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Abstract

Gossypium, as the one of the biggest genera, the most diversity, and the highest economic value in field crops, is assuming an increasingly important role in studies on plant taxonomy, polyploidization, phylogeny, cytogenetics, and genomics. Here we update and provide a brief summary of the emerging picture of species relationships and diversification, and a set of the designations for individual genomes and chromosomes in *Gossypium*. This cytogenetic and genomic nomenclature will facilitate comparative studies worldwide, which range from basic taxonomic exploration to breeding and germplasm introgression.

Keywords

Nomenclature, Individual genome, Individual chromosome, *Gossypium*

Disciplines

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REVIEW

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Designations for individual genomes and chromosomes in *Gossypium*

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Abstract

Gossypium, as the one of the biggest genera, the most diversity, and the highest economic value in field crops, is assuming an increasingly important role in studies on plant taxonomy, polyploidization, phylogeny, cytogenetics, and genomics. Here we update and provide a brief summary of the emerging picture of species relationships and diversification, and a set of the designations for individual genomes and chromosomes in *Gossypium*. This cytogenetic and genomic nomenclature will facilitate comparative studies worldwide, which range from basic taxonomic exploration to breeding and germplasm introgression.

Keywords: Nomenclature, Individual genome, Individual chromosome, *Gossypium*

Because of its diversity and economic significance, the cotton genus (*Gossypium*) has been subjected to decades of taxonomic, cytogenetic, and phylogenetic analyses. Accordingly, a reasonably well-documented phylogenetic and taxonomic understanding has developed, as recently summarized (Wendel and Grover 2015). Work published since that time also supports the emerging picture of species relationships and diversification (Grover et al. 2015a, 2015b; Chen et al. 2016; Gallagher et al. 2017). Our purpose here is to provide a brief summary of this understanding, and to introduce the chromosomal context for the genome designations that are widely used by cotton researchers worldwide.

As shown in Table 1, the genus is divided into 8 diploid genome groups (A through G, and K), as well as one allopolyploid clade (AD genome) formed from ancient merger and chromosome doubling from A and D genome ancestors. These genome groups were initially defined based on comparative chromosome sizes and chromosome behavior in interspecific hybrids (Beasley 1942; Stephens 1947; Phillips 1966; Fryxell 1992; Endrizzi et al. 1985). Subsequent phylogenetic work (reviewed in Wendel and Grover 2015) has confirmed that each of these genome groups is monophyletic; that is, they have a single origin, with each genome group comprising a natural set of more or less closely related species. Genome groups vary widely in species

diversity, from consisting of only a single species (F genome) to larger genome groups containing more than a dozen species each (D, K). The important allopolyploid clade, which includes *G. hirsutum* and *G. barbadense*, contains 7 species, including two described only in the last 10 years (*G. ekmanianum*, *G. stephensii*) (Krapovickas and Seijo 2008; Gallagher et al. 2017).

Many *Gossypium* species are taxonomically well-understood, whereas others are poorly known and not well-established as *bona fide* species; these are indicated with parentheses in Table 1. Most notable in this respect are species or putative species from the horn of Africa and the Arabian Peninsula; several of these species are poorly represented in herbarium collections and no living material has been available for study (last five in Table 2). Remarkably, new species remain to be discovered and or taxonomically described, as evidenced by the recent publication of *G. anapoides* (Stewart et al. 2014) and *G. stephensii* (Gallagher et al. 2017). Also notable is the relatively poorly understood diversity in the Mexican arborescent clade, in which additional species likely remain to be described (Wendel and Grover 2015; Feng et al. 2011). More species might be discovered in Australia and in Southern America with new exploitation.

This taxonomic framework provides a justification for a nomenclature for individual genomes and chromosomes in each species in *Gossypium*. A stable and accepted nomenclature will facilitate comparisons among the many kinds of studies that might be conducted in

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Table 1 Taxonomic, cytogenetic and geographic diversity of species of *Gossypium*. Included are descriptions of each genome group and the collective geographic distribution of the included species. Genomic placements and taxonomic status of species enclosed by parentheses remain to be established as they are poorly known

Genome group	Number of species	Species presently recognized	Geographic distribution
A	2	<i>G. arboreum</i> , <i>G. herbaceum</i>	Wild forms known only from Southern Africa, but with an indigenous domesticated range encompassing parts of Africa, the middle east, and Asia
B	3–4	<i>G. anomalum</i> , <i>G. triphyllum</i> , <i>G. capitiviridis</i> , (<i>G. trifurcatum</i>)	Africa, Cape Verde Islands
C	2	<i>G. sturtianum</i> , <i>G. robinsonii</i>	Central and Western Australia
D	13–14	<i>G. thurberi</i> , <i>G. armourianum</i> , <i>G. harknessii</i> , <i>G. davidsonii</i> , <i>G. klotzschianum</i> , <i>G. aridum</i> , <i>G. raimondii</i> , <i>G. gossypoides</i> , <i>G. lobatum</i> , <i>G. trilobum</i> , <i>G. laxum</i> , <i>G. turneri</i> , <i>G. schwendimanii</i> , (<i>G. sp.nov.</i>)	Primarily Mexico, with range extensions into Peru, the Galapagos Islands, and southern Arizona
E	5–9	<i>G. stocksii</i> , <i>G. somalense</i> , <i>G. areysianum</i> , <i>G. incanum</i> , <i>G. trifurcatum</i> , (<i>G. benidirese</i>), (<i>G. bricchettii</i>), (<i>G. vollesenii</i>), (<i>G. trifurcatum</i>)	Poorly understood native ranges of many species, but collectively in parts of the Arabian Peninsula, Northeast Africa, and Southwest Asia
F	1	<i>G. longicalyx</i>	Endemic to East Africa
G	3	<i>G. bickii</i> , <i>G. australe</i> , <i>G. nelsonii</i>	Central Australia
K	12	<i>G. anapoides</i> , <i>G. costulatum</i> , <i>G. cunninghamii</i> , <i>G. enthyale</i> , <i>G. exiguum</i> , <i>G. londonderriense</i> , <i>G. marchantii</i> , <i>G. nobile</i> , <i>G. pilosum</i> , <i>G. populifolium</i> , <i>G. pulchellum</i> , <i>G. rotundifolium</i>	Northwest Australia, Cobourg Peninsula, Northern Territory, Australia
AD	7	<i>G. hirsutum</i> , <i>G. barbadense</i> , <i>G. tomentosum</i> , <i>G. mustelinum</i> , <i>G. darwinii</i> , <i>G. ekmanianum</i> , <i>G. stephensii</i>	Wild species are from the New World tropics and subtropics, including Hawaii, NE Brazil, the Dominican Republic, and the Galapagos Islands. A recently described species (<i>G. stephensii</i>) is from the Wake Atoll near French Polynesia. The indigenous cultivated range of the two domesticated species <i>G. barbadense</i> and <i>G. hirsutum</i> encompasses many parts of the drier New World tropics and subtropics, with overlapping ranges in the Caribbean and elsewhere

Gossypium, which range from basic taxonomic exploration to breeding and germplasm introgression. As shown in Table 2, designations of genomes and chromosomes in each species, subspecies and variety in *Gossypium* are suggested, including for *G. herbaceum* subs. *africanum* with its genome as A_{1-a}, which might be useful for ongoing genomic studies, and one Mexican arborescent species with a genome designated as D₁₂, as this species may soon be described as a new D genome species. The last five species in Table 2 have not been assigned genome designations because they are poorly represented in herbarium collections and no living material has been available for study.

A comparative nomenclature of individual chromosomes in *Gossypium* is facilitated by the many early

studies in the later decades of the previous century, when cotton karyotype studies were frequently conducted (Edwards 1977, 1979a, 1979b; Wang et al. 1994; Endrizzi et al. 1985; Wendel and Grover 2015). These earlier investigations provided an important foundation for the transition into the molecular biology era. By using cultivars or wild species in *Gossypium*, there were increasingly frequent reports on genetic mapping related to linkage groups (Brubaker et al. 1999; Rong et al. 2004; Khan et al. 2016), on identifications of individual chromosomes (Wang et al. 2007, 2008; Gan et al. 2011, 2012, 2013; Shan et al. 2016), and even on microdissection and microcloning of individual chromosomes (Peng et al. 2012). *De novo* sequence-based genomic studies provided detailed information on single or pseudo-chromosomes (Wang et al.

Table 2 Nomenclature of individual genomes and chromosomes for each species in *Gossypium*, with Chinese translation of species names

Species names		Individual genome ^a	Individual chromosome
Scientific names	Chinese translations		
<i>G. hirsutum</i> Linnaeus	陆地棉	(AD) ₁	A _h 01-A _h 13; D _h 01-D _h 13
<i>G. barbadense</i> Linnaeus	海岛棉	(AD) ₂	A _b 01-A _b 13; D _b 01-D _b 13
<i>G. tomentosum</i> Nuttall ex Seemann	毛棉	(AD) ₃	A _{tt} 01-A _{tt} 13; D _{tt} 01-D _{tt} 13
<i>G. mustelinum</i> Miers ex Watt	黄褐棉	(AD) ₄	A _m 01-A _m 13; D _m 01-D _m 13
<i>G. darwinii</i> Watt	达尔文氏棉	(AD) ₅	A _d 01-A _d 13; D _d 01-D _d 13
<i>G. ekmanianum</i> Wittmack	艾克棉	(AD) ₆	A _e 01-A _e 13; D _e 01-D _e 13
<i>G. stephensii</i> J. Gallagher, C. Grover & Wendel	斯蒂芬氏棉	(AD) ₇	A _s 01-A _s 13; D _s 01-D _s 13
<i>G. herbaceum</i> Linnaeus	草棉	A ₁	A ₁ 01-A ₁ 13
<i>G. herbaceum subs. africanum</i> Hutchinson	阿非利加棉	A _{1-a}	A _{1a} 01-A _{1a} 13
<i>G. arboreum</i> Linnaeus	亚洲棉	A ₂	A ₂ 01-A ₂ 13
<i>G. anomalum</i> Wawra & Peyritsch	异常棉	B ₁	B ₁ 01-B ₁ 13
<i>G. triphyllum</i> (Harvey & Sonder) Hochreutiner	三叶棉	B ₂	B ₂ 01-B ₂ 13
<i>G. capitata-viridis</i> Mauer	绿顶棉	B ₃	B ₃ 01-B ₃ 13
<i>G. sturtianum</i> Willis	斯特提棉	C ₁	C ₁ 01-C ₁ 13
<i>G. sturtianum var. nandawarensense</i> Derera	南岱华棉	C _{1-n}	C _{1n} 01-C _{1n} 13
<i>G. robinsonii</i> Mueller	鲁滨逊氏棉	C ₂	C ₂ 01-C ₂ 13
<i>G. thurberi</i> Todaro	瑟伯氏棉	D ₁	D ₁ 01-D ₁ 13
<i>G. armourianum</i> Kearney	辣根棉	D ₂₋₁	D _{2a} 01-D _{2a} 13
<i>G. harknessii</i> Brandegees	哈克尼西棉	D ₂₋₂	D _{2h} 01-D _{2h} 13
<i>G. davidsonii</i> Kellogg	戴维逊氏棉	D _{3-d}	D _{3d} 01-D _{3d} 13
<i>G. klotzschianum</i> Andersson	克劳茨基棉	D _{3-k}	D _{3k} 01-D _{3k} 13
<i>G. aridum</i> (Rose & Standley) Skovsted	旱地棉	D ₄	D ₄ 01-D ₄ 13
<i>G. raimondii</i> Ulbrich	雷蒙德氏棉	D ₅	D ₅ 01-D ₅ 13
<i>G. gossypoides</i> (Ulbrich) Standley	拟似棉	D ₆	D ₆ 01-D ₆ 13
<i>G. lobatum</i> Gentry	裂片棉	D ₇	D ₇ 01-D ₇ 13
<i>G. trilobum</i> (DC.) Skovsted	三裂棉	D ₈	D ₈ 01-D ₈ 13
<i>G. laxum</i> Phillips	松散棉	D ₉	D ₉ 01-D ₉ 13
<i>G. turneri</i> Fryxell	特纳氏棉	D ₁₀	D ₁₀ 01-D ₁₀ 13
<i>G. schwendimanii</i> Fryxell & Koch	施温迪芒棉	D ₁₁	D ₁₁ 01-D ₁₁ 13
<i>G. sp.nov.</i>	(待命名)	D ₁₂	D ₁₂ 01-D ₁₂ 13
<i>G. stocksii</i> Masters in Hooker	司笃克氏棉	E ₁	E ₁ 01-E ₁ 13
<i>G. somalense</i> (Gurke) Hutchinson	索马里棉	E ₂	E ₂ 01-E ₂ 13
<i>G. areysianum</i> Deflers	亚雷西亚棉	E ₃	E ₃ 01-E ₃ 13
<i>G. incanum</i> (Schwartz) Hillcoat	灰白棉	E ₄	E ₄ 01-E ₄ 13
<i>G. longicalyx</i> Hutchinson & Lee	长萼棉	F ₁	F ₁ 01-F ₁ 13
<i>G. bickii</i> Prokhanov	比克氏棉	G ₁	G ₁ 01-G ₁ 13
<i>G. australe</i> Mueller	澳洲棉	G ₂	G ₂ 01-G ₂ 13
<i>G. nelsonii</i> Fryxell	奈尔逊氏棉	G ₃	G ₃ 01-G ₃ 13
<i>G. exiguum</i> Fryxell, Craven & Stewart	小小棉	K ₁	K ₁ 01-K ₁ 13
<i>G. rotundifolium</i> Fryxell, Craven & Stewart	圆叶棉	K ₂	K ₂ 01-K ₂ 13
<i>G. populifolium</i> (Bentham) Mueller ex Todaro	杨叶棉	K ₃	K ₃ 01-K ₃ 13
<i>G. pilosum</i> Fryxell	稀毛棉	K ₄	K ₄ 01-K ₄ 13

Table 2 Nomenclature of individual genomes and chromosomes for each species in *Gossypium*, with Chinese translation of species names (*Continued*)

Species names		Individual genome ^a	Individual chromosome
Scientific names	Chinese translations		
<i>G. marchantii</i> Fryxell, Craven & Stewart	马全特氏棉	K ₅	K ₅ 01-K ₅ 13
<i>G. londonderriense</i> Fryxell, Craven & Stewart	伦敦德里棉	K ₆	K ₆ 01-K ₆ 13
<i>G. enthyle</i> Fryxell, Craven & Stewart	林地棉	K ₇	K ₇ 01-K ₇ 13
<i>G. costulatum</i> Todaro	皱壳棉	K ₈	K ₈ 01-K ₈ 13
<i>G. cunninghamii</i> Todaro	肯宁汉氏棉	K ₉	K ₉ 01-K ₉ 13
<i>G. pulchellum</i> (Gardner) Fryxell	小丽棉	K ₁₀	K ₁₀ 01-K ₁₀ 13
<i>G. nobile</i> Fryxell, Craven & Stewart	显贵棉	K ₁₁	K ₁₁ 01-K ₁₁ 13
<i>G. anapoides</i> Stewart, Craven & Wendel	孪生叶面棉	K ₁₂	K ₁₂ 01-K ₁₂ 13
<i>G. anomalum</i> subsp. senarensis (Wawra & Peyritsch) Vollesen	桑纳氏棉	B	These species are excluded as they are poorly represented in herbarium collections and no living material has been available for study.
<i>G. trifurcatum</i> Vollesen	三叉棉	E / B	
<i>G. vollesenii</i> Fryxell	佛伦生氏棉	E	
<i>G. benadirensis</i> Mattei	伯纳迪氏棉	E	
<i>G. bricchettii</i> (Ulbrich) Vollesen	伯里切特氏棉	E	

^aSome designations for individual genomes were discussed with James McD Stewart (deceased) in 2007

2012; Paterson et al. 2012; Li et al. 2014, 2015; Zhang et al. 2015; Liu et al. 2015; Yuan et al. 2015).

These and many other studies collectively indicate that a clear nomenclature of individual chromosomes in *Gossypium* will be useful to facilitate communication and to provide consistency in chromosome designations. Here we suggest such designations (Table 2) for all clades in *Gossypium*, with the exception of the last five taxa that are too poorly understood taxonomically and cytogenetically to be included. For the seven allotetraploid species, the first letters of their specific names are used instead of their corresponding genome designations. A_h and D_h stand for corresponding chromosome sets of A-sub and D-sub genome, respectively, for *G. hirsutum*, as well as A_b and D_b for *G. barbadense*, A_{tt} and D_{tt} for *G. tomentosum*, A_m and D_m for *G. mustelinum*, A_d and D_d for *G. darwinii*, A_e and D_e for *G. ekmanianum*, and A_s and D_s for *G. stephensii*. A_t and D_t are more broadly used terms that designate chromosomes of A-sub and D-sub genomes in all allotetraploid cottons, respectively, from which the A_{tt} and D_{tt} for *G. tomentosum* are distinguished. Generally, in diploid species, the designations for individual chromosomes correspond to the individual genomes. There is another exception for *G. armourianum* and *G. harknessii* because of the historical use of the genome designation D₂ for both of these species; accordingly, 'a' and 'h', the first letters of their specific epithets, are used to clarify this confusion, so that the individual chromosomes of the two species are designated D_{2a}1 - D_{2a}13 and D_{2h}1 ~ D_{2h}13, respectively. The other break with tradition is the simplifying omission of dashes in individual chromosome designations for *G. herbaceum* subsp. *africanum*, *G. sturtianum* var. *nandewarense*, *G. armourianum*, *G. harknessii*, *G. davidsonii* and *G. klotzschianum*.

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Availability of data and materials

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Authors' contributions

Wang KB conceived of the subject, and participated in its design and coordination and jointly to draft the manuscript; Wendel JF participated in the design and jointly to draft the manuscript; Hua JP participated in the design and helped to draft the manuscript. All authors read and approved the final manuscript.

Ethics approval and consent to participate

Not applicable.

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Competing interests

The authors declare that they have no competing interests.

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