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Morphology of tulips (*Tulipa*, Liliaceae) in its primary centre of diversity

Davron Dekhkonov, Komiljon Tojibaev*, Ziyoviddin Yusupov, Dilmurod Makhmudjanov, Temur Asatulloev

Institute of Botany, Academy of Sciences, Durmon yuli str. 32, Tashkent 100125, Uzbekistan

✉ ktojibaev@mail.ru

ABSTRACT
The Tian Shan and Pamir-Alay mountains of Central Asia are generally regarded as the primary center of diversity of *Tulipa* species, but a comparative morphological description of Central Asian *Tulipa* species is still lacking. To fill the existing gap, we studied 48 *Tulipa* species found in Central Asia plus one outgroup (*Erythronium caucasicum*) for 24 morphological characters of bulbs, leaves, stems and flowers. The obtained data matrix was subjected to a cladistic analysis. Although bootstrap values were low, the morphology-based tree more or less corresponded to previous classifications, except for the placement of sect. *Clusianae* and *T. butkovii*.

Key words: *Tulipa*; comparative morphology; morphology based phylogeny; cladistic analysis

Introduction

Tulipa L. (Liliaceae) is a bulbous monocot genus mainly distributed in Central Asia, but extending into south-eastern Europe, the Middle East and across North Africa (Veldkamp & Zonneveld 2012; Christenhusz et al. 2013). The genus is characterized by a distinct suit of traits (leaf and flower morphology, pubescence of bulb tunic etc.) and, due to the horticultural value and cultural significance always attracted much attention (Christenhusz et al. 2013). To date, 380 tulip names have been proposed, of which 104 are currently accepted (WCVP 2021).

The Tian Shan and Pamir-Alay mountains of Central Asia are regarded as a primary center of diversity for *Tulipa* species, with the Caucasus and northern Iran as a secondary center (Botschantzeva 1962). The total number of tulip taxa in Central Asia reaches 80 species (WCVP 2021). More than 37 (less than 60%) species of tulips are endemic to this area (Vvedensky & Kovalevskaja 1971).

Although floristically well studied, new *Tulipa* species are still occasionally discovered in Central Asia. During the last decade, 15 new species have been described (WCVP 2021). Central Asian tulips were the subject of intensive taxonomic research by Vvedensky (1935), Botschantzeva (1962), Tojibaev and Kadirov (2010), Lazkov and Umralina (2015), Tojibaev and Beshko (2016), but there are many unresolved questions regarding the infrageneric relationships in this genus. A cladistic analysis based on a large number of taxonomically important morphological characters may shed light on the relationships within the genus. Unfortunately, although morphology used to be and remains the basic and key data for taxonomic classification in *Tulipa*, we are unaware of a cladistic analysis of the genus based on morphology. Therefore, the goals of this study

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are 1) produce a comparative morphological analysis and 2) construction of a morphology-based phylogenetic tree using a cladistic analysis of 48 wild tulip species sampled in Central Asia.

Material and methods

Study area and plant material

The study area, which constitutes a part of Central Asia, is shown in Fig. 1. Fresh leaves were collected in Uzbekistan during field trips. Morphology of other species (from Kyrgyzstan, Tajikistan, Turkmenistan and Kazakhstan) was studied using herbarium specimens in TASH. All vouchers were deposited in TASH.

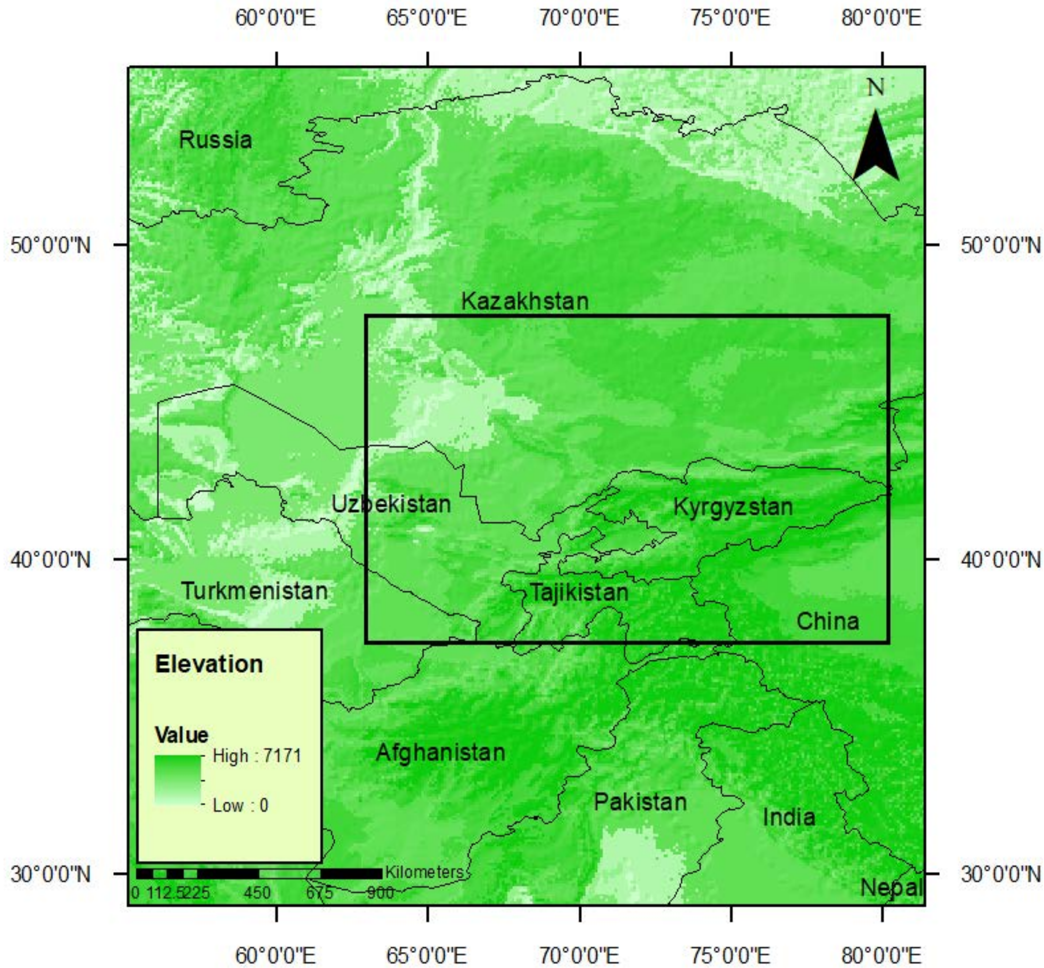

Fig. 1. Map of Central Asia and the primary center of *Tulipa* diversity denoted by a rectangle.

Morphological evaluation

Our study followed the systems of Veldkamp & Zonneveld (2012) and Christenhusz et al. (2013) that recognize four subgenera and sometimes 11 or 12 sections. Twenty-four morphological characters of bulbs, leaves, stems and flowers were measured from 49 species, including *Erythronium caucasicum* Woronow as outgroup, which represents the sister genus to *Tulipa*. The analysed morphological characters had two, three or four states (Table 1). If all members of a section have the same character state, this character is defined as uniform. If one or more species in a section have a character state that differs from a state shared by the remaining members of a section, such character is defined as varying. The uniform and varying characters

Table 1. List of morphological characters of *Tulipa* species and their abbreviations

#	Characters	Characters states	Abbreviation
1.	Bulb shape	globose (0), ovoid (1), elongated ovoid (2)	BS
2.	Type of tunic surface	papery (0), coriaceous (1)	TS
3.	Hairs at the lower part of bulb tunic	none (0), sparse (1), strong (2), woolly (3)	HLPB
4.	Hairs at the upper part of bulb tunic	none (0), sparse (1), strong (2)	HUPB
5.	Number of leaves	1 (0), 2-3 (1), 3-5 (2), more (3)	NL
6.	Width of leaves	narrow (0), middle (1), broad (2)	LW
7.	Pubescence of leaf surface	yes (0), no (1)	LSP
8.	Leaves markings	no (0), yes (1)	LM
9.	Having slender stem	yes (0), no (1)	SS
10.	Stem pubescence	yes (0), no (1)	SP
11.	Number of flowers	2-16 (0), 1 (1)	NF
12.	Colour of tepals	white (0), yellow (1), red (2), reddish (3)	COT
13.	Fading of the blotch in the bright	yes (0), no (1)	FB
14.	Blotch of flower at the base	no (0) yes (1)	BFB
15.	Occurrence of secondary blotch	no (0), yes (1)	OSB
16.	Shade at the outer side of the tepal	no (0), yes (1)	SOT
17.	Colour of anthers	black (0), yellow (1), violet (2), purple (3)	AC
18.	Anther length than filaments	longer (0), equal (1), shorter (2)	AP
19.	Anther opens gradually	no (0), yes (1)	AOG
20.	Filaments surface	glabrous (0), pubescent (1)	FS
21.	Colour of filaments	black (0), yellow (1), bicolor (2), red (3)	FC
22.	Colour of pollen	yellow (0), black (1), purple (2), violet (3)	PC
23.	Shape of ovary	columnar (0), bottle-like (1)	OS
24.	Having long style*	yes (0), no (1)	LS

* longer than ovary

for each of the eight included sections are shown in Figs. 2–9. Because we focused on Central Asian species, the analysed plant material did not include species of sections *Tulipanum*, *Tulipa* and *Sylvestris*, which potentially could affect our results.

Phylogenetic analysis

Phylogenetic analyses were performed on the data matrix (Table 2) using the maximum parsimony method (MP) as implemented in PAUP* version 4.0b10 (Swofford 2002). All characters were considered equally weighted. The heuristic search option was selected using 5000 replications of closest addition sequence with ACCTRAN optimization and TBR (tree bisection reconnection) branch-swapping with MulTrees on and steepest descent off. We then applied a successive re-weighting strategy (Farris 1969) to improve the tree indices and to decrease the effect of characters representing homoplasy

Table 2. Data matrix used in the phylogenetic analyses of *Tulipa* L.

#	Taxa	Endemism	Data
		1. Sect. *Lanatae* (Raamsd.) Zonn.	
1.	*T. affinis* Botschantz.	Nurata and Turkestan ridges	2122220010121110000000101
2.	*T. bactriana* J.de Groot & Tojibaev	South of Uzbekistan (Sherabad Valley)	1132220010121110000000001
3.	*T. carinata* Vved.	West Pamir-Alay	1122220010121110100000101
4.	*T. fosteriana* Irving	West Pamir-Alay	1112220010121110200000201
5.	*T. ingens* Hoog.	West Pamir-Alay	2132220010121100100000101
6.	*T. lanata* Regel	Mountainous Central Asia and Iran	1132220010121110100000001
7.	*T. tubergeniana* Hoog	West Pamir-Alay	1032220010121110000000001
		2. Sect. *Kolpakowskianae* Raamsd. ex Zonn. and Veldk.	
8.	*T. borszczowii* Baker	Central Asia and Iran	1132211001111110001000011
9.	*T. ferganica* Vved.	Ferghana Valley	1112210000111001110010111
10.	*T. hissarica* Popov & Vved.	South-West Pamir-Alay	2022211001111001100010111
11.	*T. intermedia* Tojibaev & J.de Groot	Northern Ferghana	1112211001111100110010111
12.	*T. kolpakowskiana* Baker	Central Asia	1112111001111000120010011
13.	*T. korolkowii* Regel	Central Asia	2112211001121100120020111
14.	*T. korolkowii* Regel f. *rosea* Zonn.	South-West Pamir-Alay	1112211001131100110000111
15.	*T. korshinskyi* Vved.	South-West Pamir-Alay	1122211001101101100010111
16.	*T. lehmanniana* Merckl.	Central Asia and Iran	1132211001111100120010011
17.	*T. scharipovii* Tojibaev	Northern Ferghana	1112211001111000110010111
18.	*T. talassica* Lazkov	West Tien Shan	1101211001111101120010111
19.	*T. zonneveldii* J.de Groot & Tojibaev	South Chatkal	1122311000111001120010111
		3. Sect. *Vinistriatae* (Raamsd.) Zonn.	
20.	*T. albertii* Regel	Central Asia	1122220010120100100010011
21.	*T. butkovii* Botschantz.	Western Chatkal ridge	1022220010121000110030111
22.	*T. greigii* Regel	West Tien-Shan	1122220110120110000000011
23.	*T. micheliana* Hoog	Central Asia and Iran	1132220110120110200000011
24.	*T. mogoltavica* Popov & Vved.	Mogoltau and Kurama ridges	1132220110120110000002111
25.	*T. vvedenskyi* Botschantz.	Kurama ridge	1022220010120100100010011
		4. Sect. *Spiranthera* Vved. ex Zonn. & Veldk.	
26.	*T. anadroma* Botschantz.	Southern Chatkal ridge	1112220010111001111010111
27.	*T. dubia* Vved.	West Tien-Shan	1022220010111001101010011
28.	*T. kaufmanniana* Regel	West Tien-Shan	1011221010111101101010011
29.	*T. tschimganica* Botschantz.	West Tien-Shan	1012220010111101101010011

30.	*T. uzbekistanica* Botschantz. & Sharipov	South-West Hissar ridge	101122001012111012101001
	5. Sect. *Biflores* A.D.Hall ex Zonn. & Veldk.		
31.	*T. bifloriformis* Vved.	West Tien Shan	110210100000110110011011
32.	*T. biflora* Pall.	Widespread	103210100100110112011011
33.	*T. buhseana* Boiss.	Central Asia	110210100100110110011011
34.	*T. dasystemon* Regel	Mountainous Central Asia	100110100111100110011011
35.	*T. dasystemonoides* Vved.	Mountainous Central Asia	110210100010110112011010
36.	*T. jacquesi* Zonn.	South Chatkal ridge	100110100100110111011111
37.	*T. orithyioides* Vved.	Hissar ridge	103210100110110110011011
38.	*T. regelii* Elwes.	Chu-Ili ridge	112200100110110112011011
39.	*T. sogdiana* Bunge	Turan deserts	110210100110110112001011
40.	*T. tarda* Stapf	Central Asia	110110100000110112011011
41.	*T. turkestanica* Regel	Pamir-Alay	110210100000110112011011
	6. Sect. *Clusianae* (Baker) Zonn.		
42.	*T. linifolia* Regel	Pamir-Alay	111230001112110021003001
43.	*T. maximowiczii* Regel	Pamir-Alay	111230001112110021000301
	7. Sect. *Orithyia* (D.Don) Vved.		
44.	*T. heteropetala* Ledeb.	North of Central Asia and Xinjiang	100110100111100112001010
45.	*T. heterophylla* (Regel) Baker	North of Central Asia and Xinjiang	200010100111100112001010
46.	*T. uniflora* Besser ex Baker	Widespread	100110100111100112001010
	8. Sect. *Multiflorae* (Raamsd.) Zonn.		
47.	*T. praestans* Hoog	Hissar ridge	110122001003100011003001
48.	*T. subpraestans* Vved.	Hissar ridge	110122001002100011003001
	Outgroup		
49.	*E. caucasicum*	Caucasus	200010010110110012001000

on tree topologies. In the next step, clade support was evaluated by bootstrapping (Felsenstein 1985) with 20,000 replications with the heuristic search option, closest addition sequence, TBR branch swapping and MulTrees off. The strict consensus tree is given in Fig. 10.

Results

Sectional comparative morphology

1. Subgen. *Tulipa* sect. *Lanatae*

This section is represented by seven species in our analysis. The inner surface with profuse hairs and the same length of the red-coloured perianth are general features of the section. Comparative morphology using *T. lanata* Regel is shown in Fig. 2. Six characters are varying within the section. All other characters were found to be uniform.

2. Subgen. *Tulipa* sect. *Kolpakowskianae*

This section is represented by 12 species in our analysis. Mainly, species of this section tend to have strongly produced bulb tunics, slender stems, yellow tepals and narrow and glaucous leaves. Most than half of the characters (14 out of 24) are varying. Comparative morphology using *T. ferganica* Vved. is shown in Fig. 3.

3. Subgen. *Tulipa* sect. *Vinistriatae*

The section is represented by six species in our analysis. Species usually have red tepals and markings on leaf surfaces. Almost half of the characters (11 out of 24) are varying.

Comparative morphology using *T. greigii* Regel is shown in Fig. 4.

4. Subgen. *Tulipa* sect. *Spiranthera*

This section is represented by five species in our analysis. The gradual and slowly (during 2–3 days) opening of anthers from tip to base is a remarkable feature of this section. Almost half of the characters (10) are varying. Comparative morphology using *T. uzbekistanica* Botschantz. & Scharipov is shown in Fig. 5. *Tulipa uzbekistanica* and *T. anadroma* Botschantz. are distinct species with four and three specific features, respectively.

5. Subgen. *Eriostemones* sect. *Biflores*

This section is represented by 11 species in our analysis. This section can be easily identified by the colour of tepals (usually white and yellow), number of leaves (2), number of flowers (2–16) and small plant size. More than half of the characters (13) were varying. Some species have unique characters such as one leaf with crest-like ridges (*T. regelii* Krasn.), the colour of tepals and absence of blotches at flower base [*T. dasystemon* (Regel) Regel], equal anther position to filaments and black coloured pollen (*T. jacquesii* Zonn.). Comparative morphology using *T. bifloriformis* Vved. is shown in Fig. 6.

6. Subgen. *Clusianae* sect. *Clusianae*

This section was represented by two species in our analysis (*T. linifolia* Regel and *T. maximowiczii* Regel). Glabrous or pubescent stamens, sessile stigmas and woolly hairs of bulbs protruding from the tip are distinct characters of the section *Clusianae*. Most of the characters in this section are shared by its members, but this can be an artefact of the small sample size (only two species). The analysed two species differ from each other in the colour of filaments and pollen, and were synonymised by Christenhusz et al. (2013). Comparative morphology using *T. linifolia* is shown in Fig. 7.

7. Subgen. *Orithyia* sect. *Orithyia*

This section is represented by three species in our analysis [*T. uniflora* (L.) Besser ex Baker, *T. heteropetala* Ledeb. and *T. heterophylla* (Regel) Baker]. Section *Orithyia* is characteristic in its glabrous bulb tunic inside and the relatively long style, which is nearly as long as the ovary. The studied species of sect. *Orithyia* differed in only two characters (HUPB and BS, only in *T. heterophylla*). Comparative morphology using *T. uniflora* is shown in Fig. 8.

8. Subgen. *Tulipa* sect. *Multiflorae*

Two species (*T. praestans* H.B.May and *T. subpraestans* Vved.) were investigated. The plants of this section differ from the other sections by a distinct set of characters including large number of flowers per stem, tough bulb skins and absence of a basal tepal spots. The studied two species differed from each other in the state of tepal colour only, and were thus synonymised by Christenhusz et al. (2013). Comparative morphology using *T. praestans* is shown in Fig. 9.

Cladistic analysis

The bootstrap values for most of the clades were below 50%, which means that the sectional classification did not receive support in the produced tree. Nevertheless, the tree (Fig. 10) roughly corresponds to Zonneveld's (2009) sectional system (except for *T. butkovii*). *Tulipa butkovii* is in our tree placed with *T. subpraestans* and *T. praestans*, i.e. it may belong to sect. *Multiflorae* rather than *Vinistriatae*. Section *Kolpakowskianae* forms a clade, but support for any of these nodes is lacking. *Tulipa regelii* appears to have a firm position in sect. *Biflores*. Like in other studies, the basalmost position is occupied by sect. *Orithyia*, but *T. heterophylla* does not render as part of this clade possibly due to lack of data. This species, originally described as *Eduardoregelia heterophylla* Popov (M 1936) has two characters distinguishing it from *T. heteropetala* and *T. uniflora* (BS-2 and HUPB-0).

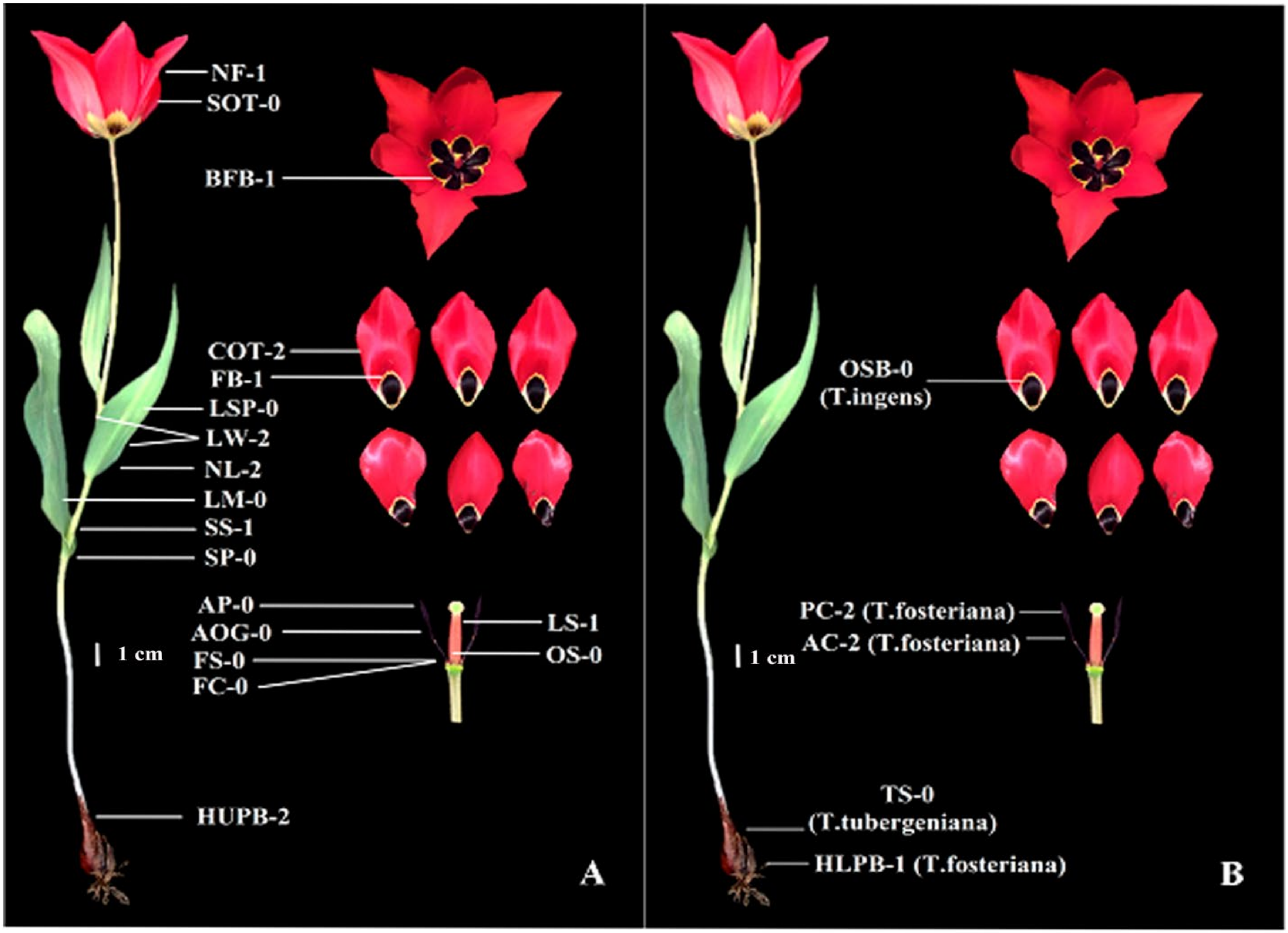

Fig. 2. Uniform (A) and varying (B) characters of species of sect. *Lanatae*

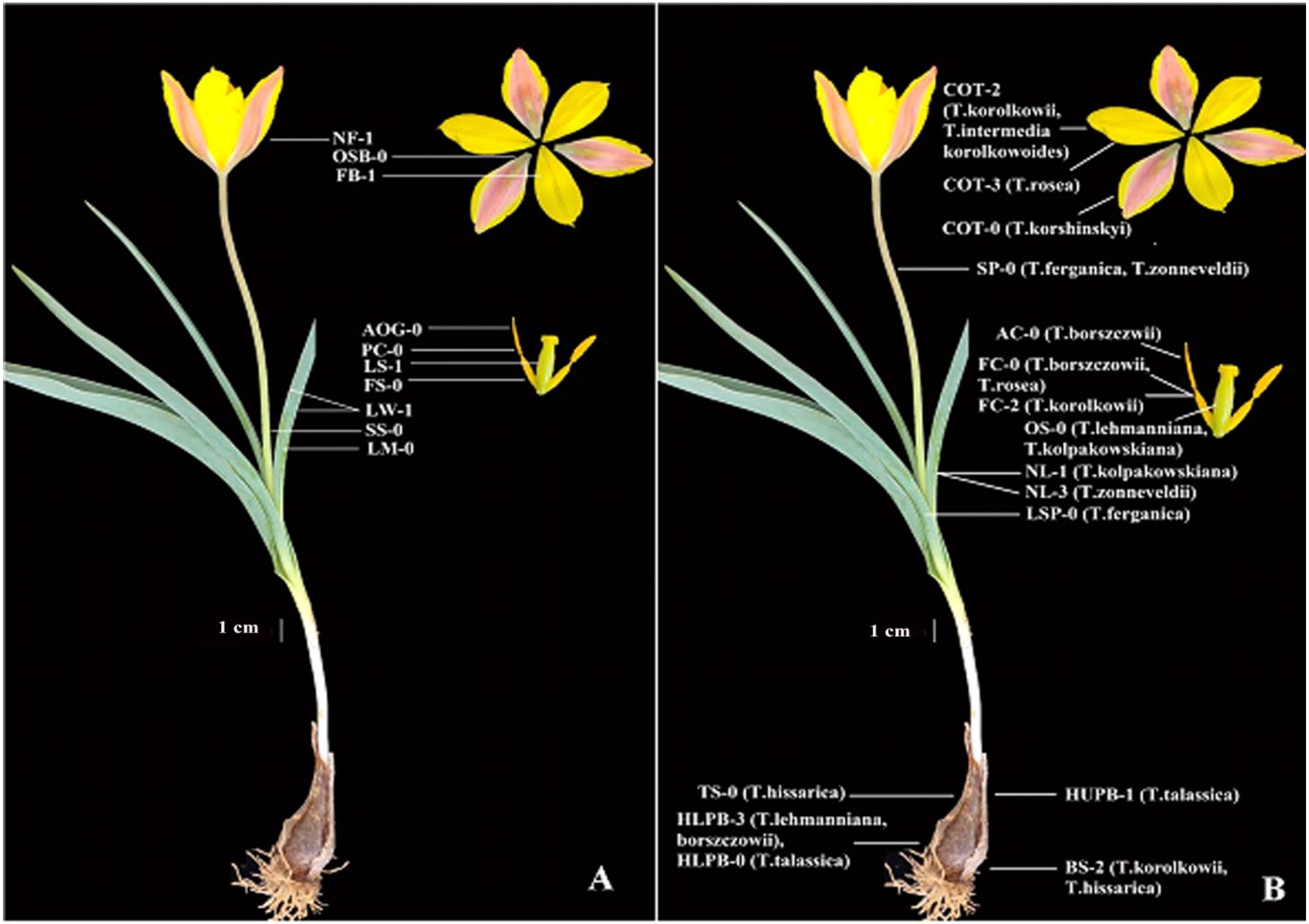

Fig. 3. Uniform (A) and varying (B) characters of species of sect. *Kolpakowskianae*

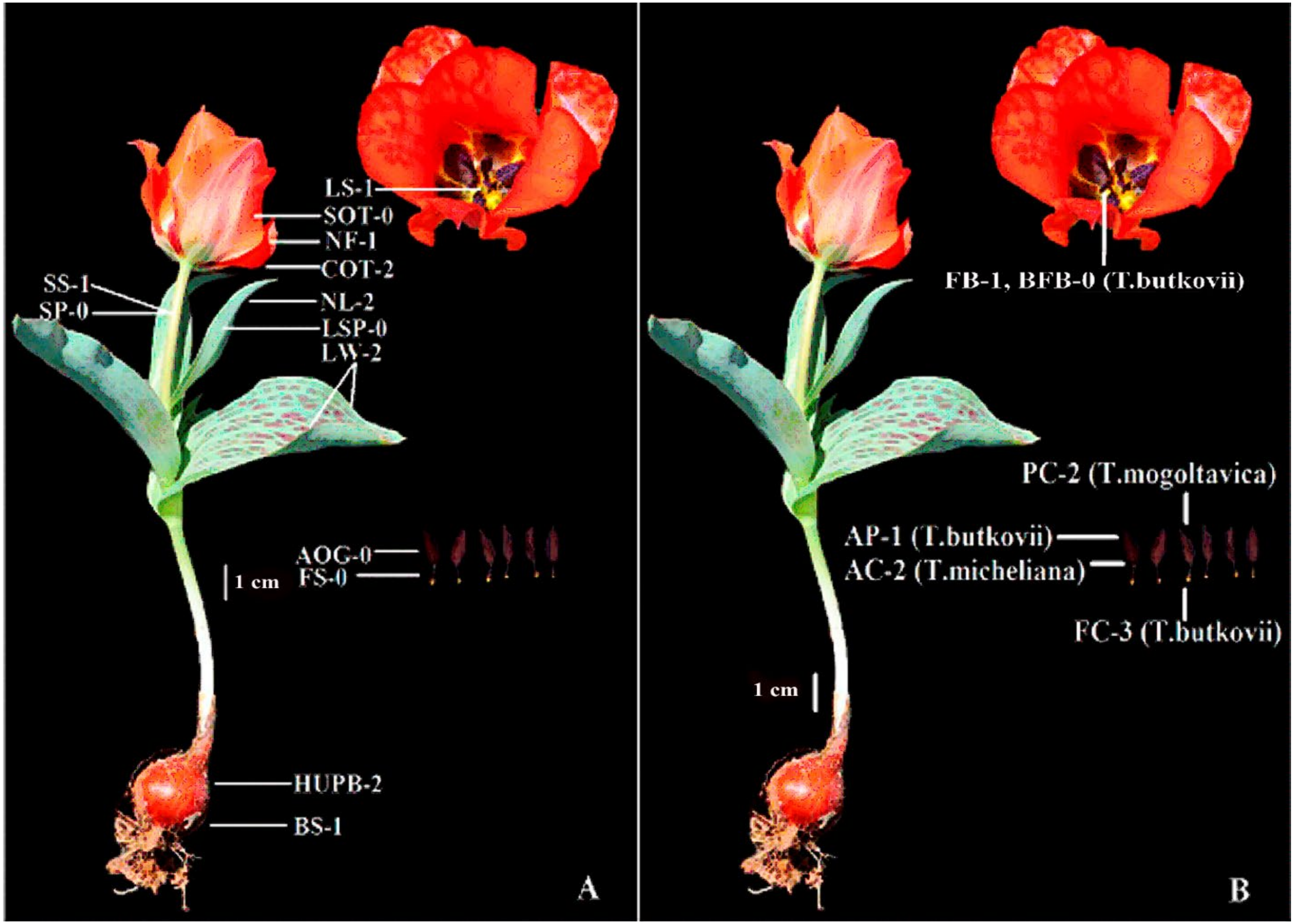

Fig. 4. Uniform (A) and varying (B) characters of species of sect. *Vinistriatae*

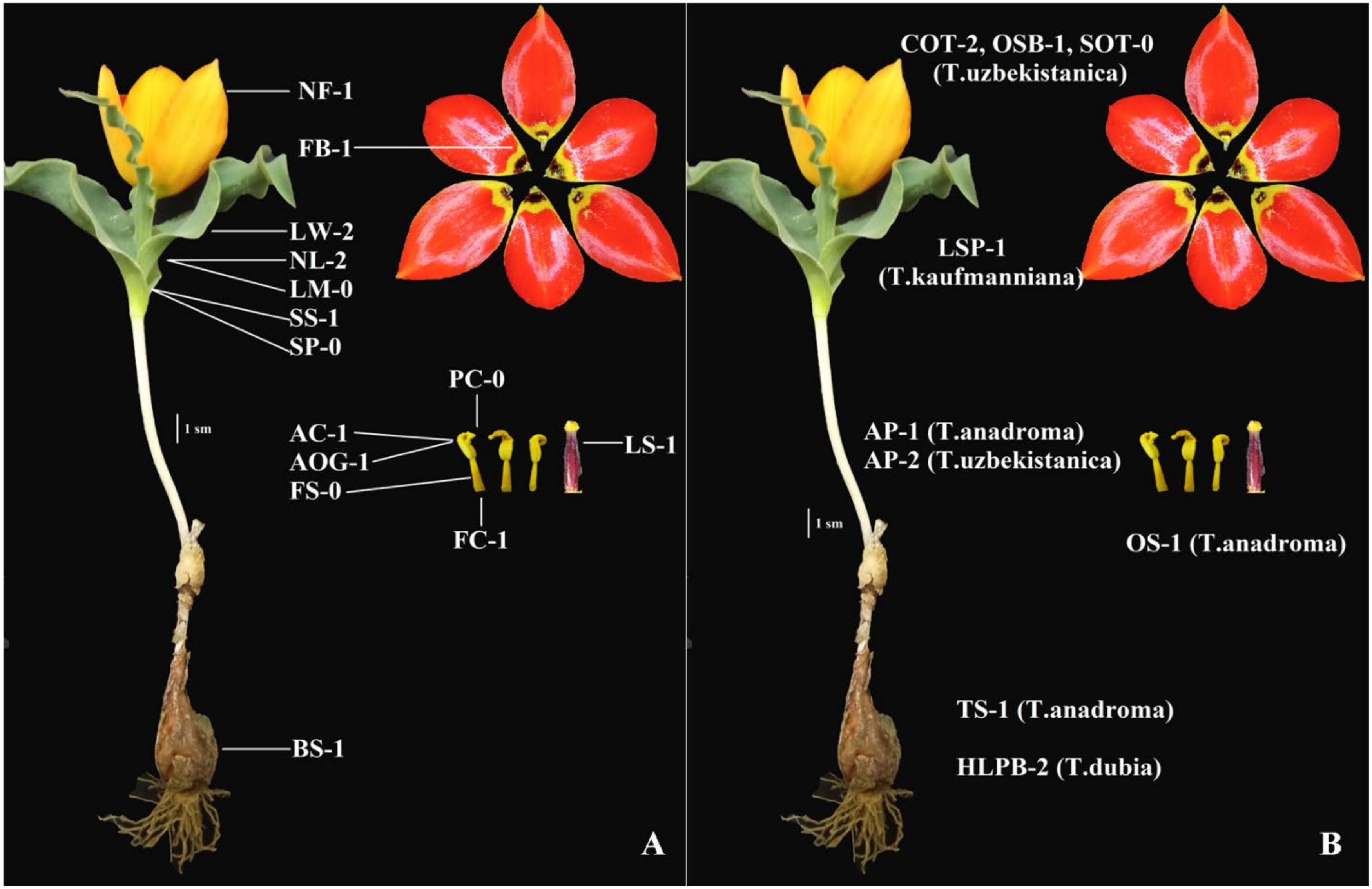

Fig. 5. Uniform (A) and varying (B) characters of species of sect. *Spiranthera.* *Explanation: Inner side of petals of *T. uzbekistanica* is red, but outer side is yellow.

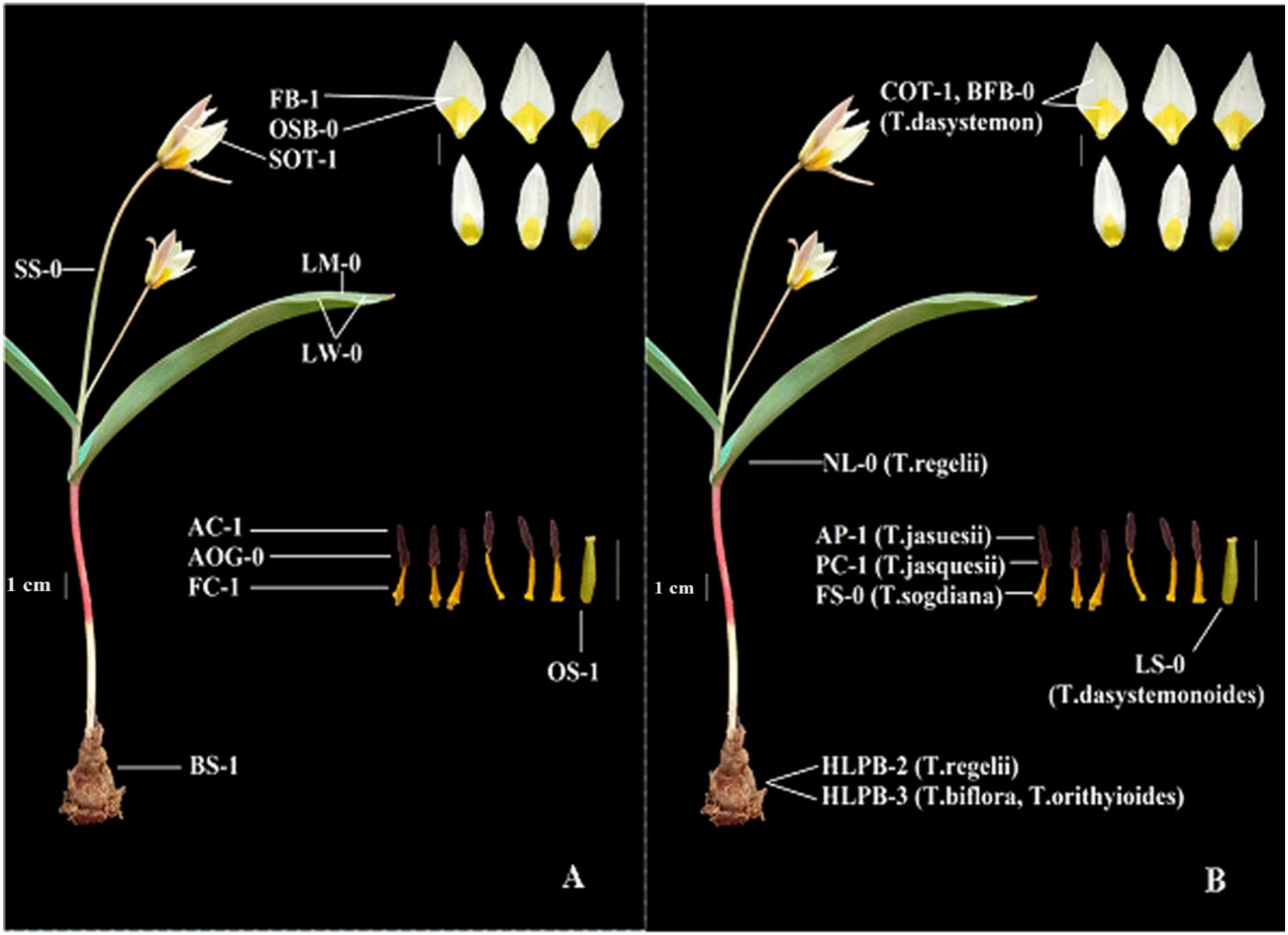

Fig. 6. Uniform (A) and varying (B) characters of species of sect. *Biflores*

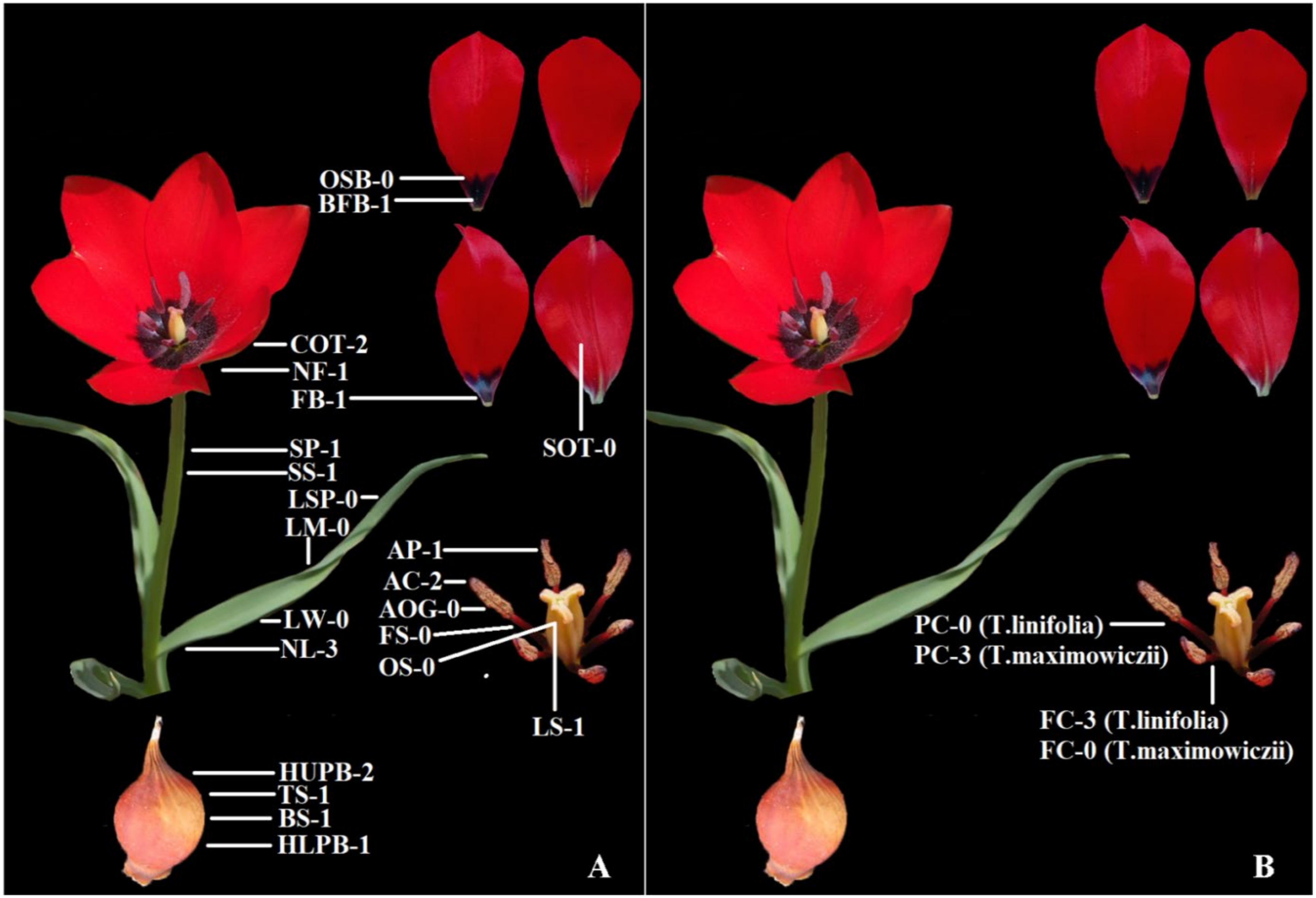

Fig. 7. Uniform (A) and varying (B) characters of species of sect. *Clusianae*

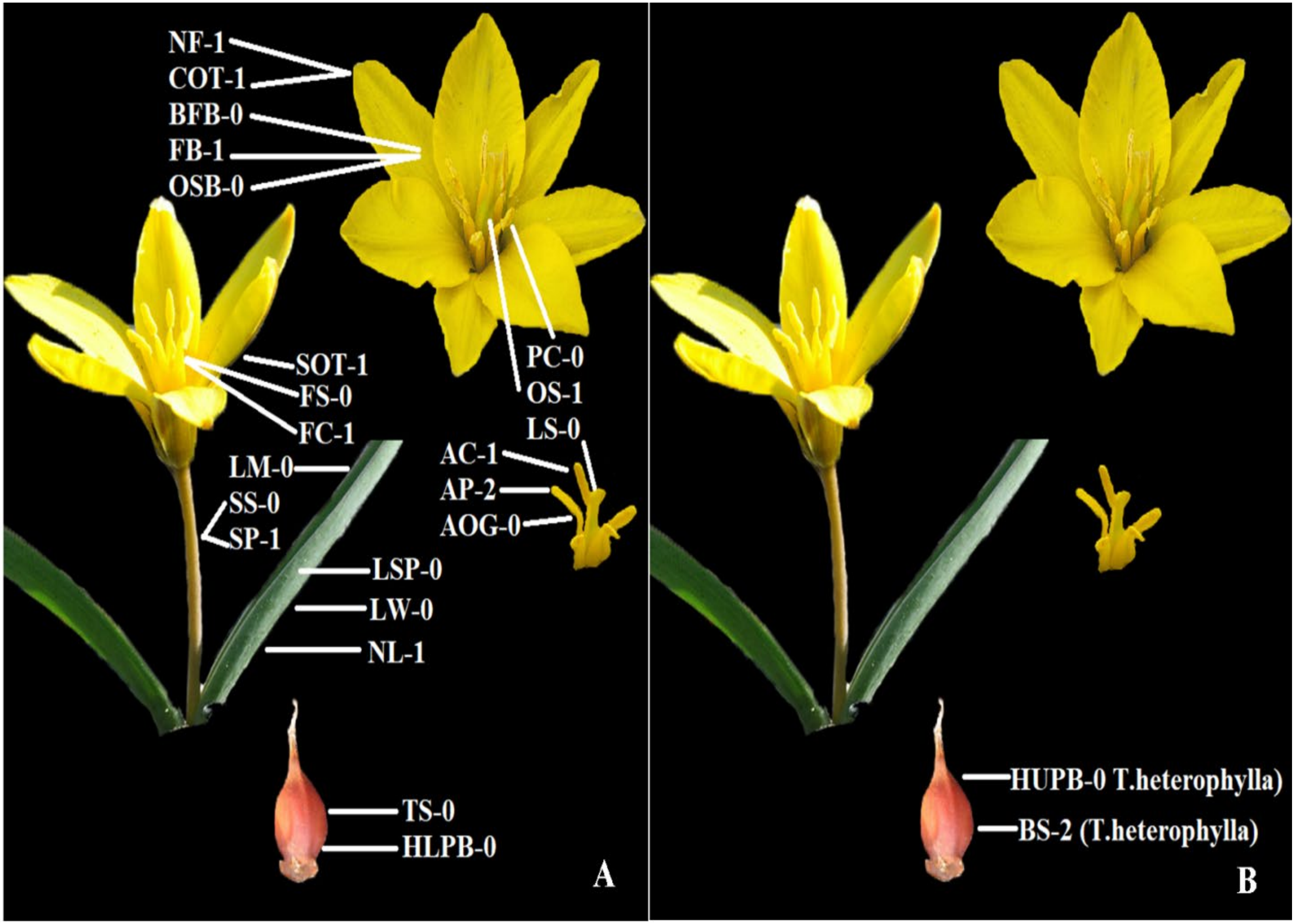

Fig. 8. Uniform (A) and varying (B) characters of species of sect. *Orithyia*

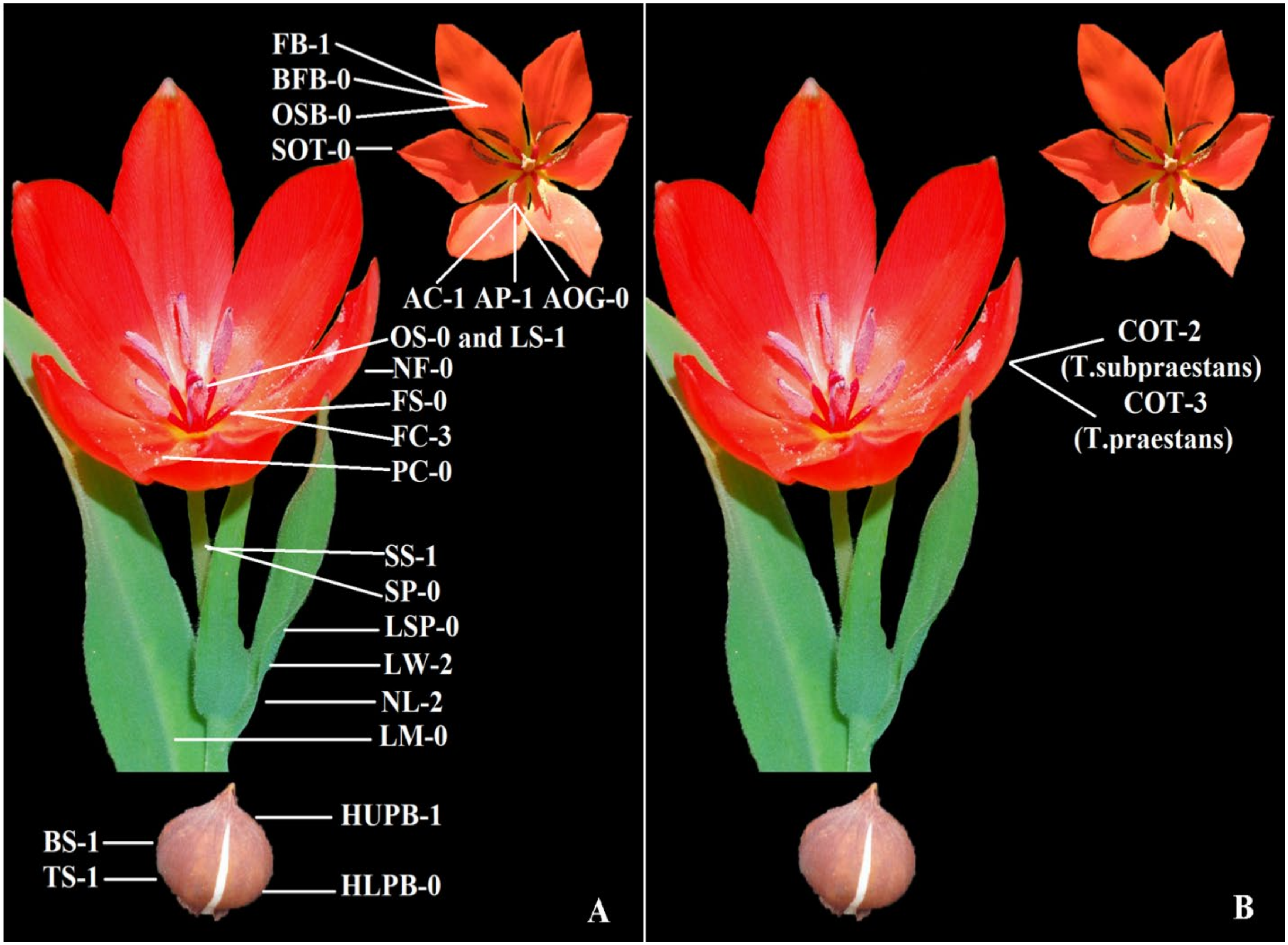

Fig. 9. Uniform (A) and varying (B) characters of species of sect. *Multiflorae*

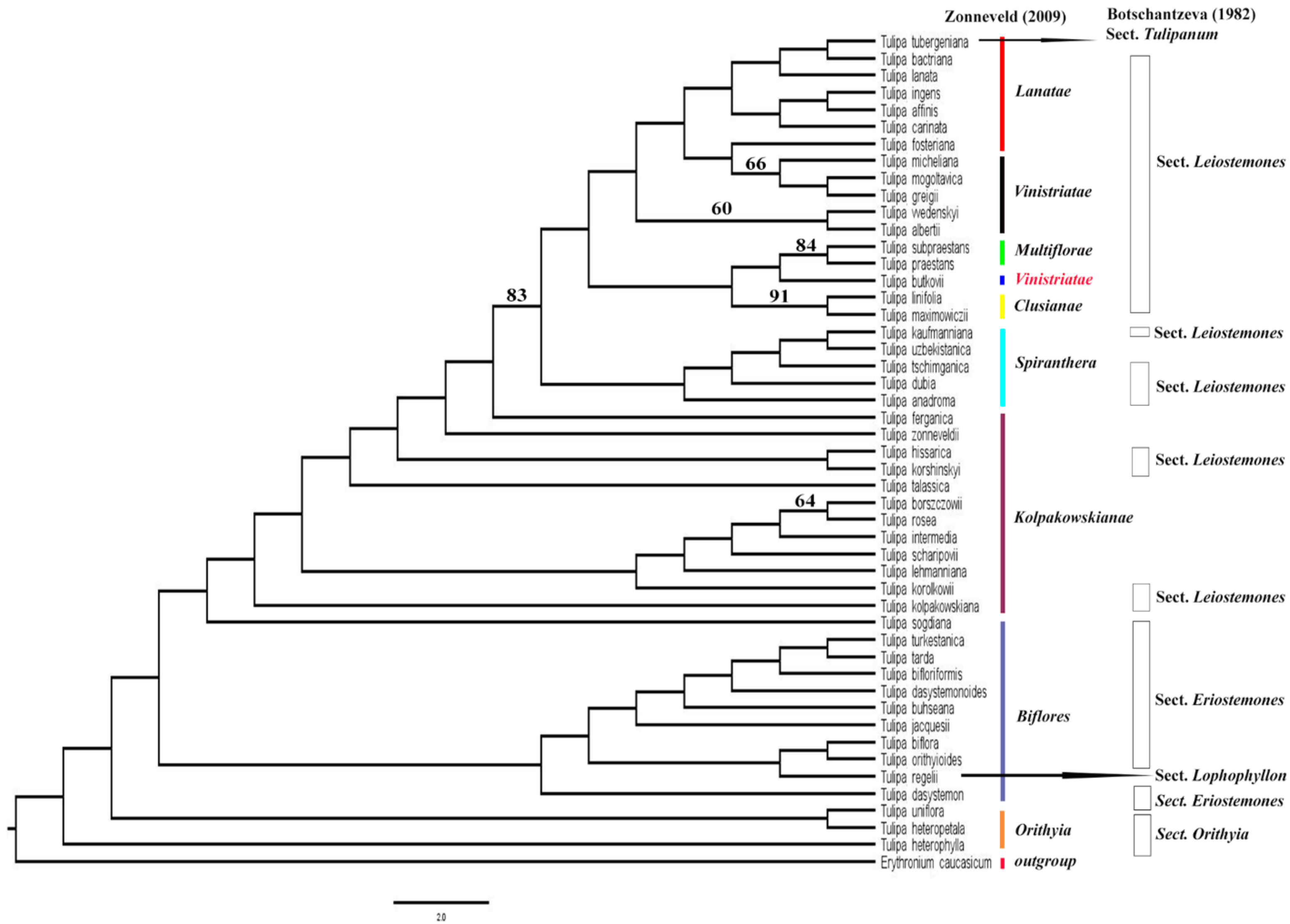

Fig. 10. Strict consensus tree derived from the morphological data matrix after successive weighting by rescaled consistency index and the correspondence of the species sectional positions to systems of Zonneveld (2009) and Botschantzeva (1962). Numbers above branches are bootstrap values. Numbers <50% are not shown.

Discussion

Until the last decade, the taxonomy of *Tulipa* was based solely on morphological data. Boissier (1882) divided the genus into two groups, *Leiostemones* (= subgenus *Tulipa*) and *Eriostemones*, based on the presence or absence of pubescence on the stamen base. Hall (1940) elevated these to subgenus level. He also subdivided *Leiostemones* into five sections (*Clusianae*, *Gesnerianae*, *Eichleres*, *Kolpakowskianae*, *Oculis-solis*) and *Eriostemones* into three sections (*Australes*, *Biflores, Saxatiles*). This classification had not been challenged until Zonneveld (2009), who proposed a 'classification' using nuclear genome size, even though this is not a technique suitable for taxonomic study, because genome size can vary even within a species and gives no indication of relationships. A molecular study by Christenhusz et al. (2013) have found the 'classification' of Zonneveld (2009) wanting and refuted some sections (i.e. *Kolpakowskianae*) and placement of some species (i.e. *T. regelii*, *T. sprengeri* Baker). Christenhusz et al. (2013) provided a historical overview of the genus and also typified the majority of *Tulipa* species and accepted a conservative 78 species, admitting that some species groups need further study.

Although molecular-based phylogenetic studies predominate in modern *Tulipa* taxonomic research (Christenhusz et al. 2013; Pourkhaloee et al. 2018; Hajdari et al. 2021; Li et al. 2021), morphological studies of the genus continue, especially in areas with high species diversity, such as Turkey (Eker et al. 2014) and Iran (Khaleghi et al. 2018). Even though we found no support for any of the clades based in our morphological cladistic scheme, and a single character could therefore change the topology, we still think that the morphological characters used are robust. We therefore discuss below how well the results of our morphology-based cladistic analysis agree with classification systems and molecular studies of the genus *Tulipa*.

I. Morphological studies (I): Baker (1874), Hall (1940) and Van Raamsdonk & De Vries (1992, 1995)

Among early *Tulipa* systems Baker (1874) is discussed in many papers. Baker (1874) divided *Tulipa* into two subgenera: *Eutulipa* (including *Gesnerianae, Eriobulbi, Scabriscapae, Silvestres* and *Saxatiles*) and *Orithyia* (including *T. uniflora* and *T. heterophylla*; and *T. edulis* (Miq.) Baker which is now placed in the genus *Amana* Honda). Hall's well-known classification system (Hall 1940) focused on ploidy and was to large extent based on cultivated plants of unknown or poorly known origin (Botschantzeva 1962). He followed Boissier (1882) in accepting the subgenera *Leiostemones* and *Eriostemones*. Furthermore, he divided *Leiostemones* into five sections (*Clusianae*, *Eichleres, Gesnerianae, Kolpakowskianae,* and *Oculus-solis*) and *Eriostemones* into three sections (*Australes, Biflores* and *Saxatiles*). In our study, only the species of sect. *Biflores* were congruent with Hall`s system, while phylogenetic positions of many species from the other sections contradicted Hall's classification.

Van Raamsdonk and De Vries (1992, 1995) investigated 35 morphological character variations by the help of principal components and canonical variates. In subgenus *Tulipa* they included sections *Tulipa, Kolpakowskianae* and *Eichleres* and subgenus *Eriostemones* more or less follows Hall's system. Section *Orithyia* was not included.

II. Morphological studies (II): Vvedensky (1935) and Botschantzeva (1962) After Regel's (1873) treatment of the genus, the taxonomic treatments of the genus *Tulipa* of by Vvedensky (1935) was perhaps the best-known. His system has been used for a long time in the Soviet Union and was studied by Hall (1940) and it became the basis for subsequent works by Vvedensky (Vvedensky 1941; Vvedensky & Kovalevskaja 1971) and his collaborators (Poljakova 1958; Botschantzeva 1962; Silina 1977). This classification system differs from other classifications in having two additional sections: *Spiranthera* and *Lophophyllon*, which were originally described as monotypic (with *T.*

kaufmanniana Regel and *T. regelii*, respectively). In his classification, Vvedensky also relocated *T. sogdiana* Bunge from sect. *Leiostemones* to sect. *Eriostemones*. The classifications of Van Raamsdonk and De Vries (1992), Veldkamp and Zonneveld (2012) and our morphology based study confirms the status of *Spiranthera* as a distinct section and the placement of *T. sogdiana* in sect. *Biflores* (=*Eriostemones*). Christenhusz et al. (2013) places *T. sogdiana* as a synonym of *T. biflora* Pall., pending further study. It differs from *T. biflora* only in having glabrous stamens, which is why it was placed among *Leiostemones* originally. In contrast, the taxonomic status of sect. *Lophophyllon* is not confirmed both in our study and molecular studies (Christenhusz et al. 2013). *Tulipa regelii* turned out to be a member of the monophyletic sect. *Biflores* (=*Eriostemones*), and it matches this morphologically. It only differs in having unusually ribbed leaves. *Tulipa tubergeniana* Hoog as a representative of sect. *Tulipanum sensu* Vvedensky together with *T. bactriana* J.de Groot & Tojibaev in our tree are members of sect. *Lanatae.* The second species is newly described and morphologically close to the species of sect. *Tulipanum sensu* Reboul and Vvedensky (De Groot & Tojibaev 2020).

Botschantzeva (1962) added 19 tulip species to Vvedensky's system and placed them into six sections (*Tulipanum, Leiostemones*, *Spiranthera, Lophophyllon*, *Eriostemones* and *Orithyia*) using solely morphological features. In our study, these placements were fully supported, except for sect. *Lophophyllon*.

III. Genome size studies: Zonneveld (2009); Veldkamp & Zonneveld (2012)

We previously expressed our concerns about the Zonneveld (2009) 'system', but we used it in a synopsis of *Tulipa* for Uzbekistan Tojibaev and Beshko (2014). Zonneveld (2009) based his classification on genome size measurements and morphology, but as mentioned, genome size is inappropriate for inferring relationships. In a subsequent revision, Veldkamp & Zonneveld (2012) subdivided *Tulipa* into four subgenera: *Tulipa, Eriostemones, Clusianae* and *Orithyia*, which they based on preliminary molecular studies (Fay et al. 2001) and these subgenera were further subdivided into a total of 12 sections.

In our phylogenetic tree, the positions of 48 Central Asian species correspond to the infrageneric *Tulipa* classification by Zonneveld (2009), except for subgenus *Clusianae* and *Tulipa butkovii* Botschantz. *Tulipa butkovii* also does not seem to be in the correct placement. The position of subgenus *Clusianae* was located among sections of subgenus *Tulipa*, probably due to the limited numer of species included in our study and the morphological characters used not being discriminating enough.

Tulipa butkovii has red tepals with brown-violet spots and red or purple filaments, traits that it shares with species of sect. *Multiflorae*. In the protologue of *T. butkovii*, Botschantzeva indicated *T. praestans* as the most closely related ally, and later, in the checklist of species known to occur in the USSR (Botschantzeva 1962), placed it between *T. praestans* and *T. subpraestans* (sect. *Leiostemones*). Based on this, it seems certain that Zonneveld's assignment of *T. butkovii* to *Vinistrae* is incorrect.

The placement of *Orithyia* in our morphology-based tree agrees with its position in the classification of Veldkamp & Zonneveld (2012) Christenhusz et al. (2013), where it is placed as the first diverging clade in *Tulipa*. However, positions of species comprising sections *Multiflorae* and *Clusiana*, and especially *T. butkovii* from *Vinistriatae* in our tree raise questions about their current section assignments, or, alternatively, validity of the sections to which they belong.

In subgenus *Eriostemones*, species of sect. *Biflores* were included in this cladistic analysis and their placement agrees with the Zonneveld's system. Species of sect. *Tulipanum* and *Tulipa* (subgenus *Tulipa*) and sect. *Sylvestris* (subgenus *Eriostemones*) were not included in this study because of its focus on Central Asian species.

Several of our findings apply to all discussed classifications. In subgenus *Tulipa*, sect. *Kolpakowskianae* was found to be polyphyletic and therefore is not supported. Earlier, there were concerns about existence of this section as a distinct group (Christenhusz et al. 2013). Thus, revision of this section and re-classification of the species comprising this section is necessary.

IV. Molecular (DNA) studies: Christenhusz et al. (2013)

The system of Christenhusz et al. (Christenhusz et al. 2013) was based on DNA sequences from five plastid regions and the internal transcribed spacer (ITS) region of nuclear ribosomal DNA. This was accompanied by a thorough taxonomic review and typification of most accepted species. The phylogenetic studies confirmed the separation of Clusianae as a subgenus, first found by Fay et al. (2001) and adopted by Zonneveld (2009) and Veldkamp & Zonneveld (2012). The classification of Christenhusz et al. (2013) largely agrees with the subdivision of Veldkamp & Zonneveld (2012), but it also has some differences. For example, Christenhusz et al. (2013) found that *T. regelii* belongs to subgenus *Eriostemones.* In our phylogenetic tree *T. regelii* has a firm position in *Biflores*. Christenhusz et al. (2013) also found that sect. *Kolpakowskianae* is an artificial group, which is corroborated by our findings.

Molecular studies are currently ongoing at regional levels (Hajdari et al. 2021; Li et al. 2021) and we hope that in the future an system can be produced using intergated taxonomy of molecular and morphological analyses when more data becomes available.

Conclusions

This cladistic analysis of morphological characters of 48 species from Central Asia, the primary center of diversity for *Tulipa*, expanded our knowledge of the genus in the region. Even though our support values are low or absent, our results generally agree with the molecular-based system of Christenhusz et al. (2013) and genome size-based system of Zonneveld (2009), but also suggest a need for incorporation of some elements of the classification of Vvedensky (1935), such as sect. *Spiranthera*. In general, approach of Vvedensky based on recognition of importance of spatial isolation in genus evolution and therefore taxonomy, needs a closer attention by modern *Tulipa* taxonomists. This morphological study is a first step in producing an integrated study on the genus *Tulipa*, which may help to study character evolution and biogeography in this intriguing group of plants.

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