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Species relationships and taxonomy in *Tulipa* subg. *Tulipa* (*Liliaceae*)

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Key words: *Liliaceae, Tulipa*, subg. *Tulipa*, sects. *Clusianae, Kolpakowskianae, Tulipanum, Eichleres, Tulipa*. – Typification, morphology, numerical taxonomy, chromosome banding, biogeography, nomenclature.

Abstract: Principal component and canonical variate analyses were used to analyse the variation of 34 morphological characters measured in 98 accessions of *Tulipa* subg. *Tulipa*, formerly known as sect. *Leiostemones*. In addition 43 accessions were analysed cytogenetically by means of C-banding methods. Based on the encountered variation and on geographical distribution data 30 species in five sections were recognized, of which the synonymy is stated. Seven new series in two different sections have been designated.

The first intergeneric subdivision of the genus *Tulipa* L. was made by de Reboul (1847). This division was incomplete and consisted primarily of species known locally in southern Europe. Later Regel (1873) and Baker (1874) produced more elaborated subdivisions. The two main groups recognized by Regel (1873) were named *Eriostemones* and *Leiostemones* (Boissier 1882), and they appeared to be clearly separated from each other. This main subdivision is still in use. Some sections designated by Baker (1874) were placed in these main groups (Boissier 1882).

Sect. *Tulipa* (*Leiostemones* Boiss.) is mainly found in the primary gene center in Central Asia and comprises about 40 species. The systematic position of several species is not clear. The cultivated tulip, *T. gesneriana* L., is part of a group of closely related species in this section with crossability relationships (van Eijk & al. 1991).

The species of the other section, *Eriostemones*, migrated from the primary as well as from the secondary gene center (Caucasus) westwards into western Europe. The approximately 20 species of this section are separated into three well divided subsections (van Raamsdonk & de Vries 1992). These results are mainly based on morphological, crossability, chromosome and chemical studies (Nieuwhof & al. 1990, van Eijk & al. 1991, van Raamsdonk & de Vries 1992).

This paper deals with a study aimed at systematic enumeration of species of sect. *Tulipa* based on morphological and cytogenetical characteristics and on data of geographical distribution.

Table 1. List of *Tulipa* accessions. Accession number, chromosome number, source and origin are mentioned. Ploidy levels are indicated for each species. * Additional accessions used for completing geographic and/or cytogenetic data but not included in the morphological analyses. All taxa are indicated on the species level with the nomenclaturally correct name

Sect. *Clusianae*		
T. aitchisonii A. D. Hall, 2×		
66336		source unknown
71337	2n = 24	C. Grey-Wilson & R. F. Hewer GWH 972: S of Kabul, Afghanistan
72103	2n = 24	Gibbons S 0725 Al
73119*	2n = 24	originally from Elburz Mts, Iran
76171	2n = 24	clone of 71336: C. Grey-Wilson & T. F. Hewer GWH 935: W of Bamian, Afghanistan
76172	2n = 24	clone of 71337
77279		clone of 72129: A. Ala, Iran: Tasham valley, Iran
79152	2n = 24	clone of 75307: Jammu, Kashmir
T. clusiana DC. (including f. *chrysantha*); 4×, 5×		
65152		van Eeden, Noordwijk, Netherlands; cv. Cynthia
68590	2n = 48	Thoolen, Overveen, Netherlands
70639		W. Kooiman, Enkhuizen, Netherlands
71328	2n = 60	C. Grey-Wilson & T. F. Hewer GWH 638: N of Ghazni, Afghanistan
75303	2n = 48	Jammu, Kashmir
T. montana Lindley, 2×		
70607	2n = 24	W. Kooiman, Enkhuizen, Netherlands
74428	2n = 24	originally Kopeth Dagh, Turkmenistan
78394	2n = 24	clone of 68065: Hort. Bot. Tashkent, Uzbekistan
T. linifolia Regel, 2×		
67261	2n = 24	C. G. van Tubergen, Haarlem, Netherlands
70596	2n = 24	W. Kooiman, Enkhuizen, Netherlands
73460		source unknown
T. maximowiczii Regel, 2×		
65470	2n = 24	J. G. van Eeden, Noordwijk, Netherlands
T. batalini Regel, 2×		
64181	2n = 24	C. G. van Tubergen, Haarlem, Netherlands
70597	2n = 24	W. Kooiman, Enkhuizen, Netherlands
70611	2n = 24	W. Kooiman, Enkhuizen, Netherlands
71328A	2n = 24	C. Grey-Wilson & T. F. Hewer GWH 638: No of Ghazni, Afghanistan
73116	2n = 24	originally from Elburz Mts, Iran
77282		clone of 73119: originally from Elburz Mountains, Iran
Sect. *Kolpakowskianae*		
T. altaica Pall. ex Sprengel		
82105*		Hort. Bot. Moscow, Russia: E. Kazakhstan
T. kolpakowskiana Regel, 2× (4×)		
68596	2n = 24, 48	Thoolen, Overveen, Netherlands
74228*	2n = 24	W. Kooiman, Enkhuizen, Netherlands
T. iliensis Regel, 2×		
74226	2n = 24	W. Kooiman, Enkhuizen, Netherlands
T. anisophylla Vvedensky, 2×		
73458*		(received as *T. korshinskyi*)
76333*	2n = 24	Hort. Bot. Dushanbe, Tadzhikistan: W Pamir Alai
T. ferganica Vvedensky, 2×		
74247	2n = 24	Hort. Bot. Tashkent, Uzbekistan
75116		van Tubergen, Haarlem, Netherlands
T. lehmanniana Mercklin, 2×		
77161		M. H. Hoog, Haarlem, Netherlands

Table 1 (continued)

T. zenaidae Vvedensky, 2×		
79161	2n = 24	clone of 77299: Z. M. Silina, Petersburg, Russia
T. tetraphylla Regel, 4×		
65302	2n = 48	Hort. Bot. Alma-Ata, Kazakhstan
67368	2n = 48	Hort. Bot. Petersburg, Russia
T. behmiana Regel, 4×		
84280	2n = 48	Hort. Bot. Salaspils, Lithuania
T. ostrowskiana Regel, 4×		
68055	2n = 48	Hort. Bot. Moscow, Russia
70600*	2n = 48	W. Kooiman, Enkhuizen, Netherlands
74102	2n = 48	Hort. Bot. Tashkent, Uzbekistan
78120*	2n = 48	W. Kooiman, Enkhuizen, Netherlands
Sect. *Tulipanum*		
T. oculus-solis St. Amans, 2×		
73109*	2n = 24	T. F. Hewer: Zagros, Iran
77310	2n = 24	W. Kooiman, Enkhuizen, Netherlands
84259*	2n = 24	P. Visser, St. Pancras, Netherlands; originally from Turkey
84260*	2n = 24	P. Visser, St. Pancras, Netherlands; originally from Turkey
86221		L. Schoorl, Lisse, Netherlands
T. systola Stapf, 2×		
79154	2n = 24	clone of 77105: Golestan forest, Iran
T. stapfii Turrill, 2×		
71341		Mrs A. Ala, Iran: Golestan forest near Tangehgol, Iran
76175*		clone of 71341
77270	2n = 24	clone of 71340: Mrs A. Ala, Iran: Golestan forest, Iran
81282		hybrid between *T. stapfii* (76175) and *T. praecox* (77101)
T. ulophylla Wendelbo, 2×		
71339*		Mrs A. Ala, Iran: Dashted Nuzir, Iran
76173		clone of 71339
77269		clone of 71339
T. kuschkensis B. Fedtschenko, 2×		
76167	2n = 24	clone of 71320: C. Grey-Wilson and T. F. Hewer GWH 494; N of Merat, Afghanistan
T. julia C. Koch, 2×		
68075		Hort. Bot. Tashkent, Uzbekistan
72119	2n = 24	Hort. Bot. Yerevan, Armenia: Monastery Gegard
T. aleppensis Boissier ex Regel; 2×, 3×		
84257		P. Visser, St. Pancras, Netherlands
84268	2n = 36	W. Kooiman, Enkhuizen, Netherlands
T. praecox Tenore, 3×		
67741*	2n = 36	Station Alpine, Lautaret, France: Le Chet, Maurienne valley, Savoy, France
77101	2n = 36	H. Q. Varekamp, Wageningen, Netherlands: Korçula, Croatia
83209		M. H. Hoog, Haarlem, Netherlands
Sect. *Eichleres*		
T. lanata Regel; 2×, 3×		
65369	2n = 36	C. G. van Tubergen, Haarlem, Netherlands
76332*	2n = 24	Hort. Bot. Dushanbe; originally Darvas, Turkmenistan
T. ingens Hoog, 2×		
70599		W. Kooiman, Enkhuizen, Netherlands
74429	2n = 24	M. H. Hoog, Haarlem, Netherlands: Kopeth Dagh, Turkmenistan
T. eichleri Regel, 2×		
67234	2n = 24	W. Kooiman, Enkhuizen, Netherlands
67235	2n = 24	C. G. van Tubergen, Haarlem, Netherlands; cv. Excelsa

Table 1 (continued)

T. micheliana Hoog, 2×		
78356	2n = 24	clone of 71315: C. Grey-Wilson & T. F. Hewer GWH 391: NE Iran
T. tubergeniana Hoog, 2×		
65391	2n = 24	C. G. van Tubergen, Haarlem, Netherlands
T. hoogiana Fedtschenko; 2×, 3×		
69169		C. G. van Tubergen, Haarlem, Netherlands
81107*	2n = 24	Hort. Bot. Askhabad: Kopeth Dagh, Turkmenistan
82116*	2n = 36	P. Visser, St. Pancras, Netherlands
T. fosteriana Hoog ex W. Irving, 2×		
71324A	2n = 24	C. Grey-Wilson & T. F. Hewer GWH 493: N of Merat, Afghanistan
82331		Veldhuizen, Hillegom, Netherlands; cv. Madame Lefeber
T. greigii Regel, 2×		
78122	2n = 24	M. H. Hoog, Haarlem, Netherlands: Samarkand
79163	2n = 24	clone of 77293: Z. M. Silina, Petersburg, Russia
T. mogoltavica M. Popov & Vvedensky		
78389		Z. M. Silina, Petersburg, Russia
T. alberti Regel, 2×		
68061	2n = 24	Hort. Bot. Tashkent, Uzbekistan
T. vvedenskyi Bochantzeva, 2×		
65249		Hort. Bot. Petersburg, Russia
68087*	2n = 24	Hort. Bot. Tashkent, Uzbekistan
80290	2n = 24	clone of 76124: Elliot, Ashford, Kent, UK; from Tashkent, Uzbekistan (received as *T. butkovii*
81120		L. Schoorl, Netherlands
86115		W. Kletzing, Germany: Choros, elev. 2300 meter, Pamir Alai
T. butkovii Bochantzeva, 2×		
76124	2n = 24	Hort. Bot. Tashkent, Uzbekistan
T. sosnovskyi Akhverdov & Mirzojeva, 2×		
67356		Hort. Bot. Yerevan, Armenia
72120	2n = 24	Hort. Bot. Yerevan, Armenia: Megri, Armenia
T. praestans Hoog, 2×		
70626	2n = 24	M. H. Hoog, Haarlem, Netherlands
71331		C. Grey-Wilson & T. F. Hewer GWH 709: Salang pass, N. of Kabul, Afghanistan
76115		B. Andreasen, Denmark; from Hort. Bot. Oxford, UK
77266		clone of 71331
80285		clone of 71331
T. kaufmanniana Regel, 2×		
65301	2n = 24	Hort. Bot. Alma Ata, Kazakhstan
65252		Hort. Bot. Petersburg, Russia
68014		Hort. Bot. Moscow, Russia
T. amblyophylla (Post) Feinbrun, 2×		
74111*	2n = 24	Hort. Bot. Jerusalem: Negev desert, Israel
T. tschimganica Bochantzeva, 2×		
68085	2n = 24	W. Kooiman, Enkhuizen, Netherlands
68086		Hort. Bot. Tashkent, Uzbekistan
76123*	2n = 24	Elliot, Ashford, Kent, UK
T. anadroma Bochantzeva, 2×		
78395	2n = 24	clone of 68068: Hort. Bot. Tashkent, Uzbekistan
T. dubia Vvedensky, 2×		
78386	2n = 24	clone of 77160: M. H. Hoog, Haarlem, Netherlands
80298*	2n = 24	clone of 77344: W. Tien Shan Mts
T. subpraestans Vvedensky, 2×		
68083	2n = 24	Hort. Bot. Tashkent, Uzbekistan

Table 1 (continued)

Sect. *Tulipa*		
T. armena Boiss., 2×		
74223	2n = 24	C. G. van Tubergen, Haarlem, Netherlands
T. galatica Freyn, 3×		
84266	2n = 36	W. Kooiman, Enkhuizen, Netherlands
T. hungarica Borbas, 2×		
66066	2n = 24	Hort. Bot. Sofia, Bulgaria
76181		clone of 74197: originally from Roman, Romania
T. rhodopea Velenovksy, 2×		
66078		Hort. Bot. Sofia, Bulgaria
75102		Hort. Bot. Budapest, Hungary
75108*	2n = 24	Hort. Bot. Sofia, Bulgaria
T. didieri Jordan, 2×		
68007	2n = 24	Hort. Bot. Göttingen, Germany
T. planifolia Jordan, 2×		
67737	2n = 24	Station Alpine, Lautaret, France: Villars-Clement, Maurienne valley, Savoy, France
T. marjolettii Perr. & Song., 2×		
66040		Hort. Bot. München, Germany
73120	2n = 24	C. G. van Tubergen, Haarlem, Netherlands
T. grengiolensis Thommen, 2×		
67738	2n = 24	Station Alpine, Lautaret, France: Grengiols, Wallis, Switzerland
T. suaveolens Roth, 2×		
65038	2n = 24	Hort. Bot. Rostow/Don, Russia
T. gesneriana L.		
78392		source unknown
82334		Hort. Bot. Balcik, Bulgaria

Material and methods

Material. Sect. *Tulipa* is raised to the level of subgenus for reasons as discussed in the second paragraph of the discussion. This indication will be used throughout the paper in order to reach uniform terminology. 120 accessions of 54 taxa of subg. *Tulipa* used are summarized in Table 1, together with their ploidy level and their origin. Vouchers were deposited in WAHO. Each accession consists either of a population propagated by seed or a clone, in most cases propagated from a population which was collected originally in the wild. However, not all data on locality are available. Data on geographic distribution of each species were taken from Hall (1940), Hoog (1973), and Bochantzeva (1982). Names of species considered to be closely related with the species used (Hall 1940, Bochantzeva 1982) are taken into account in order to discuss probable conspecificity.

Multivariate analyses. Of the total of 120 accessions, 98 were used for multivariate morphological analysis. The characters, all measured on the flowering date, are: flowering date, plant length, stem diameter, stem pubescent (y/n), number of leaves, width of second lowest leaf, leaf undulation (none, weak, strong), position of second lowest leaf (prostrate, intermediate, erect), leaf pubescent (y/n), leaf margin ciliate (y/n), number of flowers, length of outer tepal, width of outer tepal, width of inner tepal, blotch length at center of tepal, blotch length at margin of tepal, width of blotch border, occurrence of secondary blotch (y/n; 1989 dataset only), streak width at dorsal side of tepal, base of tepals bearded (y/n), outer side of tepal pubescent (y/n), tip of outer tepal pubescent (y/n), tip of inner tepal pubescent (y/n), anther length, filament length, filament colour contrasting with flower colour (y/n), stigma hairy (y/n).

The characters measured after lifting of the bulbs are: hairy coronet at base of bulb (y/n), hairs at lower part of bulb tunic (none, sparse, strong, woolly), hairs at middle part of bulb tunic (none, sparse, strong, woolly), hairs at upper part of bulb tunic (none, sparse, strong, woolly), bulb tufted at top (y/n), colour of bulb tunic (cream, light-, mediated-, dark-brown), number of offset bulbs.

The classes of discrete characters are mentioned in brackets. These characters have been measured on an ordinal scale. All other characters were measured on a continuous scale.

Four plants of each accession (two repeats with two plants each) were measured in 1988 [subsects. *Clusianae, Kolpakowskianae* and *Tulipanum* (*Oculus-solis*)] and in 1989 [subsects. *Eichleres*, including *Tulipanum* sensu Hall and *Spiranthera*, and *Tulipa* (*Gesnerianae*)]. The correlation coefficients between all characters were calculated. The character pairs width of outer and inner tepal, blotch length at center and margin of tepal, tepal outer side pubescent and bearded base of tepals, and hairs at middle and upper part of bulb tunic each were related empirically. It can be assumed that these characters are under the same genetic control. These relations were approved numerically by high correlation coefficients ($R > 0.8$). One character of each pair was removed from the final dataset in order to limit a too high level of redundancy and to avoid an effective character weight of 2 for an attribute. The character of each pair which showed the lowest correlation coefficient with the remaining characters was removed. Therefore the characters width of inner tepal, blotch length at margin of tepal, bearded base of tepals, and hairs at middle part of bulb tunic have been left out.

The raw data matrices containing 30 or 29 characters in the 1988 and 1989 dataset, respectively, were standardized prior to performing the final analyses. Multivariate analyses were carried out using the IRIS program package (van Raamsdonk 1988). Principal component analysis was calculated based on a correlation matrix with equal weight allocated to each character. Principal components are newly calculated, compound axes representing the maximum amount of linear variation in each direction of the multidimensional space. The relation between the characters and the principal components is expressed by means of factor loads, the objects are projected onto the newly calculated axes by means of component scores.

The species as assigned in literature are indicated by different signs in the figures of the principal component plots. The regions of newly combined species as designated in the current paper are indicated by straight polygons. In some other cases regions of single species are encircled when necessary. Cytotypes are indicated by broken lines (Fig. 3). The position of a hybrid population is indicated by a dotted line (Fig. 5).

Fifteen populations representing the variability in all five subsections were studied in both years, which makes it possible to transform the 1988 data into the 1989 ranges by means of linear regression. Most discrete characters remained untransformed. Five characters showed a too large year effect to be included in the combined dataset. Using the combined dataset with 24 characters Canonical variate analysis was carried out based on within and between groups covariance matrices. Canonical variates are new compound axes maximizing the distinguishing ability of character combinations between groups.

Chromosome banding. The method for C-banding of chromosomes was briefly as follows: root tips were sampled in colchicine, fixed in Carnoy and stored at –20 °C. A single root tip was macerated in 45% acetic acid at room temperature, squashed in acetic acid and air dried for several days. C-banding was achieved by incubation in $Ba(OH)_2$ (3 min, 60 °C) and in a 2× SSC solution, cooling from 60 °C to room temperature for several hours. After soaking the slides were stained in a 10% Gurr solution for 10 min. More details on the C-banding method were published by van Raamsdonk (1984). The sensibility of the different accessions showed fluctuation, so minor modifications of the general method per accession had to be used.

Table 2. Percentage of explained variation, and the factor loads and the ranking in parentheses of the 15 main determining characters for the first four principal components in the 1988 dataset with sects. *Clusianae, Kolpakowskianae*, and *Tulipanum*. * Characters with high factor loads exclusively in 1988

	First PC 28.07%	Second PC 10.53%	Third PC 7.90%	Fourth PC 6.53%
Stem diameter	0.743 (3)	–0.201 (20)	0.106 (22)	–0.212 (11)
Stem pubescence	0.255 (25)	0.460 (6)	–0.290 (12)	–0.543 (2)
Leaf position 2nd leaf*	0.437 (18)	0.326 (10)	0.584 (2)	0.247 (9)
Leaf undulation	–0.147 (27)	–0.359 (9)	–0.471 (3)	0.148 (16)
Leaf pubescence	0.319 (24)	0.185 (21)	0.027 (28)	–0.593 (1)
Width of second leaf	0.878 (1)	0.125 (26)	–0.081 (24)	–0.129 (18)
Number of flowers	–0.098 (28)	0.512 (4)	0.063 (27)	–0.442 (5)
Length of outer tepal	0.833 (2)	–0.134 (25)	–0.259 (13)	–0.101 (21)
Width of outer tepal	0.688 (5)	–0.369 (8)	–0.300 (11)	–0.166 (14)
Width streak on tepal*	0.472 (17)	0.089 (29)	0.605 (1)	–0.074 (26)
Blotch length at center	0.699 (4)	–0.518 (3)	0.115 (21)	0.099 (24)
Blotch length at margin*	0.560 (14)	–0.535 (2)	–0.077 (26)	–0.001 (30)
Hairs lower part tunic	0.679 (6)	–0.321 (11)	0.363 (5)	0.086 (25)
Hairs upper part tunic	–0.382 (22)	–0.631 (1)	0.330 (8)	–0.074 (26)
Number of offset bulbs	0.353 (23)	0.305 (14)	–0.322 (9)	0.473 (3)

Table 3. Percentage of explained variation, and the factor loads and the ranking in parentheses of the 16 main determining characters for the first four principal components in the 1989 dataset with sects. *Eichleres* and *Tulipa*. * Characters with high factor loads exclusively in 1989

	First PC 18.62%	Second PC 8.86%	Third PC 8.60%	Fourth PC 7.93%
Flowering date*	0.448 (11)	–0.060 (25)	–0.426 (4)	0.353 (7)
Plant length*	0.033 (26)	–0.475 (5)	–0.350 (8)	–0.214 (11)
Stem diameter	–0.837 (1)	–0.239 (11)	–0.096 (21)	–0.089 (23)
Stem pubescence	–0.507 (9)	0.066 (24)	0.534 (2)	0.133 (19)
Number of leaves*	–0.035 (25)	0.203 (14)	0.517 (3)	0.245 (10)
Leaf undulation	0.314 (17)	–0.129 (20)	–0.338 (9)	0.641 (2)
Leaf pubescence	–0.631 (4)	–0.029 (27)	0.385 (6)	0.387 (6)
Width of second leaf	–0.602 (5)	–0.623 (2)	0.141 (20)	–0.200 (12)
Number of flowers	0.027 (28)	–0.130 (19)	0.633 (1)	–0.005 (28)
Length of outer tepal	–0.815 (2)	–0.266 (9)	–0.059 (25)	–0.092 (22)
Width of outer tepal	–0.747 (3)	–0.398 (7)	–0.086 (23)	0.143 (17)
Tip outer tepal pub.*	–0.557 (7)	0.211 (12)	0.081 (24)	0.489 (3)
Tip inner tepal pub.*	–0.405 (13)	–0.011 (29)	–0.301 (13)	0.664 (1)
Blotch length at center	–0.579 (6)	0.136 (17)	–0.305 (11)	0.063 (24)
Hairs lower part tunic	–0.515 (8)	0.466 (6)	–0.392 (5)	–0.147 (16)
Hairs upper part tunic	–0.447 (12)	0.635 (1)	–0.303 (12)	–0.293 (9)
Bulb tufted at top*	–0.317 (16)	0.614 (3)	–0.149 (19)	–0.120 (21)
Number of offset bulbs	0.185 (20)	–0.503 (4)	–0.196 (17)	0.030 (26)

Results

The statistics of the independent analyses of the 1988 dataset with 30 characters and the 1989 dataset including 29 characters are presented in Tables 2 and 3, respectively. Every character having a factor load exceeding 0.5 is included in the tables. These characters are assumed to have a major influence on the direction of the respective principal component, which is referred to as a "high load". The first and second Principal Component (PC) in the 1988 analysis showed a higher percentage of explained variation than the same PC's in the 1989 analysis. Up to four PC's are needed in order to take a sufficient part (approx. 50%) of total variation into account. Of all characters only two show a high factor load in more than one PC, i.e., blotch length at center of the tepals in the 1988 analysis (Table 2) and width of second leaf in the 1989 analysis (Table 3). The first PC is predominantly determined by five characters, which range among the six highest factor loads in both years. For the second PC only the hairiness of the upper part of the bulb tunic appeared almost equally important in both years. Several characters range among those with the highest factor loads for more than one PC per year indicated by the ordinal numbers (Tables 2 and 3).

The general distributions of the specimens in the 1988 and 1989 analyses are shown in Figs. 1 and 2, respectively. Sect. *Clusianae* takes a separated region in the PCA diagrams of both years. The other sections cover regions which overlap partly. The main part of each section, however, possesses recognizable parts of the attribute space. Some species were found isolated from the main part of the respective sections, like *T. praecox* of sect. *Tulipanum* (Fig. 1) and *T. kuschkensis, T. lanata*, and *T. ingens* of sect. *Eichleres* (Fig. 2). In order to analyse the positions of all other species more in detail, quarter plots were made: Figs. 3, 4, and 5 show detailed parts of Fig. 1, whereas Figs. 6, 7, 8, and 9 show detailed parts of Fig. 2. For sect. *Eichleres* a vertical border, indicated by a broken line, with a value of –0.6 at the first PC is used to distinguish between several species groups.

For sect. *Clusianae* two main subregions were found, distinguished by second and third PC (Fig. 3): *T. linifolia, T. batalinii*, and *T. maximowiczii* with low values, and *T. aitchisonii* and *T. clusiana* with high values. *T. montana* takes an intermediate position. Yellow flowered specimens, originally identified as *T. chrysantha*, the yellow variety of *T. montana* (heavy cross signs, Fig. 3), appeared to be indistinguishable from *T. batalinii*. The typical variety of *T. clusiana* and variety *chrysantha* show a slight difference for the third PC. The fourth PC appeared to be of no importance for distinction between groups.

All species in sect. *Kolpakowskianae* were located in the same part of the variation denoted by the first PC, i.e. no differentiation along the horizontal axis is present (Fig. 4). The two main species of the section, *T. kolpakowskiana* and *T. ostrowskiana*, cover separated regions when taking the other PC's into account. *T. tetraphylla* is indistinguishable from *T. ostrowskiana. T. iliensis* and *T. ferganica*, and *T. behmiana* were found in the same regions as *T. kolpakowskiana* and *T. ostrowskiana*, respectively, except for some differences at the third PC. *T. zenaidae* and *T. lehmanniana* take an intermediate position.

Several species of sect. *Tulipanum* show well separated regions in the PCA diagrams (Fig. 5), especially *T. praecox*. On the other hand, *T. systola, T. stapfii*, and *T. ulophylla* were found in the same region.

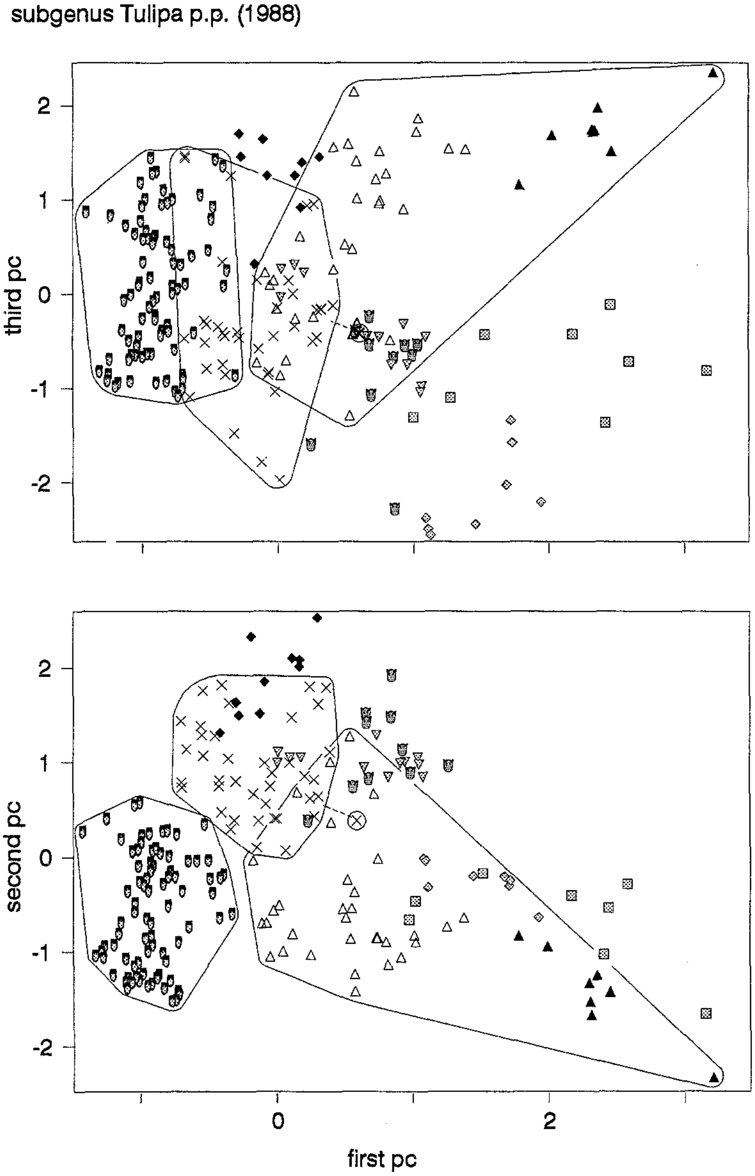

Fig. 1. Principal component plot with the first and second and first and third principal components based on an analysis of the 1988 dataset (see material and methods). Signs: small tulip flowers: sect. *Clusianae*; cross: sect. *Kolpakowskianae*; upper triangles: sect. *Tulipanum* (black upper triangles: *T. praecox*); grey-shaded rhombs and squares: sect. *Eichleres* (grey squares: *T. fosteriana*; grey rhombs: *T. vvedenskyi*; lower triangles: *T. tschimganica* and *T. kaufmanniana*; dark grey rhombs: *T. praestans*); wide tulip flowers: sect. *Tulipa*. The latter two sections were used as reference to the 1989 dataset

The species of sect. *Eichleres* with a value of less than –0.6 for the first PC are shown in Fig. 6. A group consisting of *T. tubergeniana, T. hoogiana, T. fosteriana, T. eichleri*, and *T. micheliana* can be distinguished. However, a second group with *T. greigii* and *T. mogoltavica* share the same regions for all PC's. These two groups can be distinguished by additional characters not included in the PCA dataset, like

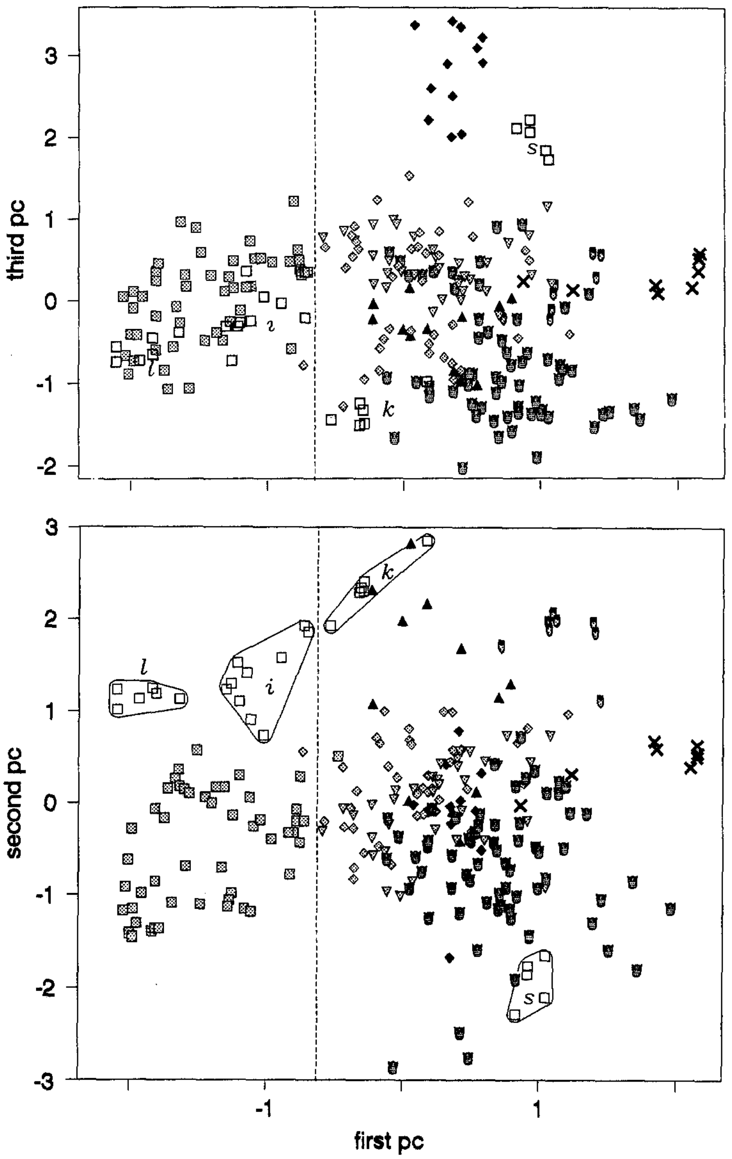
subgenus Tulipa p.p. (1989)

Fig. 2. Principal component plot with the first and second and first and third principal components based on an analysis of the 1989 dataset (see material and methods). Signs: small tulip flowers: sect. *Clusianae*; cross: sect. *Kolpakowskianae*; upper triangles: sect. *Tulipanum*; rhombs, squares and lower triangles: sect. *Eichleres* (the species indicated by their first letter are: *T. lanata, T. ingens, T. kuschkensis*, and *T. subpraestans*; grey squares: *T. eichleres* c.s. and *T. greigii* c.s.; grey rhombs: *T. vvedenskyi* c.s.; lower triangles: *T. kaufmanniana* c.s.; dark grey rhombs: *T. praestans*); wide tulip flowers: sect. *Tulipa*. The first three sections were used as reference to the 1988 dataset

anthocyanidin stripes on the upper surface of the leaves and shape and colour intensity of the blotch.

Several groups of species of sect. *Eichleres* showed values higher than –0.5 at the first PC. The species under consideration excluding those of sect. *Spiranthera* (Fig. 7) possess different areas, although overlap exists with respect to the second and fourth PC. These areas are referred to as species regions with intermediate overlapping zones. These regions allow comparison with the species of sect. *Spiranthera*, located in the same part of the total PC diagram. *T. praestans* and *T. sosnovskyi* are clearly separated. *T. vvedenskyi* shares the same region with *T. albertii* and *T. butkovii*. The species originally considered to belong to sect. *Spiranthera* are shown in Fig. 8, with an indication of the species regions as indicated in Fig. 7. These species predominantly share region 2B with *T. vvedenskyi, T. albertii, T. butkovii*, and *T. praestans*, region 3B with *T. vvedenskyi, T. albertii*, and *T. butkovii*, and region 4A with *T. sosnovskyi. T. kaufmanniana* was hardly found in the overlapping zones between regions, whereas *T. tschimganica, T. anadroma*, and *T. dubia* show similarities to specimens in adjacent regions.

In sect. *Tulipa, T. rhodopea*, and *T. hungarica* are located at the same regions in all diagrams (Fig. 9). Two specimens of *T. rhodopea* show a deviating habitus with respect to the characters as loaded on the first PC. *T. suaveolens* is located outside the region in the diagram covered by *T. rhodopea* in all but one cases. *T. armena* and the so-called Neotulipae *T. didieri, T. planifolia, T. marjolettii*, and *T. grengiolensis*, occupy two different regions with hardly any overlap in the PCA diagrams. The forms of *T. gesneriana* show considerable variation, greatly outside the regions of the species discussed.

In general the characters show high correlation coefficients ($R > 0.85$) between the years, which indicates high genetic control and reliability. Exceptions are plant length ($R = 0.705$), leaf undulation ($R = 0.786$), number of flowers ($R = 0.305$) and bulb tunic colour ($R = 0.525$). All values in the 1988 dataset of the characters measured on a continuous scale were transformed to the 1989 data ranges based on linear regression of the 15 reference populations between the years. Of these characters, only number of flowers was not excluded from the combined dataset, since the low correlation coefficient was exclusively due to the variation in *T. praestans*.

Table 4. Percentage of explained variation, and the factor loads and the relative ranking in parentheses of the eight main determining characters for the first two canonical variates in the total dataset of subg. *Tulipa*

	First CV 40.83%	Second CV 16.38%
Stem pubescence	1.858 (2)	–0.133 (14)
Leaf pubescence	1.245 (4)	1.766 (1)
Teal outside pubescent	0.837 (7)	1.364 (2)
Width streak blotch-tip	0.007 (21)	0.525 (5)
Hairy coronet at base	2.110 (1)	–0.448 (6)
Hairs lower part tunic	1.455 (3)	0.081 (15)
Hairs upper part tunic	–1.230 (5)	0.646 (3)
Bulb tufted at top	–1.162 (6)	0.637 (4)

Table 5. Global amount of heterochromatin after C-banding of *Tulipa* species. The numbers refer to the accession

Section	Heterochromatin					
	none or low		moderate		high	
Clusianae			*T. batalinii:*	64181		
				70597		
			T. linifolia:	67261		
				70596		
Kolpakowskianae	*T. kolpakowskiana:*	68596				
		74228				
	T. ostrowskiana:	68055				
		70600				
		78120				
	T. tetraphylla:	65302				
		67368				
Tulipanum						
Tulipanum	*T. agenensis:*	77310	*T. agenensis:*	84259	*T. julia:*	72119
		84260	*T. stapfii:*	71341		
			T. systola:	79154		
Aureo-fasciatae			*T. praecox:*	67741		
				77101		
Eichleres						
Lanatae	*T. ingens:*	74429				
Eichleres	*T. eichleri:*	67234				
	T. hoogiana:	82116				
	T. fosteriana:	71324A				
Vinistriatae	*T. greigii:*	78122				
Undulatae	*T. vvedenskyi:*	81120	*T. vvedenskyi:*	68087		
Multiflorae	*T. praestans:*	70626				
		77266				
Spiranthera	*T. kaufmanniana:*	65301	*T. kaufmanniana:*	65252		
	T. tschimganica:	76123		68014		
			T. amblyophylla:	74111		
Tulipa	*T. armena:*	74223	*T. hungarica:*	66066	*T. galatica:*	84266
	T. planifolia:	67737		76181		
			T. rhodopea:	75108		
			T. suaveolens:	65038		
			T. marjolettii:	66040		
				73120		
			T. grengiolensis:	67738		

The combined dataset with measurements of 1989 and those of 1988 recalculated to the 1989 data ranges and containing 24 characters, was subjected to Canonical variate analysis. The percentage of explained variation of the first and second canonical variate (CV) and the 8 characters with the highest factor loads are presented in Table 4. All most important characters showed aspects of the degree of hairiness. The characters with the highest loads on the second CV were also included in the seven most important characters of the first CV.

A CVA diagram with species groups plotted against the first and second CV is shown in Fig. 10. Sect. *Clusianae* is separated from the other sections as after PCA. *T. kuschkensis* (group 2) is located among the species of sect. *Tulipanum*. The species groups with *T. lanata* c.s., *T. eichleri* c.s., and *T. greigii* c.s., groups 1, 3, and 4, respectively, with values for the first PC lower than –0.5 are also separated from the rest of sect. *Eichleres* in Fig. 10. The pairs *T. eichleri* c.s. and *T. greigii* c.s. (groups 3 and 4), *T. armena* c.s. and the Neotulipae species (groups A and C), *T. clusiana* and *T. aitchisonii* (groups D and E), and *T. julia* and *T. aleppensis* (groups J and K) are hardly distinguishable in the CVA plot. *T. praestans* shows a tendency towards sect. *Tulipanum*.

A C-banding pattern with a high number of bands is shown in Fig. 11. The patterns appeared to be unique for each species and a relation between band positions in different species could not be established. The global amount of heterochromatin is presented in Table 5. Hardly any heterochromatin (less than 2%) was found in sects. *Kolpakowskianae* and *Eichleres*, while high levels (more than 20%) were present in some species of sect. *Tulipanum* and *Tulipa*. Accessions showing no heterochromatin were tested for several subsequent years.

Some accessions additional to those used for multivariate analysis have been identified as indicated in Table 1 and were used to complete the view on and the documentation of the species with respect to morphology, chromosome number and distribution.

Discussion

Genus typification. LINNAEUS (1753) described two species: *T. gesneriana* (subg. *Leiostemones*) and *T. sylvestris* (subg. *Eriostemones*). A third one from Ethiopia, *T. breyniana*, is now placed in the genus *Baeometra*. Presumably *T. gesneriana* fits best LINNAEUS' concept of the genus, since specimens of *T. gesneriana* were available in the CLIFFORD Herbarium, where *T. sylvestris* is not represented (LINNAEUS, 1737 a). So, *T. gesneriana* was the first species known to LINNAEUS and probably the only one at the time he wrote the first edition of Genera Plantarum (1737 b). Moreover, *T. gesneriana* is suited better to the general idea of the typical phenotype of a tulip. *T. gesneriana* is designated the type of the genus, and subg. *Leiostemones* is therefore formally named subg. *Tulipa*. This choice has been made by DASGUPTA & DEB (1985) and was followed by JARVIS & al. (1992, 1993).

Subgeneric division. Neither BOISSIER (1882) nor HALL (1940) gave an indication of the level of the two main groups in the genus, although HALL (1940) subdivided the *Leiostemones* into five subsections and the *Eriostemones* into three sections. Both main groups were considered sections by STORK (1984) and MARAIS (1984). The current subdivision in sects. *Eriostemones* and *Leiostemones* is now well documented by differences in morphology (HALL 1940, STORK 1984, VAN RAAMSDONK & DE VRIES 1992), flower pigment composition (NIEUWHOF & al. 1990) and absence of crossability relationships (VAN EIJK & al. 1991). On account of these differences the sections are raised to the level of subgenera. In addition, the groupings described as subsections (HALL 1940, STORK 1984) are raised to the level of sections. Formal descriptions are given in the chapter taxonomic enumeration.

The five sections of subg. *Tulipa* show overlapping regions in at least two of the four PC's used in this study (Figs. 1 and 2), except for sect. *Clusianae* which is clearly separated morphologically. The existing division into sections (HALL 1940: subsections) is maintained because of the general differences in morphology between the sections (Figs. 1, 2, and 10) and of the different geographical distributions (HOOG 1973), although some species are replaced from one section to another.

For priority reasons, the name *Scabriscapae* (BAKER 1874) should be used instead of one of the names used by HALL (1940). BAKER (l.c.) included species now classified in sects. *Kolpakowskianae, Eichleres*, and *Tulipa*, and the description of *Scabriscapae* covers (part of) these sections as well. BAKER (1883) did not maintain a section or subsection under the name *Scabriscapae* and he classified the species included in *Scabriscapae* (BAKER 1874) in the large sect. *Gesnerianae* (BAKER 1883). So, the meaning of this name is unclear and it must be stated a nomen nudum.

Character distribution and species delimitation. The high correlation coefficients of most characters between years point to a high repeatability. The genetic component appeared to be dominant in the phenotype. Nevertheless, the genotype-environment interaction is unknown and a straightforward conclusion of high heritability figures cannot be drawn. The absolute date of flowering may vary between years depending on temperature and rainfall but the species appeared to flower in almost identical order in the years investigated, which caused the high correlation coefficient.

Among the characters used for the several PC and CV analyses the characters concerning hairiness or pubescence, especially of the bulb tunic range as most important (Tables 2, 3, and 4). This importance supports the recognition of sects. *Clusianae* and *Tulipanum* of which the species show the characters bulbs tufted with hairs and upper parts of the bulb tunics hairy, and bulb tunics entirely woolly, respectively. A correlation with geographic distribution may occur since the species of these sections predominantly occur south of major mountain ranges, i.e., sect. *Clusianae* south of the Pamir Alai and Himalaya and sect. *Tulipanum* south of the Swiss, Austrian and Julian Alps, Caucasus and Kopeth Dagh (HOOG 1973). Any ecological relevance or selective advantage cannot be indicated. Woolly bulb tunics could be considered to be advantageous in hardish climates, but within sect. *Biflores* (subg. *Eriostemones*) species with either woolly or glabrous bulb tunics have been found in Central Asian mountain regions as well as in South Russia and the Balkan peninsula (VAN RAAMSDONK & DE VRIES 1992). Sect. *Tulipanum* shares its geographic distribution area with species of sect. *Tulipa* possessing almost glabrous bulb tunics.

Flower colour within species may differ in two respects. At first, blotch (the basal parts of the tepals, usually darker than main flower colour) and blotch margin (usually yellow) may show difference in size as well as in intensity. Secondly, within some species anthocyanidins are lacking in certain accessions resulting in yellow or very light colours (NIEUWHOF & al. 1990). After selection experiments in accessions obtained from natural provenances (EIKELBOOM, CPRO-DLO, unpubl.) as well as mutation experiments with radiation (BROERTJES & VAN HARTEN 1988) it was shown that blotch margin and flower colour can easily be influenced. In sev-

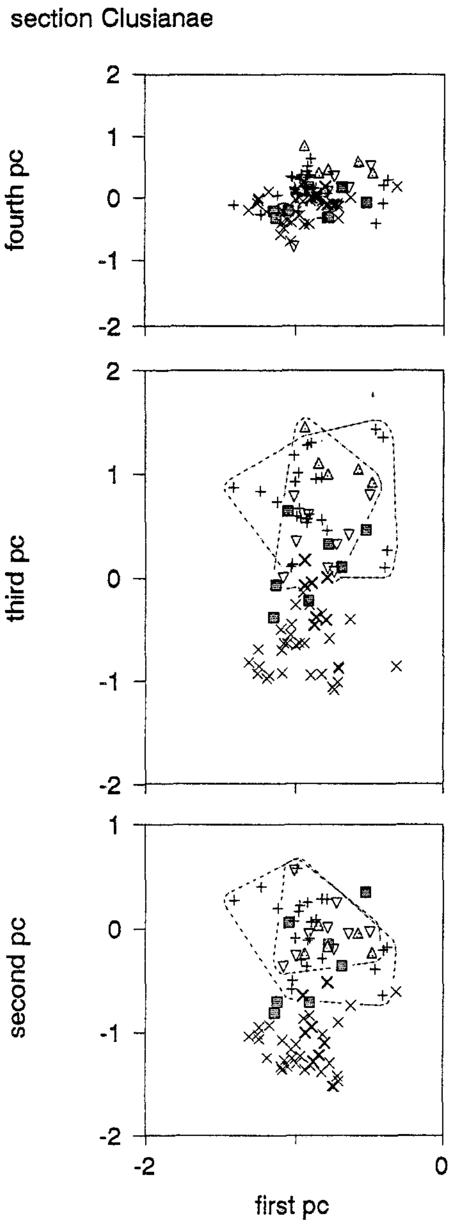

Fig.3

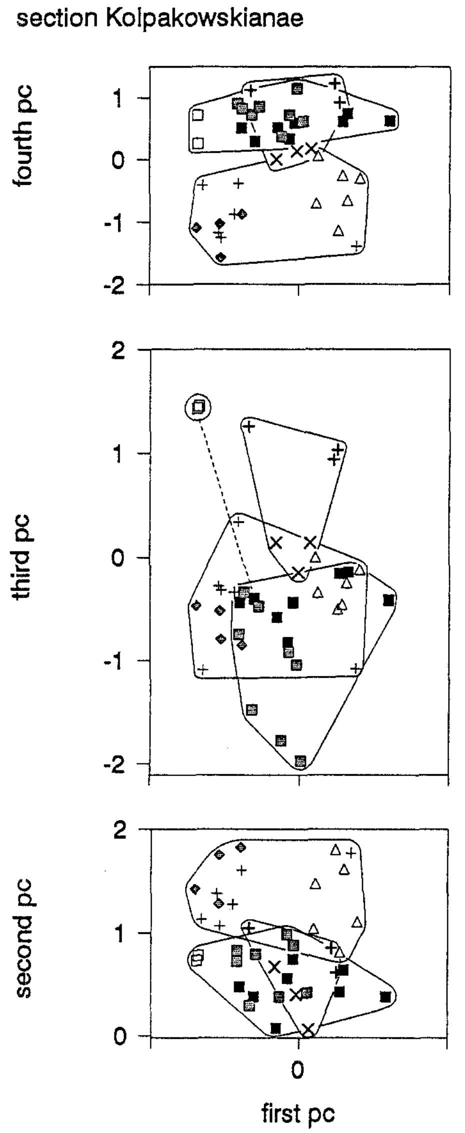

Fig. 4

Fig. 3. Part of a principal component plot with the first and second, first and third, and first and fourth principal components based on an analysis of the 1988 dataset (see material and methods). Signs: plus: *T. aitchisonii*; lower triangle: *T. clusiana* var. *chrysantha*; upper triangle: *T. clusiana* var. *clusiana*; grey squares: *T. montana*; cross: *T. linifolia* (incl. *T. batalinii* and *T. maximowiczii*); heavy cross: *T. montana* yellow variety

Fig. 4. Part of a principal component plot with the first and second, first and third, and first and fourth principal components based on an analysis of the 1988 dataset (see material and methods). Signs: plus: *T. kolpakowskiana*; grey rhombs: *T. iliensis*; upper triangles: *T. ferganica*; heavy cross: *T. zenaidae*; heavy plus: *T. lehmanniana*; open squares: *T. behmiana*; grey squares: *T. tetraphylla*; black squares: *T. ostrowskiana*

eral species a yellow blotch margin is either present or absent, i.e., in *T. stapfii, T. lanata, T. ingens, T. hoogiana*, and *T. fosteriana*. Species described as closely related (Hall 1940, Bochantzeva 1982, Stork 1984) may differ exclusively in flower colour-like *T. clusiana* and *T. stellata, T. linifolia* and *T. batalinii*, and *T. armena* and *T. galatica*. Species are described as formas when the flower colour is the only distinguishing feature.

In several cases species show slight morphological differences but differ greatly in their geographic distribution. In the present study such species pairs are treated on the level of subspecies when allopatric or as varieties when partly sympatric. New combinations are described in the chapter taxonomic enumeration.

C-banding. Data on chromosome C-banding were reported by Blakey & Vosa (1982), predominantly using material from the CPRO-DLO collection (formerly IVT). Hardly any heterochromatin was found in sect. *Kolpakowskianae* and most species of sect. *Eichleres*, although *T. fosteriana* and *T. greigii* showed moderate amounts (Blakey & Vosa 1982), which is contrary to our present results (Table 5). In sect. *Tulipa* a moderate number of C-bands were organized around the centromere (Blakey & Vosa 1982). This phenomenon was only partly found in *T. galatica*, while the minor chromosomes were significantly shorter (Fig. 11) than reported by Blakey & Vosa (1982). Moderate banding in sect. *Clusianae* and moderate to strong banding in sect. *Tulipanum* (Blakey & Vosa 1982) is in concordance with the present results (Table 5). The statement of Loidl (1983), that a high amount of heterochromatin is an advanced characteristic, should imply that sect. *Kolpakowskianae* is the most primitive and that the most advanced species were found in sects. *Tulipanum* and *Tulipa*.

Sect. *Clusianae*. Species of sect. *Clusianae* are found south of the mountain ranges Kopeth Dagh, Pamir Alai and western Himalayas, the *T. linifolia* complex originally assigned to be endemic in the Pamir Alai (Hoog 1973). *T. clusiana* f. *clusiana* shows white or cream flowers of which the outer tepals have a broad red or crimson band at the dorsal side. The blotch is purple (Hall 1940). *T. stellata* has a yellow blotch, while its form *chrysantha* is completely yellow. One collected sample (GWH 638) was provisionally identified as *T. clusiana* yellow variety (Hewer 1974) but it appeared to consist of individuals belonging to *T. batalinii* as well. *T. clusiana, T. stellata*, and "*T. stellata chrysantha*" were considered to be tetraploid or pentaploid (Hall 1938, 1940). Plants collected at the end of the 19th century with flowers like the typical *T. clusiana* proved to be diploids and were assigned to *T. aitchisonii* (Hall 1938). Later also completely yellow forms on the diploid level were collected and described as *T. aitchisonii* subsp. *cashmeriana* (Hall 1938, 1940). *T. aitchisonii* is considered synonymous to *T. clusiana* (Sealy 1948), since the variation in morphology (Fig. 3) and flower colour appeared to be identical. The four formas as described in taxonomic enumeration therefore consist of diploids as well as polyploids. The species *T. fernandezii* and *T. porphyreo-chrysantha* of the *T. clusiana* aggregate (Blatter & Fernandez 1934) both possess yellow flowers without a blotch and with a crimson dorsal band on the tepals. The type of *T. porphyreo-chrysantha* is indicated by Blatter & Fernandez (1934) as syntype of *T. fernandezii*. The cited herbarium sheets were not found; they should be present in the Bombay Blatter herbarium (Dasgupta & Deb 1985), but we were not able to locate them. Both species have been treated as nomina dubia within *T.*

clusiana (DASGUPTA & DEB 1985). The name *T. chrysantha* BOISS. was originally published to describe plants which are currently regarded as yellow variants of *T. montana* (q.v.). However, BAKER (1874) included apparently plants belonging to the *T. clusiana* aggregate. So, several combinations with the epitheton "*chrysantha*" have been used incorrectly, *T. clusiana* var. *chrysantha* (HALL) SEALY amongst them (HALL 1940, SEALY 1948). We now conclude from the discussed nomenclatural confusions that the names published by BLATTER and the combination of SEALY are invalid. *T. batalinii* and *T. maximowiczii* were described as being very closely related to *T. linifolia*, the latter with prostrate leaves and red flowers (HALL 1940). They are different from *T. linifolia* by yellow flowers and erect leaves, respectively. *T. linifolia, T. maximowiczii*, and *T. batalinii* are treated as synonymous (DYKES 1925); the name *T. linifolia* has priority. The name *T. montana* has been applied to two different taxa; REGEL (1873) used the name twice in two different species groups. LINDLEY (1827) assigned this name to a species which should be related to *T. linifolia* according to DYKES (1925), HALL (1940) and SEALY (1963). This species was later described as *T. wilsoniana* (HOOG 1902). Later the name *T. montana* was commonly used for a species of sect. *Tulipanum* with *T. systola* as correct name (BAKER 1883, HALL 1940, SEALY 1963, MOUTERDE 1966). A yellow variant of *T. montana* was described as *T. chrysantha* (BOISSIER 1882, SEALY 1948). All accessions used in the present study identified as *T. montana* appeared to be part of the variation of sect. *Clusianae* (Fig. 3). The red flowered variants are intermediate between *T. linifolia* and *T. clusiana* and designated as species. The yellow variants, however, were indistinguishable from accessions originally identified as *T. batalinii.* As a result the yellow flowering variety of *T. linifolia* has been given the name var. *chrysantha*. Some accessions of *T. clusiana* and *T. linifolia* var. *chrysantha* were found west of the known distribution area (Table 1; HALL 1940, HOOG 1973). These two taxa from Kashmir and the Pamir Alai mountains, respectively, apparently extend their distribution to Iran.

Sect. *Kolpakowskianae*. The distribution of the species of sect. *Kolpakowskianae* is predominantly in the Tien Shan mountain range; some of these species extend into western China. *T. ferganica* is located in the mountains adjacent to the Fergana Basin and the distribution of *T. lehmanniana* is extended to the Kyzyl Kum area, Hindu Kush and Kopeth Dagh (HOOG 1973). *T. iliensis, T. kolpakowskiana*, and *T. ferganica* share almost the same region in the principal component plots (Fig. 4). Only on the third PC some differences were found in this group (Fig. 4 b). The same applies to the group with the species *T. tetraphylla, T. behmiana*, and *T. ostrowskiana*. Both groups are considered to be monospecific. According to priority rules these species are designated as *T. iliensis*, primarily consisting of diploids, and *T. tetraphylla*, exclusively consisting of tetraploids (HALL, 1940, BOCHANTZEVA 1982, KROON & JONGERIUS 1986). *T. ferganica* and *T. ostrowskiana*, respectively, are treated as subspecies because of their different geographic distribution (HOOG 1973). Both species have yellow flowers tinged with red or lilac as found in sect. *Clusianae*. In *T. ostrowskiana* accessions with completely red flowers were found. *T. lehmanniana* and *T. zenaidae* from the lower slopes of the Alatau valley (BOCHANTZEVA 1982) remain as separate species, having a distinctive brown blotch.

Sect. *Tulipanum* (*Oculus-solis* sensu HALL). The name *Tulipanum* was origi-

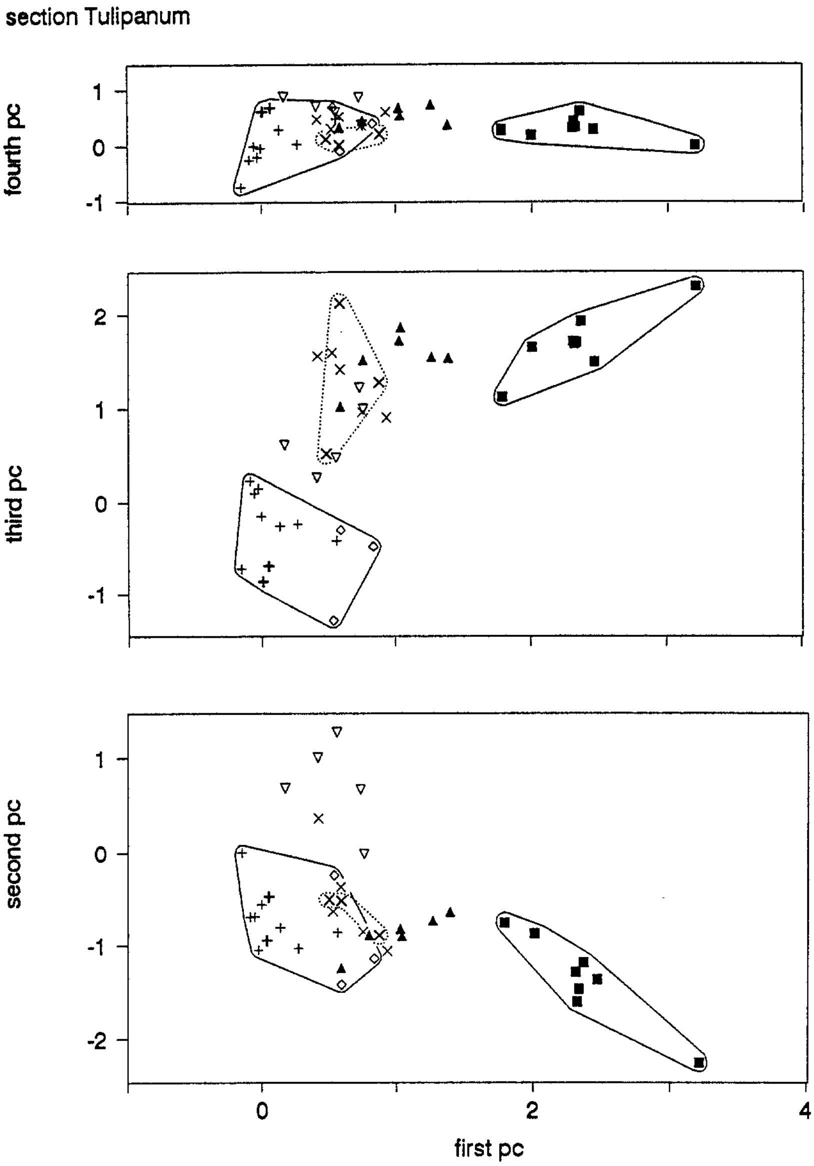

Fig. 5. Part of a principal component plot with the first and second, first and third, and first and fourth principal components based on an analysis of the 1988 dataset (see material and methods). Signs: rhombs: *T. systola*; plus: *T. stapfii*; heavy plus: *T. ulophylla*; lower triangles: *T. oculus-solis*; cross: *T. julia*; black upper triangles: *T. aleppensis*; black squares: *T. praecox*; heavy cross: hybrid between *T. stapfii* and *T. praecox*

nally used by DE REBOUL (1847) to indicate a group of species with bulb tunics woolly at the inside, containing *T. praecox, T. oculus-solis, T. clusiana, T. maleolens* and an undocumented species name. Later sect. *Tulipanum* was considered to consist of *T. tubergeniana, T. kuschkensis, T. hoogiana,* and *T. julia* (VVEDENSKY 1935); all these species appeared to be described later than 1847. The absence of the species named by DE REBOUL (1847) is due to the fact that they occur outside, section Eichleres p.p.

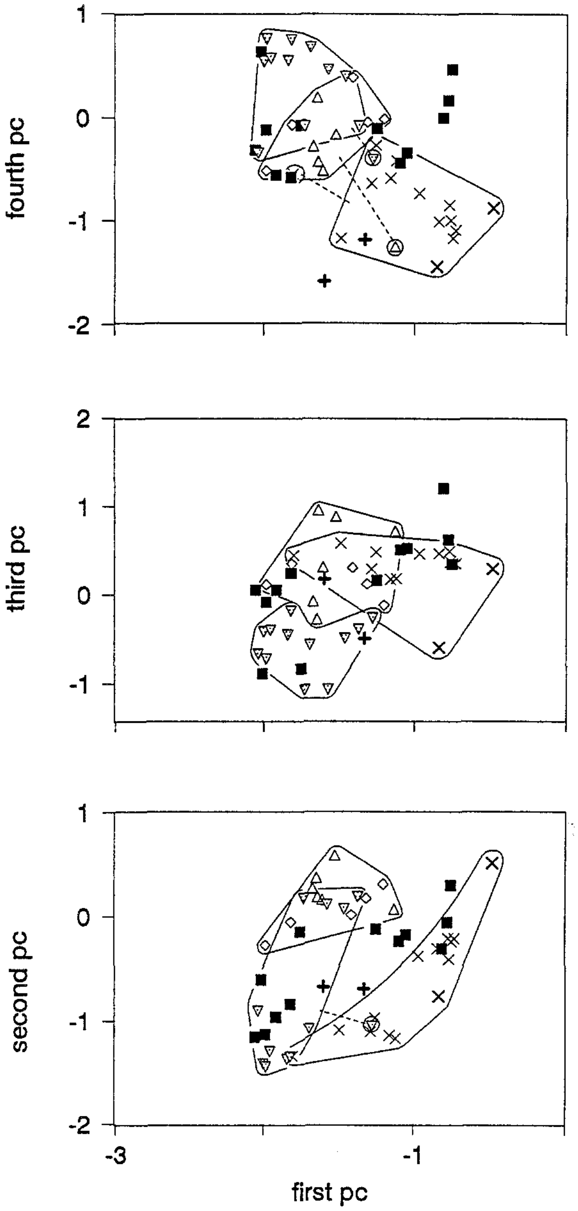

Fig. 6. Part of a principal component plot with the first and second, first and third, and first and fourth principal components based on an analysis of the 1989 dataset (see material and methods). Signs: upper triangles: *T. hoogiana*; rhombs: *T. tubergeniana*; lower triangles: *T. fosteriana*; cross: *T. eichleri*; heavy cross: *T. micheliana*; black squares: *T. greigii*; plus: *T. mogoltavica*

i.e., south of the region covered by Flora of the USSR. Hall (1940) treated the species considered to belong to sect. *Tulipanum* as a special group within subsect. *Oculus-solis*. Bochantzeva (1982) added a fifth species to Vvedensky's (1935) enumeration: *T. subquinquefolia* Vved. The lack of relationship between *T. clusiana* at one hand, and *T. praecox* and *T. oculus-solis* at the other is obvious. Therefore, the sect. usually indicated as *Oculus-solis* (*Eriobulbi*/Baker) deserves the name *Tulipanum* for priority reasons. The representatives of this section occur in central Europe, Asia Minor, Lebanon, Syria, Caucasus, Iran, Iraq, and Afghanistan (Hoog 1973). The species of this group resemble species of sect. *Tulipa* (Hall 1940) and

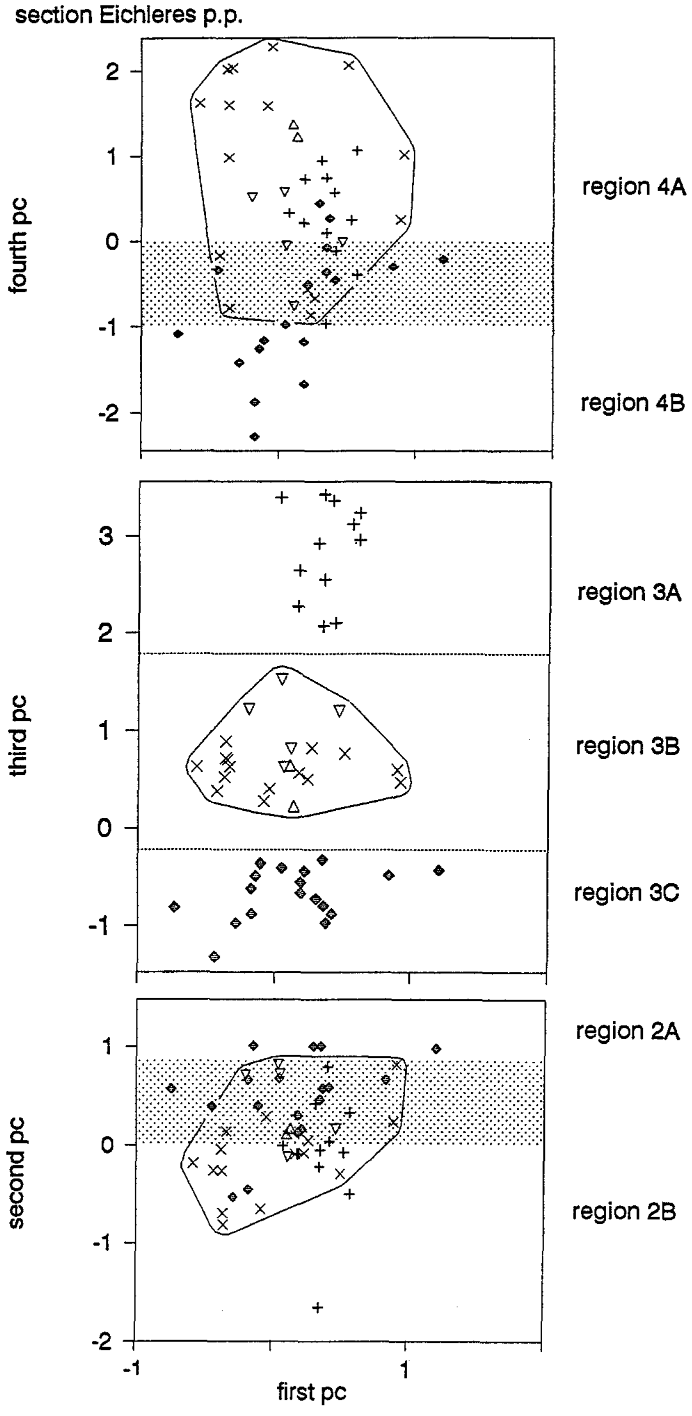

Fig. 7. Part of a principal component plot with the first and second, first and third, and first and fourth principal components based on an analysis of the 1989 dataset (see material and methods). Signs: cross: *T. vvedenskyi*; lower triangles: *T. albertii*; upper triangles: *T. butkovii*; grey rhombs: *T. sosnovskyi*; plus: *T. praestans*

some species of sect. *Eichleres* (Fig. 2) with respect to foliage and flower characteristics, but differ because of the long, interwoven hairs at the inside of the bulb tunics (Hall 1940). The name *T. agenensis* was published in February 1804 by de Candolle in Rédouté (1804). Shortly afterwards Saint Amans (1804) discussed the name *T. oculus-solis* for a species which appeared to be identical to that of de Candolle, but Saint Amans (1804) did not add a description. Therefore, the correct name of this species is *T. agenensis* (Marais 1980). *T. systola* and *T. stapfii* resemble each other very closely and are treated as conspecific. The specific status of *T. aleppensis* is doubtful (Figs. 5 and 10). It may well be a triploid derivative of *T. julia*, although diploid forms were reported (Kroon & Jongerius 1986). *T. stapfii* is treated including *T. ulophylla*.

Sect. *Eichleres*. In sect. *Eichleres*, the largest of the subg. *Tulipa*, large differences with respect to geographic distribution (Hoog 1973) and morphology (Figs. 2, 6–8) were found. *T. kuschkensis* with woolly bulb tunics is placed in sect. *Tulipanum* by Hall (1940) and Hewer (1974), which is confirmed by the present results (Fig. 10). *T. ingens* and *T. lanata* (Pamir Alay and Eastern Kopeth Dagh; Hoog 1973), and *T. subpraestans* (Pamir Alay; Hoog 1973) are separated from the main part of the section (Fig. 2), and placed in two series.

The main part of species of sect. *Eichleres* consists of several groups of closely related species. Two groups with values lower than –0.6 for the first PC sharing the same region for all four PC's (Fig. 6), are separated geographically: *T. fosteriana, T. hoogiana, T. tubergeniana*, and *T. eichleri* were found in the Pamir Alay and the mountain ranges west of it, whereas *T. greigii* and *T. mogoltavica* occur in montane Kyzyl-Kum and Tien Shan, north of the geographic area of the first group. Both groups are described as series. *T. tubergeniana* and *T. hoogiana* differ in area of distribution: *T. tubergeniana* is endemic in the western Pamir-Alai mountain range (Bukhara and environs), while *T. hoogiana* occurs in montane Turkmenistan extending to NE Iran. Both distribution ranges are divided by the river Amu Darya (Hoog 1973). *T. hoogiana* is treated as synonymous to *T. tubergeniana*, as indicated by Hall (1940) and Bochantzeva (1982), for the absence of clear morphological differences (Fig. 6). The close relationship of *T. micheliana* from the Pamir Alai (Hoog 1973) with *T. eichleri* (Hall 1940) is confirmed and they are treated as conspecific.

Similarly, in the region with scores for the first PC higher than –0.6 several groups of closely related species were found (Figs. 7 and 8). *T. sosnovskyi* (Caucasus), *T. albertii, T. vvedenskyi* and *T. butkovii* – both treated as conspecific (Tien Shan), and *T. praestans* (Pamir Alai) are separated by the third PC (Fig. 7 b). Because of morphological (Hall 1940 and present study) and geographical differences (Hoog 1973) these groups are treated as series.

The species *T. kaufmanniana, T. dubia*, and *T. tschimganica*, endemic in western Tien Shan (Hoog 1973) share the geographic area with *T. albertii*. *T. anadroma* is treated as conspecific with *T. tschimganica*, and *T. amblyophylla* with *T. kaufmanniana*. Red flowering accessions have been assigned to *T. dubia*. The group of species related to *T. kaufmanniana* has been described as sect. *Spiranthera* (Vvedenskyi 1935, Bochantzeva 1982). In each principal component plot of the 1989 analysis different species combine in the same region with the species of sect. *Spiranthera* (Figs. 7 and 8), but these species are separated after the 1988

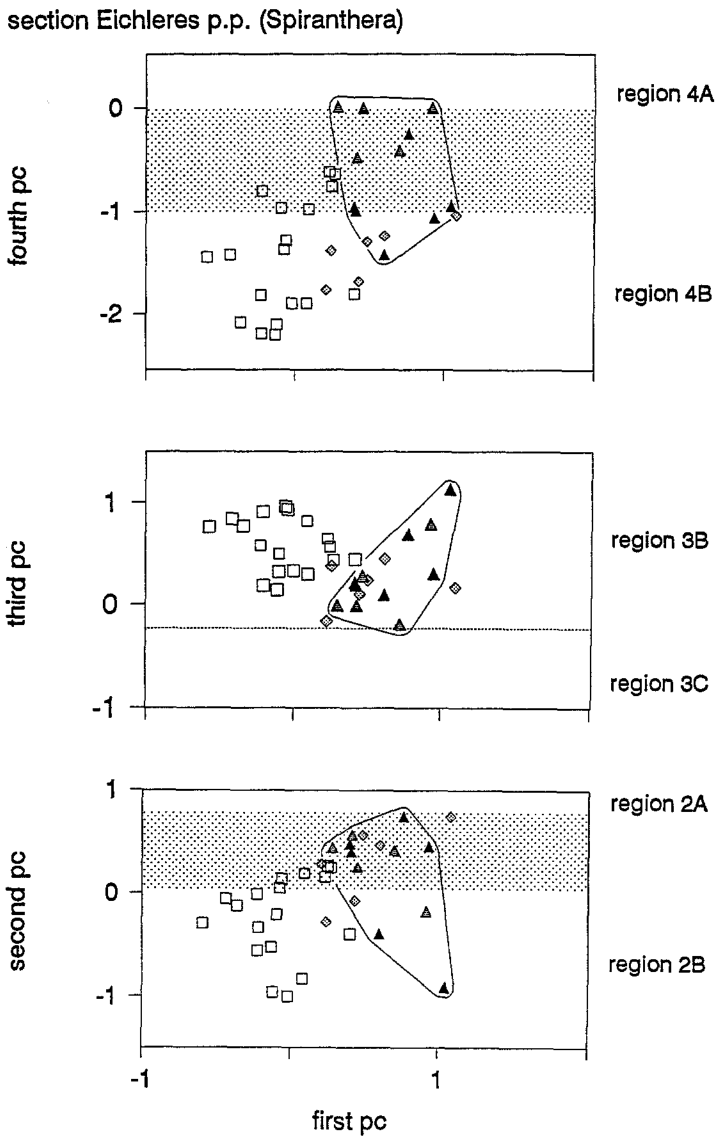

Fig. 8. Part of a principal component plot with the first and second, first and third, and first and fourth principal components based on an analysis of the 1989 dataset (see material and methods). Signs: squares: *T. kaufmanniana*; grey rhombs: *T. dubia*; black upper triangles: *T. tschimganica*; grey upper triangles: *T. anadroma*

analysis (Fig. 1). This section can easily be recognized by means of some characteristics, which were not included in the presently used set of characters for multivariate analyses, like leaf colour, flower shape, and a red spot at the inner side of the tepals at the place where the margin of the blotch should be located (Hall 1940). Besides totally red flowers in *T. dubia* as found in all other species of sect. *Eichleres*, cream or yellow flowers tinged with red on the dorsal side occur, comparable to the flower colour in sect. *Clusianae* and *Kolpakowskianae* (Bochantzeva 1982). The accessions of *T. kaufmanniana* and *T. amblyophylla* show moderate

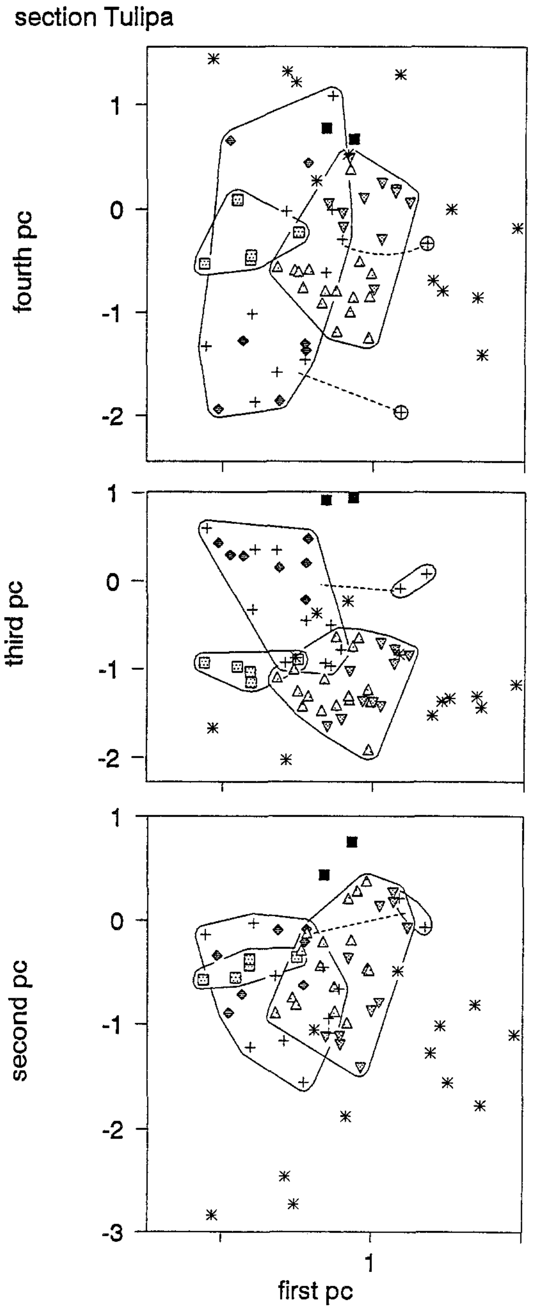

Fig. 9. Part of a principal component plot with the first and second, first and third, and first and fourth principal components based on an analysis of the 1989 dataset (see material and methods). Signs: dotted squares: *T. armena*; grey rhombs: *T. hungarica*; plus: *T. rhodopea*; black squares: *T. suaveolens*; upper triangles: *T. marjolettii* and *T. grengiolensis*; lower triangles: *T. didieri* and *T. planifolia*; stars: *T. gesneriana*

levels of heterochromatin in contrast to most other species in sect. *Eichleres* (Table 5). However, a separate section can not be maintained and the section is therefore treated as series.

Sect. *Tulipa* (*Gesnerianae* sensu Hall). The section *Tulipa* is found in Europe and the Middle East (Hoog 1973). The species are generally closely related to the cultivated tulip, *T. gesneriana, T. rhodopea* is regarded to be a subspecies of *T.*

hungarica, occurring in Rumania and Bulgaria, respectively (HOOG 1973). *T. armena* and *T. galatica* are treated as conspecific, sympatric in Asia minor, and differing in flower colour (HALL 1940), chromosome number and amount of heterochromatin (Table 5). In *T. galatica* two similar and one deviating haploid set of chromosomes with respect to C-banding pattern was found (Fig. 11), which could indicate an alloploid origin. *T. gesneriana* has crossability relationships with some species of sect. *Eichleres* (VAN EIJK & al. 1991), but differences in the mean amount of heterochromatin occur between sect. *Tulipa* and sect. *Eichleres*. *T. suaveolens* has been mentioned to be the ancestor of the *T. gesneriana* "Duc van Tol" types (JANSE 1966). The large variability of *T. suaveolens* together with that of the two accessions of *T. gesneriana* used will be dealt with in a separate paper. In sect. *Tulipa* a group of Neotulipae was described in the nineteenth century, mainly found on the western and southern borders of the Alps, and most of the species known from only one locality (LEVIER 1884, HALL 1940). Because of their western, isolated distribution they should be regarded as garden escapes of *T. gesneriana* and they are treated as one species. Some forms included in the Neotulipae show hairy bulb tunics and red or scarlet flower colours with a distinctive black blotch, yellow margined. These forms like *T. maleolens* should be designated as part of sect. *Tulipanum* (BAKER 1874: *Eriobulbi*), of which species occur in the same region.

Taxonomic enumeration

Tulipa L. Sp. Pl.: 305 (1753)

Subgenus *Tulipa*. Basionym: sect. *Leiostemones* BOISSIER, Fl. Orientalis **5**, p. 192 (1882). Homotypic synonym: sect. *Tulipa* MARAIS, in DAVIS, P. H., (Ed.): Flora of Turkey and the East Aegean Islands **8**, p. 306 (1984). Type species: *T. gesneriana* L. (1753).

Section *Clusianae* BAKER, Gard. Chr. n.s. **19**: 691 (1883). Homotypic synonym: subsect. *Clusianae* HALL, The genus *Tulipa*, p. 80 (1940). Type species: *T. clusiana* DC. (1803) (lectotype, designated here).

T. clusiana DC. in REDOUTÉ, Les Liliacées **1**, t. 37 (1803). Heterotypic synonym: *T. aitchisonii* A. D. HALL, J. Bot. **76**: 313 (1938; "*aitchesonii*").

Forma *clusiana*. Heterotypic synonyms: *T. chitralensis* auct., Kew Bull. app. **2**: 53 (1898); HALL, The genus *Tulipa*, p. 85 (1940); *T. aitchisonii* HALL var. *clusianoides* WENDELBO, Symb. Afghan. **4**: 162 (1968). The flowers show a white basic color with a crimson or purple dorsal band, and a dark purple blotch with filaments and anthers in the same colour. The anthers may be either shorter or longer (var. *clusianoides*) than the filaments.

Forma *stellata* (HOOK.) DASGUPTA & DEB, Candollea **40**: 165 (1985). Basionym: *T. stellata* HOOKER, Curt. Bot. Mag. **54**: 2762 (1827). Homotypic synonym: *T. clusiana* var. *stellata* (HOOK.) REGEL, Acta Hort. Petrop. **1**: 54 (1873). Flowers possess a white basic colour with a crimson or purple dorsal band. Blotch, filaments and anthers are yellow.

Forma *diniae* VAN RAAMSDONK, forma nova. Heterotypic synonyms: *T. fernandezii* BLATT., J. Bombay Nat. Hist. Soc. **37**: 420 (1934), nomen dubium; *T. porphy-*

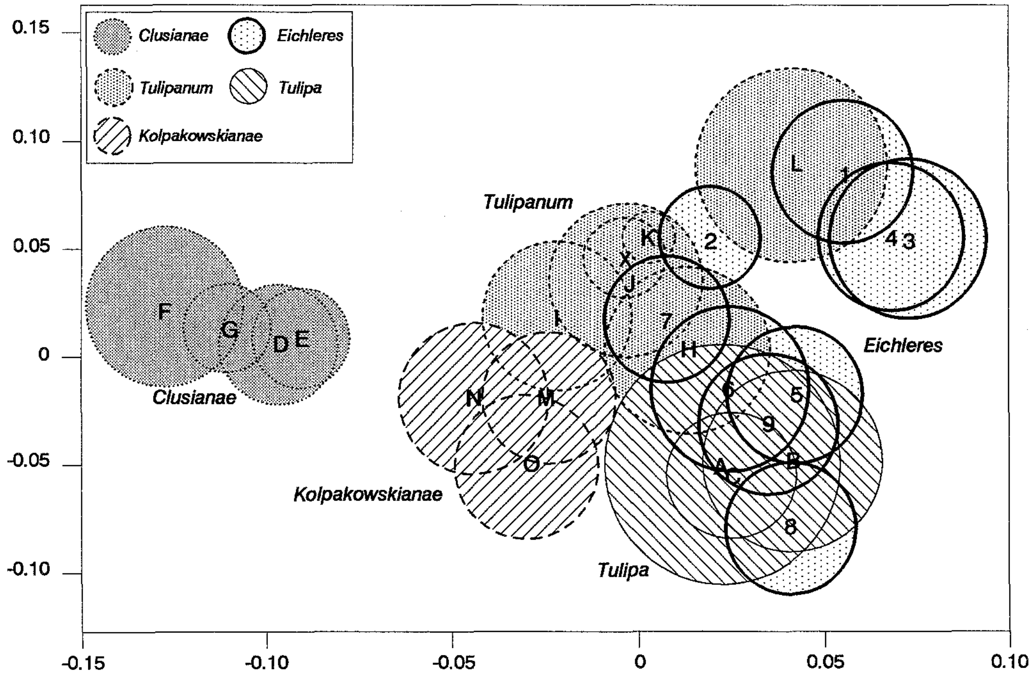

Fig. 10. Regions of species groups in a plot with the first and second canonical variate based on the combined dataset of 1988 and 1989. 1 *T. lanata, T. ingens*; 2 *T. kuschkensis*; 3 *T. eichleri, T. micheliana, T. fosteriana, T. tubergeniana, T. hoogiana*; 4 *T. greigii, T. mogoltavica*; 5 *T. vvedenskyi, T. albertii, T. butkovii*; 6 *T. sosnovskyi*; 7 *T. praestans*; 8 *T. subpraestans*; 9 *T. kaufmanniana, T. tschimganica, T. anadroma, T. dubia*; A *T. armena, T. suaveolens, T. gesneriana*; B *T. hungarica, T. rhodopea*; C *T. marjoletti, T. planifolia, T. didieri, T. grengiolensis*; D *T. clusiana*; E *T. aitchisonii*; F *T. linifolia, T. batalinii, T. maximowiczii*; G *T. montana*; H *T. oculus-solis*; I *T. stapfii, T. systola, T. ulophylla*; J *T. julia*; K *T. aleppensis*; L *T. praecox*; M *T. kolpakowskiana, T. iliensis, T. ferganica*; N *T. zenaidae*; O *T. ostrowskiana, T. tetraphylla, T. behmiana*; X hybrid between *T. stapfii* (I) and *T. praecox* (L)

reochrysantha Blatt., J. Bombay Nat. Hist. Soc. **37**: 421 (1934), nomen dubium; *T. stellata chrysantha* Hort ex Hall (1940), non Boissier; *T. clusiana* var. *chrysantha* (Hall) Sealy, Curtis Bot. Mag. n.s. **16S**: 13 (1948), nomen nudum. Tepala lutea intus basi macula pollide violacea vel sine macula extus stria coccina dorsali. Holotype: T. de Vries 1106, acc.nr. 68590, IVT, Wageningen; paratype: T. de Vries 1115, acc.nr. 70639, IVT, Wageningen (WAG). Flowers show a yellow basic colour without or with a light purple blotch, but with a crimson dorsal band on the tepals, and yellow filaments and anthers. The anthers may be either shorter (*T. porphyreochrysantha*) or longer than the filaments. Cultivar ‘Cynthia’ is included in this forma.

Forma *cashmeriana* (Hall) van Raamsdonk, comb. & stat. nov. Basionym: *T. aitchisonii* subsp. *cashmeriana* Hall, J. Bot. **76**: 313 (1938). The flowers are completely yellow, sometimes with a brown blotch, but without a crimson dorsal band.

T. montana Lindley, Bot. Reg., t. 1106 (1827). Synonym: *T. wilsoniana* Hoog, Gard. Chron. n.s. **32**: 50 (1902).

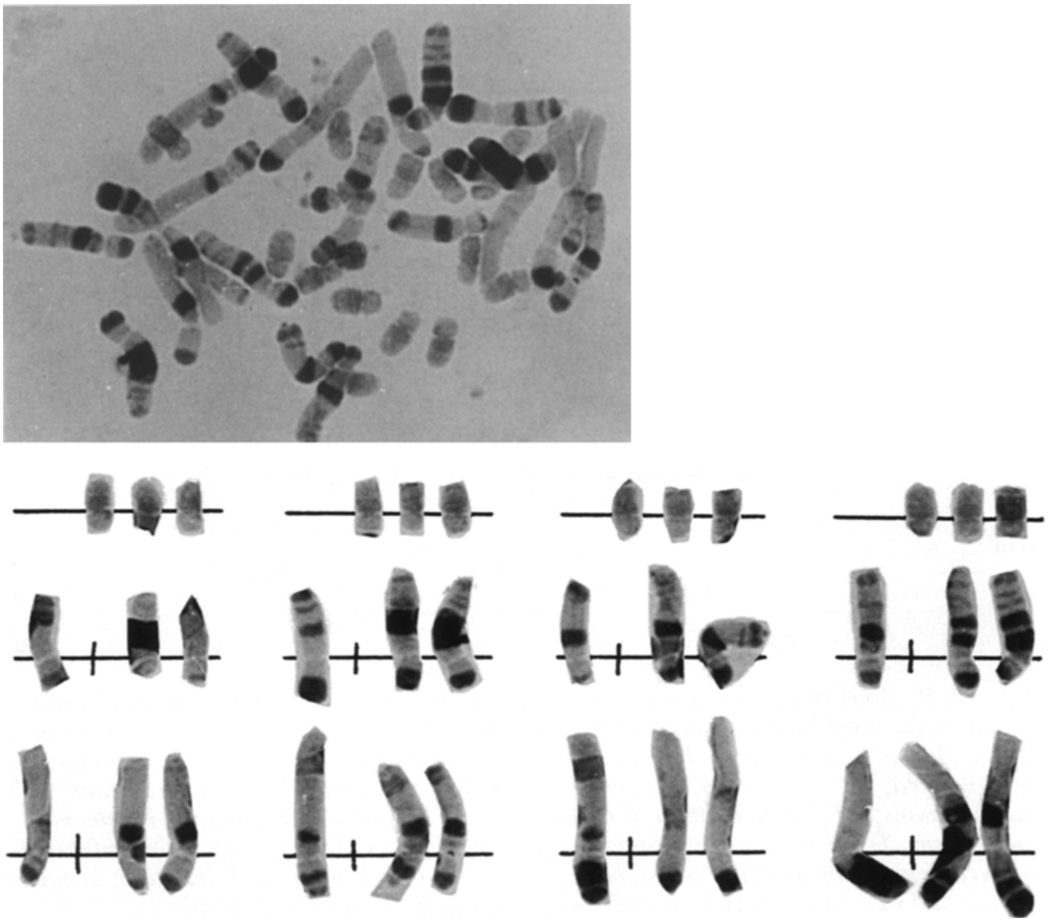

Fig. 11. Idiogram of the triploid species *T. galatica* (84266)

T. linifolia Regel, Acta Hort. Petrop. **8**: 648 (1884). Synonym: *T. maximowiczii* Regel, Gartenflora **38**: 505 (1889).

Forma *linifolia*.

Forma *chrysantha* (Boissier) van Raamsdonk, comb. nova. Basionym: *T. chrysantha* Boissier in Kotschy, Fl. Pers. Bor, p. 78 (1846); Boissier, Fl. Orientalis **5**: 193 (1882). Heterotypic synonym: *T. batalinii* Regel, Gartenflora **38**: 506 (1889). This forma differs from f. *linifolia* in having yellow flowers instead of red. Both colour formas are indistinguishable concerning other characters. *T. chrysantha* Boissier was considered by Hall (1940) to be the yellow forma of *T. montana*, but almost all accessions in our collection identified as yellow *T. montana* turned out to be yellow *T. linifolia* (Fig. 3).

Section *Kolpakowskianae* (Hall) van Raamsdonk, stat. nov. Basionym: subsect. *Kolpakowskianae* Hall, The genus *Tulipa*, p. 134 (1940). Type species: *T. kolpakowskiana* Regel (1877) (lectotype, designated here; = *T. altaica*).

T. altaica Pall. ex Sprengel, Syst. **2**, p. 63 (1825). Heterotypic synonyms: *T. kolpakowskiana* Regel, Acta Hort. Petrop. **8**: 650 (1877), *T. iliensis* Regel, Gartenflora **28**: 162 (1879), *T. anisophylla* Vvedensky, Bjul. Sredn. Gos. Univ. **21 (16)**: 147 (1935).

Var. *altaica*.

Var. *ferganica* (Vved.) van Raamsdonk, comb. nova. Basionym: *T. ferganica* Vved., Bjul. Sredn. Gos. Univ. **21 (16)**: 148 (1935). Var. *ferganica* show wider stems and leaves, and larger floral parts than var. *altaica* (Fig. 4), and differ in area of distribution: var. *altaica* is found in the Tien-Shan mountain range, and in some parts of western China, whereas var. *ferganica* is endemic in the Pamir-Alai mountain range and Fergana basin (Hoog 1973).

T. lehmanniana Mercklin, Mem. Acad. Pet. Sav. Etr. **7**: 513 (1854). Heterotypic synonym: *T. zenaidae* Vvedensky, Bjul. Sredn. Gos. Univ. **21 (16)**: 150 (1935).

T. tetraphylla Regel, Acta Hort. Petrop. **3**: 296 (1875). Heterotypic synonym: *T. behmiana* Regel, Acta Hort. Petrop. **6**: 505 (1880).

Subsp. *tetraphylla*.

Subsp. *ostrowskiana* (Regel) van Raamsdonk comb. nova. Basionym: *T. ostrowskiana* Regel, Acta Hort. Petrop. **8**: 649 (1884). Subsp. *ostrowskiana* has more erect and less undulated leaves than subsp. *tetraphylla* (Fig. 4), and differs in area of distribution: subsp. *tetraphylla* is found in the NE part of the Tien-Shan mountain range and some parts of western China, whereas subsp. *ostrowskiana* is found in the eastern part of Turkestan (Hoog 1973).

Section *Tulipanum* de Reboul, Giorn. Bot. Ital. **2**: 60 (1847). Homotypic synonyms: sect. *Eriobulbi* Baker, J. Linn. Soc. **14:** 276 (1874), subsect. *Oculus-solis* Hall, The genus *Tulipa,* p. 104 (1940). Type species: *T. oculus-solis* St. Amans (1804) (lectotype, designated here).

Series *Tulipanum.* Type species: *T. agenensis* DC. (1804).

T. agenensis DC. in Redouté: Les Liliacées **1**, p. 60 (1804). Heterotypic synonyms: *T. oculus-solis* St. Amans, Rec. Soc. Agri. Agen. **1**: 75 (1804), nomen nudum; *T. maleolens* de Reboul, Nonnul. sp. tulip. not. App.: 1 (1823).

T. systola Stapf, Denkschr. Akad. Wien **50**: 17 (1885). Heterotypic synonyms: *T. stapfii* Turrill, Curtis Bot. Mag. **157**: t. 9356 (1934), *T. ulophylla* Wendelbo, Nytt. Mag. Bot. **14**: 99 (1967).

T. kuschkensis B. Fedtschenko, Bot. Jahrb. **50**: 612 (1914, nomen; 1932, descr.)

T. julia C. Koch, Linnaea **22**: 225 (1849).

T. aleppensis Boissier ex Regel, Acta Hort. Petrop. **2**: 450 (1873).

Series *Aureo-fasciatae* van Raamsdonk, ser. nova. Plantae magnae caule longo et crasso foliis latis floribus magnis et tepalis distincte luteo-fasciatis. Type species: *T. praecox* Tenore (1811). The species of this series has a large habit (stem length 40–55 cm), thick stem (6–8 mm), broad leaves (50–75 mm), large flowers (7–9 cm) and a distinct yellow dorsal band on the tepals. The yellow band is very occasionally found in *T. systola. T. aleppensis* is intermediate by having broad leaves and being triploid like *T. praecox.*

T. praecox Tenore, Flora Napolitana **1**, p. 179 (1811).

Section *Eichleres* (Hall) van Raamsdonk, stat. nov. Basionym: subsect. *Eichleres* Hall, The genus *Tulipa,* p. 122 (1940). Type species: *T. eichleri* Regel (1874) (lectotype, designated here).

Series *Lanatae* van Raamsdonk, ser. nova. Tunica parte superiore lanata indumento apice bulbi visibili. Basi tepalorum macula nigra acute marginata saepe margine lutea distincta et stigmate perpallide viride. Type species: *T. lanata* Regel (1884). The species of this series are distinct by having a woolly layer of hairs in the upper part of the tunics, a tuft of hairs visible on top of the bulb, a sharply edged, black heart ("blotch") with or without a distinct yellow border at the base of the tepals and a colourless stigma. Only the slight hairiness in the lower part of the bulb differs from that of the species of sect. *Tulipanum*. The species are related to the next series.

T. lanata Regel, Acta Hort. Petrop. **8**: 647 (1884).

T. ingens Hoog, Gard. Chron. n.s. **32**: 14 (1902).

Series *Eichleres*. Type species: *T. eichleri* Regel (1874). Species of this series show a sharply edged, black blotch usually with a distinct yellow border in the center of the flower, and either a red-coloured stigma (*T. tubergeniana*) or a pale yellowish-green stigma.

T. eichleri Regel, Gartenflora **23**: 193 (1874).

Var. *eichleri*.

Var. *micheliana* (Hoog) van Raamsdonk, comb. nova. Basionym: *T. micheliana* Hoog, Gard. Chron. n.s. **32**: 350 (1902). Var. *eichleri* and var. *micheliana* are comparable in morphology (Fig. 6) but var. *micheliana* shows a much dwarfer habit. The varieties differ in area of distribution: var. *eichleri* is endemic in S Caucasus and N Iran, while var. *micheliana* occurs in NE Iran, extending to Pamir Alai; a transient zone with both varieties may occur in N Iran (Hoog 1973).

T. tubergeniana Hoog, Gard. Chron. n.s. **35**: 358 (1904). Heterotypic synonym: *T. hoogiana* B. Fedtschenko, Gard. Chron. n.s. **48**: 53 (1910).

T. fosteriana Hoog ex W. Irving, Gard. Chron. n.s. **39**: 322 (1906).

Series *Vinistriatae* van Raamsdonk, ser. nova. Folia supra striis vinaceis suffulta. Tepala macula fusca vel nigra colore vivide et lucente rubro transiente. Type species: *T. greigii* Regel (1874). The species of this series is distinct by having anthocyanin stripes on the upper surface of the leaves and a brown or black blotch, fading in the bright, shiny red colour of the flower. Anthocyanin stripes are only occasionally found in some other species, like *T. eichleri* (ser. *Eichleres*), *T. albertii* (ser. *Undulatae*) and *T. kaufmanniana* (ser. *Spiranthera*).

T. greigii Regel, Gartenflora **22**: 290 (1873). Heterotypic synonym: *T. mogoltavica* M. Popov & Vvedensky, Herb. Fl. As. Med. no. 594 (1935).

Series *Undulatae* van Raamsdonk, ser. nova. Folia margine saepe undulato. Caules breves. Macula lutea plerumque gradatim marginem versus atrans et colore rubro tepalorum transiens. Type species: *T. albertii* Regel (1877). The species in this series shows leaves with often undulated margins, short stems (10–35 cm) and usually a yellow blotch, in some populations gradually darkening towards the blotch margin, fading away in the red flower colour.

T. albertii Regel, Acta Hort. Petrop. **5**: 264 (1877). Heterotypic synonyms: *T. vvedenskyi* Bochantzeva, Not. Syst. Herb. Uzb. **14**: 3 (1954), *T. butkovii* Bochantzeva, Not. Syst. Herb. Uzb. **16**: 8 (1961).

Series *Luteo-apiculatae* van Raamsdonk, ser. nova. Caules flaccidis irregulariter flectantes. Flores rubri macula nigra. Filamenta antherae pollenque atropurpurea vel nigra. Type species: *T. sosnovskyi* Akhverdov & Mirzojeva (1950). The species of this series shows flaccid stems, bending irregularly, and red flowers with a black blotch and very dark filaments, anthers and pollen. The filaments have a distinct yellow tip.

T. sosnovskyi Akhverdov & Mirzojeva, Tr. Bot. Inst. Ac. Sc. Arm. **7**: 31–32 (1950).

Series *Multiflorae* van Raamsdonk, ser. nova. Tunica bulba dura. Flores rubri vel armeniaci since macula. Filamenta colore tepalis simila rariter atropurpurea. Antherae atropurpureae vel luteolae. Plant plerumque plusquam florem unum et etiam usque flores septem gerens. Type species: *T. praestans* Hoog (1903). The species of this series is distinct by showing hard bulb tunics. Flowers are entirely red or golden yellow, which means the absence of a blotch and usually filaments with the same colour as the tepals and with dark purple or yellow anthers. The plants have usually more than one and up to seven flowers per stem. This characteristic is extremely rare in some other species of subg. *Tulipa*, i.e., *T. fosteriana* (ser. *Eichleres*) and *T. kaufmanniana* (ser. *Spiranthera*) may occasionally show two flowers. It was not found in *T. sosnovskyi* (ser. *Luteo-apiculatae*) as reported by Bochantzeva (1982). One population in our collection shows dark purple filaments. Besides the type species *T. praestans* with red flowers a second taxon endemic to Afghanistan has to be described possessing yellow or ochre flowers.

T. praestans Hoog, Gard. Chron. n.s. **33**: 364 (1903).

Series *Spiranthera* (Vved.) van Raamsdonk, stat. nova. Basionym: sect. *Spiranthera* Vvedensky (1935). Type species: *T. kaufmanniana* Regel (1877).

T. kaufmanniana Regel, Gartenflora **26**: 194–195 (1877). Heterotypic synonym: *T. montana* var. *amblyophylla* Post, Pl. Post. **1**, p. 13 (1890).

T. tschimganica Bochantzeva, Not. Syst. Herb. Uzb. **16**: 10 (1961). Heterotypic synonym: *T. anadroma* Bochantzeva, Not. Syst. Herb. Uzb. **16**: 7 (1961).

T. dubia Vvedensky, Bjull. Sredn. Gos. Univ. **21 (16)**: 148 (1935).

Series *Glabrae* van Raamsdonk, ser. nova. Facies interior tunicae bulbi glaberrima. Etiam coronula pilifera basi bulbi absens. Type species: *T. subpraestans* Vvedensky (1935).

The inner side of the bulb tunics of the species in this series is completely glabrous. Especially the hairy coronet at the base of the bulb is lacking, which is not found in any other species. Flowering time is approximately one week later than the other species of this section.

T. subpraestans Vvedensky, Herb. Fl. As. Med. no 597 (1935).

Section *Tulipa*. Basionym: sect. *Gesnerianae* Baker, J. Linn. Soc. **14:** 276 (1874). Homotypic synonyms: sect. *Dulipanum* de Reboul, Giorn. Bot. Ital. **2**: 60 (1847), subsect. *Gesnerianae* Hall, The genus *Tulipa*, p. 92 (1940). Type species: *T. gesneriana* L. (1753).

T. armena Boiss., Diagn. **2 (4)**: 99 (1859).

Forma *armena*.

Forma *galatica* (Freyn) van Raamdonk, comb. nova. Basionym: *T. galatica*

Freyn, Bull. Herb. Boiss. **4**: 186 (1896). This forma differs from f. *armena* in having yellow flowers instead of red ones with a black blotch. F. *galatica* is triploid (Fig. 11). Both colour formas are indistinguishable as for other characters.

T. hungarica Borbas, Foldmuv. Erdek., p. 561 (1882). Heterotypic synonyms: *T. orientalis* Levier, Bull. Soc. Sci. Nat. Neuchatel **14**: 201–312 (1884); *T. urumoffii* Hayek, Verh. Zool.-Bot. Ges. Wien **61**: 110 (1911).

Subsp. *hungarica*.

Subsp. *rhodopea* (Velenovsky) van Raamsdonk, comb. nova. Basionym: *T. rhodopea* Velenovsky, Reliquiae Mrkvickanae, p. 28 (1922), *T. orientalis* var. *rhodopea* Velenovsky, Sitz. Böhm. Ges. Wiss. **40**: 8 (1899). Subsp. *hungarica* has yellow, or red flowers with a black blotch, and in combination with both flower colours yellowish-green pollen grains. Flowers of subsp. *rhodopea* are always purple-red with a black blotch and purple pollen grains. The subspecies are alike concerning other characteristics (Fig. 9). The areas of distribution are different: subsp. *rhodopea* is found in the Rhodope mountains (Bulgaria), whereas subspecies *hungarica* occurs in Rumania and presumably also in Hungary. Both distribution ranges are divided by the Danube river (Hoog 1973).

T. suaveolens Roth, Ann. Bot. **10**; Neue Ann. Bot. **4**: 44 (1794). Heterotypic synonym: *T. schrenkii* Regel, Acta Hort. Petrop. **2**: 452 (1873).

T. didieri Jord., Fragm. **1**, p. 36 (1846). Heterotypic synonyms: *T. planifolia* Jordan in Jord. & Fourr., Icones **1**, p. 19 (1858); *T. marjoletti* Perr. & Song., Bull. Herb. Boiss. ser. 1, **2**: 425 (1894); *T. grengiolensis* Thommen, Bull. Mur. Soc. Val. Sc. Nat. 63: 67 (1946).

T. gesneriana L., Sp. Pl., p. 306 (1753).

Subgenus *Eriostemones* (Boissier) van Raamsdonk, stat. nov. Basionym: "section" *Eriostemones* Boissier Fl. Orientalis **5**: 196 (1882).

Type: *T. sylvestris* L., Sp. Pl., p. 305 (1753).

The sections and species have been treated in van Raamsdonk & de Vries (1992).

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