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ORIGINAL ARTICLE

The systematic value of nuclear genome size for "all" species of *Tulipa* L. (*Liliaceae*)

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Abstract Nuclear genome size, as measured by flow cytometry with propidium iodide, was used to investigate the relationships within the genus *Tulipa* L. (*Liliaceae*). More than 400 accessions representing 123 taxa from mainly wild-collected plants were investigated. Most species of *Tulipa* have the same basic chromosome number, $2n = 2x = 24$. However, the somatic DNA 2*C* value (2*C*) is shown to range from 32 to 69 pg for the diploids. The largest genome contains roughly 3.4×10^{10} more base pairs than the smallest and has chromosomes that are more than twice as large. These large differences in the amount of nuclear DNA predict that the hybrids, if any arise, are usually sterile. Depending on the size of the total genome, 1 pg amounts to several thousand genes. Moreover, genome sizes are evaluated here in combination with available morphological, geographical, and molecular data. Therefore, the taxonomy proposed here is not a single-character taxonomy based on genome size alone. The genus *Tulipa*, as here determined, has 87 species, 29 more than accepted by van Raamsdonk et al. [Acta Hort (ISHS) 430:821–828, 1997], but including 25 species that were not available to them. Of these 87 species, 28 were not seen by Hall (*The genus* Tulipa, The Royal Horticultural Society, London, 1940) in a living state and placed by him in an addendum. Species of the subgenus *Clusianae* (Baker) Zonn. differ strongly in nuclear DNA content (DNA 2*C* value), 32 versus 40–68 pg for all other tulips, and are placed here in a separate subgenus. Also *Orithyia*, the only group with a style and with only 38–39 pg is placed in a separate subgenus. Therefore, all tulips are attributed to four subgenera, *Clusianae* (Baker) Zonn., *Tulipa*, *Eriostemones* Raamsd., and *Orithyia* (D. Don) Baker and divided further into 12 sections. Seven of the eight series of section *Eichleres* (A.D. Hall) Raamsd. are now placed in four sections: (1) section *Lanatae* (Raamsd.) Zonn., mainly confined to species from the Pamir-Alay and including series *Lanatae* Raamsd., (2) section *Multiflorae* (Raamsd.) Zonn. (including series *Glabrae* Raamsd.), (3) section *Vinistriatae* (Raamsd.) Zonn. (including series *Undulatae* Raamsd.), and (4) section *Spiranthera* Vved. ex Zonn. and Veldk. Triploids, tetraploids, and pentaploids were found in several species. DNA content confirmed the close relationships of the species within the different sections. The rather similar looking and therefore often confused *T. armena* Boiss. (51.8 pg), *T. systola* Stapf (56.3 pg), and *T. julia* K., Koch (61.6 pg) could be clearly distinguished. The same is true for *T. biebersteiniana* Schult. f. (56.9 pg), *T. sylvestris* ssp. *australis* (Link) Pamp. (62.0 pg), and *T. primulina* Baker (64.6 pg). *T. doerfleri* Gand. and *T. whittalli* (Dykes) Hall could be placed as polyploid forms of *T. orphanidea* Boiss. ex Heldr. On the basis of DNA content, a systematic association between *T. julia* K. Koch and the triploid *T. aleppensis* Boiss. and between *T. systola* Stapf and the triploid *T. praecox* Tenore was suggested. The new species *T. lemmersii* Zonn., Peterse, and de Groot is described, and four possible new species are indicated. Genome size as measured by using flow cytometry may conveniently be used to produce systematic data. It is applicable even in the case of dormant bulbs or sterile plants for monitoring the trade in bulbous species.

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Introduction

The genus *Tulipa* L. (*Liliaceae*) comprises 40 (Stork 1984) to 55 (van Raamsdonk et al. 1997) to more than 100 species (Hall 1940). In the World Checklist for *Tulipa* (Govaerts 2008), 418 are named and 112 were accepted there. Tulips occur naturally in southern Europe, North Africa, the Middle East, and central Asia, including China. The Tien Shan and Pamir-Alay mountain ranges in central Asia are considered the primary gene centers for *Tulipa* species (Botschantzeva 1962), with the Caucasus as a secondary center. They are popular spring-flowering garden plants; millions of bulbs are sold annually and over 5,000 cultivars are registered (van Scheepen 1996). Several species are in cultivation, but they cover less than 7% of the total tulip area in the Netherlands. The boundaries between taxa of various ranks are still a subject of dispute (van Raamsdonk et al. 1997). All species counted (with exception of the polyploid forms and *T. maximowiczii* Regel) have the same chromosome number, $2n = 2x = 24$ (De Mol 1928; Woods and Bamford 1937; Plavcova 1969). To elucidate the relationships between *Tulipa* species, the classical taxonomic traits based on morphological characters and geographical distribution are here supplemented with data on DNA 2*C*-values. These were not investigated earlier to any extent in the systematic study of *Tulipa*. In the list of DNA *C*-values (Bennett and Leitch 2004), data on 23 accessions of tulips were recorded, but these are hard to interpret as they come from different sources and methods, and they are intrinsically inconsistent.

Despite the existence of a large body of literature on *Tulipa*, taxonomy is generally considered to be difficult. Sentences to this effect are encountered in every taxonomic treatment but are especially applicable in this case. The main reason is that there is hardly any character that is not variable within a species. The main characteristics are as follows, but not a single one is without exceptions: leaf/stem hairiness, a black blotch at the base of the tepals with or without a yellow edge, the presence and type of hairs on the inside of the bulb tunic, flower color, flowering time, and hairs on the base of the filaments. To circumvent this, van Raamsdonk (1992) and van Raamsdonk and De Vries (1995) used principal component and canonical variate analyses to investigate the variation of 35 morphological characters, and they substantially clarified systematic relationships within *Tulipa*. In this study, DNA 2*C*-value (nuclear DNA content) is introduced as an additional method for the study of *Tulipa* taxonomy. More than 400 different accessions representing nearly all accepted species were measured in an attempt to understand the relationships within *Tulipa* better.

Nuclear DNA content can conveniently be measured by flow cytometry using propidium iodide, a stoichiometric DNA stain that intercalates in the double helix. Where many species in a genus have the same chromosome numbers, differences in DNA 2*C*-value, when present, have proven to be very effective in delimiting infrageneric divisions in a number of taxa (Ohri 1998). Flow cytometry can therefore be considered as a fast and useful method for understanding systematic relationships. Genome size has been demonstrated to differ between taxa with identical chromosome numbers. Moreover, Greilhuber (1998, 2005) has clearly shown that intraspecific variation of genome size is much less than assumed.

The evolution of genome size (*Cx* value; Greilhuber 1979) has received increased attention during recent years. Primitive angiosperms are now believed to have had small genomes; increases up to a factor of 1,000 have occurred independently in various modern taxa (Leitch et al. 1998). Flow cytometry has successfully been used to measure the 2*C* value for the genera *Hosta* Tratt., *Helleborus* L., *Clivia* Lindl., *Nerine* Herb., *Agapanthus* L'Her., *Galanthus* L., *Narcissus* L., *Gasteria* Duval., and others by Zonneveld et al. (2001–2008). In this paper it is shown, using several accessions for most species, that many species can be discriminated based on their genome size and intraspecific variation is low in most *Tulipa* species. Details of the revised nomenclature for the infrageneric taxa are submitted by Veldkamp and Zonneveld.

Materials and methods

Plant material

Plant material was obtained from the collections of the Bulb Research Center of the Koninklijke Algemeene Vereeniging voor Bloembollencultuur (KAVB), Lisse via E. Breed; W. Lemmers, Lisse; J. van Tuyl, Wageningen University; J. de Groot, de Zilk; J.P. Tyssen, M. van den Brink, and J. Zonneveld (Hortus Bulborum, Limmen), all in the Netherlands; L. Lieser, France; J. Ruksans, Latvia; G. Knoche, Germany; and H. and M. Aanesen, Norway. Where possible, material of known wild origin was used, and care was taken to ensure correct identification of all material. Vouchers of most species are in the Herbarium of Wageningen University (WAG) and the Royal Botanic Garden, Kew, UK (K).

Flow cytometric measurement of nuclear DNA content

For the isolation of nuclei, about 0.5 cm^2 of adult leaf tissue was chopped together with a piece of *Agave americana* L. 'Aureomarginata' or *Clivia miniata* (Lindl.) Regel as an internal standard (see below). The chopping was done with a new razor blade in a Petri dish in 0.25 ml nuclei-isolation buffer to which 0.25 mg RNase/ml was added (Zonneveld and Van Iren 2001). After adding 1.75 ml propidium iodide solution (50 mg PI/l in isolation buffer), the suspension with nuclei was filtered through a 30-μm nylon filter. The fluorescence of the nuclei was measured 30 min and 1 h after addition of propidium iodide, using a Partec CA-II flow cytometer. The optical path contained a HBO mercury lamp, filters KG1 and BG12, dichroic mirror TK500, filter OG570, and a Leitz 50 × 1 water immersion objective. Data were analyzed by means of DPAC software (Partec). The 2*C* DNA content of the sample was calculated as the sample peak mean, divided by the *Agave*/*Clivia* peak mean, and multiplied by the amount of DNA of the *Agave*/*Clivia* standard. At least three different samples, with at least 5,000 nuclei each, were measured twice for each clone. Most histograms revealed a coefficient of variation of less than 5%. The standard deviation was calculated for the DNA content of each species, using all relevant measurements.

Internal standard and absolute DNA content values

When measuring nuclear DNA content by means of flow cytometry, it is necessary to chop tissue from the plant of interest together with an internal standard: this standard must be as close as possible to the plants of interest. In this way, variation in signal intensities due to staining kinetics, to light absorption and quenching by sample components, as well as to instrument and other variables, is reduced to a minimum. *Agave americana* was chosen as internal standard for tulips of subgenus *Clusianae* (Baker) Zonn. and section *Kolpakowskianae* Raamsd. ex Zonn. and Veldk. (including their polyploids) with about 32–45 pg of DNA for the diploids; *Clivia miniata* was used for all other tulips. *Clivia miniata* and *A. americana* are available year-round, do not mind several weeks without water and, being large plants, a single specimen can serve a lifetime, thereby further reducing variation in readings. They also have a low background in propidium iodide measurements and show a single G_0 peak, almost lacking G_2 arrest. Fresh male human leucocytes ($2C = 7.0$ pg; $1 \text{ pg} = 10^{-12}$ gram $= \pm 10^9$ bp) were chosen as primary standard (Tiersch et al. 1989). This yields $2C = 15.9$ pg for nuclei of *Agave americana* L. and 39.0 pg for *Clivia miniata*.

Results and discussion

Genome size

Tulips, as with most species that arouse a strong horticultural interest, are not easy to investigate as it is often difficult to discriminate between wild tulips and escaped ones. Moreover, very few characters are constant in tulips. Even with a strong character such as hairs on the filaments that discriminate between subgenus *Eriostemones* Raamsd. and all other tulips, species are found among bonafide *Eriostemones* where the hairs are absent, e.g., in *T. sprengeri* Baker and *T. sogdiana* Bunge. Another important character is the number and shape of the hairs inside the bulb tunic. Here also differences are found within a population (Botschantzeva 1962), and moreover seem also to depend strongly on conditions of cultivation. Flower color is often of minor importance, as especially in the Tien Shan (Pratov et al. 2006) and adjacent desert areas, several species, including *T. schrenkii* Regel, *T. alberti* Regel, *T. greigii* Regel, *T. kaufmanniana* Regel, and *T. ostrowskiana* Regel, range from white, yellow, and orange to red colors. Even in species with mainly red flowers, being most prominent in the Pamir-Alay, an occasional yellow (edged) flower can be found. Furthermore a yellow margin to a black blotch on the base of a tepal, even the blotch itself, can be present or absent within a species (Van Raamsdonk and De Vries 1995). Genome size as investigated here (see Table 1), complements the work based mainly on morphological characters of Hall (1940) and of morphological characters, crossability studies and geographical distribution of van Raamsdonk et al. (1991–1997). Although van Raamsdonk et al. used about 35 characters to discriminate among the species, they remark that some species come out identical in their scheme yet can be distinguished by characters not used in their investigations. Our start was to see how few species we could distinguish; Van Raamsdonk et al. (1997) with 55 species seemed a very good basis, but in the end, we could not be avoid restoring several more taxa to species status. Moreover, 25 additional species could be investigated that were not available to Van Raamsdonk and De Vries (1995).

Subdivision of the genus *Tulipa*

Traditionally genus *Tulipa* is divided in two sections: *Tulipa* (syn.: *Leiostemones* Boiss.) and *Eriostemones*. Van Raamsdonk et al. (1997) raise these to subgenus status and divide the subgenus *Tulipa* into five sections: *Clusianae* Baker, *Kopalkowskiana* (A.D. Hall) Raamsd., *Eichleres* (A.D. Hall) Raamsd., *Tulipanum* Reboul, and *Tulipa*. Section *Eichleres* was further divided into eight series. Section *Eriostemones* is simpler. Since Hall (1940), most

Table 1 All species of *Tulipa* with their amount of DNA 2*C*, average, standard deviation, place of origin, and the names under which the clones were received

Genus *Tulipa L.* (*Liliaceae*)

Coll. no.		2*C* DNA (pg)	Average	SD	Ploidy[b]	Origin	Received as/ cultivar
Subgenus *Clusianae* (Baker) Zonn.							
Section *Clusianae* Baker							
sg219	*T. clusiana* f. *cashmeriana* (A.D. Hall) Raamsd.	30.9	32.1	1.9	2*X*	Hindu Kush, NW Kabul, Afghan.	HB76172-3, ex G.Wilson
sg213	*T. clusiana* f. *cashmeriana* (A.D. Hall) Raamsd.	31.1			2*X*	Hindu Kush, NW Kabul, Afghan.	
23.6	*T. clusiana* f. *cashmeriana* (A.D. Hall) Raamsd.	32.0			2*X*	CPRO	As ***T. aitchisonii***
7.1	*T. clusiana* f. *cashmeriana* (A.D. Hall) Raamsd.	34.6			2*X*	Bulb Research Centre, Lisse	As ***T. aitchisonii***
D 5081	*T. clusiana* DC.	41.0	41.0	1.7	“2–3*X*”	ex J. de Groot	As *T. stellata*
BZ2	*T. clusiana* DC.	46.1	47.3	1.5	3*X*	ex commerce	
	T. clusiana DC.	46.2			3*X*	Bulb Research Centre, Lisse	‘Sheila’ (clus × stellata)
3lim20	*T. clusiana* DC.	47.2			3*X*	Hortus Bulborum. Limmen	‘Taco’
22.2	*T. clusiana* DC.	47.5			3*X*	ex commerce	‘Tubergen’s Gem’
96.1	*T. clusiana* DC.	49.3			3*X*	Bulb Research Centre, Lisse	‘Z1065-2’
86.1	*T. clusiana* f. *diniae* Raamsd.	64.3	65.8	1.2	4*X*	Bulb Research Centre, Lisse	‘Tinker’
23.7	*T. clusiana* f. *diniae* Raamsd.	64.8			4*X*	Bulb Research Centre, Lisse	As ***T. cashmeriana***[a]
23.2	*T. clusiana* f. *diniae* Raamsd.	65.1			4*X*	Bulb Research Centre, Lisse	‘Cynthia’
23.8	*T. clusiana* f. *diniae* Raamsd.	66.8			4*X*	Bulb Research Centre, Lisse	‘Lady Jane’
3lim18	*T. clusiana* f. *diniae* Raamsd.	68.2			4*X*	ex commerce	
cb33	*T. clusiana* f. *clusianae*	78.9	79.8	2.5	5*X*	ex C. Breed	
23.1	*T. clusiana* f. *clusianae*	78.9			5*X*	Bulb Research Centre, Lisse	
23.3	*T. clusiana* f. *clusianae*	81.5			5*X*	ex R. vd Zalm	
30.8	*T. linifolia* Regel	32.0	31.8	1.7	2*X*	ex C. Breed	As ***T. batalini***[a]
55.1	*T. linifolia* Regel	32.1			2*X*	(real one $2n = 22$!)	As *T. maximowiczii* Hort.
100.1	*T. linifolia* Regel	31.9			2*X*	Bulb Research Centre, Lisse	‘Red Hunter’
lim23	*T. linifolia* Regel	31.2			2*X*	(real one $2n = 22$!)	As *T. maximowiczii* Hort.
16.3	*T. linifolia* Regel	32.3			2*X*	Bulb Research Centre, Lisse	As ***T. batalini***[a]
16.1	*T. linifolia* Regel	31.0			2*X*	Bulb Research Centre, Lisse	‘Bronze Charm’
16.4	*T. linifolia* Regel	31.0			2*X*	sel. J. de Winter	
16.2	*T. linifolia* Regel	31.2			2*X*	Bulb Research Centre, Lisse	‘Yellow Jewel’
cb57	*T. linifolia* Regel	33.6			2*X*	ex C. Breed	
w11	*T. montana* Lindley	31.4	32.5	1.5	2*X*	ex Wageningen BG	
w10	*T. montana* Lindley	31.5			2*X*	ex Wageningen BG	
w09	*T. montana* Lindley	31.6			2*X*	ex Wageningen BG	
cb60	*T. montana* Lindley	32.1			2*X*	ex C. Breed	
57.1	*T. montana* Lindley	32.4			2*X*	Bulb Research Centre, Lisse	
cb73	*T. montana* Lindley	32.9			2*X*	ex C. Breed	As ***T. wilsoniana***[a]
D 5039	*T. montana* Lindley	33.3			2*X*	ex J. de Groot	As ***T. wilsoniana***[a]
57.3	*T. montana* Lindley	33.4			2*X*	Bulb Research Centre, Lisse	
57.2	*T. montana* Lindley	33.8			2*X*	CPRO	

Table 1 continued

Genus *Tulipa L.* (*Liliaceae*)

Coll. no.		2*C* DNA (pg)	Average	SD	Ploidy[b]	Origin	Received as/ cultivar
Subgenus *Orithyia (D.Don) Baker*							
Section *Orithyia* (D.Don) Vved.							
sg12/4	*T. heterophylla* (Regel) Baker	37.5	37.5	0.3	2*X*	Tien Shan, N. Almaty, Kazak.	On acid soil
sg8/5	*T. uniflora* (L.) Besser ex Baker	38.3	38.3	0.4	2*X*	W. Tarbagatai, Kazakhstan	
testc	*T. heteropetala* Ledeb.	38.4	39.1	0.6	2*X*	Altai, Kazakhstan	
sg314 c	*T. heteropetala* Ledeb.	39.2			2*X*	Altai, Marble Pass, Kazakhstan	
sg314a	*T. heteropetala* Ledeb.	39.4			2*X*	Altai, Chin. border, Kazakhstan	
sg314b	*T. heteropetala* Ledeb.	39.4			2*X*	Altai, E Irtich river, Kazakhstan	
Subgenus *Tulipa*							
Section *Kolpakowskianae* Raamsd. ex Zonn & Veldk.							
112-1	*T. lemmersii* Zonn., A. Peterse, J. de Groot sp.nov.	36.4	36.4	0.5	2*X*	Mashad Pass, Chimkent, Kaz.	
112-2	*T. lemmersii* Zonn., A. Peterse, J. de Groot sp. nov.	36.4			2*X*	Mashad Pass, Chimkent, Kaz.	
BZ08	*T. nitida* Hoog	38.3	38.6	0.8	2*X*	Dehqanabad, Uzbekistan	
	T. nitida Hoog	38.9			2*X*	Dehqanabad, Uzbekistan	
BZ07	*T. zenaidae* Vved.	39.3	39.8	1.0	2*X*	Merke valley, Kazakhstan	
97.1	*T. zenaidae* Vved.	39.7			2*X*	Bulb Research Centre, Lisse	
	T. zenaidae Vved.	40.5			2*X*	Merke Valley, Kazakhstan	
42.2	*T. iliensis* Regel	39.4	41.0	0.9	2*X*	Bulb Research Centre, Lisse	
testc.	*T. iliensis* Regel	40.3			2*X*	Bulb Research Centre, Lisse	As *T. ferganica*
81	*T. iliensis* Regel	40.3			2*X*	Bulb Research Centre, Lisse	
D5303	*T. iliensis* Regel	40.8			2*X*	HB77268	
42.1	*T. iliensis* Regel	41.1			2*X*	Bulb Research Centre, Lisse	
D5403b	*T. iliensis* Regel	41.4			2*X*	ex J. de Groot	
D 5080a	*T. iliensis* Regel	41.6			2*X*	Marni 01, China	
D 5080b	*T. iliensis* Regel	41.9			2*X*	Ketmen Range, Kazakhstan	
D5403d	*T. iliensis* Regel	42.0			2*X*	HB74247	
sg	*T. iliensis* Regel	62.1	62.1	1.2	3*X*	ex commerce	
D5420	*T. brachystemon* Regel	39.3	41.0	0.9	2*X*	Dzjungaric foothills, Kazakhstan	
BZ07	*T. brachystemon* Regel	40.9			2*X*	Kazakhstan	
sg	*T. brachystemon* Regel	41.6			2*X*	Kazakhstan	
D5419	*T. brachystemon* Regel	41.7			2*X*	Kazakhstan	
sg	*T. brachystemon* Regel	41.6			2*X*	Ili River	
sg	*T. brachystemon* Regel	40.7			2*X*	Dzjungaric Ala-Tau	
BZ07	*T. korolkowii* Regel	40.6	41.5	0.9	2*X*	Mogoltau, Uzbekistan	
	T. korolkowii Regel	41.0			3*X*	Iron Gate, Uzbekistan	
BZ08	*T. korolkowii* Regel f. *rosea* Zonn.	42.1			2*X*	Turkestansky range	As ***T. rosea***[a]
BZ07	*T. korolkowii* Regel f. *rosea* Zonn.	42.2			2*X*	Turkestansky range	As ***T. rosea***[a]
D 5136	*T. borszczowii* Baker	41.6	41.6	1.4	2*X*	Kyzyl-kum Lake, Kazakhstan	
	T. kolpakowskiana Baker	39.2	41.8	1.5	2*X*		
sg211	*T. kolpakowskiana* Baker	40.0			2*X*	Charyn Canyon, Kazakhstan	

Table 1 continued

Genus *Tulipa L.* (*Liliaceae*)

Coll. no.		2*C* DNA (pg)	Average	SD	Ploidy[b]	Origin	Received as/ cultivar
D5400	*T. kolpakowskiana* Baker	40.9			3*X*	Kazakhstan	
	T. kolpakowskiana Baker	41.0			2*X*	Merke Valley, Kazakhstan	
BZ07	*T. kolpakowskiana* Baker	41.3			2*X*	Near Ili River, Kazakhstan	
	T. kolpakowskiana Baker	41.5			2*X*	Merke Valley, Kazakhstan	
	T. kolpakowskiana Baker	42.0			2*X*	Kabchagal, Kazakhstan	As *T. alberti* small
59.2	*T. kolpakowskiana* Baker	42.1			2*X*	CPRO 82337	As *T. neustruevae*
D 5021a	*T. kolpakowskiana* Baker	43.2			2*X*	fr coll seed JJA02, Kazak.	
cb68	*T. kolpakowskiana* Baker	44.3			2*X*	ex C. Breed	
D5415	*T. lehmanniana* Merckl.	42.0	42.4	1.0	2*X*		As ***T. behmiana***[a]
BZ07	*T. lehmanniana* Merckl.	42.1			2*X*	Kabchagal Kazakhstan no 1	As ***T. behmiana***[a]
BZ07	*T. lehmanniana* Merckl.	42.7			2*X*	Kabchagal Kazakhstan no 2	As ***T. behmiana***[a]
	T. lehmanniana Merckl.	42.7			2*X*	Badhyz, Turkmenistan	
52.1	*T. lehmanniana* Merckl.	67.6	67.6		3*X*	CPRO 77161, ex M. Hoog	
D 5066a	*T. hissarica* Popov & Vved.	42.8	42.8	1.3	2*X*	Hodji-obi-garm, Tajikistan	
D 5066	*T. hissarica* Popov & Vved.	42.8			2*X*	ex P.Christian 1999.	
testc.	*T. anisophylla* Vved.	42.0	43.4	1.2	2*X*	Bulb Research Centre, Lisse	
5.2	*T. anisophylla* Vved.	43.5			2*X*	Bulb Research Centre, Lisse	
5.1	*T. anisophylla* Vved.	44.4			2*X*	CPRO76333-2,BG Dunshanbe	
47.1	*T. korshinskyi* Vved.	43.5	44.0	0.7	2*X*	Bulb Research Centre, Lisse	
	T. korshinskyi Vved.	44.5			2*X*	Darwas Mnt, Z. Tadjikistan	
D 5041	*T. ferganica* Vved.	44.3	44.8	1.8	2*X*	ex J. de Groot	
cb44	*T. ferganica* Vved.	44.7			2*X*	ex C. Breed	
D5405a	*T. ferganica* Vved.	45.6			2*X*	HB80291-1, d yellow	
sg208	*T. altaica* Pall. ex Spreng.	43.2	44.9	1.6	2*X*	Altai 2005, broad lf	
sg210	*T. altaica* Pall. ex Spreng.	43.6			2*X*	Marble pass, Altai 2004	
sg9/5	*T. altaica* aff. Pall. ex Spreng.	44.5			2*X*	Dzjungaric Ala-Tau	
2008	*T. altaica* Pall. ex Spreng.	44.7			2*X*	Saur Mountains, Kazakhstan	
D5401b	*T. altaica* Pall. ex Spreng.	44.7			2*X*	ex J. de Groot	
testc.	*T. altaica* Pall. ex Spreng.	45.5			2*X*	Altai, Kazakhstan	
	T. altaica Pall. ex Spreng.	45.5			2*X*	Altai, Kazakhstan	
2008	*T. altaica* Pall. ex Spreng.	45.7			2*X*	W. Tarbagatai, Kazakhstan	
testc.	*T. altaica* Pall. ex Spreng.	46.5			2*X*	Marble Pass, Altai 2005	
D5403a	*T. ostrowskiana* Regel	76.7	77.7	1.9	4*X*	Chu & Ily Mnts	
D5407	*T. ostrowskiana* Regel	77.1			4*X*	ex J. de Groot,HB78120-0	
D5400	*T. ostrowskiana* Regel	77.6			4*X*	HB93194-1	
84.3	*T. ostrowskiana* Regel	77.7			4*X*	Bulb Research Centre, Lisse	
84.1	*T. ostrowskiana* Regel	79.4			4*X*	Bulb Research Centre, Lisse	
sgl	*T. tetraphylla* Baker	39.0	40.1	1.5	2*X*	W. China	
sgl	*T. tetraphylla* Baker	41.1			2*X*	Ketman Range, ZO. Kazakhstan	
cb31	*T. tetraphylla* Baker	77.7	79.9	1.4	4*X*	ex C. Breed	
84.2	*T. tetraphylla* Baker	78.5			4*X*	CPRO 93151	
	T. tetraphylla Baker	78.8			4*X*	Kyrgyzstan	
84.7	*T. tetraphylla* Baker	79.6			4*X*	CPRO 93149	
17642	*T. tetraphylla* Baker	80.4			4*X*	Ene of Kordai 1,800 m, Kazak.	
4.1	*T. tetraphylla* Baker	80.6			4*X*	Bulb Research Centre, Lisse	As *T. altaica*

Table 1 continued

Genus *Tulipa* L. (*Liliaceae*)

Coll. no.		2*C* DNA (pg)	Average	SD	Ploidy[b]	Origin	Received as/ cultivar
D 5099	*T. tetraphylla* Baker	81.0			4*X*	HB 87136	As *T.* sp.
4.2	*T. tetraphylla* Baker	82.5			4*X*	Bulb Research Centre, Lisse	As *T. altaica*
Section *Multiflorae* (Raamsd.) Zonn.							
81.1	*T. subpraestans* Vved.	46.8	45.7	1.2	2*X*	Bulb Research Centre, Lisse	
cb05	*T. subpraestans* Vved.	44.6			2*X*	ex C. Breed	
41.2	*T. heweri* Raamsd.	46.9	47.7	1.2	2*X*	Bulb Research Centre, Lisse	Short form
2lim26	*T. heweri* Raamsd.	47.6			2*X*	Hortus Bulborum, Limmen	
41.1	*T. heweri* Raamsd.	47.9			2*X*	Bulb Research Centre, Lisse	Long form
cb09	*T. heweri* Raamsd.	48.3			2*X*	ex C. Breed	
2lim33	*T. praestans* Hoog	48.8	50.1	0.6	2*X*	Hortus Bulborum, Limmen	‘Princess Red Sun’
2lim32	*T. praestans* Hoog	49.1			2*X*	Hortus Bulborum, Limmen	‘Princess Shogon’
69.2	*T. praestans* Hoog	49.7			2*X*	Bulb Research Centre, Lisse	‘Tubergen’s var’
CB68	*T. praestans* Hoog	50.7			2*X*	Bulb Research Centre, Lisse	‘Fuselier’
69.1	*T. praestans* Hoog	51.0			2*X*	Bulb Research Centre, Lisse	‘Zwaneburg’(wild coll.)
CB67	*T. praestans* Hoog	51.0			2*X*	Bulb Research Centre, Lisse	‘Unicum’
Section *Lanatae* (Raamsd.) Zonn. comb. et stat. nov.							
CB70	*T. hoogiana* B.Fedtsch.	47.9	48.8	1.2	2*X*	ex C. Breed	
CB207	*T. hoogiana* B.Fedtsch.	48.0			2*X*	ex C. Breed	
cb15	*T. hoogiana* B.Fedtsch.	48.4			2*X*	ex C. Breed	
sg310	*T. hoogiana* B.Fedtsch.	49.3			2*X*	ex J. de Groot	
39.1	*T. hoogiana* B.Fedtsch.	50.6			2*X*	Bulb Research Centre, Lisse	
sg	*T. hoogiana* B.Fedtsch.	73.6	73.6		3*X*	ex J. de Groot	
32.1	*T.* sp.	49.7	50.8	0.9	2*X*	Bulb Research Centre, Lisse	As *T. eichleri horT.*
cb06	*T.* sp.	50.5			2*X*	ex C. Breed	As *T. eichleri horT.*
32.3	*T.* sp.	51.1			2*X*	Bulb Research Centre, Lisse	As *T. eichleri horT.*
32.2	*T.* sp.	51.3			2*X*	Bulb Research Centre, Lisse	As *T. eichleri horT.*
D5205	*T.* sp.	51.4			2*X*	ex J. de Groot	‘Clare Benedict’
cb12	*T. fosteriana* Hoog	51.2	51.9	1.0	2*X*	ex C. Breed	‘Rockery Beauty’
cb10	*T. fosteriana* Hoog	51.5			2*X*	ex C. Breed	‘Madame Lefeber’
cb11	*T. fosteriana* Hoog	51.9			2*X*	ex C. Breed	‘Cantata’
99.1	*T. fosteriana* Hoog	51.9			2*X*	Bulb Research Centre, Lisse	‘Mrs. Dagnia’
D 5004a	*T. fosteriana* Hoog	52.0			2*X*	Seravschan, Uzbekistan	
cb13	*T. fosteriana* Hoog	53.2			2*X*	ex C. Breed	
sg224	*T. affinis* Botschantz.	52.4	52.5	1.3	2*X*	ex J. de Groot	
3.1	*T. affinis* Botschantz.	52.6			2*X*	Bulb Research Centre, Lisse	
50.1	*T. lanata* Regel	52.1	52.5	0.4	2*X*	CPRO 65369, ex v Tubergen	
sg220	*T. lanata* Regel	51.9			2*X*	ex J. de Groot	
Lim19	*T. lanata* Regel	53.4			2*X*	Hortus Bulborum, Limmen	
50.2	*T. lanata* Regel	78.9	78.9	0.1	3*X*	No. 1256	
89.4	*T. tubergeniana* Hoog	52.4	53.5	1.1	2*X*	Bulb Research Centre, Lisse	‘Splendens’
cb03	*T. tubergeniana* Hoog	52.5			2*X*	ex C. Breed	As ***T. ingens***[a]
89.1	*T. tubergeniana* Hoog	53.9			2*X*	CPRO 65391, ex v Tubergen	
43.1	*T. tubergeniana* Hoog	54.0			2*X*	Bulb Research Centre, Lisse	As ***T. ingens***[a]
sg106	*T. tubergeniana* Hoog	54.0			2*X*	Baisun, Uzbekistan	
89.3	*T. tubergeniana* Hoog	54.1			2*X*	Bulb Research Centre, Lisse	
D 5055a	*T. carinata* Vved.	53.9	54.2	1.2	2*X*	Sangardak Valley, Uzbekistan	

Table 1 continued

Genus *Tulipa L.* (*Liliaceae*)

Coll. no.		2*C* DNA (pg)	Average	SD	Ploidy[b]	Origin	Received as/ cultivar
BZ	*T. carinata* Vved.	54.5			2*X*	Sangardak Valley, Uzbekistan	
Section *Vinistriatae* (Raamsd.) Zonn.							
cb75	*T. micheliana* Hoog	47.4	48.0	0.8	2*X*	ex C. Breed	
sg302	*T. micheliana* Hoog	48.2			2*X*	ex J. de Groot	
D 5114	*T. micheliana* Hoog	48.7			2*X*	Kopet Dagh, Cambridge B03	
sg226	*T. micheliana* Hoog	49.2			2*X*	ex J. de Groot	
sg	*T. micheliana* Hoog	47.4			2*X*	Kopet Dagh, Iran	
sg	*T. micheliana* Hoog	47.3			2*X*	Kopet Dagh, Iran	
93.1	*T. vvedenskyi* Botschantz.	50.2	51.4	1.7	2*X*	Bulb Research Centre, Lisse	
93.3	*T. vvedenskyi* Botschantz.	50.4			2*X*	Bulb Research Centre, Lisse	
8.1	*T. vvedenskyi* Botschantz.	50.8			2*X*	Bulb Research Centre, Lisse	
93.4	*T. vvedenskyi* Botschantz.	51.0			2*X*	CPRO 81139	
93.2	*T. vvedenskyi* Botschantz.	51.3			2*X*	CPRO large form	
93.5	*T. vvedenskyi* Botschantz.	51.4			2*X*	Bulb Research Centre, Lisse	
093.7?	*T. vvedenskyi* Botschantz.	51.5			2*X*	Bulb Research Centre, Lisse	
cb02	*T. vvedenskyi* Botschantz.	51.7			2*X*	ex C. Breed	
cb20	*T. vvedenskyi* Botschantz.	51.8			2*X*	ex C. Breed	
93.8	*T. vvedenskyi* Botschantz.	51.9			2*X*	Bulb Research Centre, Lisse	
CB63	*T. vvedenskyi* Botschantz.	52.4			2*X*	ex Potterton & Martin	'Hanka'
D5113	*T. vvedenskyi* Botschantz.	52.7			2*X*	Karakorum Mtns, Tadjikistan	
	T. alberti Regel	51.4	52.4	1.6	2*X*	Kabchagal, Kazakhstan	
D5323a	*T. alberti* Regel	52.3			2*X*	Kara-Tau, Kazakhstan	
D5323a	*T. alberti* Regel	52.3			2*X*	Kara-Tau, Kazakhstan	
	T. alberti Regel	52.5			2*X*	Kabchagal, Kazakhstan	
BZ07	*T. alberti* Regel	53.3			2*X*	Kabchagal, Kazakhstan	
56.1	*T. mogoltavica* Popov & Vved.	51.4	51.6	1.5	2*X*	Mogoltau, Tadjikistan	
	T. mogoltavica Popov & Vved.	51.7			2*X*	Mogoltau, Tadjikistan	
cb01	*T. greigii* Regel	52.2	53.4	1.0	2*X*	ex C. Breed	
cb19	*T. greigii* Regel	53.4			2*X*	Dzambul desert	
	T. greigii Regel	53.5			2*X*	Berkara Valley, Kazakhstan	
BZ7	*T. greigii* Regel	54.7			2*X*	Red Hill, Dzabagly, Kazakhstan	
D 5115	*T. butkovii* Botschantz.	53.9	53.9	0.9	2*X*	Akbulak Valley, Chimgan, Uzbek.	
Section *Spiranthera* Vved. ex Zonn. & Veldk.							
sg215	*T. berkariensis* Ruksans nom. ill.	50.7	50.8	0.2	2*X*	Kshi Kaindy, Kazakhstan	As *T. kaufmanniana* aff.
sg214	*T. berkariensis* Ruksans nom. ill.	51.1			2*X*	Ulken Kaindy, Kazakhstan	As *T. kaufmanniana* aff.
sgl	*T. berkariensis* Ruksans nom. ill.	50.7				Aksu-Djabagly Res. Kazakhstan	As *T. kaufmanniana* aff.
	T. berkariensis Ruksans nom. ill.	75.9	75.9	1.7	3*X*	Kazakhstan	As *T. kaufmanniana* aff.
	T. kaufmanniana Regel	52.2	53.2	1.4	2*X*	Tubergen selection	'Gaiety'
CB220	*T. kaufmanniana* Regel	52.7			2*X*	type in general culture	
cb64	*T. kaufmanniana* Regel	53.1			2*X*	Urun Gachsai, Uzbekistan	
CB218	*T. kaufmanniana* Regel	53.2			2*X*	type ex P. Nyssen	
sg5	*T. kaufmanniana* Regel	53.3			2*X*	ex J. de Groot	
D65318e	*T. kaufmanniana* Regel	53.6			2*X*	Urun Gachsai, Uzbekistan	
cb69	*T. kaufmanniana* Regel	54.5			2*X*	Ugan, Uzbekistan via J.Ruksans	'Ice Sticks'
87.4	*T. tschimganica* Botschantz.	52.4	53.7	0.9	2*X*	Bulb Research Centre, Lisse	Type 4

Table 1 continued

Genus *Tulipa L.* (*Liliaceae*)

Coll. no.		2*C* DNA (pg)	Average	SD	Ploidy[b]	Origin	Received as/ cultivar
87.2	*T. tschimganica* Botschantz.	54.0			2*X*	Bulb Research Centre, Lisse	Type 2
87.1	*T. tschimganica* Botschantz.	54.3			2*X*	Bulb Research Centre, Lisse	Type 1
87.3	*T. tschimganica* Botschantz.	54.3			2*X*	Bulb Research Centre, Lisse	Type 3
D 5060	*T. dubia* Vved.	54.0	54.7	0.9	2*X*	Chimgan, Uzbekistan	
31.2	*T. dubia* Vved.	54.0			2*X*	Bulb Research Centre, Lisse	Type 2
cb70	*T. dubia* Vved.	54.5			2*X*	Beldersai, Uzbekistan	
31.1	*T. dubia* Vved.	55.1			2*X*	Bulb Research Centre, Lisse	Type 1
D 5059	*T. dubia* Vved.	55.9			2*X*	Ruksans 1999, Beldersai	
Section *Tulipanum* Reboul							
2lim40	*T. undulatifolia* Boiss.	51.2	51.2	0.5	2*X*	Hortus Bulborum, Limmen	
Aanesen	*T. undulatifolia* Boiss.	76.8	76.8	0.8	3*X*	Didyma, Peloponesus, Greece	As ***T. boeotica***[a]
Knoche	*T. cypria* Stapf ex Turill	78.8	78.8	0.8	3*X*	Akamas peninsula, Cyprus	
62.1	*T. armena* Boiss.	50.8	51.8	1.7	2*X*	Bulb Research Centre, Lisse	As *species* 2 fr Turkey
sg303	*T. armena* Boiss.	51.1			2*X*	ex J. de Groot	As *species* 1 fr Turkey
63.1	*T. armena* Boiss.	51.2			2*X*	Bulb Research Centre, Lisse	As *species* 3 fr Turkey
60.1	*T. armena* Boiss.	51.2			2*X*	Bulb Research Centre, Lisse	As *T. oculus-solis,* short
1.2	*T. armena* Boiss.	51.2			2*X*	Bulb Research Centre, Lisse	CPRO 74223
1.3	*T. armena* Boiss.	51.4			2*X*	Bulb Research Centre, Lisse	
tc60.1	*T. armena* Boiss.	52.2			2*X*	Bulb Research Centre, Lisse	As *T. agenensis*
sg221	*T. armena* Boiss.	53.3			2*X*	ex J. de Groot from Tsechie	'Excelsa'
1.1	*T. armena* Boiss.	53.9			2*X*	Bulb Research Centre, Lisse	CPRO88036
1.4	*T. armena* Boiss.	75.5	75.5	0.8	3*X*	Bulb Research Centre, Lisse	As *T. armena* ssp. *lycica*
sg110	*T. kuschkensis* Fedtsch.	53.3	53.3	0.4	2*X*	Turkmenistan	
5208c	*T. stapfii* Turill	52.3	52.7	0.6	2*X*	Kordestan, Iran	
sg	*T. stapfii* Turill	53.1				Khoshyeylag Pass, Iran	
D 5079	*T. systola* Stapf	55.1	56.1	1.1	2*X*	V.S. 2000	As ***T. stapfii***[a]
w02	*T. systola* Stapf	55.4			2*X*	Wageningen BG	
w04	*T. systola* Stapf	55.6			2*X*	Wageningen BG	
sg56	*T. systola* Stapf	55.8			2*X*	ex J. de Groot	As *T. ulophylla*
w03	*T. systola* Stapf	55.9			2*X*	Wageningen BG	
88036	*T. systola* Stapf	56.2			2*X*	Bulb Research Centre, Lisse	As *T. julia*
w07	*T. systola* Stapf	56.3			2*X*	Wageningen BG	
D5105	*T. systola* Stapf	56.5			2*X*	Erzurum, Turkey, ex BG Got.	As ***T. sintenisii***
w06	*T. systola* Stapf	56.7			2*X*	Wageningen BG	
5079	*T. systola* Stapf	56.7			2*X*	ex J. de Groot	As ***T.stapfii***[a]
w05	*T. systola* Stapf	57.2			2*X*	Wageningen BG	
sgl	*T. schmidtii* Fomin	57.9	57.9	0.9	2x	W. of Calilabad S. Azerbaijan	
D5202a	*T. julia* K. Koch	60.4	61.6	2.0	2*X*	Lebanon	As *T. aleppensis*
cb58	*T. julia* K. Koch	61.0			2*X*	ex Cambridge BG	
D 5117a	*T. julia* K. Koch	61.0			2*X*	ex Seed ES01	As *T. arm.* ssp *lycica*
101.1	*T. julia* K. Koch	61.3			2*X*	Bulb Research Centre, Lisse	As *T. stapfii*
cb61	*T. julia* K. Koch	61.5			2*X*	ex C. Breed	As *T. armena*
44.2	*T. julia* K. Koch	63.2			2*X*	Bulb Research Centre, Lisse	Long form
44.1	*T. julia* K. Koch	64.1			2*X*	BG Yerevan, Armenia	CPRO 72119-16
sg	*T. julia* K. Koch	62.4			2*X*	Mt. Arai, N.Yerevan, Armenia	
D5119	*T. praecox* Tenore	57.9	57.9	0.7	2*X*	Salda Lake,W Turkey	Seed ES01 as *T. ndulata*

Table 1 continued

Genus *Tulipa L.* (*Liliaceae*)

Coll. no.		2C DNA (pg)	Average	SD	Ploidy[b]	Origin	Received as/ cultivar
w01	*T. praecox* Tenore	87.3	88.3	0.6	$3X$	ex Wageningen BG	
sg7	*T. praecox* Tenore	87.3			$3X$	ex J. de Groot	
tc68,1	*T. praecox* Tenore	88.3			$3X$	Bulb Research Centre, Lisse	
tc60,2	*T. praecox* Tenore	88.3			$3X$	Bulb Research Centre, Lisse	As ***T. oculus-solis***[a]
2lim39	*T. praecox* Tenore	90.4			$3X$	Hortus Bulborum, Limmen	As ***T. agenensis***[a]
6.2	*T. aleppensis* Boiss. ex Regel	93.6	95.3	1.4	$3X$	CPRO 84258 ex P Visser	
2lim37	*T. aleppensis* Boiss. ex Regel	94.3			$3X$	Hortus Bulborum, Limmen	
6.1	*T. aleppensis* Boiss. ex Regel	94.8			$3X$	Bulb Research Centre, Lisse	
sg1	*T. aleppensis* Boiss. ex Regel	96.7			$3X$	ex J. de Groot	
sg7	*T. aleppensis* Boiss. ex Regel	97.3			$3X$	ex J. de Groot	
Section *Tulipa*							
JPT1	*T. suaveolens* Roth	60.2	61.7	1.7	$2X$	ex J. Tyssen	
cb63	*T. suaveolens* Roth	60.8			$2X$	ex C. Breed	As *T. schrenkii* hort.
JPT2	*T. suaveolens* Roth	60.9			$2X$	ex J. Tyssen	As *T. schrenkii* hort.
1620	*T. suaveolens* Roth	61.4			$2X$	Hortus Bulborum, Limmen	As *T. schrenkii* hort.
cb34	*T. suaveolens* Roth	62.9			$2X$	ex C. Breed	‘Duc van Tol’
w12	*T. suaveolens* Roth	64.2			$2X$	ex Wageningen BG	
BZ	*T. schrenkii* Regel	60.3	61.5	1.3	$2X$	Karalar plain, Crimea	ex J. Ruksans
BZ07	*T. schrenkii* Regel	61.7			$2X$	Korgalzhin, Tengislake, Kazak.	2. Yellow flower
BZ07	*T. schrenkii* Regel	61.7			$2X$	Korgalzhin, Tengislake, Kazak.	3. White flower
BZ07	*T. schrenkii* Regel	61.8			$2X$	Korgalzhin, Tengislake, Kazak.	1. Pink flower
76.2	*T. schrenkii* Regel	62.1			$2X$	Bulb Research Centre, Lisse	
sgl	*T. eichleri* Regel	62.7	62.7	1.8	$2X$	W. of Quba, N. Azerbaijan	
78.1	*T. sosnovskyi* Achv.& Mirz.	62.6	63.4	1.6	$2X$	Bulb Research Centre, Lisse	
lim16	*T. sosnovskyi* Achv.& Mirz.	63.9			$2X$	Hortus Bulborum, Limmen	
D5314	*T. sosnovskyi* Achv.& Mirz.	64.3			$2X$	ex J. de Groot	
cb25	*T. sosnovskyi* Achv.& Mirz.	64.5			$2X$	ex C. Breed	
sgl	*T. sosnovskyi* Achv.& Mirz.	62.1			$2X$	Meghri, Z. Armenia	
sgl	*T. sosnovskyi* Achv.& Mirz.	62.9			$2X$	Meghri, Z. Armenia	
sgl	*T. florenskyi* Woronow	64.2	64.2	0.8	$2X$	Meghri, Z. Armenia	
45.1	*T. karabachensis* Grossh.	64.0	65.6	1.6	$2X$	Caucasus	
45.2	*T. karabachensis* Grossh.	64.7			$2X$	ex Letland	
cb72	*T. karabachensis* Grossh.	65.6			$2X$	ex C. Breed	
2lim38	*T. karabachensis* Grossh.	65.6			$2X$	Hortus Bulborum, Limmen	
Lim20	*T. karabachensis* Grossh.	65.8			$2X$	Hortus Bulborum, Limmen	
D5104	*T. karabachensis* Grossh.	67.9			$2X$	ex J. de Groot	
sgl	*T. karabachensis* Grossh.	67.0			$2X$	Meghri, Z. Armenia	As ***T. confusa***[a], pink flower
sgl	*T. karabachensis* Grossh.	66.1			$2X$	Meghri, Z. Armenia	As ***T. confusa***[a], red flower
sgl	*T. karabachensis* Grossh.	65.5			$2X$	Meghri, Z. Armenia	As ***T. confusa***[a], pink flower
sgl	*T. karabachensis* Grossh.	67.8			$2X$	Meghri, Z. Armenia	As ***T. confusa***[a], pink flower
26.1	*T. karabachensis* Grossh.	65.6			$2X$	Azerbaijan	
40.2	*T. hungarica* Borbas	64.7	65.6	2.3	$2X$	CPRO 78392-2	
40.1	*T. hungarica* Borbas	64.8			$2X$	CPRO 78392-6, Budapest BG	
lim28	*T. hungarica* Borbas	65.5			$2X$	Hortus Bulborum, Limmen	

Table 1 continued

Genus *Tulipa L.* (*Liliaceae*)

Coll. no.		2*C* DNA (pg)	Average	SD	Ploidy[b]	Origin	Received as/ cultivar
40.3	*T. hungarica* Borbas	66.0			$2X$	Bulb Research Centre, Lisse	
	T. hungarica var. *urumoffii* Hayek	65.7			$2X$	ex commerce	As ***T. urumoffii***[a]
91.1	*T. hungarica* var. *urumoffii* Hayek				$2X$	Budapest BG 75102-1	As ***T. urumoffii***[a]
cb26	*T. rhodopaea* (Velen.) Velen.	67.6	68.6	2.1	$2X$	Rhodope Mntns, Bulgaria	
72.1	*T. rhodopaea* (Velen.) Velen.	68.2			$2X$	Rhodope Mntns, Bulgaria	
72.2	*T. rhodopaea* (Velen.) Velen.	68.5			$2X$	Bulb Research Centre, Lisse	
lim14	*T. rhodopaea* (Velen.) Velen.	70.0			$2X$	Rhodope Mntns, Bulgaria	
sg309	*T. gesneriana?* L.	68.6	69.2	1.2	$2X$	Kordestan SW Negel, Iran	Seed JJA02
sg233	*T. gesneriana?* L.	69.0			$2X$	Macedonia, ex BG Got.	a***s T. scardica***[a]
cb40	*T. gesneriana?* L.	69.9			$2X$	N Cauc., Piatogorsk, Krasnodar	*as T. schrenkii?*
cb18	*T. gesneriana* L.	67.3	68.7	2.0	$2X$	ex C. Breed	As ***T. viridiflora***[a]
30.1	*T. gesneriana* L.	67.9			$2X$	Bulb Research Centre, Lisse	As ***T. didieri***[a]
2.1	*T. gesneriana* L.	67.7			$2X$	Bulb Research Centre, Lisse	As ***T. acuminata***[a]
cb17	*T. gesneriana* L.	68.2			$2X$	ex C. Breed	As ***T. fulgens***[a]
cb21	*T. gesneriana* L.	68.2			$2X$	ex C. Breed	As ***T. marjolettii***[a]
2lim27	*T. gesneriana* L.	67.3			$2X$	Hortus Bulborum, Limmen	As ***T. marjolettii***[a]
66.1	*T. gesneriana* L.	68.7			$2X$	Bulb Research Centre, Lisse	As ***T. platystigma***[a]
54.1	*T. gesneriana* L.	68.8			$2X$	Bulb Research Centre, Lisse	As ***T. mauritiana***[a] 'Cindy'
cb24	*T. gesneriana* L.	69.3			$2X$	ex C. Breed	As ***T. aximensis***[a]
95	*T. gesneriana* L.	69.4			$2X$	Bulb Research Centre, Lisse	As ***T. saracenica***[a]
cb22	*T. gesneriana* L.	70.1			$2X$	ex C. Breed	As ***T. didieri***[a]
cbd27	*T. gesneriana* L.	70.1			$2X$	ex C. Breed	As ***T. passeriniana***[a]
34.1	*T. gesneriana* L.	68.8			$2X$	red flower, Grengiols, Suisse	As ***T. grengiolensis***[a]
cb23	*T. gesneriana* L.	70.4			$2X$	ex C. Breed	As ***T. grengiolensis***[a]
TC	*T. gesneriana* L.	67.7			$2X$	Yellow fl., Grengiols, Suisse	As ***T. grengiolensis***[a]
36.2	*T. gesneriana* L.	67.0			$2X$	CPRO 84266, ex W. Kooiman	As ***T. galatica***[a] Hort.
cb47	*T. gesneriana* L.	68.1			$2X$	ex P. Nyssen	As ***T. galatica***[a] Hort.
sg232	*T. gesneriana* L.	68.9			$2X$	ex J. de Groot	As ***T. galatica***[a] Hort.
36.1	*T. gesneriana* L.	69.0			$2X$	Bulb Research Centre, Lisse	As ***T. galatica***[a] Hort.
lim25	*T. gesneriana* L.	67.7			$2X$	Hortus Bulborum, Limmen	As ***T. galatica***[a] Hort.
Lieser	*T. gesneriana* L.	70.2			$2X$	L. Lieser France, bulblet	As ***T. rubidusa***[a] Lieser
Lieser	*T. gesneriana* L.	70.5			$2X$	L. Lieser France, bulblet	As ***T. sedunii***[a] Lieser
Subgenus *Eriostemons (Boiss.) Raamsd.*							
Section *Sylvestres* (Baker) Baker							
D5706	*T. patens* C.Agarth ex Schult.	54.2	55.0	1.3	$2X$	Altai, Kazakhstan	
sg201	*T. patens* C.Agarth ex Schult.	54.5			$2X$	Kamenogorsk	
BZ07	*T. patens* C.Agarth ex Schult.	54.8			$2X$	Tengis lake, Kazakhstan no 3	
BZ07	*T. patens* C.Agarth ex Schult.	55.4			$2X$	Tengis lake, Kazakhstan no 1	
sg	*T. patens* C.Agarth ex Schult.	55.4			$2X$	Kamenogorsk	
BZ07	*T. patens* C.Agarth ex Schult.	55.5			$2X$	Tengis lake, Kazakhstan no 2	
18.1	*T. biebersteiniana* Schult. f	56.1	56.7	1.4	$2X$	CPRO 73108, ex Stavropol BG	
cb51	*T. biebersteiniana* Schult. f	56.5			$2X$	ex C. Breed	
10.2	*T. biebersteiniana* Schult. f	56.7			$2X$	France	As *T. australis*

Table 1 continued

Genus *Tulipa L.* (*Liliaceae*)

Coll. no.		2*C* DNA (pg)	Average	SD	Ploidy[b]	Origin	Received as/ cultivar
CB65	*T. biebersteiniana* Schult. f	56.7			2*X*	ex C. Breed	
D 5022	*T. biebersteiniana* Schult. f	57.0			2*X*	ex J. de Groot	
82.3	*T. biebersteiniana* Schult. f	57.1			2*X*	Bulb Research Centre, Lisse	As *T. sylvestris*
102.1	*T. biebersteiniana* Schult. f	57.9			2*X*	Peloponesus, Greece	As *T. australis*
D5705a	*T. biebersteiniana* Schult. f	56.0			2*X*	Karalar Steppe	As ***T. ophiophylla***[a]
cb35	*T. hageri* Heldreich	57.7	57.7	0.7	2*X*	ex C. Breed	'Splendens'
37.3	*T. hageri* Heldreich	85.9	85.9	1.1	3*X*	Large form	
cb37	*T. orphanidea* Boiss. ex Heldr.	59.0	59.6	1.3	2*X*	ex C. Breed	As *T. sprengeri* Hort.
cb38	*T. orphanidea* Boiss. ex Heldr.	59.1			2*X*	ex C. Breed	
64.4	*T. orphanidea* Boiss. ex Heldr.	59.4			2*X*	Bulb Research Centre, Lisse	As *T. orphanidea* 'Flava'
testc.	*T. orphanidea* Boiss. ex Heldr.	59.4			2*X*	Bulb Research Centre, Lisse	As ***T. goulimyi***[a]
D5711	*T. orphanidea* Boiss. ex Heldr.	59.9			2*X*	BG Gotenburg	As ***T. goulimyi***[a]
Aanesen	*T. orphanidea* Boiss. ex Heldr.	60.7			2*X*	Kythira, Greece	As ***T. goulimyi***[a]
64.2	*T. orphanidea* Boiss. ex Heldr.	88.5	88.7	1.5	3*X*	CPRO 95192	
D5713	*T. orphanidea* Boiss. ex Heldr.	88.4			3*X*	Lesbos, Greece	As ***T. theophrasti***[a]
Aanesen	*T. orphanidea* ssp. *doerfleri* (Gand.) Zonn.	86.6			3*X*	Gious-Kambos, Crete	As ***T. doerfleri***[a]
29.2	*T. orphanidea* ssp. *doerfleri* (Gand.) Zonn.	87.2			3*X*	Mt .Kedros, Spili, Crete	As ***T. doerfleri***[a]
Aanesen	*T. orphanidea* ssp. *doerfleri* (Gand.) Zonn.	87.9			3*X*	Spili, Crete	As ***T. doerfleri***[a]
29.1	*T. orphanidea* ssp. *doerfleri* (Gand.) Zonn.	89.1			3*X*	Spili, Crete	As ***T. doerfleri***[a]
cb62	*T. orphanidea* ssp. *doerfleri* (Gand.) Zonn.	93.2			3*X*	Spili, Crete	As ***T. doerfleri***[a]
64.3	*T. orphanidea* ssp. *whittallii* Boiss. ex Heldr.	115.1	115.9	3.2	4*X*	CPRO 89109	As ***T. whittallii***[a]
94.1	*T. orphanidea* ssp. *whittallii* Boiss. ex Heldr.	116.6			4*X*	Bulb Research Centre, Lisse	As ***T. whittallii***[a]
10.1	*T. sylvestris* ssp. *australis* (Link) Pamp.	61.2	62.0	1.5	2*X*	Andorra	
10.4	*T. sylvestris* ssp. *australis* (Link) Pamp.	61.9			2*X*	CPRO 89103	
10.5	*T. sylvestris* ssp. *australis* (Link) Pamp.	62.8			2*X*	Ronda, Spain	
Aanesen	*T. sylvestris* ssp. *sylvestris* L.	89.8	90.4	1.0	3*X*	Mandal, Norway	
Aanesen	*T. sylvestris* ssp. *sylvestris* L.	89.9			3*X*	Arendal, Norway	
Aanesen	*T. sylvestris* ssp. *sylvestris* L.	91.4			3*X*	Little Torungen, Norway	
cb41	*T. sylvestris* ssp. *sylvestris* L.	118.6	120.9	3.2	4*X*	Rich flowering	
D 5133	*T. sylvestris* ssp. *sylvestris* L.	119.0			4*X*	V·S.03.	
82.1	*T. sylvestris* ssp. *sylvestris* L.	119.4			4*X*	CPRO 73143	
82.4	*T. sylvestris* ssp. *sylvestris* L.	120.7			4*X*	Tatra Mntms	*T. sylvestris* 'Tatrensis'
82.5	*T. sylvestris* ssp. *sylvestris* L.	121.0			4*X*	CPRO	
BGL	*T. sylvestris* ssp. *sylvestris* L.	122.8				Bot. Garden, Leiden	
82.2	*T. sylvestris* ssp. *sylvestris* L.	122.8			4*X*	CPRO	As *T. australis*
D 5133a	*T. sylvestris* ssp. *sylvestris* L.	123.0			4*X*	Tabriz, Iran (V.S. 04)	
cb46	*T. sprengeri* Baker	63.7	64.6	1.8	2*X*	ex C. Breed	
79.1	*T. sprengeri* Baker	64.5			2*X*	Bulb Research Centre, Lisse	

Table 1 continued

Genus *Tulipa* L. (*Liliaceae*)

Coll. no.		2*C* DNA (pg)	Average	SD	Ploidy[b]	Origin	Received as/ cultivar
Z026	*T. sprengeri* Baker	65.5			2*X*	Bulb Research Centre, Lisse	
70.1	*T. primulina* Baker	63.7	64.2	1.9	2*X*	Bulb Research Centre, Lisse	
2lim41	*T. primulina* Baker	63.7			2*X*	Hortus Bulborum, Limmen	
CB64	*T. primulina* Baker	64.4			2*X*	ex Monocot nursery	
cb71	*T. primulina* Baker	65.2			2*X*	ex C. Breed	
10.3	*T. celsiana* DC	65.6	66.0	0.4	2*X*	CPRO 75106	As *T. australis*
BZ01	*T. celsiana* DC	65.9			2*X*	Katara Pass, Greece	As *T. australis*
cb43	*T. celsiana* DC	66.2			2*X*	ex C. Breed	
70.2	*T. celsiana* DC	66.3			2*X*	CPRO 69308, Dar-UlBaider, Leb.	As *T. primulina*
Section *Biflores* A.D.Hall ex Zonn. & Veldk.							
sg9/5	*T.* sp.	48.0	48.0	0.4	2*X*	Dzjungaric Ala-Tau	
cb81	*T. tarda* Stapf	50.2	51.5	1.3	2*X*	ex van Tubergen	
cb45	*T. tarda* Stapf	50.7			2*X*	ex C. Breed	As ***T. urumiensis***[a]
	T. tarda Stapf	50.9			2*X*	ex commerce	As ***T. urumiensis***[a]
83.2	*T. tarda* Stapf	51.2			2*X*	Almaty, Kazakhstan	
cb82	*T. tarda* Stapf	51.5			2*X*	ex C. Breed	
92.2	*T. tarda* Stapf	51.5			2*X*	Bulb Research Centre, Lisse	As ***T. urumiensis***[a]
Lim22	*T. tarda* Stapf	51.9			2*X*	Hortus Bulborum, Limmen	As ***T. urumiensis***[a] 'Tity Star'
sg'08	*T. tarda* Stapf aff.	51.9			2*X*	Kyrgyzstan	As *T.* sp.
	T. tarda Stapf	52.0			2*X*	Bulb Research Centre, Lisse	As hybrid?
83.1	*T. tarda* Stapf	52.0			2*X*	Bulb Research Centre, Lisse	
83.3	*T. tarda* Stapf	52.1			2*X*	Bulb Research Centre, Lisse	Dark form
92.1	*T. tarda* Stapf	52.5			2*X*	CPRO 64177	As ***T. urumiensis***[a]
D5900	*T. turcomanica* B. Fdtsch.	76.3	76.3	1.2	**3*X***	Foothills Kopet Dagh, Turkmenistan	
sg40	*T. dasystemon* Regel	51.2	51.5	1.3	2*X*	Coll. seed: 44	
28.2	*T. dasystemon* Regel	51.4			2*X*	CPRO 97263	
D 5017b	*T. dasystemon* Regel	53.3			2*X*	Kugart valley, Kyrgyzstan	
sgl	*T. dasystemon* Regel	50.0			2*X*	Kyrgyzstan	
sgl	*T. dasystemon* Regel	99.6	99.6	1.2	4*X*	Kyrgyzstan	As *T. dasystemonoides*
103.1	*T. regelii* Elwes.	52.4	52.4	1.5	2*X*	Tamgalitas, Kazakhstan	
sg	*T.* sp. nov.	51.9	52.4	0.4	2*X*	Altai, Kazakhstan	As *T. biflora*
4.3	*T.* sp. nov.	52.3			2*X*	Altai, Kazakhstan	As *T. biflora*
D5500	*T.* sp. nov.	52.6			2*X*	Altai, Kazakhstan 2005	As *T. biflora*
D5901b	*T.* sp. nov.	52.9			2*X*	Altai, Kazakhstan 2006	As *T. biflora*
	T. neustruevae Pobed.	53.9	54.8	0.7	2*X*	ex Commerce	As *T. dasystemon*
	T. neustruevae Pobed.	54.2			2*X*	ex Commerce	As *T. dasystemon*
28.1	*T. neustruevae* Pobed.	54.2			2*X*	Bulb Research Centre, Lisse	As *T. dasystemonoides?*
cb83	*T. neustruevae* Pobed.	54.4			2*X*	ex C. Breed	As *T. dasystemon*
D 5018	*T. neustruevae* Pobed.	54.7			2*X*	ex J. de Groot	
59.1	*T. neustruevae* Pobed.	55.0			2*X*	Bulb Research Centre, Lisse	
cb84	*T. neustruevae* Pobed.	55.4			2*X*	ex C. Breed	
D 5018a	*T. neustruevae* Pobed.	55.6			2*X*	ex J. de Groot	
D 5017	*T. neustruevae* Pobed.	56.0			2*X*	ex J. de Groot	As *T. dasystemon*
cb42	*T. biflora* Pall.	53.4	55.7	1.8	2*X*	ex C. Breed	
20.2	*T. biflora* Pall.	54.4			2*X*	Bulb Research Centre, Lisse	'Yellow Form'

Table 1 continued

Genus *Tulipa L.* (*Liliaceae*)

Coll. no.		2*C* DNA (pg)	Average	SD	Ploidy[b]	Origin	Received as/ cultivar
D 5013	*T. biflora* Pall.	54.5			2*X*	ex J. Ruksans	'Starlight'
D 5134	*T. biflora* Pall.	55.2			2*X*	Kara-Tau Mntns	As *T. orthopoda*
cb59	*T. biflora* Pall.	55.6			2*X*	ex C. Breed	As ***T. binutans***[a]
20.1	*T. biflora* Pall.	56.1			2*X*	Bulb Research Centre, Lisse	
D 5014	*T. biflora* Pall.	56.2			2*X*	ex J. de Groot	
BZ07	*T. biflora* Pall.	56.3			2*X*	Kabchagal, Kazakhstan	As ***T. talievii***[a]
D5914	*T. biflora* Pall.	57.3			2*X*	Kyzyl-Kul, Kazakhstan	As ***T. busheana***[a]
D5914a	*T. biflora* Pall.	57.6			2*X*	Kabchagal, Kazakhstan	As ***T. talievii***[a]
cb32	*T. biflora* Pall.	109.1	110.0		4*X*	ex C. Breed	
D 5011f	*T. biflora* Pall.	110.8			4*X*	Chimgan, Kazakhstan	
D 5012	*T. turkestanica* Regel	55.7	56.2	0.5	2*X*	Aman-Kutan, Uzbekistan	Coll. J. Ruksans
cb67/Tc	*T. turkestanica* Regel	56.3			2*X*	Dshizak, Nuratau mnts	Coll. J. Ruksans
cb55	*T. turkestanica* Regel	56.6			2*X*	Cambridge BG	As ***T. bifloriformis***[a]
sg	*T. turkestanica* Regel	112.4	113.4		4*X*	ex J. de Groot	Sprout brown, hairy
sg	*T. turkestanica* Regel	114.3			4*X*	ex J. de Groot	Sprout brown, hairy
D5901b	*T. polychroma* Stapf	54.5	56.7	2.0	2*X*	Yugoslavia, CPRO 79103	As ***T. mariannae***[a]
sgl	*T. polychroma* Stapf	55.3			2*X*	Vayak, M2, Armenia	
cb30	*T. polychroma* Stapf	55.6			2*X*	ex C. Breed	
67.1	*T. polychroma* Stapf	57.5			2*X*	ex C. Breed	
67.4	*T. polychroma* Stapf	58.7			2*X*	CPRO 91106	
sg	*T. polychroma* Stapf	58.8			2*X*	RRW00123	As *T. biflora*
67.3	*T. polychroma* Stapf	84.4	84.4	2.1	3*X*	CPRO 95201	
77.2	*T. sogdiana* Bunge	57.2	57.4	1.4	2*X*	CPRO 95200	
w08	*T. sogdiana* Bunge	57.5			2*X*	ex Wageningen BG	
sg39	*T. dasystemoniodes* Vved.	57.3	57.7	1.3	2*X*	Kyrgyzstan	sp. 43, flower white
D 5013a	*T. dasystemoniodes* Vved.	57.7			2*X*	Zaamin Reserve, Uzbekistan	
D 5111	*T. dasystemoniodes* Vved.	58.0			2*X*	ex J. Ruksans 02./03	
D 5088	*T. orithyioides* Vved.	58.3	58.3	1.7	2*X*	ex J. de Groot	
D 5086a	*T. orithyioides* Vved.	87.1	87.1		3*X*	Tajikistan	
sg28	*T. orthopoda* Vved.	58.5	59.3	1.4	2*X*	Kujuk Pass, Kazakhstan	
BZ07	*T. orthopoda* Vved.	60.1			2*X*	Kujuk Pass, Kazakhstan	
D5905	*T. binutans* Vved.	59.3	59.4	1.5	2*X*	Muyun Kum desert, Kazakhstan	
BZ07	*T. binutans* Vved.	59.4			2*X*	Dzabagly, Kazakhstan	
Section *Saxatiles* (Baker) Baker							
cb74	*T. cretica* Boiss. & Heldr.	57.9	60.5	2.2	2*X*	ex C. Breed	
25.2	*T. cretica* Boiss. & Heldr.	60.8			2*X*	Ida Plateau, Crete	
25.1	*T. cretica* Boiss. & Heldr.	61.6			2*X*	CPRO76122	
25.3	*T. cretica* Boiss. & Heldr.	61.7			2*X*	Bulb Research Centre, Lisse	
74.2	*T. saxatilis* ssp. *bakeri* (Hall) Zonn.	60.7	62.7	1.3	2*X*	White Mntsn, Crete	
Aanesen	*T. saxatilis* ssp. *bakeri* (Hall) Zonn.	62.1			2*X*	W. Omalos plateau, Crete, cult land	As ***T. bakeri***[a]
17.1	*T. saxatilis* ssp. *bakeri* (Hall) Zonn.	62.3			2*X*	Bulb Research Centre, Lisse	'Lilac Wonder'
Aanesen	*T. saxatilis* ssp. *bakeri* (Hall) Zonn.	62.9			2*X*	Gious-Kambos, Spili, Crete	
cb48	*T. saxatilis* ssp. *bakeri* (Hall) Zonn.	63.2			2*X*	ex M. Salmon	As ***T. bakeri***[a]

Table 1 continued

Genus *Tulipa L.* (*Liliaceae*)

Coll. no.		2*C* DNA (pg)	Average	SD	Ploidy[b]	Origin	Received as/ cultivar
13.1	*T. saxatilis* ssp. *bakeri* (Hall) Zonn.	63.6			2*X*	Bulb Research Centre, Lisse	'Little Beauty' (× aucher.?)
Aanesen	*T. saxatilis* ssp. *bakeri* (Hall) Zonn.	63.9			2*X*	W.Omalos plateau, Crete, rocks	As ***T. bakeri***[a]
74.1	*T. saxatilis* Sieber ex Spreng.	92.8	93.1	1.7	3*X*	Bulb Research Centre, Lisse	
cb49	*T. saxatilis* Sieber ex Spreng.	93.4			3*X*	ex M. Salmon	
71.11	*T. pulchella* (Fenz ex Regel) Baker	60.3	61.7	0.7	2*X*	Bulb Research Centre, Lisse	Type 11
71.1	*T. pulchella* (Fenz ex Regel) Baker	60.4			2*X*	Bulb Research Centre, Lisse	Type 7
71.7	*T. pulchella* (Fenz ex Regel) Baker	61.2			2*X*	Bulb Research Centre, Lisse	Rose 48a
71.17	*T. pulchella* (Fenz ex Regel) Baker	61.4			2*X*	Bulb Research Centre, Lisse	'Liliput'
71.19	*T. pulchella* (Fenz ex Regel) Baker	61.7			2*X*	Bulb Research Centre, Lisse	'Pegasus' (wild coll.)
71.14	*T. pulchella* (Fenz ex Regel) Baker	61.7			2*X*	Bulb Research Centre, Lisse	Type 14
49.3	*T. pulchella* (Fenz ex Regel) Baker	61.8			2*X*	Bulb Research Centre, Lisse	As ***T. kurdica***[a]
71.13	*T. pulchella* (Fenz ex Regel) Baker	61.8			2*X*	Bulb Research Centre, Lisse	Red form
71.5	*T. pulchella* (Fenz ex Regel) Baker	62.1			2*X*	Bulb Research Centre, Lisse	Type 5
11.1	*T. pulchella* (Fenz ex Regel) Baker	62.2			2*X*	Bulb Research Centre, Lisse	'Red Cup'
49.4	*T. pulchella* (Fenz ex Regel) Baker	62.2			2*X*	IPTS	As ***T. kurdica***[a]
71.2	*T. pulchella* (Fenz ex Regel) Baker	62.6			2*X*	Bulb Research Centre, Lisse	'Zephyr' (wild coll.)
49.1	*T. pulchella* (Fenz ex Regel) Baker	62.8			2*X*	no 60	As ***T. kurdica***[a]
71.3	*T. humilis* Herb.	64.0	65.0	0.7	2*X*	Sel. J. de Winter	As ***T. pulchella***[a]
71.15	*T. humilis* Herb.	64.0			2*X*	Bulb Research Centre, Lisse	'Albocoerulea-oculata'
cb52	*T. humilis* Herb.	64.4			2*X*	ex C. Breed	As ***T. aucheriana***[a]
9.1	*T. humilis* Herb.	64.6			2*X*	Bulb Research Centre, Lisse	As ***T. aucheriana***[a]
71.2	*T. humilis* Herb.	64.8			2*X*	Bulb Research Centre, Lisse	'Magenta Queen'
71.16	*T. humilis* Herb.	65.2			2*X*	Bulb Research Centre, Lisse	'Eastern Star'
38.2	*T. humilis* Herb.	65.4			2*X*	Bulb Research Centre, Lisse	As ***T. pulchella***
71.22	*T. humilis* Herb.	65.7			2*X*	Bulb Research Centre, Lisse	As *T. violacea* hort.
71.18	*T. humilis* Herb.	65.8			2*X*	Bulb Research Centre, Lisse	'Odalisque'
71.21	*T. humilis* Herb.	66.0			2*X*	Bulb Research Centre, Lisse	'Persian Pearl'
Genus *Amana* Honda							
sg50	*A. edulis* (Miq.) Honda	114.7	114.7	4.3	4*X*	ex G. Knoche	
D 5057	*A. erythronioides*? (Baker) Tan & Hong	50.7	50.7	3.0	2*X*	Hythe Alpines 1999	As *T. edulis*

[a] Synonym

[b] Ploidy was based on published chromosome numbers and here determined genome sizes

people accept three sections here: *Biflores* A.D. Hall ex Zonn. and Veldk., *Sylvestres* (Baker) Baker (syn.: *Australes)* and *Saxatiles* (Baker) Baker. Botschantzeva (1962), based mainly on Vvedenskii (1935), divided the tulips into six sections and section *Tulipa* (as *Leiostemones*) into eight groups that only partially coincide with the sections and series of van Raamsdonk.

It is proposed here to introduce two new subgenera. This would lead to four subgenera: subgenus *Tulipa* with seven sections, subgenus *Eriostemones* Raamsd. with three sections, and subgenus *Clusianae* (Baker) Zonn. and subgenus *Orithyia* (D. Don) Baker with one section each. These four subgenera are based on strong differences in DNA 2*C* values, morphological differences (Van Raamsdonk 1992; Van Raamsdonk and De Vries 1995), molecular studies at Kew (Wilford 2006), and absence of crossability relations (van Eyk et al. 1991). The eight series of section *Eichleres* (A.D. Hall) Raamsd. showed large differences in geographic distribution (Hoog 1973) and morphology (Van Raamsdonk and De Vries 1995). Therefore they are placed here in four separate sections, *Lanatae* (Raamsd.) Zonn. with eight species from mainly the Pamir-Alay,

Table 2 All species of T*ulipa* with their nuclear DNA content and ploidy, compared with the systematics of Van Raamsdonk et al. (1997)

Subgenera, sections, and species of *Tulipa* in this article	2*C* DNA (pg)	SD	Ploidy[a]	Subgenera, sections, and species of T*ulipa* acc. to van Raamsdonk et al. (1997)
Genus *Tulipa* L.				**Genus *Tulipa***
Subgenus Clusianae (Baker) Zonn.				
Section *Clusianae* Baker				**Section *Clusianae***
T. clusiana de Candolle	32.1	1.9	2*X* /4*X*/5*X*	*T. clusiana* de Candolle
T. linifolia Regel	31.8	1.7	2*X*	*T. linifolia* Regel
T. montana Lindley	32.5	1.5	2*X*	*T. montana* Lindley
Subgenus *Orithyia* (D. Don) Baker				
Section *Orithyia* (D.Don) Vved.				
T. heterophylla (Regel) Baker	37.5	0.3	2*X*	nd
T. uniflora (L.) Besser ex Baker	38.3	0.4	2*X*	nd
T. heteropetala Ledeb.	39.1	0.6	2*X*	nd
Subgenus *Tulipa*				**Subgenus *Tulipa***
Section *Kolpakowskianae* Raamsd. ex Zonn.& Veldk.				**Section *Kolpakowskianae***
T. lemmersii Zonn., A. Peterse, J. de Groot sp. *nov.*	36.4	0.5	2*X*	nd
T. nitida Hoog	38.6	0.8	2*X*	*T. tetraphylla* ssp. *ostrowskiana* (Regel) Raamsd.
T. zenaidae Vved.	39.8	1.0	2*X*	*T. lehmanniana* Mercklin
T. tetraphylla Regel	40.1	1.2	2*X*/4*X*	*T. tetraphylla* Regel
T. iliensis Regel	41.0	0.9	2*X*	*T. altaica* Pall ex Spreng.
T. brachystemon Regel	41.0	0.9	2*X*	nd
T. kolpakowskiana Baker	41.8	1.7	2*X*/4*X*	*T. altaica* Pall ex Spreng.
T. korolkowii Regel	41.5	0.9	2*X*	*T. tetraphylla* Regel
T. borszczowii Baker	41.6	1.4	2*X*	nd
T. lehmanniana Mercklin	42.3	1.0	2*X*/3*X*	*T. lehmanniana* Mercklin
T. hissarica Popov & Vved.	42.8	1.3	2*X*	*T. hissarica* Popov & Vved.
T. anisophylla Vved.	43.3	1.2	2*X*	*T. altaica* Pall ex Spreng.
T. korshinskyi Vved.	44.0	0.7	2*X*	*T. altaica* Pall ex Spreng.
T. ferganica Vved.	44.8	1.8	2*X*	*T. altaica* Pall ex Spreng.
T. altaica Pall ex Spreng.	44.9	1.6	2*X*/4*X*	*T. altaica* Pall ex Spreng.
T. ostrowskiana Regel	77.7	1.9	4*X*	*T. tetraphylla* ssp. *ostrowskiana* (Regel) Raamsd.
Section *Multiflorae* (Raamsd.) Zonn.				**Section *Multiflorae/Glabrae***
T. subpraestans Vved.	45.7	1.2	2*X*	*T. subpraestans* Vved.
T. heweri Raamsd.	47.7	1.2	2*X*	*T. heweri* Raamsd.
T. praestans Hoog	50.6	1.0	2*X*	*T. praestans* Hoog
Section *Lanatae* (Raamsd.) Zonn. comb.et stat. nov.				**Series *Eichleres/Lanatae***
T. hoogiana B. Fedtsch.	48.8	1.2	2*X*/3*X*	*T. tubergiana* Hoog
T. sp.	50.8	0.9	2*X*	*T. eichleri horT.*
T. fosteriana Hoog	51.9	1.0	2*X*	*T. fosteriana* Hoog
T. lanata Hoog	52.5	0.4	2*X*/3*X*	*T. lanata* Hoog
T. affinis Botschantz.	52.5	1.3	2*X*	nd
T. tubergeniana Hoog	53.5	1.1	2*X*	*T. tubergeniana* Hoog
T. tubergeniana Hoog				*T. ingens* Hoog
T. carinata Vved.	54.2	1.2	2*X*	nd
Section *Vinistriatae* (Raamsd.) Zonn.				**Series *Vinistriatae/Spiranthera/Undulatae***
T. micheliana Hoog	48.0	0.8	2*X*	*T. eichleri* var. *micheliana* (Hoog) Raamsd.
T. vvedenskyi Botschantz.	51.4	1.7	2*X*	*T. albertii* Regel
T. mogoltavica Popov & Vved.	51.6	1.5	2*X*	*T. greigii* Regel
T. alberti Regel	52.4	1.6	2*X*	*T. albertii* Regel
T. butkovii Botschantz.	53.9	1.8	2*X*	*T. albertii* Regel

Table 2 continued

Subgenera, sections, and species of *Tulipa* in this article	2*C* DNA (pg)	SD	Ploidy[a]	Subgenera, sections, and species of T*ulipa* acc. to van Raamsdonk et al. (1997)
T. greigii Regel	53.4	1.0	2*X*	*T. greigii* Regel
Section *Spiranthera* Vved. ex Zonn. & Veldk.				
T. berkariensis Ruksans nom ill.	50.9	0.3	2*X*	*T. kaufmanniana* Regel
T. kaufmanniana Regel	53.2	1.4	2*X*/3*X*	*T. kaufmanniana* Regel
T. tschimganica Botschantz.	53.7	0.9	2*X*	T. *tschimganica* Botschantz.
T. dubia Vved.	54.7	0.9	2*X*	T. *dubia* Vved.
Section *Tulipanum* Reboul				**Section *Tulipanum/Aureofasciatae***
T. undulatifolia Boiss.	51.2		2*X*/3*X*	*nom. nud.*
T. armena Boiss.	51.8	1.7	2*X*/3*X*	*T. armena* Boiss.
T stapfii Turill	52.7	0.6	2*X*	*T. julia* K. Koch
T. kuschkensis B.Fedtsch.	53.3	0.4	2*X*	*T. kuschkensis* B.Fedtsch.
T. systola Stapf	56.3	1.1	2*X*	*T. systola* Stapf
T. schmidtii Fomin	57.9		2*X*	nd
T. julia K. Koch	61.6	2.0	2*X*	*T. julia* K. Koch
T. cypria Stapf ex Turill	78.8	0.8	3*X*	nd
T. praecox Tenore	88.3	0.6	2*X*/3*X*	*T. praecox* Tenore
T. praecox Tenore				*T. agenensis* DC.
T. aleppensis Boiss.	95.3	1.3	3*X*	*T. aleppensis* Boiss.
Section *Tulipa*				**Section *Tulipa/Luteo-apiculatae***
T. schrenkii Regel	61.5	1.3	2*X*	*T. suaveolens* Roth
T. suaveolens Roth	61.7	1.7	2*X*	*T. suaveolens* Roth
T. eichleri Regel	62.7		2*X*	nd
T. sosnovskyi Akhv.& Mirz.	63.4	1.6	2*X*	*T. sosnovskyi* Akhv.& Mirz.
T. florenskyi Woronow	64.2		2*X*	nd
T. karabachensis Grossh.	65.6	1.6	2*X*	*T. suaveolens* Roth
T. hungarica Borbas	65.6	2.3	2*X*	*T. hungarica* Borbas
T. rhodopaea (Velen.) Velen.	68.6	2.1	2*X*	*T. hungarica* ssp. *rhodopaea* (Velen.) Raamsd.
T. gesneriana L.	68.6	1.2	2*X*	*T. gesneriana* L.
T. gesneriana L.			2*X*	*T. didieri* Jord.
Subgenus *Eriostemones* (Boiss.) Raamsd.				**Subgenus *Eriostemones***
Section *Sylvestres* Baker				**Section *Australes***
T. patens C.Agardh ex Schult&Schult. f	55.0	1.3	2*X*	*T. biebersteiniana* Schult. f
T. biebersteiniana Schult. f	56.7	1.4	2*X*	*T. biebersteiniana* Schult. f
T. hageri Heldreich	57.7	nd	2*X*/3*X*	*T. hageri* Heldreich
T. orphanidea Boiss. ex Heldr.	59.6	1.3	2*X*	*T. orphanidea* Boiss. ex Heldr.
T. orphanidea ssp. *doerfleri* (Gand.) Zonn.	88.7	1.5	3*X*	*T. doerfleri*
T. orphanidea ssp. *whittallii* (Dykes) Zonn.	115.9	3.2	4*X*	*T. whittallii* Dykes
T. sylvestris L.	120.9	3.2	3*X*/4*X*	*T. sylvestris* L.
T. sylvestris ssp. *australis* (Link) Pamp.	62.0	1.5	2*X*	*T. australis* Link
T. primulina Baker	64.2	1.9	2*X*	*T. primulina* Baker
T. sprengeri Baker	64.6	1.8	2*X*	nd
T. celsiana DC	66.0	0.4	2*X*	*T. australis* Link
Section *Biflores* A.D.Hall ex Zonn. & Veldk.				**Section *Biflores***
T. sp. *nov*. from Dzjungaric Ala-Tau	48.0	0.4	2*X*	nd
T. tarda Stapf	51.5	1.3	2*X*	*T. tarda* Stapf
T. dasystemon Regel	51.5	1.3	2*X*	*T. dasystemon* Regel
T. regelii Elwes.	52.4	1.5	2*X*	nd
T. sp. nov. from Altai, Kazakhstan	52.4	0.4	3*X*	nd

Table 2 continued

Subgenera, sections, and species of *Tulipa* in this article	2*C* DNA (pg)	SD	Ploidy[a]	Subgenera, sections, and species of *Tulipa* acc. to van Raamsdonk et al. (1997)
T. neustruevae Pobed.	54.8	0.7	2*X*	*T. neustruevae* Pobed.
T. biflora Pallas	55.7	1.8	2*X*/4*X*	*T. biflora* Pallas
T. turkestanica Regel	56.2	0.5	2*X*/4*X*	*T. turkestanica* (Regel) Regel
T. polychroma Stapf	57.0	2.0	2*X*/3*X*	*T. polychroma* Stapf
T. sogdiana Bunge	57.4	1.4	2*X*	*T. sogdiana* Bunge
T. dasystemonoides Vved.	57.7	1.3	2*X*	*T. dasystemon* Regel
T. orithyioides Vved.	58.3	1.7	2*X*	*T. orithyioides* Vved.
T. orthopoda Vved.	59.3	1.4	2*X*	nd
T. binutans Vved.	59.4	1.5	2*X*	*T. sogdiana* Bunge
T. turcomanica B.Fedtsch.	76.3	1.2	3*X*	nd
Section *Saxatiles* (Baker) Baker				**Section *Saxatiles***
T. cretica Boiss. &Heldr.	60.5	2.2	2*X*	nd
T. saxatilis A.D.Hall	93.1	1.7	3*X*	*T. saxatilis* A.D.Hall
T. saxatilis ssp. *bakeri* (Hall) Zonn.	62.7	1.3	2*X*	*T. bakeri* A.D.Hall
T. pulchella (Fenz ex Regel) Baker	61.7	0.7	2*X*	*T. pulchella* (Fenz.ex Regel) Baker
T. humilis Herb.	65.0	0.7	2*X*	*T. humilis* Herb.
T. humilis Herb.			2*X*	*T. aucheriana* Baker
Genus *Amana* Honda				
A. edulis (Miq.) Honda	114.7	4.3	4*X*	nd
A. erythronioides (Baker) Tan & Hong	50.7	3.0	2*X*	nd

[a] Ploidy was based on published chromosome numbers and here determined genome sizes

nd Not determined

Vinistriatae (Raamsd.) Zonn. from mainly the Tien Shan with six species, section *Spiranthera* Vved. ex Zonn. and Veldk. comb. nov. with four species and *Multiflorae* (Raamsd.) Zonn. comb. nov. with three species (Table 2). *Tulipa armena* Boiss. from the Caucasus and surroundings is added to section *Tulipanum* Reboul. Crosses between these four subgenera, to the extent they have been tried, have never been successful (Van Raamsdonk and De Vries 1995).

This scheme with four subgenera and 12 sections has the attraction of simplicity and does not suggest any higher order relationship. The latter can better wait until the species have been sequenced. Details of the new nomenclature for the infrageneric taxa are in development (Veldkamp and Zonneveld, submitted). The genus *Amana* Honda (syn: *Tulipa*) is considered to be a separate genus as molecular sequence data have shown that even the mainly American genus *Erythronium* L. is closer to *Tulipa* than *Amana* (Rudall et al. 2000). All species are grouped by increasing DNA 2*C* value (Table 1) into sections, and some species are moved from one section to another. Notes on the sections discussed below follow this classification. A low intraspecific variation is found in most cases. The interspecific variation shows that genome size in diploid *Tulipa* ranges from 32 to 69 pg (Tables 1, 2).

Genus *Tulipa* L.

Subgenus *Clusianae* (Baker) Zonn., **comb. nov**. Lectotype: *T. clusiana* DC. (Veldkamp and Zonneveld, submitted).

Section *Clusianae* Baker: *T. clusiana* DC., *T. linifolia* Regel, *T. montana* Lindl., *T* . *maximowiczii* Regel (not seen).

Subgenus *Clusianae* is distinguished from the remaining tulips by its low amount of DNA—32 pg instead of 36–69 pg for the other tulips (Table 1). Moreover, meiosis takes place at the start of spring in March in contrast to other species of section *Tulipa* where it occurs in the period September–November (Darlington, *fide* Hall 1940). Also DNA studies at Kew (Wilford 2006) have shown that the three species are clearly separated from the rest of *Tulipa*. All three species have a near identical DNA content, dissimilar to any other species, suggesting that they are closely related. Twelve accessions were grouped under *T. clusiana* (syn: *T. aitchisonii* A.D. Hall, *T. stellata* Hook., *T. chrysantha* Boiss.), 11 under *T. linifolia* Regel (syn: *T. batalinii* Regel and *T. montana* Hort. yellow form), and 5 accessions under *T. montana* Lindl. (syn: *T. wilsoniana* Hoog). The true *T. maximowiczii* Regel was not available for study as it could not be maintained in culture

(W. Lemmers, personal observation). It is morphologically similar to *T. linifolia* but has upright leaves, acuminate tepals and at the base of the tepals, a small blue-black spot flanked by a white to cream edge. There is, moreover, a striking difference in karyotypes as it is the only species with $2n = 22$ (Botschantzeva 1962). The plants in culture under *T. maximowiczii* turned out to be *T. linifolia*. According to Botschantzeva (1962), *T. wilsoniana* differs both morphologically and in typical features of its karyotype from *T. linifolia*. *Tulipa wilsoniana* grows in the Kopet Dagh, Kazhakstan, and only red flowered forms are present. The yellow *T. batalini* is considered by A.D. Hall (1940) to be a form of *T. montana* but according to Van Raamsdonk and De Vries (1995), it is a form of *T. linifolia*. As both have the same amount of nuclear DNA, it was impossible to discriminate them on that account. In the Elburz Mountains, Iran, both yellow and red forms of *T. linifolia* occur, often in mixed colonies in roughly equal numbers (Hewer 1974). The opinion of Van Raamsdonk and De Vries (1995) is followed here, and *T. batalinii* and the yellow form of *T. montana* Hort. are treated as *T. linifolia*. *T. linifolia* differs from *T. montana* by its more numerous (7–9), more linear leaves, crowded at the base, and they have a low crossibility (Van Raamsdonk and De Vries 1995). Several forms of *T. linifolia* were in culture in the Netherlands but only the one that provided the largest number of new bulbs each year has survived (W. Lemmers, personal communication).

The references to *T. montana* [often described as var. *julia* (K. Koch) Baker] in Turkey, Lebanon, and Syria should be referred to *T. julia* K. Koch or *T. systola* Stapf, both distinguished by having a substantially higher amount of nuclear DNA.

Six of the *T. clusiana* accessions had a cultivar name but were indistinguishable in DNA 2*C* value from authentic *T. clusiana.* Van Raamsdonk and De Vries (1995) report that crosses between the three species of subgenus *Clusianae* can be successful. Diploid *T. clusiana* has been referred to f. *cashmeriana* (A.D. Hall) Raamsd. and tetraploids to f. *diniae* Raamsd. All triploids of *T. clusiana* found were cultivars, supposedly from crossing diploids and tetraploids. Subgenus *Clusianae* can be found from Kashmir, northern Pakistan, and northern Afghanistan to northwestern Iran (Dasgupta and Deb 1985). A pentaploid form can be found naturalized from Turkey to Spain. It is very uniform and could constitute a single clone. Its stoloniferous habit could be an adaptation to cultivated fields, similar to that found in some other species. A *T. clusiana* that was received as *T. stellata* is—with 41 pg—probably an aneuploid as was earlier reported by Hall (1940).

Tulipa* subgenus *Orithyia (D. Don) Baker. Lectotype: *Tulipa uniflora* (L.) Besser ex Baker

Section *Orithyia* (D. Don) Vved.: *T. heterophylla* (Regel) Baker, *T. heteropetala* Ledeb., *T. uniflora* (L.) Besser ex Baker.

Next to *T. clusiana* with 32 pg, the species of this section have the lowest amount of nuclear DNA ranging from 38 to 39 pg (Table 1).

Species of the subgenus *Orithyia* are mainly confined to Siberia, northwestern China, and adjacent Kazakhstan. The stigma of most tulip species “sits” on the ovary with no discernable style. The species of subgenus *Orithyia* are characterized by a style nearly as long as the ovary and bulb tunics that are usually naked on the inside (Vvedenskii 1935). These three species have small, yellow flowers. Moreover, they have a DNA 2*C* value of only 38–39 pg and are found at the eastern/northern border of the tulip area, suggesting an isolated position. *Tulipa uniflora* from northern Kazakhstan and adjacent countries has rounded tepal tops and has a hanging bud. *Tulipa heteropetala* from the same area has pointed tepals, anthers with a small black tip, and a style protruding clearly above the anthers. The flowers of *T. heterophylla* from southern Kazakhstan are held in a more or less horizontal position when flowering. It is found growing together with *T. dasystemon* (Regel) Regel (Lemmers and de Groot, personal communication). Molecular studies at Kew suggest they are rather deviating from subgenus *Tulipa* (Wilford 2006). Therefore, they are placed anew in a separate subgenus. *Tulipa sinkiangensis* Z.M. Mao and *T. thianshanica* Regel, which likely belong to this subgenus, were not available for study.

Tulipa* subgenus *Tulipa

Section *Kolpakowkianae*, Raamsd. *ex* Zonn. and Veldk., **sect. nov.** Type: *Tulipa kolpakowskiana* Regel. (*T. altaica* Pall. ex Spreng., *T. anisophila* Vved., *T. brachystemon* Regel, *T. ferganica* Vved., *T. hissarica* Popov & Vved., *T. iliensis* Regel, *T. kopalkowskiana* Regel, *T. korolkowii* Regel, *T. korshinskyi* Vved., *T. lehmanniana* Merckl., *T. lemmersii* Zonn., A. Peters & J. de Groot, *T. nitida* Hoog, *T. ostrowskiana* Regel, *T. tetraphylla* Regel).

After subgenus *Clusianae* with 32 pg and subgenus *Orithyia* with 38 pg, the species of this section have the lowest amount of nuclear DNA ranging from 36 to 45 pg (Table 1). This fits with the results of Van Raamsdonk and De Vries (1995) who found less than 2% heterochromatin in section *Kopalkowskiana*. This contrasts with sections *Tulipanum* and *Tulipa* were more than 20% heterochromatin was found and where accordingly more than 60 pg was measured here. Also Newton (1927) and Blakey and Vosa (1962) found that the chromosome size of *T. kopalkowskiana* was in between subgenus *Clusianae* and the other *Tulipae*. Species of this section can be divided into two groups (J. de Groot, personal communication), those that are multiflowered, with yellow flowers and hairy scapes: *T. iliensis*, *T. ferganica*, *T. anisophylla*, and

T. tetraphylla (*T. tetraphylla* glabrous). The others are single-flowered with red or yellow flowers and have glabrous scapes. Exceptions are *T. korolkowii*, which has only red (pink) flowers and *T. hissarica* which only has yellow flowers. Hall states that *T. lehmanniana* has affinity to *T. korolkowii* and the latter to *T. ostrowskiana*, and Van Raamsdonk and De Vries (1995) also place it in synonymy with *T. ostrowskiana*. However having seen them in the wild in Kazakhstan in April 2007, there is no doubt that they are different species. The pink form of *T. korolkowii*, described as *T. rosea* Vved., is considered conspecific as f. *rosea*. This is based on my observation of an occasional red form amidst pink *T. rosea* in the wild. *Tulipa kopalkowskiana* is a mainly yellow-flowering lowland form; higher up, the tetraploid (amphidiploid?; Botschantzeva 1962) *T. ostrowskiana* with mixed colors is found; and stiller higher up, the mainly yellow-flowered *T. tetraphylla* (Botschantzeva 1962). The karyotype of *T. tetraphylla* is unique (Botschantzeva 1962) with some chromosome pairs more "related" to those of subgenus *Eriostemones*. Moreover, garden tulips have never been crossed successfully with species of section *Kopalkowskianae* (Van Raamsdonk and De Vries 1995).

In nature, *T. kopalkowskiana* is said to hybridize frequently with *T. tetraphylla* and *T. ostrowskiana* (Vvedenskii 1935). It is remarked that very few true intermediates are found, in most cases there seems to be introgression of some characters (flower color?) only. It could be that this observation is based on the premise that *T. kolpakowskiana* has yellow flowers, but it can also have reddish colors, obviating the need for the involvement of hybridization. Only a single triploid was found among 30 accessions of section *Kopalkowskianae*. Botschantzeva suggests that one of the parents of *T. ostrowskiana* is *T. kopalkowskiana*. Van Raamsdonk et al. (1995) have found that *T. altaica*, despite a high morphological similarity, does not cross with *T. kopalkowskiana*, considered by them to be a synonym of it. They are kept here as separate species as they clearly differ in DNA 2*C* values. *T. iliensis* with a hairy scape and the tetraploid *T. tetraphylla* with a glabrous scape both have bell-shaped and typically colored flowers: yellow with a red back upon which there is a green stripe. Based on their similar DNA 2*C* values, *T. anisophylla* could be united with *T. altaica*, but that is not executed here. *Tulipa schrenkii* was also placed in this section by Botschantzeva (1962), but its amount of nuclear DNA indicates that it should be placed in section *Tulipa* as was already done by Van Raamsdonk and De Vries (1995).

From the nearly vertical rocks in the Mashad pass, south of Dzabaghly and east of Chimkent in Kazakhstan, a tulip was found that looked most like *T. kolpakowskiana*. However, it has a 5 pg lower amount of DNA, 36 instead of 41 pg, and flowers 14 days later. As there is no other species with a similar amount of DNA, it is described below as a new species: *T. lemmersii* Zonn., A. Peterse, J. De Groot.

Tulipa* section *Lanatae (Raamsd.) Zonn. stat. et comb. nov. Type: *Tulipa lanata* Regel (including series *Lanatae* Raamsd. and series *Eichleres* A.D. Hall, p.p.). ([T. *affinis* Botschantz., *T. carinata* Vved., *T.* sp. (*T. eichleri hort.*), *T. fosteriana* Irving, *T. hoogiana* B. Fedtsch., *T. lanata* Regel, *T. tubergeniana* Hoog)].

Van Raamsdonk et al. (1997) placed the largest number of species in section *Eichleres* (A.D. Hall) Raamsd. and divided this further into eight series of which five are monotypic. These eight series are combined here into four sections. This is based on their DNA 2*C* values (Table 1) and also on the results of crossability studies of Van Raamsdonk et al. (1995, 1997) and on geographical proximity. Here series *Multiflorae* (Raamsd.) Zonn. (including series *Glabrae* Raamsd.), series *Spiranthera* Vved. ex Zonn. and Veldk. and *Vinistriatae* (Raamsd.) Zonn. (including series *Undulatae* Raamsd.) are given sectional status. Section *Lanatae* (Raamsd.) Zonn. is now confined to species from the Pamir-Alay and includes series *Lanatae sensu* Raamsd. Tulips in culture as *T. eichleri*, without locality data, clearly belong to the tulips around section *Lanatae*, including in terms of nuclear DNA content. However authentic material of *T. eichleri* from Azerbaijan turned out to have 10 pg more DNA, so fits better with the other tulips of the Caucasus in section *Tulipa*. So the section *Eichleres* is now without its type plant and is named here after its most widespread species, *T. lanata*. In *T. lanata*, diploid and triploid forms are found. The latter, confined to cultivated fields and roofs of temples, is rather uniform morphologically. Due to morphological similarities, *T. hoogiana* has been considered to represent a synonym of *T. tubergeniana* (Van Raamsdonk and De Vries 1995). Their more distant relationship is suggested on the basis of their DNA 2*C* values, strongly felted tunics [*T. tubergeniana* had only a few silky hairs in culture, but apparently is strongly felted in nature (Botschantzeva 1962)] and their different geographical distributions. Van Raamsdonk and De Vries (1995) found *T. hoogiana* also to be distinct from *T. fosteriana*. Hall (1940) remarked that *T. lanata*, *T. ingens* Hoog, *T. tubergeniana*, and *T. fosteriana* might constitute one variable species. The similarity in average DNA content for members of this section corroborates their close systematic relationships. Furse (1966) remarks that, whereas *T. micheliana* has in nature only a black blotch on the tepals, in culture this black blotch often has a yellow edge, showing again the variability of this character. *Tulipa micheliana* is included here in section *Vinistriatae.*

Tulipa* section *Multiflorae (Raamsd.) Zonn. **comb. nov**. Type: *Tulipa praestans* Hoog (*T. heweri* Raamsd., *T. praestans* Hoog, *T. subpraestans* Vved.; the latter from series *Glabrae* Raamsd.).

Tulipa praestans is nearly completely generatively isolated from the other species in section *Eichleres* Zonn. and Veldk. This separate and revised section seems justified on morphological grounds (multiflowered, tough bulb skin, absence of a basal tepal spot) but also based on the lower amount of DNA compared with the other species of section *Eichleres*.

Tulipa* section *Vinistriatae (Raamsd.) Zonn. **comb. nov**. (including series *Undulatae* Raamsd.). Type: *Tulipa greigii* Regel. (*T. affinis* Botschantz., *T. alberti* Regel, *T. butkovii* Botschantz., *T. carinata* Vved., *T. greigii* Regel, *T. micheliana* Hoog, *T. mogoltavica* Popov & Vved., *T. vvedenskyi* Botschantz.).

Tulipa greigii usually has anthocyan markings on the leaves, a character that occasionally can also be found in the largely sympatric other species of this section in the Tien Shan. *Tulipa greigii* is itself not that easy to cultivate, being sensitive to the fungus *Fusarium.* As it is fairly easy to cross with *T. kaufmanniana*, *T. alberti*, and *T. vvedenskyi*, it is mainly the hybrids that are in culture. For *T. micheliana* from the Kopet Dagh, it is reported that plants with striped and unicolored leaves grow in the same locality (M. van den Brink, personal communication). Therefore the above-mentioned species are included here in section V*inistriatae*. Botschantzeva (1962) placed, based on morphological grounds, *T. alberti*, *T. micheliana*, *T. greigii*, and *T. mogoltavica* together in the same group. The rare yellow forms of both *T. greigi* and *T. alberti* can have a crimson blotch on the inner side of the petal (also in *T. heweri* and *T. kopalkowskiana*), a character supposed to be typical of *T. tschimganica*. *Tulipa alberti* with occasionally a dark leaf with some green stripes is not synonymous with *T. vvedenskyi.* The latter has long narrow wavy leaves, whereas *T. alberti* has short broad gray leaves close to the ground. Characteristically the three inner tepals of *T. alberti* are folded to the inside and the three outer tepals are folded to the outside (W. Lemmers, personal communication).

Tulipa* section *Spiranthera Vved. ex Zonn. and Veldk. Type *T. kaufmanniana* Regel. (*T. berkariensis* Ruksans nom. invalid., *T. dubia* Vved., *T. kaufmanniana* Regel, *T. tschimganica* Botschantz.).

Tulips of section *Spiranthera* were originally named for anthers that open up from apex to bottom, becoming contorted afterwards. They usually have flowers with a yellow or white background, in contrast to section *Vinistriatae*, whose flowers are all mainly red. *Tulipa dubia* is very similar to the sympatric *T. kaufmanniana* (Ivaschenko 2005) differing mainly in its smaller overall size and less-spiraling anthers. It could be classified as a subspecies of *T. kaufmanniana. Tulipa dubia* crosses in the wild with *T. kaufmanniana* and the result of such a cross may be *T. tschimganica*. It fits with its in-between amount of nuclear DNA. Also numerous hybrids between *T. kaufmanniana* and *T. greigii* are reported from the Karshan-tau mountains (Vvedenskii 1935, in transl.). The invalid *T. berkariensis* from the Berkara valley and other places in Kazakhstan has a lower amount of nuclear DNA than authentic *T. kaufmanniana* from Uzbekistan and might present a new species.

Tulipa* section *Tulipanum Reboul. Type: *Tulipa agenensis* DC (as *T. oculus-solis* St. Amans, nom. invalid.) (*T. aleppensis* Boiss. ex Regel, *T. armena* Boiss., *T. cypria* Stapf ex Turill, *T. julia* K. Koch, *T. praecox* Ten., *T. stapfii* Turill, *T. schmidtii* Fomin, *T. systola* Stapf, *T. undulatifolia* Boiss.).

These species are reported from Turkey, northwestern Iran, northern Iraq, Lebanon, Israel, Egypt, and Syria. They are thus largely geographically isolated from the Asiatic centers of diversity. *Tulipa armena* is added to this section based on its DNA content, although it does not have a tunic thickly lined with wool as have the other species. Strongly felted bulb tunics are not only found in section *Tulipanum* but also in section *Lanatae*, including *T. lanata*, *T. hoogiana*, and *T. tubergeniana.* A thickly felted tunic, although it could be discriminatory in the field, is often strongly influenced by cultural conditions. It does not seem to offer a strong argument to attribute species or to separate sections.

Tulipa undulatifolia, with 51.2 pg, seems related to *T. armena* with 51.8 pg. *Tulipa boeotica* Boiss. & Heldr. is reported in Flora Europaea to have $2n = 24$. However a plant from Didyma, Peloponnesus, Greece, turned out to be a triploid with 76.8 pg. It differs in that respect both from *T. praecox* and *T. aleppensis* and is here suggested to be the triploid form of *T. undulatifolia.*

According to Hall (1940), *Tulipa armena* is synonymous with *T. gesneriana*. M. van den Brink (personal communication, 2008) showed me pictures of *T. armena* from Erzurum, Turkey, with pointed petals like *T. schrenkii.* Therefore it is understandable that Phillips and Rix (1981) also assumed a close relationship between *T. armena* from Erzurum and *T. schrenkii.* However, these opinions are not corroborated by DNA content values. Van Raamsdonk and De Vries (1995) placed *T. armena* in section *Tulipa*, but noted that it differed from the *Neotulipae.* Also Booy and Van Raamsdonk (1998) remark that the esterase patterns from *T. armena* are different from those of *T. gesneriana.* The results here indicate, for 10 accessions of *T. armena* (two accessions identical to the ones used by van Raamsdonk), that *T. armena* is not related to *T. gesneriana* or *T. schrenkii.* Moreover, it fits best with its 51.8 pg in section *Tulipanum* and not in section *Tulipa*, where all species have more than 62 pg of DNA.

Two accessions received as "*T. armena*" were found to have about 62 pg. These are likely wrongly diagnosed and are placed here with the sympatric *T. julia*, which also has pointed petals (M. van den Brink, personal communication, 2008), a similar yellow-edged black blotch at the base of the tepals, and the same amount of nuclear DNA. This might explain the suggestion of Hall (1940), Van Raamsdonk and De Vries (1995), and Phillips and Rix (1981) that "*T. armena*" has a close relationship with section *Tulipa*. *T. galatica* Hort. investigated here has about 68 pg. Up to 12 B-chromosomes are reported in *T. galatica* Freyn (Hall 1940). If the length of these is measured from the published karyotype of *T. galatica* (van Raamsdonk and De Vries 1995) and converted to DNA content, they could contribute 10–15% of total DNA. If subtracted this would give a value of around 60 pg similar to the "deviating" "*T. armena.*" Both "*T. armena*" and *T. galatica* Hort. can then be considered to be forms of *T. julia.* An expedition to Azerbaijan in 2009 was able to locate *T. schmidtii* Fomin described in 1909 of which Hall (1940) says that "its chromosomes are twice as long as in other species." However with its nuclear DNA content of 57.9 pg, this is not confirmed. *T. schmidtii* has some characters in common with *T. hoogiana*, such as strongly keeled leaves; a high number of leaves, up to 8 (up to 12 in *T. schmidtii*); similar red flowers with a yellow-edged black blotch (see figures in Hall 1940); and middle to late flowering period. However the nearly 10-pg difference in nuclear DNA content points to a distant relationship. Moreover *T. schmidtii* has only a small, threatened territory in Azerbaijan, whereas *T. hoogiana* is described from the Kopet Dagh on the border of Turkmenistan and Iran and even further east.

According to Marais (1984), the triploids *T. praecox* and *T. agenensis* may well be clonal selections of the same species. This is not corroborated by their DNA 2*C* values. Based on the DNA 2*C* values, *T. praecox* (88.3 pg) might be the triploid form of *T. systola* (56.1 pg), and *T. aleppensis* (95.3 pg) might be a triploid *T. juliae* (62.0 pg) [already suggested by Van Raamsdonk and De Vries (1995)]. It cannot be excluded that both are allo-triploids. The two triploid accessions *T. praecox* and *T. aleppensis*, with about 88 and 95 pg, cannot be derived from the so-called *Neotulipae* with about 69 pg as that would give around 103 pg for the triploid. Moreover, it cannot be excluded that triploids as such have a bulb tunic that is more hairy inside than their diploid counterparts.

Tulipa* section *Tulipa. Type: *Tulipa gesneriana* L. [*T. eichleri* Regel, *T. florenskyi* Woronow, *T. gesneriana* L., *T. hungarica* Borbas, *T. confusa Gabrielian*, *T. schrenkii* Regel, *T. sosnovskyi* Achv. & Mirz. (formerly of series *Luteo-apiculatae* Raamsd.), *T. suaveolens* Roth].

The description of *T. gesneriana* L. s.l., was based on cultivated material, and it is generally considered to cover the late-flowering cultivars, including the so-called *Neotulipae* from western Europe (Levier 1884; Grey-Wilson and Mathews 1980). It is characterized by large bulbs with a papery tunic with a few addressed hairs near the base and apex, by green buds, often a yellow-edged black base to the (red) tepals, and deep purple pollen. It has about 69 pg of DNA, higher then any other tulip species. "Species" such as *T. didieri* Jord., *T. grengiolensis* Thommen, *T. marjolettii* E.P. Perr. & Song., and other *Neotulipae* (Hall 1940) are easily hybridized with cultivars of *T. gesneriana* s.l. (Van Raamsdonk et al. 1995) and are considered escapes from cultivation. *Tulipa confusa* (*syn. T. karabachensis)* has yellow, red, and pink flowers, usually without a black blotch at the base of the tepals. It is from Azerbaijan and southeastern Armenia (Shikahogh reserve) and is further characterized by short and comparatively broad leaves. Sometimes it is considered to belong to *Neotulipae*, and Van Raamsdonk considers *karabachensis* to be a synonym of *T. suaveolens*, but its DNA 2*C* value of 65.6 pg contradicts both suggestions. *Tulipa sosnovskyi* is characterized by prostrate flower buds lying on the leaves or the ground, erecting only at the time of flowering. This plant from Armenia was placed in section *Eichleres* (series *Luteo-apiculatae* Raamsd.) by Van Raamsdonk and De Vries (1995). Based on its DNA 2*C* value of 63.2 pg, it is better placed in section *Tulipa. T. eichleri* Regel is considered by Marais (1984) to be a synonym of *T. undulatifolia* Boiss., both from cultivated fields. In that case, *T. undulatifolia* must have priority. However, Van Raamsdonk and De Vries (1995) consider *T. undulatifolia* to be a *nomen nudum* and accept *T. eichleri. T. undulatifolia* is described from western Turkey, whereas *T. eichleri* is described from the Caucasus and western Iran, a 3,000 km distance. Therefore, and because of the more than 10 pg difference in nuclear DNA content, they are placed in different sections. A wild counterpart of *T. gesneriana* has so far not been found (see however, B. J. M. Zonneveld, personal communication).

The early-flowering *T. suaveolens* has bulbs similar to those of *T. gesneriana*, but has hairy stems, buds that often show color, fragrant flowers with a yellow base to the tepals, and yellow pollen. It has on average 61.6 pg of DNA. I propose here that *T. suaveolens* Roth, originally described from the red and yellow cultivar *T.* 'Duc van Tol' and indistinguishable from it, be applied to the cultivated 'Duc van Tol' tulips only. The multicolored *T. schrenkii* Regel (mainly yellow in northern Kazakhstan, but also white, pink, orange, and pinkish red) has a bell-shaped flower, with a mainly yellow base to the tepals, and mainly yellow anthers. However occasionally plants with a black base and black anthers can also be found (W. Lemmers/J. de Groot, personal communication). It grows in a large area, stretching from the Crimea up to N. Kazakhstan and has the same amount of nuclear DNA as *T. suaveolens* and is likely (one of) its wild progenitor. *T. schrenkii* from Kazakhstan is reported to be highly fertile with garden tulips (Kudryavtseva in Ivaschenko 2006).

Tulipa* subgenus *Eriostemones (Boiss.) Raamsd. Lectotype: *Tulipa sylvestris* L.

Subgenus *Eriostemones* is characterized by filaments with a bundle of hairs at the basis or with at least a swollen basis. The flowers are funnel-shaped with a slight constriction just above the base. They have mainly lanceolate leaves and three short and three long anthers. Most are multiflowered caused by a branching of the apical bud, a derived character phylogenetically supported by the high amount of DNA found for the species of this section. The occasionally multiple flowers in subgenus *Tulipa*, on the contrary, grow from the axils of the leaves (Botschantzeva 1962).

Tulipa* section *Sylvestres (Baker) Baker. Type: *Tulipa sylvestris* L. (*T. biebersteiniana* Schult. and Schult. f., *T. celsiana* DC in *R. hageri* Heldreich, *T. orphanidea* Boiss. ex Heldr., *T. patens* C. Agardh *ex* Schult. and Schult. f., *T. primulina* Baker, *T. sprengeri* Baker, and *T. sylvestris* L.).

Tulipa biebersteiniana with yellow flowers is often equated with *T. sylvestris* ssp. *australis* (Link) Pamp. as they can hardly be distinguished morphologically (Vvedenskii 1935; Hall 1940). However, the difference in DNA content between *T. biebersteiniana* with 56.7 pg and *T. sylvestris* with 62.3 pg supports the conclusion that these taxa are distinct and worthy of recognition. *T. patens* with a similar geographical spread and DNA 2*C* value seems closely related to *T. biebersteiniana. Tulipa patens* grows from the Wolga area, via western Siberia and Kazakhstan to the Altai Mountains. According to Mathew (2005), it is morphologically close to *T. biflora*, but Van Raamsdonk (1992) consider it to be a form of *T. biebersteiniana.* It has white but also often pink flowers and is here considered a good species of the section *Sylvestres. Tulipa riparia* Knyasev, not measured here, is suggested to be an allotriploid form of *T. biebersteiniana. Tulipa sylvestris* is found in both diploid and tetraploid forms. The diploids are named ssp. *australis* and the tetraploids ssp. *sylvestris*. Surprisingly, three accessions from three separate locations in the south of Norway, likely arriving there due to human intervention, turned out to be triploid. They might be derived from a single clone. *Tulipa primulina* is set apart from *T. sylvestris* ssp. *australis*. *Tulipa primulina* has a different geographical distribution in the north of Africa (Algeria) and is also 3 pg higher in DNA 2*C* value. Moreover, it has the peculiar habit of opening its flowers on a sunny day at the end of the day instead of around noon as all other tulips do. *T. hageri* is here considered a good species with 57.7 pg, a bit lower in DNA 2*C* value than *T. orphanidea* with 59.6 pg. Based on cytological evidence and because it has at most 30% good pollen (*fide* Hall 1940), *T. orphanidea* could be an old hybrid of *T. hageri* × *T. sylvestris* as suggested by Hall. This fits with its in-between genome size. *Tulipa doerfleri* from Crete was earlier placed in section *Saxatilis* based on geographical arguments. However, based on DNA content and morphology, it is considered here as a triploid ssp. of *T. orphanidea. Tulipa whittallii* (Dykes) A.D. Hall is here considered a tetraploid subspecies of *T. orphanidea*. *T. sprengeri* has a similar amount of nuclear DNA as *T. sylvestris* and does not seem strongly related to the other red-flowering plants included in *T. orphanidea. Tulipa sprengeri*, found in northern Turkey and thought to be extinct in the wild, has maintained itself only in private gardens. There it is grown from seed, but it cannot be grown sustainably from bulbs. Instead of a bundle of hairs on the filaments, these are only swollen at the base in this species.

Tulipa* section *Biflores A.D. Hall ex Zonn. and Veldk**.**, **sect. nov.** Type: *Tulipa biflora* Pall. [*T. biflora* Pall., *T. binutans* Vved., *T. dasystemon* (Regel) Regel, *T. dasystemonoides* Vved., *T. orithyoides* Vved., *T.orthopoda* Vved., *T. polychroma* Stapf, *T. regelii* Krassn., *T. sogdiana* Bunge, *T. tarda* Stapf, *T. turcomanica* B. Fedtsch., *T. turkestanica* (Regel) Regel].

Species of this section look very similar. All have whitish-yellow flowers, mainly differing in the number and consequently size of the flowers on a stalk. *T. regelii* was placed in a separate section *Lophophyllon* by Vvedenskii (1935), based on its unique ridges on the leaf. However based on DNA content and flower morphology, it belongs to this section.

Tulipa tarda [syn: *T. urumiensis* Stapf, contrary to the opinion of Hall (1940) who considered *T. urumiensis* to be a form of *T. australis* Link*]* has, with 51.5 pg, the lowest amount of DNA in this section. *Tulipa neustruevae* Pobed is mainly distinguished from *T. dasystemon* by its glossy green leaves, a firmer bulb tunic, and brighter yellow flowers. They do differ slightly in DNA 2*C* value with 52.0 and 54.8 pg for *T. dasystemon* and *T. neustruevae*, respectively, so here they are kept separate. Apart from a greater amount of nuclear DNA, *T. dasystemoniodes* is mainly differentiated from *T. dasystemon* by its densely woolly inner surface of the bulb tunic (Hall 1940). It emerges from the soil in a flowering state. All accessions of *T. biflora* s.l. have a rather narrow range of variation in the nuclear DNA values and similar types of flower, mainly differing in the number and size of the flowers. These data strengthen the viewpoint, based also on morphological evidence, that *T. bifloriformis* Vved., *T. busheana* Boiss., and *T. talievii* Klokov & Zoz. cannot be upheld as species. Four accessions of "*T. biflora*" are geographically isolated in the Altai Mountains, Kazakstan. As also their DNA 2*C* value is 2 pg lower than authentic *T. biflora*, they might constitute a new species.

Tulipa sogdiana's main points of difference are its geographic isolation in the desert and the absence of hairs on the filaments, a character also occasionally found in some plants of *T. biflora*. This is not unique for this section as also *T. sprengeri* and *T. orphanidea* (Marais 1984) of section *Sylvestres* are devoid of hairs on the filaments. *Tulipa sogdiana* with a slightly higher amount of DNA is kept apart here. A triploid form of *T. polychroma* was found for the first time. Earlier Kroon and Jongerius (1986) reported on a tetraploid and even a hexaploid form of *T. polychroma*. This is so far the only hexaploid reported for the genus. Also the form of *T. turcomanica* measured here turns out to be triploid.

Tulipa* section *Saxatiles (Baker) Baker. Type: *Tulipa saxatilis* Sieber ex Spreng. [*T. cretica* Boiss. & Heldr., *T. humilis* Herb., *T. pulchella* (Fenzl ex Regel) Baker, *T. saxatilis* Sieber ex Spreng.].

Section *Saxatiles* contains four species, *T. humilis* with 65.0 pg (syn: *T. aucheriana* Baker, *T. violacea* Boiss. & Bushe), *T. pulchella* (syn: *T. kurdica* Wendelbo) with 61.7 pg, *T. saxatilis* ssp. *bakeri* A.D. Hall with 62.5 pg, and its triploid form ssp. *saxatilis* and *T. cretica* with 60.5 pg. The last three are confined to Crete. *T. bakeri* might well be a stabilized hybrid between T. *cretica* and the diploid form of *T. saxatilis*, but there are no arguments based on DNA 2*C* value. All three are closely related and have shiny green leaves.

Main flower colors in *T. humilis*/*pulchella* are very variable (*fide* Hall 1940; W. Lemmers, personal communication). In addition, two flower color types are found, those with violet/black (*T. pulchella*) and those with yellow bases (*T. humilis*) to the tepals. If the plants from this complex are arranged according to ascending genome size, most of those with a black base to the tepals are in the lower part and those with a yellow base in the higher segment (Table 1). If averaged, they show a strong difference in DNA 2*C* value with 61.7 pg for *T. pulchella* and 65.0 for *T. humilis s. str.* Therefore they are here considered separate species, and in this we follow Van Raamsdonk et al. (1997).

Genus Amana Honda

Amana Honda, Bull Biogeogr Soc Japan 6:20, 1935. *Tulipa* sect. *Amana* (Honda) Z.M. Mao, Fl Reipubl Pop Sin 14:89 (1980). Type: *Amana edulis* (Miq.) Honda [Syn: *Orithyia edulis* Miq., *Tulipa edulis* (Miq.) Baker]. [*A. edulis* (Miq.) Honda, *A. erythronioides* (Baker) Tan, *A. anhuiensis* (X.S. Shen) D.Y. Tan and D.Y. Hong, *A. kuocangshanica* D.Y. Tan and D.Y. Hong (the latter two not available for study).

Earlier this genus was considered as belonging to *Tulipa* but recent DNA investigations have shown that *Amana* is a distinct genus (Rudall et al. 2000). Two of the four species were measured. They are most likely a diploid and a tetraploid taxon, but the DNA 2*C* values indicate that the tetraploid taxon is not derived from this diploid.

In Table 2, all taxa have been arranged according to their amount of DNA. They are compared to the most recent treatment of *Tulipa* of Van Raamsdonk et al. (1992, 1995, 1997). In accordance with earlier results from the genus *Helleborus* and the genus *Narcissus* (Zonneveld 2001, 2008), in *Tulipa* DNA amounts do largely coincide with this earlier infrageneric classification.

Polyploidy

Ploidy seems to play a bigger role than envisioned in the speciation of *Tulipa*. Earlier cytological investigation of *Tulipa* have shown that most species are diploid ($x = 12$) (Kroon and Van Eijk 1977), and this is confirmed here indirectly (Table 1). In addition to the diploid species, triploidy in *T. aleppensis*, *T. clusiana*, *T. cypria*, *T. hoogiana*, *T. kopalkowskiana*, *T. lanata*, *T. orphanidea*, *T. orithyoides*, *T. praecox*, and *T. saxatilis* was confirmed. For the first time, triploids were also found in *T. kaufmanniana*, *T. polychroma*, *T. boeotica*, *T. sylvestris*, *T. turcomanica*, and *T. undulatifolia*. Moreover, tetraploidy is found in *T. biflora*, *T. dasystemon*, *T. clusiana*, *T. orphanidea*, *T. sylvestris*, *T. ostrowskiana*, *T. tetraphylla*, and *T. turkestanica*. Only in *T. clusiana* were pentaploids found, and in *T. polychroma* hexaploids are recorded (Kroon and Jongerius 1986).

Botschantzeva (1962) stated that the polyploids are concentrated in the middle and upper mountains, whereas the diploids are mainly found in the deserts and lower mountains. The exception must be the stoloniferous plants that are clearly well adapted to cultural conditions as found, e.g., in vineyards. The largest numbers of polyploids are found along the western and eastern boundaries of the distribution area of the genus.

In most cases in tulips, polyploidy is not an argument (any longer) to give a taxon a specific status as also stated by Woods and Bamford (1937). The autotetraploid (Botschantzeva 1962) *T. tetraphylla* has 79.9 pg. Also diploid forms of *T. tetraphylla* were encountered here. Botschantzeva showed that *T. ostrowskiana* is an amphidiploid, which in the wild easily crosses (back) with *T. kopalkowskiana*, one of its parents. Only one triploid, possibly resulting from such a cross, was encountered here. The other parent of *T. ostrowskiana* is unknown; however judging from its amount of DNA it must have $77.7-41.3 = 36.4$ pg. Plants from the Mashad Pass received as aff. *T. kopalkowskiana* have a unique amount of DNA with 36 pg and are described below as a new species. They could be the unknown other parent. This would be in accordance with the amount of DNA found for *T. ostrowskiana*. So the suggestion is that *T. ostrowskiana* could be the doubled offspring of *T. kopalkowskiana* with 41 pg × *T. lemmersii* Zonn., A. Peterse, & J. de Groot from Mashad Pass with 36 pg. This would give 78 pg for *T. ostrowskiana.*

The speed and cost effectiveness of measuring nuclear DNA content and its predicative accuracy makes it useful as a tool for identifying *Tulipa* species of wild origin. This has particular potential for the monitoring of trade in *Tulipa* species, as plants are usually imported as bulbs and only limited identification can be undertaken at this stage of the yearly life cycle. Before identification of a *Tulipa* species can be undertaken, any bulb has to be grown at a nursery for naming at a later date—a costly and time-consuming exercise. The nuclear DNA content of samples can be measured in a short time from bulb tissue. Although the DNA content is not unique to every taxon, many species (and some subspecies and varieties) can be identified using this method. Moreover, controversial imports, such as those in which trade is banned, can be distinguished from those for which large-scale commercial trade is allowed.

Evolutionary considerations

Botschantzeva (1962), considering mainly the tulips of the former Soviet Union and leaving out completely subgenus *Clusianae*, recognized four main centers of speciation for the genus. The first is the Tien Shan with mainly yellow or at most orange tulips. The second area is the Pamir-Alay, floristically isolated from the Tien Shan with fiercely red tulips. The third center includes the desert and steppes of Kazakhstan extending to eastern Europe. Mountainous Turkmenistan, Iran, and the Caucasus form the fourth center and are floristically connected with the Pamir-Alay. In western Siberia and western China mainly species of subgenus *Orithyia* are found.

Going from east to west, from northern Pakistan to the Balkans, there seems to be a gradual increase in nuclear DNA content (DNA 2*C* value) from 32 pg in section *Clusianae* to up to 69 pg in section *Tulipa.* There is a concomitant decrease in the time it takes for meiosis to take place, starting from a dormant bulb. Darlington (in Hall 1940) investigated this in about 20 species. Accordingly, these could be divided in three groups. In subgenus *Tulipa*, meiosis took place in autumn. (Within this subgenus, the *T. gesneriana* varieties with up to 69 pg underwent meiosis in September/early October, *T. fosteriana* with 52 pg in early November, and the *Kolpakowskianae* with about 40 pg at the end of November). Then in subgenus *Eriostemones* meiosis happens in the winter period, December to February. The latest meiosis took place was in subgenus *Clusianae* with about 32 pg at the start of spring in March (Darlington in Hall 1940).

The relationship shown above between an increase in the amount of nuclear DNA and a decrease in time to meiosis seems in disagreement with nucleotypic theory (Bennett 1972), which would predict that the more DNA the longer it takes to perform mitosis (also meiosis?). Moreover, early or late meiosis does not lead to a large difference in flowering time. *Clusianae* have rather small bulbs, but they have their leaves at an early time in spring. This might provide the necessary energy input to perform meiosis. However the *Gesnerianae* could already, early in autumn, rely on the starch storage in their much bigger bulbs. So they might have a sufficient energy level to have an early meiosis. This may have been (inadvertently) encouraged by several centuries of selection for bigger, fast-growing bulbs. It cannot be excluded that the change to a more maritime climate could also have attributed to a different timing of meiosis.

Clusianae are placed in a subgenus separate from the remaining tulips because of their low amount of DNA, 32 pg instead of 36–69 pg for the other tulips. This might indicate a primitive position within the genus. *Tulipa clusiana*, *T. linifolia*, and *T. montana* have identical amounts of DNA, so each one is, on this account, equally eligible for being the most plesiomorphic species. However, the higher variability both in ploidy and flower colors and larger geographical spreading of *T. clusiana* could point to a more ancient origin. Although it has sometimes been suggested in popular literature, tulips of the section *Clusianae* do not cross with species outside this section. A further distinctive feature is a pair of long chromosomes in which the long arm is more than thrice as long as the short arm, giving a subterminal kinetochore instead of the submedian kinetochore in other tulips (Woods and Bamford 1937). Based on these facts, *Clusianae* is regarded as a separate subgenus. Subgenus *Orithyia* is discriminated by a style that is as long as the ovary and a low amount of DNA of about 38 pg. They are small plants with yellow flowers and found mainly in the eastern part of the area, the mountains on the border of Kazakhstan and China and adjacent Siberia.

Sections

The main center of distribution for *T. clusiana* is in Kashmir, Pakistan, northern Iran, Iraq, and northern Afghanistan. The diploid form is from Chitral (northern Pakistan) and Kashmir and grows as far east as the Kumaon Hills in Uttar Pradesh at altitudes of 3,000–4,000 m but also in northern Afganistan. Probably the plants of *T. clusiana* found in southern Europe as far south as Spain are escapees from cultivation. They produce stolons and might be the pentaploid form. Diploid, tetraploids, and pentaploid forms of *T. clusiana* were measured here, and in culture, triploid forms have been created. For *T. linifolia* and *T. montana* thus far only diploid forms are found. *Tulipa linifolia* has more but narrower leaves compared with *T. montana.Tulipa linifolia* occupies a more westerly position relative to *T. clusiana*, growing in the Pamir-Alay, Afghanistan, and northern Iran. The related *T. montana* (including *T. wilsoniana*) can be considered as the most westerly extension, being mainly found in the Kopet Dagh and the Elburz mountains of northwesten Iran. In both cases an increase in DNA was not found.

If an increase in DNA 2*C* value during evolution is the character to go for, section *Kopalkowskiana* from the Tien-Shan seems to form the next step with 40–45 pg for the diploids and a concomitant increase in leaf width. The subgenus *Orithyia* with 38 pg seems to be an early split-off. From section *Kopalkowskiana*, a further increase in leaf width seems to have given rise to subgenus *Tulipa.* This was accompanied by a further increase in DNA 2*C* value to 50–69 pg and a more westerly position. On the other hand in subgenus *Eriostemones* with 52–64 pg, an increase in DNA content seems to coincide with an increase in the number of flowers and more northerly locations. In this subgenus *T. tarda* with 51.5 pg might occupy a plesiomorphic position. Both subgenus *Eriostemones* and section *Kopalkowskiana* have narrow leaves with often multiple slender stems, seemingly springing from ground level as elongated pedicels, and often drooping buds in common. Sections *Lanatae*, *Multiflorae*, *Spiranthera*, and *Vinistriatae* with 45–54 pg might be the next step in the evolution. From these, section *Tulipanum* and section *Tulipa* of subgenus *Tulipa* with 52–69 pg might have originated.

Conclusions

Flow cytometry can be considered as a quick and useful method to produce a systematic data source. Moreover, imported *Tulipa* bulbs can be used for investigation, precluding the need to grow them to maturity for identification purposes. The difference between the highest and lowest DNA contents in *Tulipa* is about 37 pg. This doubling in DNA content without changing the number of chromosomes must be the result of a vast number of genomic changes. Depending on the size of the total genome, 1 pg amounts to several thousand genes. Therefore, flow cytometry is not a one-character-based taxonomy as the largest genome contains roughly 3.4×10^{10} more base pairs than the smallest and has chromosomes that are more than twice as large. Moreover these large differences in the amount of nuclear DNA predict that the hybrids are usually sterile.

The genus *Tulipa* is here divided into four subgenera: *Clusianae*, *Tulipa*, *Eriostemones*, and *Orithyia.* The eight series of section *Eichleres sensu* Raamsd. were united in four sections: section *Lanatae*, section *Multiflorae* (including series *Glabrae*), section *Spiranthera*, and section *Vinistriatae* (including series *Undulatae*). Some species were placed in another section based on morphology but also on their genome size. These are *T. armena* from section *Tulipa* to section *Tulipanum*; *T. alberti*, *T. vvedenskyi*, and *T. micheliana* to section *Vinistriatae*, also based on the presence of dark stripes on the leaf; *T. sosnovskyi* and *T. eichleri* from section *Lanatae* to section *Tulipa.*

Van Raamsdonk reduced the number of species to 55 (excluding the not investigated subgenus *Orithyia*). I was in the fortunate position to accompany a tour in April 2007 to visit Kazakhstan, Uzbekistan, and Tajikistan to observe wild tulips. Nearly 30 species were seen, many of them in flower. This company had several people that had repeatedly visited these and other nearby countries. Moreover expeditions to northern Iran and Azerbaijan in 2009 resulted in some new material. Based on intensive discussions and the nuclear DNA content (DNA 2*C* value) as measured here, several more species are recognized. They are *T. anisophylla*, *T. boeotica* (*undulatifolia*), *T. brachystemon*, *T. butkovii*, *T. celsiana*, *T. confusa*, *T. cypria*, *T. dasystemonoides*, *T. florenskyi*, *T. orphanidea* ssp. *doerfleri*, *T. ferganica*, *T. hoogiana*, *T. iliensis*, *T. karabachensis*, *T. kolpakowskiana*, *T. korolkowii*, *T. korshinskyi*, *T. lemmersii* sp. nov., *T. micheliana*, *T. mogoltavica*, *T. nitida*, *T. orithyoides*, *T. ostrowskiana*, *T. patens*, *T. schmidtii*, *T. schrenkii*, *T. stapfii*, *T. turkestanica*, *T. undulatifolia*, *T. vvedenskyi*, *T. zenaidae.*

In synonymy went (compared to van Raamsdonk) *T. didieri* (included in *T. gesneriana*), *T. doerfleri* and *T. whitallii* (both to *T. orphanidea*) and *T. aucheriana* (to *T. humilis*).

Plants not investigated by van Raamsdonk et al. (1997) are *T. affinis*, *T. alberti* (the authentic one), *T. boeotica*, *T. borsczowii*, *T. brachystemon*, *T. cypria*, *T. confusa*, *T. cretica*, *T. doerfleri*, *T. eichleri* (the authentic one), *T. florenskyi*, *T. goulimyi*, *T. korolkowii*, *T. kurdica*, *T. lehmanniana* (the authentic one), *T. lemmersii*, *T. mariannae*, *T. patens*, *T. regelii*, *T. rosea*, *T. schmidtii*, *T. sintenisii*, *T. sprengeri*, *T. teophrasti*, *T. zenaidae* (the authentic one), and the species of subgenus *Orithyia: T. heteropetala*, *T. uniflora*, *T. heterophylla*, and the genus *Amana.*

Flow cytometry is shown here to be a very useful tool to indicate the relationship or taxonomic status of *Tulipa* taxa. Apart from the presence or absence of B-chromosomes, each species has a certain amount of nuclear DNA, which is of systematic value. Taxa clearly different in nuclear

DNA amounts are considered "good" species. This does not mean that taxa with identical DNA amounts must always be considered as constituting a single species. The nuclear DNA amounts should always be evaluated in combination with morphological data, just as any other taxonomic characters. In general, there is strong congruency between these characters and DNA 2*C* value. The data presented here for DNA content agree in most respects with the most recent classification of *Tulipa* (Van Raamsdonk et al. 1997). In some cases, the measured DNA value gives rise to questions about the perceived taxonomic relationship of certain taxa, which are identified as requiring further investigation. Flow cytometry as a taxonomic and diagnostic tool is applicable even in the case of dormant bulbs or sterile plants, and therefore has applications for conservation monitoring.

Lectotypification of the genus *Tulipa*

There are differences of opinion on the lectotypification of the genus *Tulipa*. To summarize the relevant data: Linnaeus (1753) described three species of tulips: *T. sylvestris* (p. 305), *T. gesneriana* (p. 306), and *T. breyniana* (the latter now in the genus *Baeometra*). It can be argued that *T. gesneriana* fits best his concept of the genus as only *T. gesneriana* was available in the Clifford Herbarium and probably the only species known to him when he wrote the first edition (1737). Boissier (1882) divided the tulips into two groups although he did not indicate the level: *Leiostemones* with 12 species, one of which is *T. gesneriana*, and *Eriostemones* with 13 species, one of which is *T. sylvestris*. According to the rules, Marais (1984) replaced *Leiostemones* with *Tulipa*. Britton and Brown (1913) just stated under Tulipa: typeplant *T. sylvestris*. They seemed just to have chosen the first binomial species in order. Hitchcock and Green (1929) selected *T. gesneriana* as the lectotype as "the best known of the three species." According to rule 10.5 (Code 2006) the choice of a lectotype may be superseded by a later one if it was based on a largely mechanical method of selection. As only the name is mentioned by Britton and Brown and just the first one of Linnaeus was chosen, this rule seem applicable here. The choice for *T. gesneriana* has been made already by Dasgupta and Deb (1985) and was followed by Jarvis et al. (1992, 1993). Moreover, it follows the general usage of *T. gesneriana* as the type of the genus *Tulipa* (Vvedenskii 1935; Hall 1940; Botschantzeva 1962; Marais 1984; Stork 1984; Van Raamsdonk and De Vries 1995; Wilford 2006). *T. gesneriana* is therefore accepted here as the lectotype as designated by Hitchcock and Green (1929) (see also Veldkamp and Zonneveld, submitted).

Possible new species

Based on the amount of nuclear DNA, several possible, as yet not described, species emerged. Unfortunately there is not sufficient material yet to describe them in detail and to deposit a type. They include the following:

1. *T. sp.* from the Berkara valley in the Kara-Tau mountains of Kazakhstan. Morphologically it is a smaller form of *T. kaufmanniana*. However, it is geographically isolated from *T. kaufmanniana* from Uzbekistan and has 2 pg less nuclear DNA. It also has smaller, round bulbs, emerges later, has only two leaves instead of three or four and makes stolons. It was found and described as "a dwarf relative of *T. kaufmanniana*" in a book by J. Ruksans as *T. berkariense* (*nom. invalid., anglice*). Based on these data it could be a new species.
2. *T. sp.* from Kyrgyzstan. It is a dwarf plant and looks like a plain yellow *T. tarda*. However, it has more leaves that are purplish coloured and a glabrous scape. Based on these characters and its DNA 2*C* value it could be a new species or a subspecies of *T. tarda*.
3. *T. sp.* from Altai, Kazakhstan. It is considered in the local floras (Botschantzeva 1962; Ivaschenko 2005; Pratov et al. 2006) to be *T. biflora.* However they are geographically isolated from the more westerly growing "true" *T. biflora*. Moreover they have 2 pg less DNA, so might constitute a new species.
4. *T. sp.* from Dzjungaric Ala-Tau, Kazakhstan. Based on a plant in seed, it was first considered to be *T. busheana*, but with only 48 pg of DNA instead of 52 pg, it is not that species. Again it might be an undescribed species.
5. And then there are tantalizing measurements such 45.3 pg (instead of 56.7 pg) for a large "*T. biebersteiniana*" growing in cultivated fields west of Quba, northern Azerbaijan and 51.9 pg (instead of 40.1 pg) for a "*T. tetraphylla*" from Toragyr Range, ZO Kazakhstan, that cannot be explained by ploidy.

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Appendix: New species and combinations

A detailed explanation of the infrageneric nomenclature of *Tulipa* as mentioned above can be found in Veldkamp and Zonneveld (submitted).

New species ***Tulipa lemmersii*** **Zonn.**, **A. Peterse**, **J. de Groot**, **sp. nov**.

Planta erecta, parva. *Bulbus* 2–2.5 cm diametro; *tunicae* brunneae, tenerae, intus e basi ad apicem pilis inspersae.

Caulis glaber, uniflorus, parte supraterranea c. 7 cm.

Folia 3, undulata, glabra, marginem non ciliatum, inferiore 15 × 3 cm, supra 15 × 1.5 cm.

Perianthi segmenta intus lutea, extus pallidiora coccinea suffusa, 3.5 × 2 cm, interiora obovata, exteriora ovata. *Staminum filamenta* lutea, glabra, 8 × 1.5 mm; antherae nigrae 6 mm; pollen ferrugineum vel isabellinum. *Ovarium* 10 mm longum, viride, stigma sessile lutea, 3 mm. *T. lemmersii a T. iliensis*, *T. ferganica*, *T. anisophylla*, *T. tetraphylla* caulis glaber et uniflorus differt. Ceterum speciorum sectio Kolpakowskianae floribus et rubris et luteis differt. Species diploidea, optime distinguitur a toto specie sectio Kolpakowskianae infimus DNA contento nucleorum 36 pg.

Distributia in Mashad Pass, Chimkent, Kazakhstan.

Type Herbarium Lugdunum Batavorum deposit.

Tulip erect, small. Bulb 2–2.5 cm in diam.; tunic thin, brown, at base and top lightly hairy.

Stem glabrous, single-flowered, aboveground part 7 cm, excluding flower of 3.5 cm. Leaves 3, glabrous and without cilia, lower leaf 15 × 3 cm, upper leaf 15 × 1.5 cm.

Inner tepals 3.5 × 2 cm, obovate, outer tepals ovate, flower yellow with a red hue on the outside. Filaments yellow, glabrous, 8 × 1.5 mm; anthers 6 mm, black with light brown pollen. Ovarium 1 cm high, green, with sitting yellow stigma.

T. lemmersii differs from *T. iliensis*, *T. ferganica*, *T. anisophylla*, and *T. tetraphylla* by its glabrous stem, thin tunic, and single flower. It can be distinguished from the other species of section *Kolpakowskianae* as the latter have mainly both red flowers and yellow flowers. It is a diploid species that has the lowest nuclear DNA content (36 pg) of all species of section *Kolpakowskianae*.

The tulip was collected by A. Peterse on top of the steep cliffs in the Mashad Pass. He accompanied a tulip expedition organized by W. Lemmers, the eminent connoisseur of the wild middle Asiatic tulip flora, to whom this tulip is dedicated.

Tulipa orphanidea subsp. ***doerfleri*** (Gand.) Zonn., **comb. et stat. nov.** Basionym: *Tulipa doerfleri* Gand., Fl. Cretica 102. 1916.

Note: The Flora cretica is a lithographed manuscript and is a valid publication (Art. 30.2; the work is not listed in Appendix V of the ICBN on the Opera utique oppressa for Gandoger).

Tulipa orphanidea **Boiss**. **ex Heldr. subsp**. ***whittalii*** (**A.D. Hall**) Zonn.**, comb. et stat. nov**.

≡*Tulipa whittallii* Elwes ex W.C.F. Newton. J Linn Soc Bot 47:341, 342. 1926, *nom. inval.*, *sine descr.* ≡ *Tulipa whittallii* A.D. Hall, Book Tulip.: 70. 1929; Gen. Tulipa, 64, t. 5. 1940; Bot Mag Lond 164:t. 9649. 1943. ≡ *Tulipa orphanidea* Boiss. ex Heldr. var. *whittallii* (A.D. Hall) Boiss. ex Dykes, Not. Tulip Sp.: 34, t. 8. 1930 (*sine ref.*, see note) ≡ *Tulipa orphanidea* (var.) *whittallii* A. Baker, J. Roy. Hort Soc Lond 56:242, 243. 1931 ("*orphanidesii*"). Type: Not indicated.

Dykes (1930) refers to a *T. orphanidea* " var. *whittallii*" and his plate is subtitled *T. orphanidea* var. *whittallii* Boiss. No. 1560. We suspect that "Boiss." is a printing error, for Boissier was the author of the species, but we have found no reference to any "*whittallii*" so named by him. Dykes gives no reference to previous uses of or descriptions for this variety, but the use of the epithet suggests that Art. 33.3 applies here and that Hall is the author in parentheses. We have only seen the relevant pages and surmise that 1560 may be the accession number.

Tulipa saxatilis **subsp.** ***bakeri*** (A.D. Hall) Zonn. **comb. et stat. nov.** Basionym: *T. bakeri* A.D. Hall J Bot 76: 316 (1938).

Tulipa korolkowii **forma** ***rosea*** (Vved.) Zonn. **comb. et stat. nov**.

Basionym *T. rosea* Vved. Opred Rast Sred Azii 2: 319 (1971).

Flowers are pink instead of red.

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