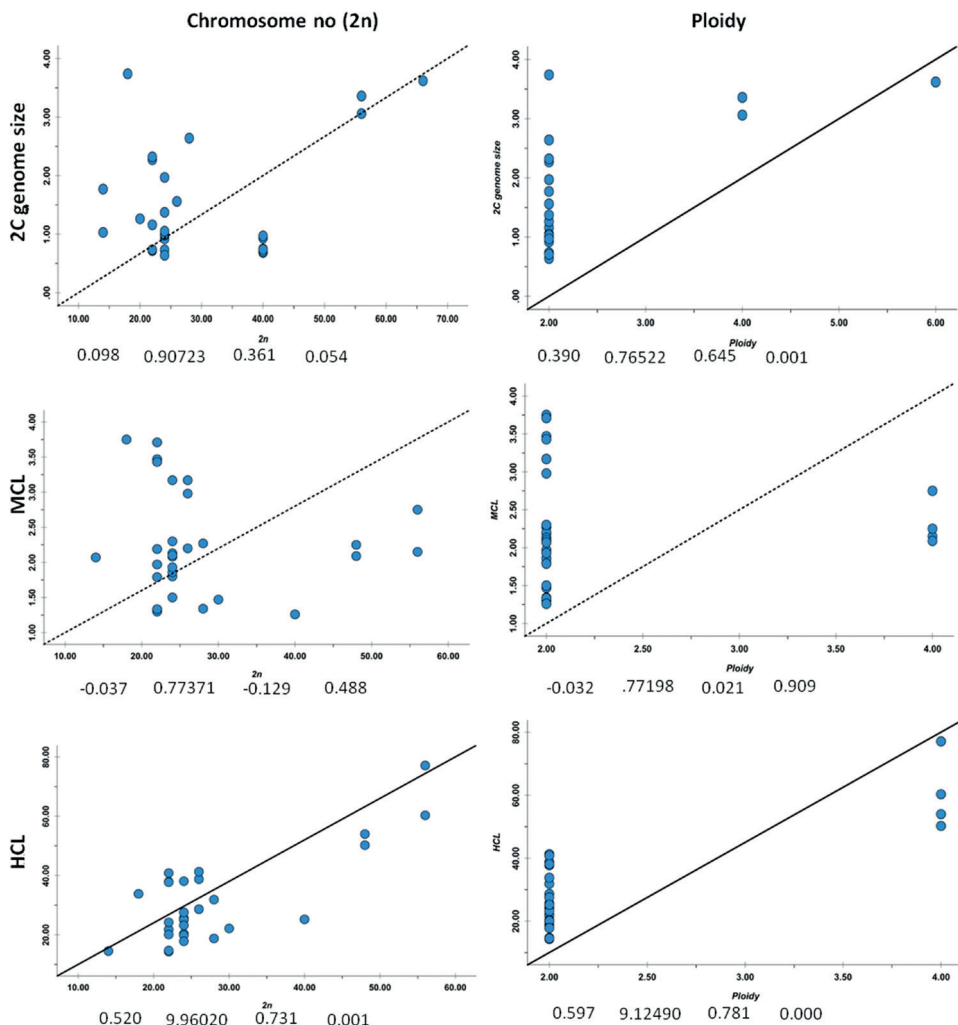


Figure 6. Scatter plots of 2n chromosome number and ploidy level (predictor variables) versus 2C genome size, MCL (mean chromosome length) and HCL (total length of haploid chromosome set) in Cucurbitaceae taxa. Symbols below plots depict regression analysis parameters; square: adjusted R square, circle: standard error of the estimate, triangle: Pearson Correlation, star: 2-tailed significance of Pearson Correlation. Regular lines indicate significant linear regression and dotted lines indicate not significant linear regress

Future directions

Chromosome number and genome size information in the basal clades (understudied tribes) should be given attention to infer ancient base numbers. The parameters of fundamental and molecular cytogenetics are inevitable for genomic interpretation (Weiss-Schneeweiss and Schneeweiss 2013; Deakin et al. 2019) and hence relevant to spot genetic resources and relationships with wild relatives. The current review is not exhaustive but supersedes the scopes of general web resources and brings an offline resource exclusive for Cucurbitaceae.

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