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Tiptoe through the tulips – cultural history, molecular phylogenetics and classification of *Tulipa* (Liliaceae)

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Tulipa (tulips; Liliaceae) is a genus of geophytes comprising c. 76 species, occurring from southwestern Europe and North Africa to Central Asia. The taxonomy and classification of the genus have been contentious in the past. We investigated the phylogenetic relationships in the genus using DNA sequences from five plastid regions (trnL intron and trnL-trnF spacer, rpl16 intron, rps12-rpl20 intergenic spacer and matK) and the internal transcribed spacer (ITS) region of nuclear ribosomal DNA. Amana and Erythronium were used as outgroups. Sequences were obtained from 25 Tulipa taxa representing all major lineages previously identified as distinct and four outgroups (two Amana spp. and two Erythronium spp.). In the combined maximum parsimony analysis, Tulipa was strongly supported as monophyletic and four clearly defined clades in the genus were obtained, although the relationships between them were unclear. In support of previous molecular studies, the results suggest that section Clusianae should be excluded from subgenus Tulipa and accepted at subgeneric rank. Subgenus Eriostemones and subgenus Tulipa (excluding Clusianae) were both strongly supported. Tulipa sprengeri, traditionally placed in subgenus Tulipa, was shown to be a member of Eriostemones. Orithyia, in this study represented by T. uniflora, formed a fourth lineage, also to be treated at subgeneric level. In the Bayesian analysis, the genus Tulipa was strongly supported and the same four lineages (subgenera) were identified. In this case, Orithyia was sister to the rest of the genus (with moderate support) and subgenera Clusianae and Eriostemones together formed a clade with strong support. Original species descriptions and type specimens of as many names as possible were reviewed and, on this basis, a revised checklist with full synonymy, typification and distribution is provided. The status of T. xgesneriana and its synonyms is discussed. All accepted species are classified into the four subgenera supported by our phylogenetic study. © 2013 The Linnean Society of London, Botanical Journal of the Linnean Society, 2013, 172, 280 - 328.

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INTRODUCTION

☐ Come tiptoe through the tulips with me

(A. Dubin, 1929)

Tulipa L. (Liliaceae) is a genus of bulbous monocots with, depending on the author, 50–60 (Van Raamsdonk & De Vries, 1992, 1995), 87 (Zonneveld, 2009), c. 100 (Hall, 1940; Botschantzeva, 1982) or 114 (WCSP, 2013) species. We accept 76 species in this paper (Appendix).

The bulbs of *Tulipa* spp. are covered with a thin tunic that is glabrous or hairy inside. The usually large flowers are trimerous, consisting of two whorls of three tepals that are brightly coloured, with the two whorls sometimes differing in colour or having different coloured blotches at the base of each tepal. There are two whorls of three stamens that vary in length and may be glabrous or hairy. Many vegetative and floral characters traditionally used to characterize species appear to be plastic, sometimes even within populations of a species. In past classifications, some of these characters were employed to describe new taxa or to define sections or subgenera. As a consequence of population variability and hybridization and selection in early horticulture and subsequent naturalization, the classification of tulips has been contentious and notoriously complicated. Many species were described from cultivated bulbs and, even though they were collected from the wild, variability in natural populations was often not studied when species were described. This was complicated by 'species' only known in cultivation, but never retrieved from the wild. As noted by Marais (1984), less than one-half of the tulip species found in Turkey

are native to that country, and no tulips are native to Europe west of the Balkans. Tulipa sylvestris L. subsp. australis (Link) Pamp. is, however, known to be native in the mountains of southern Portugal. Spain and North Africa (Güemes, 2013), and so Marais' statement is not entirely true. Wild tulips from Italy, France or Switzerland are certainly naturalized and are often referred to as neo-tulipae (Hall, 1929, 1940). Natural populations of *Tulipa* occur from the southern Iberian Peninsula and Morocco, northern Tunisia and Libya, Sicily, Greece, the southern Balkans, the southern Ukraine to central Siberia, around the Black Sea coast south to Anatolia, through the Levant to Egypt and Saudi Arabia, the Caucasus, Iraq, Iran, and Central Asia east to western China. Mongolia and the Himalayas (Fig. 1), from sea level up to c. 3000 m in the Tien Shan Mountains. Tulipa sylvestris is naturalized throughout Europe, as far north as Norway, Scotland and Finland, and in North America. Tulipa spp. usually grow in meadows, steppes and chaparral (Hall, 1940), but also commonly occur in fields, orchards, roadsides and abandoned gardens, where they may have been introduced in earlier times, either intentionally or accidentally.

Modern classifications have focused on use of stable characters, such as tunic and stamen pubescence, rather than flower colour or tepal shape. Hall (1938, 1940) focused on ploidy and described several species on that basis, even though they are morphologically difficult to distinguish. Ploidy has also been used in deciding which taxa should be treated at subspecific levels (e.g. in the case of subspecies treated under *T. saxatilis* Sieber ex Spreng. and *T. sylvestris*), although this concept appears to be flawed. Polyploid

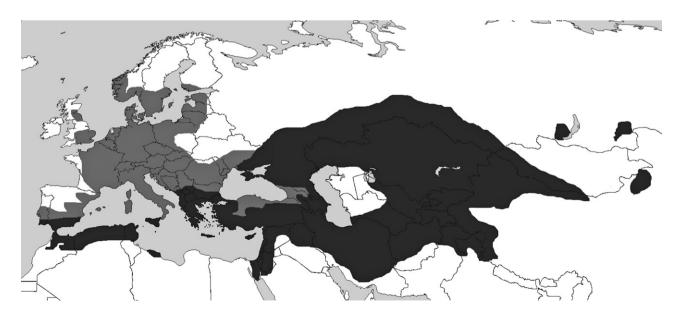


Figure 1. Distribution map of Tulipa. The native range is indicated in dark grey, the naturalized range in light grey.

taxa are often sterile and only maintained in cultivation, sometimes becoming naturalized through vegetative reproduction, but they should not automatically be treated as separate species. Polyploidy is common, and several ploidies can be found in native populations of various species (Botschantzeva, 1982).

A few species with a more eastern distribution (China, Korea, Japan) are now generally separated as the genus Amana Honda (1935). Recent phylogenetic studies (Fay & Chase, 2000; Fay et al., 2001; Allen, Soltis & Soltis, 2003; Rønsted et al., 2005; Clennett et al., 2012) have supported this separation, with all studies indicating a close relationship between Erythronium L., Amana and Tulipa (Fig. 2); these form a well-supported clade in Lilioideae of Liliaceae. usually with Amana as part of the Erythronium clade (Clennett et al., 2012), and Tulipa being monophyletic in the traditional sense, excluding T. edulis (Miq.) Baker [= *Amana edulis* (Miq.) Honda]. We prefer to maintain these three genera, for the sake of traditional usage and taxonomic stability of names, although the three genera are close, share many morphological characters and could easily be united. If it were not for the wide usage of these names in horticulture, the genera would probably have been treated as a single genus.

The infrageneric classification of *Tulipa* has been the subject of numerous treatments, varying mainly in the level at which the infrageneric taxa were recognized (Table 1). Table 1 is discussed below in the light of our phylogenetic findings. Because the literature on *Tulipa* is extensive and often confusing, we here 'tiptoe through the tulips', first providing an historical overview of their cultural importance, taxonomic history and classification, followed by a molecular phylogenetic analysis and discussion of the evolution in the group.

CULTURAL HISTORY OF TULIPS

Persian poets, such as Omar Khayyam, already celebrated the beauty of tulips in the early 12th century (Segal, 1993), but they were most probably known in earlier times, because a steppe full of flowering tulips must have been a sight that travellers would have included in their travel stories. Tulips were an intrinsic part of the early Islamic gardens in Persia and Bactria, where gardeners had a choice of an array of species collected from the wild.

When Seljuk tribes moved west from their homelands in Central Asia into Anatolia, they brought tulips with them (Van der Goes, 2004), resulting in a larger number (18; Baytop, 1993) of *Tulipa* spp. currently occurring in Turkey, only about seven of which are native, the others having escaped from cultivation and established themselves in the suitable climate of

the Anatolian plains and mountains. In present-day Turkey, there are several places called Laleli (place of the tulips), and tulips feature dominantly in decorative motifs on tiles, ceramics, textiles, carpets, manuscripts, miniatures, sculptures, reliefs, murals and headstones (Roding & Theunissen, 1993; Van der Goes, 2004).

Tulips do not appear in Byzantine manuscripts, not because these flowers were unappreciated, but more likely because the artists were not familiar with tulips. According to the *Defter-i Lalezar-i Istanbul* (Book of tulip gardens in Istanbul), only one kind of tulip was known in the surroundings of Byzantium before the Seljuk invasion of Baghdad in 1055 (Pavord, 1999). The earliest record of tulips in present-day Turkey is from tiles in the Kubadabad Sarayı, the palace of Alaeddin Keykubad I in Beyşehir (built c. 1236; Meinecke, 1986).

Under Ottoman rule, tulips flourished in the cities of Anatolia, especially in Istanbul, where, after conquering Constantinople in the 15th century, Sultan Mehmed II laid out vast gardens in the city and around his newly built palace, the Topkapı Sarayı, containing many tulips (Segal, 1993). The Turkish word for tulip is *lale*, which is spelt with the same Arabic letters as Allah, and hence it was often used as a religious symbol (Van der Goes, 2004). The tulip also became the symbol of the ruling family of Osman, increasing the usage in artefacts and on murals and buildings, especially those ordered by the Sultan (Van der Goes, 2004). Most tulips were dug up from the wild and planted in gardens, and so no selections were initially made, although rare aberrant forms or colour variations were valued and multiplied vegetatively in gardens. Tulips were also brought from other parts of the expanding empire and, on Sultan Murad IV's expedition to the east, the accompanying historian Hodja Hasan Efendi brought seven kinds of tulips with him from Persia to grow in the gardens of Istanbul (Baytop, 1993; Payord, 1999).

Under Suleyman the Magnificent (c. 1495–1566), tulips became established in Ottoman horticulture, spreading them to all corners of the empire, and, during the 16th century, tulips became so much part of Ottoman culture that almost no design was made without a tulip, changing it into a national symbol. In this period, later called the 'tulip era' by historians (Roding & Theunissen, 1993; Van der Goes, 2004), tulips started to appear in Iznik ceramics, and the brilliant red colour that made Iznik glazing famous appears to have been employed, or maybe even developed, especially to illustrate tulips (Van der Goes, 2004). In this period, Ottoman horticulturalists began to specialize in tulips, and Sultan Selim II ordered large numbers of tulip bulbs from various parts of his empire (usually gathered from the wild) to be used in



Figure 2. The *Tulipa* clade of Liliaceae tribe Tulipae. A, *Erythronium dens-canis*. B, *Amana edulis*. C, *Tulipa uniflora* (subgenus *Orithyia*). D, *Tulipa clusiana* (subgenus *Clusianae*). E, *Tulipa turkestanica* (subgenus *Eriostemones*). F, *Tulipa agenensis* (subgenus *Tulipa*). Photograph C by Natalia Ostromenskaya, all others by Maarten Christenhusz.

 Table 1. Historical overview of infrageneric classification in Tulipa

Baker (1874)	4)	Boissier (1882)	Hall (1940)		Stork (1984)		Van Raamsdoi (1992, 1995)	Van Raamsdonk & De Vries (1992, 1995)	Veldkamp & Zonneveld (2012)	12)
${\rm subgenus}\\ Eutulipa*$	Gesnerianae + Eriobulbi	\$ Leios temones	subgenus <i>Leiostemones</i> †	subsection Gesnerianae‡	$\begin{array}{c} {\rm section} \\ Tulipa \end{array}$	group Gesnerianae¶	subgenus <i>Tulipa</i>	$section \ Tulipa$	${\rm subgenus} \\ Tulipa$	$\begin{array}{c} {\rm section} \\ Tulipa^{**} \end{array}$
	P.P. Scabriscapae p.p.			subsection Kolpakowskianae		group Kolpakowskianae		section Kolpakowskianae		section Kolpakowskianae
	Scaoriscapae p.p.			Eichleres		group <i>Eichler</i> es		Eichleres		Section $Lanatae$ $Section$
										Spiranthera section Multiflorae
	Eriobulbi			subsection		group		section		section
	p.p. + Scabriscapae			Oculus-solis		Oculus-solis		Tulipanum		Tulipanum
	p.p. $Eriobulbi$ $p.p.$			$subsection \ Clusianae$		${\rm group} \\ Clusianae$		section Clusianae	$subgenus$ $Clusianae \dagger \dagger$	I
	Silvestres (including	$\S Erios temones$	subgenus $Eriostemones$	$section \\ Australes$	$rac{ m section}{Eriostemones}$	$rac{ ext{group}}{ ext{Australes}}$	$rac{1}{2}$ subgenus	$section \\ Australes$	subgenus Eriostemones	$section \\ Sylvestres$
	Saxatiles p.p. + Biflores			$section \ Biflores$		group <i>Biftores</i>		'section' $Biflores\ddagger$		section Biflores
	sensu Hall)									
	Saxatiles			$section \\ Saxatiles$		group Saxatiles		$section \\ Saxatiles$		section Saxatiles
subgenus Orithyia¶¶	1	[not included]	$ m section \ Orithyia$	I	$section \ Orithyia$	I	[not included]	I	subgenus <i>Orithyia</i>	I
			genus Amana	I					genus Amana	I

*Including Eriobulbi, Gesnerianae, Scabriscapae, Saxatiles, Silvestres, but these divisions only approximately relate to the sections/subsections of later authors. Hall stated that Leiostemones do not constitute a single natural sub-genus, but are a gathering of all tulips other than the Eriostemones.

Hall used 'subsection' for groups in Leiostemones and 'section' for groups in Eriostemones. He discussed Orithyia without making a decision about its affiliation as he did not have access to material. He treated Amana as a distinct genus. Tulipa schmidtii and T. sprengeri were treated as solitary species.

¶Stork used 'group', 'series' and 'subsection' interchangeably for the divisions at this level.

**Section Tulipa includes section Eichleres p.p. sensu Van Raamsdonk & De Vries.

††Invalidly published by Zonneveld (2009) and validated by Veldkamp & Zonneveld (2012).

#In their second paper, the authors referred to sections, but did not change the status of subsection Biflores to a section. This was eventually validated by Veldkamp & Zonneveld (2012). Some sections were subdivided into series.

Ill Including Amana edulis (as Tulipa edulis).

mass plantings (Pavord, 1999). High prices were paid for special types of tulip bulbs, and fixed prices were set by the Mayor of Istanbul to keep speculation under control, an omen of what was to come in Europe a century later.

The western name for the tulip is derived from the Persian dulband, or the equivalent Turkish türbent, meaning a turban, and one explanation is that the flower was compared with turbans commonly worn by Ottoman men in 16th century Anatolia. This is in line with a Turkish chronicler comparing the battlefield at Kossovo Field (where the Ottomans fought the Serbians in 1389) with a bed of tulips, because the field was strewn with heads and turbans (Pavord, 1999). An alternative explanation of the etymology of the name is the fashion of noblemen in Istanbul to wear a tulip on their turbans and, when asked what was the name of the flower, the translator may have confused the name for the headdress with the flower. Whatever the origin of the name, it most probably spread from Spanish tulipan or Italian tulipano into German tulpe or Dutch tulp (where, in the Germanic languages, the '-an' was mistaken for a suffix) and into other European languages including Latin, hence its scientific name Tulipa. In Ottoman times, tulips with thin pointed tepals, similar to T. cornuta Delile (= T. 'Cornuta'; in cultivation erroneously as T. acuminata hort., non Vahl), were preferred over those with round tepals that would become popular in Europe. Tulipa 'Cornuta' is not known in the wild and should be treated as a cultivar, not a species. Tulips with pointed tepals probably arose from complex hybridization and selection from the various cultivars grown in Istanbul and from bulbs imported into the city from the east and west. Breeding tulips became popular in the east and west, but, whereas the tulip in Turkish culture was more or less a symbol of paradise on earth and had almost a divine status, in the Netherlands it represented the briefness of life (Roding & Theunissen, 1993). Hall (1940) suggested that the favourite Turkish needle tulips arose from hybridization between T. gesneriana L. and T. suaveolens Roth, although the first is itself a complex garden hybrid, possibly derived from the latter. Other species, such as T. armena Boiss, T. agenensis Redouté and T. lanata Regel, or other species from Central Asia, were involved in producing the large diversity of garden tulips.

No tulips appear in the flower-strewn borders of European medieval manuscripts (Pavord, 1999), and therefore they must have been unknown in most of Europe (with the exception of southern Spain, Greece and the Balkans). Dodonaeus (1568) wrote that tulips were not indigenous to Italy and the Netherlands. Travellers to the Ottoman Empire, such as Ghiselin de Busbecq (1522–1591) and Belon (1517–1564),

noted tulips in their travel accounts and were probably responsible for the change in name from 'lale' (used in both Turkish and Arabic languages) to 'tulipan' (of Latin and Germanic languages). Belon additionally mentioned that merchants had already started a trade in tulips, with the first tulip bulbs reaching the harbour of Antwerp in 1562. However, these were mistaken for onions and were roasted over a fire or were planted in gardens with vegetables where they soon perished (Hall, 1929; Pavord, 1999).

Even though tulips were already in cultivation in Portugal, where they were introduced in 1530 (Pavord, 1999), the first illustration of a tulip in cultivation is by Gesner, who described a tulip that he saw flowering in Herwart's garden in Augsburg. Bavaria, in April 1559 (Gesner, 1561). This was presented as an important event. Gesner's tulips were scented, whereas Belon and De Busbecq stated that the flowers were beautiful but without scent. From this, it is probable that Gesner's tulip was similar to T. suaveolens (or an early selection of it), and the tulips described by Belon and De Busbecq were more complex garden tulip hybrids. Clusius (1601) mentioned two names of tulips offered by the traders of Istanbul: cafe lale and cavala lale. The first, an early flowering tulip named 'T. praecox' by Clusius, must refer to Kefe (Feodosya) in the Crimea; the second, a late flowering tulip, must refer to Kavalla in Macedonia (Mordak, 1990); however, these were probably already complex garden hybrids frequent in the Istanbul bulb trade.

Clusius was responsible for many botanical introductions into European Renaissance gardens, and he was particularly keen on flower bulbs. As director of the Imperial Court in Vienna, he received numerous plants through diplomatic channels, among others from De Busbecq who sent some bulbs to Clusius in Vienna in 1593. At the end of his Flora Iberica, written after his travels in Spain and Portugal (Clusius, 1576), he listed plants that he had received from Thrace and was growing in the Imperial Gardens, including some tulips. In 1593, Clusius accepted the title of Horti Praefectus at the newly established botanic garden of the then recently established University of Leiden, Holland, where Clusius introduced a fine collection of plants obtained through his numerous contacts around Europe. Clusius also sent bulbs and seeds to many parts of Europe, thus spreading the popularity of the tulip, but he was possessive of his collections and no one in Leiden could buy them. Some bulbs were subsequently stolen from the garden, and soon these were multiplied and grown throughout the United Provinces of the Netherlands. Because Clusius' tulips were stolen, the bulb collection of Clusius was henceforth grown behind a wooden fence where people could not access them easily. A reconstruction of this can be

seen in the present-day Clusius Garden in the *Hortus botanicus* in Leiden.

Tulips were already in Leiden and Amsterdam before Clusius brought them there; they had probably arrived with tradesmen from Istanbul (the Ottoman Empire was the first nation to recognize the Dutch independence from Spain, resulting in flourishing trade relationships). To the amazement of local gardeners, the first tulip flowered in Amsterdam in Zieuwertsz's apothecary garden in 1625 (Van Wassenaer, 1622–1635).

After Gesner described the first flowering tulip, numerous publications appeared describing flowering tulips, but these were often confused with other bulbous plants or grouped under 'Lilionarcissus', which included a variety of bulb species (e.g. Dodonaeus, 1568). Clusius (1601) attempted to make sense of the confused nomenclature of Lilionarcissus, and he accepted the name Tulipa (after Gesner) and sorted them into groups based on flowering time. A tulip is featured in the centre of the frontispiece of his book, showing the importance of this flower to Clusius.

Tulips spread rapidly across Europe, and breeders enthusiastically selected different shapes and colour forms. Double tulips were already known in the early 17th century, and these curiosities fitted well in an age when natural oddities were cherished and exhibited to friends. Scholars, such as Clusius and Lobelius, collected botanical curiosities (to advance their scientific careers), but collections were also popular with royalty and the middle classes, especially in the Netherlands, where the spice trade with the East Indies had made many people wealthy, and in France, Germany and England. These nouveaux riches wanted to show off their wealth and status. Lavishly illustrated, hand-coloured garden manuals, such as the Florilegium (Sweert, 1612) and the Hortus Eystettensis (Besler, 1613), started to appear, in which a variety of garden tulips with flamed and fringed tepals was depicted. These guides helped to expand the market for exotic garden plants, and this was especially embraced by people in the Low Countries, where gardens had become fashionable in the 1620s and much breeding of tulips and other exotic flower bulbs (Fritillaria L., Hyacinthus L., Narcissus L. etc.) was carried out. A craze for bulbs started in France, where, in the early 17th century, entire properties were exchanged as payment for a single tulip bulb. The value of the flower gave it a special 'aura' of mystique, and numerous publications describing the various varieties were published at this time, cashing in on the value of the flower (Pavord, 1999). An export business was built up in France, and Dutch, Flemish, German and English buyers were plentiful. The trade drifted slowly from the French to the Dutch. The

French tulip craze probably sparked the infamous tulip mania in Holland, which started in 1634 and reached its height in 1636 (Cos, 1637; Blunt, 1950; Goldgar, 2007); the market collapsed three years later as a result of oversupply, leaving many people bankrupt and causing the Dutch government to introduce trading restrictions on bulbs (Thompson, 2007). This did not decrease the interest in tulips, and there remained a steady demand for well known and new varieties throughout Europe. This type of 'mania' is neither unique to tulips nor to the Netherlands; when hyacinths replaced tulips as the flower of fashion, a similar pattern was found because demand was high and supply was low (Garber, 1989), but prices also fell dramatically as they became more common. Even in more modern times, exorbitant prices are paid for new varieties; Garber (1989) mentioned a small quantity of lily bulbs of a new variety being sold for nearly half a million US dollars. Despite criticisms (Garber, 1989; Thompson, 2007), tulip mania appears to have been a financial speculative bubble with major social impacts (Maurits van der Veen, 2009), similar to what we see today in the banking sector.

Less well known is a tulip fraud case in the Netherlands revolving around a couple of investors providing millions of euros to a tulip fund, with the idea of developing new tulip varieties based on previous success. This sounded like a good idea in 2003, but the bulbs were used to create money, and with high percentages on top of the selling price and bulbs changing owners up to ten times, the money invested in the fund quickly disappeared. The following year, the tulip fund collapsed, investors lost their money and bulb speculators took their profit abroad. The tulip fund remained open until 2006, after which the owners were charged with fraud (Janssen, 2008).

Demand for tulips did not decline and, during the 18th century, numerous new tulip cultivars were developed, many of which became commonly grown around Europe and elsewhere in temperate parts of the world. Tulips and other flower bulbs had become an important export product supporting the Dutch economy.

At present, nearly 6000 cultivars are registered; some, like the Duc van Tol group, date back to the 16th century, but most are more recently developed. On average, there are about 40 new cultivars registered every five years (KAVB, 2012). Tulips remain a culturally important symbol in the Netherlands. Holland became the main hub in the global trade of cut flowers, ornamental plants and bulbs, and the trade in tulip bulbs is now a billion euro industry. Tulips are even cultivated in the Southern Hemisphere, allowing tourist shops in the Netherlands to offer tulip bulbs throughout the year, and, as far afield as Michigan, Canada, Japan, Australia and

New Zealand, Dutch communities organize tulip festivals attracting many tourists.

TAXONOMIC HISTORY OF TULIPA

On his visit to the Netherlands, Linnaeus would have seen tulips flowering in the Dutch gardens, but he dismissed all fancy cultivars and colour forms created by humans and did not deal with their taxonomy (Linnaeus, 1737). He based the genus Tulipa on Clusius' account (1583), including three species in Species Plantarum (T. sylvestris, T. gesneriana L. and T. breyniana L.; Linnaeus, 1753). The last was based on a poor illustration that most closely resembles Homeria collina (Thunb.) Salisb. (Iridaceae), a name later synonymized under Moraea Mill. (Iridaceae) (Goldblatt, 1973; Goldblatt et al., 2002). The first was placed in the genus Liriopogon Raf. by Rafinesque (1837), and T. gesneriana should therefore be treated as the type of *Tulipa* by exclusion. It was also designated as the type by Hitchcock & Green (1929). Tulipa gesneriana is a garden tulip of complex hybrid origin, a single, late flowering, unicoloured, tall tulip, which was the progenitor of the flamed Rembrandttype tulips popular at the time. Despite its name, it is not the tulip described and illustrated by Gesner (1561), which is more similar to T. suaveolens. Tulipa gesneriana is typified with a specimen from the Linnean herbarium (no. 425.2 LINN; Fig. 3), which was one of the common garden tulips at Linnaeus' time. Linnaeus does not deal with the great diversity of tulips grown in European gardens, and this has created issues related to the interpretation of the Linnaean tulip, often erroneously referred to as the Gesnerian tulip. All references to wild T. gesneriana (Mordak, 1990) refer to T. suaveolens, which occurs in the Caspian deserts and may have been the 'cafe lale' from the Crimea and the early tulip ('T. praecox') of Clusius (1583). Linnaeus did not consider the late and early tulips as separate species, and, as a result of intentional interbreeding, the two initially separate types have been integrated. Therefore, we believe that there probably is no extant garden tulip to which the name T. gesneriana really applies, although some are still in cultivation under that name. Some cultivars grown at the Hortus Bulborum in Limmen, the Netherlands, may still be close to the original Linnaean tulips, but this cannot be verified, and thus it is preferable to treat all garden tulip cultivars without a species epithet and the Linnaean tulip as a complex hybrid of unknown parentage: T. xgesneriana. Associated with T. xgesneriana are most of the so-called neo-tulipae (Hall, 1929, 1940), a range of naturalized garden tulips described as species, mainly from France, Italy and Switzerland. Some of these may represent early introductions, e.g. the tulip

painted by Hoefnagel c. 1590 (depicted in Pavord, 1999: 3) closely resembles plants cultivated as *T. grengiolensis* Thommen, one of the neo-tulipae, from Switzerland. It thus seems that some neo-tulipae may be the closest approaching true *T. xgesne-riana*, but we will never be sure about the identity of the tulip of Linnaeus.

Under the name Ornithogalum uniflorum L., Linnaeus (1770) described another tulip, now known as Tulipa uniflora (L.) Besser ex Baker, an unusual species that later formed the basis for the genus Orithyia D.Don. Several species were added in the 18th century by various authors, of which only T. biflora Pallas (Pallas, 1776), a specimen of which is in the Linnean Herbarium, and T. suaveolens (Roth, 1794) are presently in use. Link (1800) added T. australis Link, a small species from Spain and North Africa, which has often been considered as a subspecies of T. sylvestris (the typical subspecies being from Libya, commonly naturalized in Europe). In the elaborate Liliacées of Redouté (1803-1815), a number of tulips were beautifully illustrated and described, including T. clusiana Redouté and T. agenensis Redouté. The plant named *T. clusiana*, a name now in common use, had, however, already been described as T. praecox Cav. (Cavanilles, 1802), based on the account of Clusius (1601), a name that was later taken up for a form of T. agenensis (T. praecox Ten.; Tenore, 1811). Christenhusz, Fay & Govaerts (2013) accordingly proposed the rejection of T. praecox Cav. in favour of T. clusiana Redouté. Tulipa agenensis (described in an added note and based on a tulip thought to be indigenous to Agen, France) was later corrected by Redouté (vol. 2, 1805) as T. oculis-solis Saint-Amans (1804), but in that publication the name was not validly published. Tulipa oculis-solis has since been widely applied, but the oldest and correct name is *T. agenenesis*.

Roemer & Schultes (1829) and subsequent authors placed Tulipa between Fritillaria and Erythronium L., but several new genera were subsequently described. Don (1836) described Orithvia on the basis of T. uniflora, and Rafinesque (1837) described Liriactis Raf. (based on T. stellata Hook.), Liriopogon (based on T. sylvestris) and Podonix Raf. (based on T. biflora) from naturalized material in North America. Endlicher (1836) accepted *Orithyia* at the generic level and placed it between Erythronium and Tulipa. These segregate genera were not, however, accepted by Baker (1874) or by most subsequent authors. Meanwhile, numerous new species were described, many from cultivation or from cultivated bulbs collected originally from the wild. Notable contributions were those by Reboul (1822, 1823, 1838), Sprengel (1825) and Roemer & Schultes (1829). Regel (1873, 1877) studied tulips, often collected by his son



Figure 3. Lectotype specimen of Tulipa ×gesneriana L. Linnean Herbarium no. 425.2 (LINN).

Albert from the Russian and Central Asian steppes, from where he also described numerous new taxa.

Baker (1874) provided a revision of the genus and divided *Tulipa* into two subgenera: *'Eutulipa'* (= *Tulipa*) with rudimentary styles and subgenus *Orithyia* (D.Don) Baker with long styles. Regel (1873) and many subsequent authors recognized two major groups in Baker's *'Eutulipa'*, namely *Eriostemones* (= *Liriopogon*), characterized by an enlarged boss covered with hairs at the base of the stamen filament, and *'Leiostemones'* (= *Tulipa*), characterized by the lack of these hairs. In addition, a small number of taxa have been treated as segregrate genera, notably *Orithyia* and *Amana*.

Boissier (1882) divided Baker's (1874) *Eutulipa* into two sections, *Eriostemones* and *Leiostemones*, considering the presence of hair at the base of the filaments and at the edges of the inner segments of the perianth to be the defining character for the species belonging to section *Eriostemones*. At the beginning of the 20th century, a greater number of Central Asian tulips became known to European gardens, not least because of the introductions of Hoog, who propagated and distributed numerous botanical tulips through the Van Tubergen nursery in Haarlem, the Netherlands (Stork, 1984).

Hall (1929) followed Boissier's classification of Tulipa, also dividing the genus into two. However, he named one part a subgenus, Eriostemones (as 'Eriostemon'), and the other a section, Leiostemones (= Tulipa). Later, Hall (1938) described three new species on the basis of differences in ploidy, and this practice has remained common in tulip taxonomy. Hall (1940) provided an extensive revision of the genus in his book 'The genus Tulipa', although he was not able to revise many of the more complicated names, especially those published in Russian periodicals, because of the lack of fresh material for him to determine ploidy. He accepted the division into Eriostemones and Leiostemones, stating that these 'differ in so many respects that it will be convenient to consider their morphology separately (Hall, 1940). In Eriostemones, he also noted that the filaments associated with the inner perianth segments are longer than the outer three, the edges of the inner segments of the perianth are hairy near the base and the ovary tapers towards the apex, almost forming a style below the stigma. Although he accepted subgenus Leiostemones Boiss., Hall (1940) stated that it was an unnatural group, calling it 'a gathering of all tulips other than Eriostemones'. He did note, however, that Leiostemones is usually larger than Eriostemones and often has a central stem carrying a single flower.

Marais (1984) pointed out that the autonym 'section *Tulipa*' should replace the 'section *Leiostemones*' because it includes the type of the genus *Tulipa* (as

designated by Hitchcock & Green, 1929). This was followed by Van Raamsdonk & De Vries (1995), who followed Hall (1929) in treating the two sections as subgenera. Botschantzeva (1982) used a different sectional treatment of Tulipa, dividing the genus into six sections. To test these classifications, Van Creij, Kerckhoffs & Van Tuyl (1997) studied fertilization barriers in interspecific crosses in *Tulipa* by observing pollen tube growth patterns. In crosses between species belonging to subgenus Eriostemones and a garden tulip they called 'T. gesneriana' (subgenus Tulipa), they observed an absence of penetration of the ovule by the pollen tube, although the number of pollen tubes reaching the ovary and the lengths of the pollen tubes were similar to those of compatible 'intraspecific' garden tulip crosses. As both studies (Van Eijk, Van Raamsdonk & Eikelboom, 1995; Van Creij et al., 1997) were carried out for horticultural purposes, the garden tulip T. xgesneriana (a complex hybrid) was always one of the parents in their experimental crossing, and no crosses between Eriostemones and other members of subgenus Tulipa were attempted.

Nieuwhof, Van Raamsdonk & Van Eijk (1990) analysed pigment composition in *Tulipa* flowers. They found little resolution at the specific level, but the subgeneric classification was confirmed by the species in the different subgenera having either pelargonidin or delphinidin. Van Raamsdonk & De Vries (1992, 1995) carried out biosystematic studies of the two large subgenera of *Tulipa*, but these studies did not include members of *Amana*, *Orithyia* or any of the morphologically isolated species identified by Vvedensky (1935b), Hall (1940) and others (e.g. *T. sprengeri* Baker, *T. regelii* Elwes).

A molecular analysis of *Tulipa* based on five plastid DNA regions (partial matK, trnL intron, trnL-trnF, rps12-rpl20 and rpl16) was reported in an abstract (Fay et al., 2001), using Amana and Erythronium as outgroups (see also Rønsted et al., 2005; Clennett et al., 2012; Kim et al., 2013). The genus was strongly supported as monophyletic (100% bootstrap support), and Amana appeared to be more closely related to Erythronium than to Tulipa. Tulipa uniflora, representing section Orithyia (D.Don.) Vved., was found to be sister to the rest of the genus, and T. montana Lindl. (section Clusianae Baker) was sister to the remaining Tulipa spp. These relationships were, however, not well supported. The remainder of subgenera Tulipa and Eriostemones were each strongly supported. Tulipa sprengeri, which Hall (1940) treated as an isolated species, emerged as a member of Eriostemones (see also Wilford & Fay, 2007). The filaments of T. sprengeri have a boss at their base but are not clothed with hair, and Fay et al. (2001) suggested that the defining character for subgenus Eriostemones is the presence of a boss alone, with or without hairs. Based on these results, it was suggested that raising sections *Clusianae* and *Orithyia* to subgeneric rank would be appropriate (Fay et al., 2001). Zonneveld (2009) attempted to raise section *Clusianae* to the rank of subgenus, not attributing this discovery to Fay et al. (2001), but failed to do so validly. In 2012, Veldkamp & Zonneveld validated this and the other invalidly published names of Zonneveld (2009).

A study on Iranian *Tulipa* spp. (Kiani, Memariani & Zarghami, 2012) focused on the diversity of T. lehmanniana Merckl., but there was little resolution. Yanigawa et al. (2012) presented a molecular phylogenetic study based on plastid regions but also found little resolution because of a lack of variation in the regions used. They included a number of cultivars and found T. suaveolens (as T. schrenkii Regel) to be embedded in this group. This may indicate that T. suaveolens is a potential maternal parent of the complex garden tulips, but the samples were apparently not vouchered; the sequences are not available in GenBank. Therefore, this study is not reproducible and the identity of their T. suaveolens sample cannot be easily verified. Türktas et al. (2013) presented a molecular phylogenetic study based on species from Turkey, but their study lacked some critical taxa needed to address the remaining questions.

This leaves us with some unresolved questions relating to the infrageneric relationships in *Tulipa*, especially relating to inclusion or exclusion of *Orithyia*, the monophyly of subgenus *Tulipa s.l.* (including *Clusianae*), validity of the usage of sections and placement of several previously unsampled species. We present a phylogenetic analysis of *Tulipa* and its closest relatives based on plastid and internal transcribed spacer (ITS) sequence data in an attempt to shed some light on these questions. On the basis of the results and a thorough literature and herbarium study, we also propose a revised classification of the genus and provide an annotated checklist, citing types, synonyms and distribution (Appendix).

MATERIAL AND METHODS

TAXON SAMPLING

All species, apart from *T. lehmanniana*, were sampled from the living collections at the Royal Botanic Gardens, Kew, and voucher specimens are preserved in the Herbarium at Kew (K). The sample of *T. lehmanniana* was wild collected in Iran, and the voucher is also held at K. Sampling was designed to include taxa from all subgeneric groupings recognized by Vvedensky (1935b), Hall (1940), Van Raamsdonk &

De Vries (1992, 1995), Wilford (2006), Zonneveld (2009) and Veldkamp & Zonneveld (2012). Tulipa regelii and T. sprengeri, regarded by Hall (1940) and other authors as isolated species, were also included. In total, 25 accessions of Tulipa, representing 23 species of all previously recognized sections (Hall, 1940), were sequenced for this analysis. Representatives of Amana and Erythronium were used as outgroups, as indicated by the analyses of, for example, Rønsted et al. (2005) and Clennett et al. (2012). Species and voucher details are given in Table 2. Names were verified by comparison of the plants with herbarium specimens (Appendix), preferably type specimens, from B, BM, BRNM, C, COI, E, FI, G, H, K. L. M. P. PRC, S. WAG, WU and Z and associated illustrations and literature.

DNA EXTRACTION, AMPLIFICATION AND SEQUENCING

Total genomic DNA of all samples was extracted using a modified $2 \times \text{cetyltrimethylammonium}$ bromide (CTAB) protocol (Doyle & Doyle, 1987). Five plastid regions (trnL intron, trnL-F intergenic spacer, rpl16 intron, rps12 intron, partial matK) and one nuclear region (ITS) were amplified using polymerase chain reaction (PCR), employing the primers listed in Table 3. [For amplification details, see references in Table 3.]

PCR was performed in 50-µl volumes containing 45 µl of ReddyMix commercial PCR mastermix (ABGene, Epsom, Surrey, UK), 0.5 µl of bovine serum albumin, 0.5 µl of each primer and 2.0 µl of DNA. PCR products were purified using the NucleoSpin Extract Kit (Macherey-Nagel, Duren Germany) following the manufacturer's protocol.

Cycle sequencing reactions were carried out in 10-µl reaction volumes containing 1.0 µl of BigDye Terminator Mix (Applied Biosystems Inc, ABI, Warrington, Cheshire, UK), 1.5 µl of cycle sequencing buffer, 0.75 µl of primer and c. 50 ng of the purified PCR product template. Cycle sequencing products were cleaned by ethanol precipitation and run on an ABI 3100 automatic sequencer.

PHYLOGENETIC ANALYSES

Sequencher 4.1.2 software (Gene Codes Corp, Ann Arbor, MI, USA) was used to assemble and edit the sequences. The edited sequences were visually aligned in PAUP* ver. 4.0b10 (Swofford, 2003). In addition to the sequences, six indel characters were coded and included in the matrix.

For the maximum parsimony (MP) analyses, heuristic analyses were performed in PAUP* ver. 4.0b10 under equal weights, using 1000 random taxonaddition replicates and subtree-pruning-regrafting

Japan

AF485283

HF953091 HF953092

HF953065 HF953066

HF953037 HF953038

HF953008 HF953009

Sheahan 136 (K) Chase 8456 (K)

Erythronium Erythronium

D.Y.Tan & D.Y.Hong
Erythronium dens-canis

E. japonicum Decne.

Table 2. Samples included in this study. Subgenera are abbreviated as follows: E, Eriostemones; T, Tulipa. Subgenera and sections follow Wilford (2006) (—, no sequence available)

т									
ho Ti	Species	Subgenus; Section*	Voucher	trnL- $trnF$	rps12- $rpl20$	rpl16	matK	ITS	Origin
	Tulipa biflora Pall.	E; $Biflores$	Chase 6117 (K)	HF952983	HF953011	HF953039	HF953069	HF952957	Turkey
	T. bifloriformis Vved.	E; $Biflores$	Chase 18533 (K)	HF952984	HF953012	HF953040	HF953067	HF952958	Kyrgyzstan
e.	T. borszczowii Regel	T; $Tulipanum$	Chase 12000 (K)	HF952985	HF953013	HF953041		HF952959	Kazakhstan
o : o	T. clusiana Redouté (as	T; $Clusianae$	Chase 11432 (K)	HF952986	HF953014	HF953042	1	HF952960	Afghanistan
<i>-</i>	T. aitchisonii A.D.Hall)								
·t t	T. cretica Boiss. & Heldr.	E; $Saxatiles$	Chase 18532 (K)	HF952987	HF953015	HF953043	HF953070	HF952961	Greece
	T. humilis Herb.	E; $Saxatiles$	Chase 6107 (K)	HF953010	HF953016	HF953044	HF953071	HF952962	Turkey
dos	T. humilis Herb. (as	E; $Saxatiles$	<i>Chase 6111</i> (K)	HF952988	HF953017	HF953045	HF953068	HF952963	Garden origin
. 1	T. aucheriana Baker)								
204	T. julia K.Koch	T; $Tulipanum$	Chase 6114 (K)	HF952989	HF953018	HF953046	HF953072	HF952964	Armenia
~n:	T. kolpakowskiana Regel	T; Kolpakowskianae	Chase 438 (K)	HF952990	HF953019	HF953047	HF953073	HF952965	Garden origin
001	T. korolkowii Regel	T; Kolpakowskianae	Chase 11756 (K)	HF952991	HF953020	HF953048	HF953074	HF952966	Uzbekistan
T _o ,	T. lehmanniana Merckl.	T; Kolpakowskianae	Zarrei & Golzarian	EU912324	I	EU912240	EU912163	EU912094	Iran
			35228A (TUH)						
1	T. linifolia Regel	T; Clusianae	Chase 12001 (K)	HF952992	HF953021	HF953049	HF953075	HF952967	Garden origin
o.f	T. montana Lindl.	T; $Clusianae$	Chase 6112 (K)	HF952993	HF953022	HF953050	HF953076	HF952968	Turkey
<i>+l</i> ₁ .	T. orphanidea Boiss. (as	E; Australes	Chase 6110 (K)	HF952994	HF953023	HF953051	HF953083	HF952969	Greece
	T. theophrasti Candargy)								
inn	T. regelii Krassn.	E; Lophophyllon	Chase 6109 (K)	HF952995	HF953024	HF953052	HF953077	HF952970	Kazakhstan
00.	T. saxatilis Sieber	E; $Saxatiles$	<i>Chase 6119</i> (K)	HF952996	HF953025	HF953053	HF953078	HF952971	Greece
	T. sprengeri Baker	E; Australes	RBG Kew (K)	HF952997	HF953026	HF953054	HF953080	HF952972	Garden origin
00:	T. suaveolens Roth (as	T; $Tulipa$	Chase 6115 (K)	HF952998	HF953027	HF953055	HF953079		Russia
	T. schrenkii Regel)								
90	T. sylvestris L. subsp. sylvestris	E; Australes	Chase 6108 (K)	HF952999	HF953028	HF953056	HF953081	HF952974	Tunisia
119	T. systola Stapf	T; $Tulipanum$	Chase 6120 (K)	HF953000	HF953029	HF953057	HF953082	HF952975	Iran
11	T. xtschimganica Botschantz.	T; Eichleres	<i>Chase 6113</i> (K)	HF953001	HF953030	HF953058	HF953084	HF952976	Uzbekistan
70	T. turkestanica (Regel) Regel	E; $Biflores$	Chase 18534 (K)	HF953002	HF953031	HF953059	HF953085	HF952977	Uzbekistan
90	T. ulophylla Wendelbo	T; $Tulipanum$	Chase 6116 (K)	HF953003	HF953032	HF953060	HF953086	HF952978	Iran
Λ '	T. uniflora (L.) Besser	T; Orithyia	<i>Chase 751</i> (K)	HF953004	HF953033	HF953061	HF953087	HF952979	Russia
990	T. vvedenskyi Botschantz.	T; Eichleres	Chase 18889 (K)	HF953005	HF953034	HF953062	HF953088	HF952980	Kyrgyzstan
	Amana edulis (Miq.) Honda	Amana	Chase 2397 (K)	HF953006	HF953035	HF953063	HF953089	HF952981	Garden origin
	A. erythronioides (Baker)	Amana	Chase 742 (K)	HF953007	HF953036	HF953064	HF953090	HF952982	Japan

*Sections Clusianae and Orithyia are recognized by various authors as separate subgenera (see text). Molecular studies by Fay et al. (2001) and those presented in this article support this separation.

Table 3. Primers used for amplification and sequencing

Locus	Primers	Reference or sequence
matK	-19F	Molvray, Kores & Chase (2000)
	trnK-2R	Johnson & Soltis (1994)
	Internal reverse primer 900R	5'-GAAGCCAGAATTGCTTTTCCT-3'
trnL intron/trnL-trnF intergenic spacer	c and f, plus internal primers d and e	Taberlet <i>et al.</i> (1991)
rpl16 intron	71F, 1661R	Jordan, Courtney & Neigel (1996)
	158F	Zarrei <i>et al.</i> (2009)
rps12-rpl20 intergenic spacer	rps12, rpl20	Hamilton (1999)
ITS	17SE and 26SE	Sun et al. (1994)

(SPR) branch swapping, and saving multiple trees (MULTREES on), holding ten trees per replicate. Trees from all replicates were then used as starting trees for a final round of heuristic search, with a tree limit of 10 000 (MAXTREES). Internal support for clades was assessed using bootstrap analysis (Felsenstein, 1985) employing 1000 replicates with SPR swapping, with no more than ten trees being retained per replicate. All changes were assessed as unordered and were equally weighted (Fitch parsimony: Fitch, 1971). Bootstrap scores (BS) of 50–74% were considered as weak, 75-89% as moderate and > 90% as strong support. Scores of < 50% are not reported. As the plastid genome is inherited uniparentally as a unit and does not undergo recombination (Soltis & Soltis, 1998), all plastid sequences were combined in one matrix and analysed together. The ITS data was then analysed separately. These preliminary single-partition analyses were performed to rule out incongruence between the DNA regions (none was found, and so results not shown). In the third analysis, plastid and ITS data matrices were combined and analysed together.

A combined (plastid + ITS) Bayesian analysis was performed as follows. Bayesian analyses were performed using a Markov-chain Monte-Carlo (MCMC) approach, as implemented in MrBayes v3.2.1 (Ronquist et al., 2012) and following recommendations by Nylander (2004). Best-fit models for each region were selected using MrModeltest v.3.0 (Nylander, 2004) based on the Akaike information criterion (see Table 1), and the restriction model implemented in MrBayes was used for the gap partition. A partitioned analysis was performed on the basis of the combined matrix by unlinking all parameters (except the topology). This approach allowed the partitions to vary independently and contribute to the analysis. Two Metropolis-coupled MCMCs with an incremental heating temperature of 0.2 were run for 10 million generations, with the parameters and the resulting phylogenetic trees being sampled every 1000 generations. The analysis was repeated twice, starting with random trees. Convergence was accepted when standard deviations attained values below 0.01 and when the effective sampling size (ESS) was > 200. After a burn-in period of 25%, a half-compatible consensus tree (and its associated Bayesian posterior probabilities, BPPs) was reconstructed using MrBayes v3.2.1 (Ronquist *et al.*, 2012).

RESULTS

The matrix statistics (number of sequences, alignment length, best-fit model for Bayesian analysis and numbers of constant, variable and potentially parsimony informative characters) are presented in Table 4.

PARSIMONY ANALYSIS

No conflicting strongly supported clades were found in the separate analyses of plastid and nuclear sequences (results not shown). The parsimony analysis of the combined plastid + ITS matrix yielded 1647 most-parsimonious trees with a length of 514 [consistency index (CI) = 0.76; retention index (RI) = 0.84]. All strongly supported relationships were the same as found in the Bayesian analysis (see below).

BAYESIAN ANALYSIS

The half-compatible consensus tree is shown in Figure 4. Amana, Erythronium and Tulipa all received maximum support [bootstrap percentage (BP), 100; posterior probability (PP), 1.0] for their monophyly. In Tulipa, all four subgenera were strongly supported (BP, 99–100; PP, 1.0; subgenus Orithyia by default as only one species was sampled). The relationships between the subgenera were, however, not strongly supported. Subgenus Orithyia was sister (BP, 58; PP, 0.87) to the rest of the genus. Subgenera Clusianae and Eriostemones together (BP > 50; PP, 0.97) were sister to subgenus Tulipa, albeit with weak support (BP, 58; PP, 0.87).

Table 4. Statistics for the matrix used for maximum parsimony and Bayesian analyses

	ITS region	matK	rpl16 intron	rps12-rpl20 IGS	trnL-trnF region	Combined matrix*
Number of sequences (all/ingroup)	29/25	28/24	30/26	29/25	30/26	30/26
Alignment length (bp)	908	945	852	873	935	4417
Best-fit model	GTR + G + I	HKY + I	GTR + G + I	HKY + I	HKY + G + I	
Number of constant characters (all/ingroup)	908//89	901/945	765/852	834/873	875/935	4014/4417
(%)	(79.0/81.6)	(95.3/97.0)	(89.8/92.4)	(95.5/97.2)	(93.6/95.2)	(90.9/92.9)
Number of variable characters (all/ingroup)	169/148	44/28	87/65	39/24	60/45	403/314
(%)	(21.0/18.4)	(4.7/2.9)	(10.2/7.6)	(4.5/2.7)	(6.4/4.8)	(9.1/7.1)
Number of potentially parsimony informative characters (all/ingroup)	106/87	11/4	35/24	16/7	23/15	195/141
(%)	(13.1/10.8)	(1.2/0.4)	(4.1/2.8)	(1.8/0.8)	(2.5/1.6)	(4.4/3.2)

Fincluding six indel characters.

Relationships within the subgenera were not generally strongly supported, at least in part as a result of the relatively low level of divergence between accessions. In subgenus Clusianae, T. linifolia Regel was weakly supported as sister to T. clusiana and T. montana. In subgenus Eriostemones, T. biflora, T. bifloriformis Vved. and T. turkestanica (Regel) Regel (all section Biflores sensu Hall, 1940) were together strongly supported as sister to the rest of the subgenus (sections Australes and Saxatiles sensu Hall, 1940, plus two of the 'solitary' species sensu Hall, 1940: T. regelii and T. sprengeri). Relationships in the clade formed by the combined Australes and Saxatiles were totally unresolved. In subgenus Tulipa, T. korolkowii Regel and T. kolpakowskiana Regel were weakly supported as successive sisters to the rest of the subgenus. Apart from this, there was relatively little resolution, the remaining eight taxa forming four pairs, with weak to strong support (Fig. 4). Further subdivisions of the subgenus were not supported; e.g. T. korolkowii, T. kolpakowskiana and T. lehmanniana Merckl. (all section Kolpakowskianae sensu Wilford, 2006) were separated in our phylogenetic trees, whereas T. vvedenskyi Botschantz. and T. xtschimganica Botschantz. (both Eichleres sensu Wilford, 2006) were sisters with strong support (Fig. 4).

DISCUSSION

Monophyly of *Tulipa*, excluding *Amana*, was well supported and agrees with previous analyses of the genus (Fay et al., 2001; Türktaş et al., 2013). Amana, although sharing morphological characters with *Tulipa* and *Erythronium*, appears to be sister to (or possibly embedded in) *Erythronium* (Clennett et al., 2012). Sparse sampling of *Erythronium* and the absence of more distant outgroups precludes us from commenting on the relationship between *Amana* and *Erythronium*. The three genera are closely related, forming a clade in wider analyses (e.g. Fay & Chase, 2000), and could be united into a single genus. On balance, we recommend that the three genera should be maintained to prevent nomenclatural instability.

Within *Tulipa*, subgenera *Tulipa*, with glabrous stamens, and *Eriostemones*, with bossed, usually hairy stamens, were confirmed by this study, with some amendments. The monophyly of *Orithyia*, with only one species sampled, is still untested and should be a focus of future studies. *Clusianae* emerged as monophyletic with strong support and separate from subgenus *Tulipa*, where it had previously been included (Hall, 1940; Van Raamsdonk & De Vries, 1995), in agreement with Fay *et al.* (2001). This separation from subgenus *Tulipa* is also supported by morphology (Van Raamsdonk & De Vries, 1995), karyotypes (Woods & Bamford, 1937; Southern, 1967;

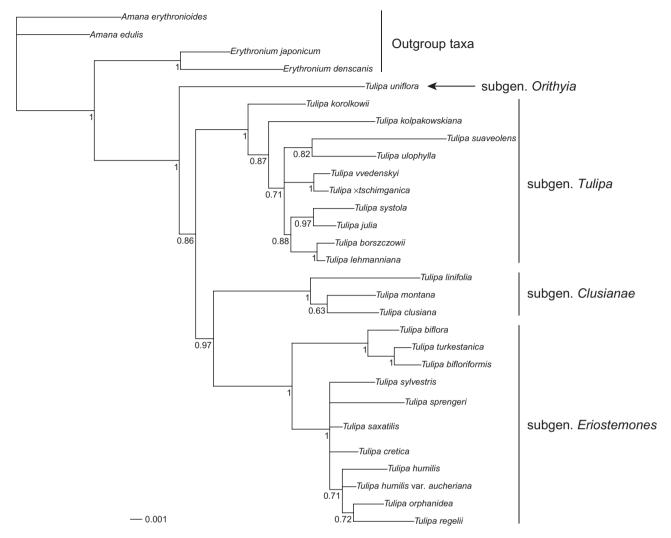


Figure 4. The half-compatible consensus tree from the Bayesian analysis of the combined plastid and internal transcribed spacer (ITS) sequence data. Bayesian posterior probabilities are displayed below the branches. (*Amana erythronioides* was defined as the outgroup as the program MrBayes only allows one most external outgroup.)

Blakey & Vosa, 1981, 1982), chromosome C-banding pattern (Blakey & Vosa, 1982) and genome size (Zonneveld, 2009). Because the group is also reproductively isolated (Van Raamsdonk & De Vries, 1995; Van Creij *et al.*, 1997; Van Raamsdonk *et al.*, 1997), we agree with Fay *et al.* (2001), Zonneveld (2009) and Türktaş *et al.* (2013) that *Clusianae* should be treated at the rank of subgenus.

In subgenus *Tulipa*, section *Kolpakowskianae* is not supported. The section was always poorly defined, including mostly yellow-flowered, small species with spear-shaped stamen filaments and several narrow leaves, but Hall (1940), who defined the group, also stated that the species may 'not belong to the same natural group or subgenus'. The representatives of *Kolpakowskianae* included here did not form a clade, and this section should be abandoned. The two taxa of

section *Eichleres* (*T.* ×*tschimganica* and *T. vvedenskyi*) fell together with strong support. Both taxa are found in the western Tien Shan. Botschantzeva (1982) assigned T. xtschimganica to a separate section Spiranthera Vved. (followed by, for example, Zonneveld, 2009), but this taxon appears to be intermediate between T. dubia Vved. and T. kaufmanniana Regel (Zonneveld, 2009) and has been suggested to be a natural hybrid (Phillips & Rix, 1981). Tulipa vvedenskyi was placed by Zonneveld (2009) in section Vinistriatae (Raamsd.) Zonn., but neither Spiranthera nor Vinistriatae is supported. Section Tulipanum (T. julia K.Koch, T. systola Stapf, T. borszczowii Regel and T. ulophylla Wendelbo) emerges as a weakly supported clade in the ITS analysis (results not shown), but, in the combined analysis, the support for section Tulipanum found in ITS is lost and the clade collapses into a polytomy. The branches involved are short, and additional data will be required to clarify the situation. At this time, it does not appear to be necessary or, indeed, warranted to accept sections in subgenus *Tulipa*.

Among the species of *Eriostemones*, there is little resolution, but section Biflores is sister to the rest of the subgenus. Van Raamsdonk & De Vries (1992) placed T. turkestanica as 'basal' (presumably meaning first-branching) in section Biflores. Although we had little resolution in our combined analysis, our ITS analysis indicated that T. biflora was the first species to branch off from the rest of section Biflores, and so the hypothesis of Van Raamsdonk & De Vries (1992) is not supported. The distribution of T. biflora is more westerly than the remaining members of this section. Species in sections Australes and Saxatiles, of mainly Middle Eastern and Mediterranean distribution, seem to be closely related and the branches are short (with the exception of that leading to T. sprengeri, also placed here). Based on morphological characteristics, Van Raamsdonk & De Vries (1992) stated that the monophyly of these sections could not be confirmed, and our molecular results agree with this. The placement of T. regelii in a separate section Lophophyllon Vved., based on its plicate leaves, is also not supported by our data, although the lack of resolution among species of Eriostemones means that a relatively isolated placement for T. regelii cannot be refuted. On the basis of floral morphology and genome size, Zonneveld (2009) placed T. regelii in section Biflores, but that placement is not supported by our analysis. It does, however, belong in subgenus *Eriostemones*.

Hall (1940) placed *T. sprengeri* as a 'solitary' species of Leiostemones (= subgenus Tulipa). He did, however, describe the filaments having a swollen boss near the base and, as in species belonging to subgenus Eriostemones, the filaments are also alternately long and short. In the study of Woods & Bamford (1937), the chromosome morphology of T. sprengeri shared characteristics with species of subgenus Eriostemones, but they did not comment on this, instead stating that the chromosome morphology sets T. sprengeri apart from other species of subgenus Tulipa. Based on the distribution of heterochromatin on the chromosomes (with only one C-band at the distal end of chromosome 7), Blakey & Vosa (1982) also concluded that T. sprengeri differs from the rest of the species in subgenus Tulipa. Further support for the defining character in *Eriostemones* being the swollen boss. pubescent or glabrous at the base of the filaments, is provided by the morphological description by Botschantzeva (1982) of T. sogdiana Bunge, a member of *Eriostemones* from Central Asia (included in the Appendix below under T. biflora s.l.). She described individuals of this species as having either glabrous bosses at the base of the filaments or bosses with scattered hairs. Marais (1984) also noted the absence of hairs in some Turkish populations of *T. orphanidea* Boiss. ex Heldr. Based on DNA content, Zonneveld (2009) placed *T. sprengeri* in section *Sylvestres* and considered it to be closely related to *T. sylvestris*. Our results showed *T. sprengeri* to be deeply embedded in subgenus *Eriostemones*, but not with a particularly close association with *T. sylvestris*.

TAXONOMY AND NOMENCLATURE

The taxonomy of tulips is notoriously difficult for several reasons.

- 1. Species have been described from cultivation, based on plants of unknown origin. This has resulted in clones of single, sometimes aberrant, forms that may be different from the species in the strict sense being named, but these fall within the diversity of another species observed in the wild.
- 2. Species have been described from populations that are not natural, but rather naturalized populations of garden plants. Recognition of these so-called neo-tulipae has resulted in a long list of synonyms for *T. agenensis*, *T. ×gesneriana* and *T. suaveolens*, many of which are difficult to assign to any natural population.
- 3. *Tulipa* ×*gesneriana* is not known in a truly wild state; it is a complex hybrid that has been cultivated for centuries.
- 4. Hybridization occurs easily in cultivation when closely related species are grown together; when these plants of garden origin are described, they may not be assignable to another species.
- 5. Many species lack proper typification, have no original material cited or have no herbarium material preserved, making comparison between species difficult (and, in these cases, only possible on the basis of the description or an illustration). The names of untypified species have been, however, commonly used, and have often been perpetuated through cultivation. Sometimes these names have been erroneously applied.
- 6. In the past it was common practice to describe every form found in the wild or of putative wild origin in gardens as new species, without much understanding of the natural range of variation of the taxa, resulting in a large number of poorly understood and unsatisfactory names, particularly in the horticultural literature. The nomenclature of these taxa can be problematic to resolve as they often lack good descriptions of preserved specimens with which the names can be interpreted.
- 7. Some species names are based on differences in ploidy alone. These can sometimes be easily recognized in horticulture but do not represent natural species.

Table 5. Accepted subgenera with their characteristics, type species and other accepted species

Tulipa subgenus Clusianae (Baker) Zonn. & Veldkamp, Pl. Syst. Evol. 298: 89. (2012)

Characters: bulbs with a tuft of woolly hairs protruding from the tip. Stamens without hairs or boss. Stigmas sessile

Accepted species:

Tulipa clusiana Redouté (type)T. linifolia RegelT. harazensis Rech.f.T. montana Lindl.

Tulipa subgenus Eriostemones (Boiss.) Hall, Book of the Tulip: 60 (1929), as Eriostemon.

Characters: bulb tunics felty to glabrous inside. Stamens with boss, usually with hairs. Stigmas sessile

Accepted species:

Tulipa biflora Pall. T. saxatilis Sieber ex Spreng.

T. bifloriformis Vved.T. sprengeri BakerT. cinnabarina K.Perss.T. subbiflora Vved.

T. cretica Boiss. & Heldr. T. sylvestris L. subsp. australis (Link) Pamp.

T. dasystemon (Regel) Regel T. sylvestris L. subsp. primulina (Baker) Maire & Weiller

T. humilis Herb. T. sylvestris L. subsp. sylvestris (type)

T. kolbintsevii Zonn. T. turkestanica (Regel) Regel

T. koyuncui Eker & Babaç T. urumiensis Stapf

T. orithyioides Vved.

T. orphanidea Boiss. ex Heldr.

T. regelii Krassn.

Tulipa subgenus Orithyia (D.Don) Baker J. Linn. Soc. Bot. 14: 277. (1874)

Characters: bulb tunics hairy at the tip or glabrous. Stamens without hairs or boss. Stigma placed on a clearly defined style

Accepted species:

 ${\it Tulipa\ heteropetala\ Ledeb}. \hspace{1.5cm} {\it T.\ sinkiangensis\ Z.M.Mao}$

T. heterophylla (Regel) Baker T. uniflora (L.) Besser ex Baker (type).

Tulipa subgenus Tulipa

Characters: bulb tunics densely lined inside with rippled or silky hairs or (nearly) glabrous. Stamens without hairs or boss. Stigmas sessile

Accepted species:

Tulipa agenensis RedoutéT. kaufmanniana RegelT. albanica Kit Tan & ShukaT. kolpakowskiana RegelT. alberti RegelT. korolkowii Regel

T. aleppensis Boiss. ex Regel

T. kosovarica Kit Tan, Shuka & Krasniqi

T. altaica Pall. ex Spreng.

T. kuschkensis B.Fedtsch.

T. anisophylla Vved.

T. lanata Regel

T. armena Boiss.T. lehmanniana Merckl.T. banuensis Grey-WilsonT. lemmersii Zonn.T. borszczowii RegelT. ostrowskiana Regel.

T. borszczowii Regel T. ostrowskiana Regel.
T. botschantzevae S.N.Abramova & Zakal.
T. persica (Lindl.) Sweet
T. butkovii Botschantz.
T. platystemon Vved.
T. carinata Vved.
T. praestans H.B.May

T. cypria Stapf ex Turrill
T. scardica Bornm.
T. dubia Vved.
T. scharipovii Tojibaev

T. faribae Ghahr., Attar & Ghahrem.-Nejad T. schmidtii Fomin
T. ferganica Vved.
T. serbica Tatic & Krivošej

T. foliosa StapfT. sosnowskyi Achv. & MirzoevaT. fosteriana W.IrvingT. suaveolens RothT. xgesneriana L. (type)T. subquinquefolia Vved.T. greigii RegelT. systola Stapf

T. heweri Raamsd.

T. talassica Lazkov
T. hissarica Popov & Vved.
T. tetraphylla Regel
T. hoogiana B.Fedtsch.
T. ×tschimganica Bo

 $\begin{array}{ll} \textit{T. hoogiana B.Fedtsch.} & \textit{T. xtschimganica Botschantz.} \\ \textit{T. hungarica Borbás} & \textit{T. ulophylla Wendelbo} \\ \textit{T. iliensis Regel} & \textit{T. undulatifolia Boiss.} \end{array}$

T. ingens Hoog T. uzbekistanica Botschantz. & Sharipov

T. julia K.Koch T. vvedenskyi Botschantz.

It has been difficult to create a natural species concept, but the appended checklist is an approach to create order out of the plethora of Tulipa names. Several names placed in synonymy in our list are certainly easily recognizable entities in horticulture, and the names can continue to be used in the trade, although we believe it would be better to treat them as varieties, cultivars or cultivar groups. We have made an attempt to study most publications describing new taxa and to typify as many names as possible, but, undoubtedly, some names will have escaped our attention or their status is uncertain at this stage. Using the framework of our phylogenetic analyses presented here, we compile a new classification with full synonymy, distribution and type information for all known species of tulips (Appendix). The accepted names and their subgeneric placement are listed in Table 5.

The placement of *T. heteropetala* Ledeb., *T. heterophylla* (Regel) Baker and *T. sinkiangensis* Z.M.Mao in subgenus *Orithyia* remains to be tested. It is possible that some of these belong to other subgenera of *Tulipa* or may even have to be segregated as the genus *Eduardoregelia* Popov. Further studies of these enigmatic species are needed.

Bulbous plants, especially those that hybridize readily, present problems as a result of falling at the interface between horticultural and botanical taxonomy. Tulips, because of their long history of cultivation, have proved particularly complex in terms of developing an acceptable and workable taxonomy. We hope that our attempt to 'tiptoe through the tulips' will lead to an increased stability in the nomenclature of this horticulturally important group.

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APPENDIX

CHECKLIST OF THE GENUS *TULIPA* (LILIACEAE) *Tulipa* L., Sp. Pl.: 305 (1753) Seventy-six accepted species (excluding hybrids).

Type: Tulipa ×gesneriana L. (designated by Hitchcock & Green, 1929).

Distribution: Southern Spain and Portugal, northern Africa (Morocco, Algeria, Tunisia, Libya), Sicily, Greece, Cyprus, Balkans (Albania, Kosovo, Montenegro, Macedonia, Serbia, Bulgaria, Romania), Crimea, Ukraine and southern Russia and to the Caucasus (Armenia, Azerbaijan, Georgia), Turkey, throughout Anatolia and the Levant (Israel, Lebanon, Palestine, Syria), south to Sinai and Jordan, Iraq, Iran, East to Central Asia (Afghanistan, Kazakhstan, Kyrgyzstan, Tajikistan, Turkmenistan, Uzbekistan), Central Siberia, southern Mongolia, western China and Inner Mongolia, south to Waziristan, Kashmir and the western Himalayas. Naturalized elsewhere. The genus is most diverse in the area between Cappadocia and Bactria, with many species in northern Iran, the Pamir Alai and the Tien Shan Mountains.

Synonyms

Orithyia D.Don in R.Sweet, Brit. Fl. Gard. 7: t. 336 (1836). Type: Orithyia uniflora (L.) D.Don = Tulipa uniflora (L.) Baker.

 $\begin{array}{c} \it Liriactis \ Raf., \ Fl. \ Tellur. \ 2: \ 97 \ (1837). \ Type: \it Liriactis \ albiflora \ Raf. = \it Tulipa \ clusiana \ DC. \end{array}$

Liriopogon Raf., Fl. Tellur. 2: 35 (1837). Type: Liriopogon sylvestre (L.) Raf. = T. sylvestris L.

Podonix Raf., Fl. Tellur. 4: 28 (1838). Type: Podonix albiflora Raf. = T. biflora Pall.

Eduardoregelia Popov, Index Seminum (AA) 3: 9 (1936). Type: Eduardoregelia heterophylla (Regel) Popov = Tulipa heterophylla (Regel) Baker.

We accept four subgenera, indicated in the checklist below with their initials:

(C) *Tulipa* subgenus *Clusianae* (Baker) Zonn. & Veldkamp, Pl. Syst. Evol. 298: 89 (2012). *Tulipa* section *Clusianae Baker* (1883).

Type: Tulipa clusiana DC.

Liriactis Raf. (1837)

(E) *Tulipa* **subgenus** *Eriostemones* (Boiss.) Hall, Book of the Tulip: 60 (1929), as *Eriostemon. T.* § *Eriostemones* Boiss. (1882).

Type: Tulipa sylvestris L.

Liriopogon Raf. (1837), Podonix Raf. (1838), Tulipa § Leiobulbos C.Koch (1849), T. § Saxatiles Baker (1874), T. § Sylvestres Baker (1874), T. section Saxatiles (Baker) Baker (1883), T. section Sylvestres (Baker) Baker (1883), T. § Albae Levier (1884), T. section Eriostemones (Boiss.) Boiss. ex Levier (1884), T. § Luteae Levier (1884), T. § Rubrae Levier (1884), T. subgenus Eriostemones (Boiss.) Raamsd., nom. superfl. (1995), T. section Biflores A.D.Hall ex Zonn. & Veldk. (2012).

(O) *Tulipa* subgenus *Orithyia* (D.Don) Baker, J. Linn. Soc., Bot. 14: 277 (1874). *Orithyia* D.Don (1836). *Type:* Tulipa uniflora (L.) Baker.

Tulipa section Orithyia (D.Don) Baill. (1894), Eduardoregelia Popov (1936).

(T) Tulipa subgenus Tulipa.

Type: Tulipa ×gesneriana L.

Tulipa section Dulipanum Reboul (1847), T. section Tulipanum Reboul (1847), T. § Lanigera C.Koch (1849), T. § Eriobulbae Baker (1874), T. subgenus Eutulipa Baker (1874), nom. superfl., T. § Gesnerianae Baker (1874), T. § Scabriscapae Baker (1874), T. § Leiostemones Boiss. (1882), T. section Eriobulbae (Baker) Baker (1883), nom. superfl., T. section Gesnerianae (Baker) Baker (1883), T. § Ambiguae Levier (1884), T. section Leiostemones (Boiss.) Boiss. ex Levier (1884), T. series Aureofasciatae Raamsd. (1995), T. series Lanatae Raamsd. (1995), T. series Luteoapiculatae Raamsd. (1995), T. series Multiflorae Raamsd. (1995), T. series Tulipanum (Reboul) Raamsd. (1995), T. series Undulatae Raamsd. (1995), T. ser Vinistriatae Raamsd. (1995), T. section Kolpakowskianae Raamsd. ex Zonn. & Veldk. (2012), T. section Lanatae (Raamsd.) Zonn. (2012), T. section Multiflorae (Raamsd.) Zonn. (2012), T. section Spiranthera Vved. ex Zonn & Veldk. (2012), T. section Vinistriatae (Raamsd.) Zonn. (2012).

The taxonomy of *Tulipa* is notoriously difficult, as a result of hybridization, polyploidy, naturalization of cultivated plants, unrecorded horticultural practices and the frequent absence of type specimens. Many species are described from cultivated plants that do not reflect the natural variability of species in the field. These names often represent a single clone in cultivation showing little variability, resulting in names being applied to a single genotype or to aberrant forms. Different colour forms often occur in mixed populations from which selections for garden use have frequently been made, and subsequently described as new species, in many cases without type specimens being studied. We have studied all type specimens available to us and typified species when necessary. This should solve some of the longstanding nomenclatural debates in Tulipa.

Horticultural hybrids are often of such old or obscure origin that the parentage cannot be known. For instance, many names are associated with garden tulips, which are complex hybrids of unknown origin, probably first appearing sometime in mediaeval Persia. They include T. *gesneriana, the type of the genus, a complex hybrid without typical plants currently in cultivation, although some of its lineal descendents are: these should be treated as cultivars rather than species. In addition to issues surrounding garden hybrids, there are a number of species described from outside the natural range of Tulipa. These are usually referred to as neo-tulipae (e.g. Hall, 1929, 1940), indicated with (N) in the list below. Several of these clearly belong to T. agenensis (in Cultivar Groups of that species), but the majority of these are naturalized early garden hybrids, here placed as synonyms of the poorly defined T. ×gesneriana for lack of better placement. Neo-tulipae brought into cultivation should be treated as Cultivar Groups of T. ×gesneriana or (perhaps preferable) as Cultivar Groups independent of an epithet, but certainly not as natural species. We place these here in the 'Didieri Group' (unicolorous tepals) and in the 'Grengiolensis Group' (tepal margins discolorous).

Taxa synonymized here that are common in cultivation and have known cultivars should also be treated in Cultivar Groups (ICNCP; Brickell et al., 2009). These Cultivar Groups are pointed out in the list. Cultivars of these synonymized taxa are placed under these Group names. The application of Cultivar Group names to entities formerly treated as botanical taxa has already been followed in horticulture (Cubey et al., 2013). Well-known examples are T. saxatilis Bakeri Group 'Lilac Wonder' and T. orphanidea Hageri Group 'Splendens'. Taxa representing size or colour variants known from wild populations can be accepted at the varietal level, but these have not been treated here separately; an example is T. undulatifolia var. micheliana differing from typical T. undulatifolia in its striped leaves.

In this checklist, we attempt to organize the numerous names published in the genus *Tulipa*, many of which are used in horticulture. We aim to use species names only for taxa that are known to have (or have had) native, natural populations, even though they may be originally described from cultivation. There are still some dubious taxa of which we know little, and these are tentatively accepted or synonymized here (depending on their usage). Further research at natural sites may resolve the status of these names in the future.

ALPHABETICAL LIST OF ACCEPTED TAXA

Tulipa (T) agenensis Redouté, Liliac. 1: 60 (add. & corr.) (1804)

Ind. loc.: 'M. Lamouroux a découvert dans les environs d'Agen une nouvelle tulipe indigène', no material cited. Neotype (**designated here**): *Tulipa oculis-solis* in Redouté, Liliac. 4: t. 219 (1808).

Note: The name was coined in an annotation, but was later transferred by Redouté under *T. oculus-solis*, which is why we chose that plate here as neotype. *Distribution:* Native to north-western Iran, naturalized in Cyprus, Greece, eastern Aegean, Turkey, Lebanon, Syria, Israel, Palestine, France, Italy, Portugal and Tunisia.

Note: A number of the names below are described from cultivated plants or naturalized populations (e.g. Neo-tulipae), but it is preferable to treat it as a single variable taxon. A few other taxa accepted as species here (e.g. *T. aleppica*, *T. cypria*) may also have to be included in the future pending further study.

Tulipa oculus-solis St.-Amans, Recueil Soc. Agr. Agen. 1: 75 (1804), nom. inval.

Tulipa oculus-solis DC. in J.B.A.M. de Lamarck & A.P. de Candolle, Fl. France, ed. 3, 3: 200 (1805). Ind. loc.: 'In arvis cultis circa Aginnum, et in Galloprovincia', no material cited. Neotype (**designated here**): FRANCE. Agen (Lot et Garonne), De Franqueville (ex Herb. Richard) s.n. (P-06797254!).

Tulipa acutiflora Poir. in J.B.A.M.de Lamarck, Encycl. 8: 134 (1808), nom. inval. pro syn.

Tulipa praecox Ten., Fl. Napol. 1: 170 (1811), nom. illeg. Tulipa praecox var. tenoris Reboul, Antologia (Florence) 28(2): 291 (1827), nom. inval. pro syn. Tulipa oculus-solis var. praecox Regel, Trudy Imp. S.-Peterburgsk. Bot. Sada 2: 447 (1873). Ind. loc.: 'Habitat in Italia et insula Chio'. Lectotype (designated here): without locality, Tenore s.n. (K!). Note: This should be treated as a cultivar, T. agenensis 'Praecox'.

Tulipa acuminata Vahl ex Hornem., Hort. Bot. Hafn. 1: 328 (1813). Holotype: CULTIVATED: Hort. Bot. Copenhagen, Anon. ex herb. Liebmann (C!). Note: The type specimen is unlike material offered in the trade under this name, which should be treated as T. 'Cornuta'.

Tulipa (N) raddii Reboul, Nonnul. Sp. Tulip. Not.: 5 (1822). Tulipa praecox subsp. raddii (Reboul) K.Richt., Pl. Eur. 1: 214 (1890). Tulipa praecox var. raddii (Reboul) Reboul, Antologia (Florence) 28(2): 291 (1827). Ind. loc.: ITALY. Careggi, no material cited. Note: Reboul (1838) synonymized his species under T. praecox Ten., but the epithet will have priority at the species level because of the older name T. praecox Cav. As a cultivar, the name T. agenensis 'Praecox' may be used.

Tulipa (N) maleolens Reboul, Nonnul. Sp. Tulip. Not., App.: 1 (1823). Tulipa oculus-solis var. maleolens (Reboul) Regel, Trudy Imp. S.-Peterburgsk. Bot. Sada 2: 446 (1873). Ind. loc.: 'Flos odorem exhalat injucundum, a quo nomen desumpsi. Ruribus muris cinctis, dirutam Divi Miniatis arcem inter et Divi Leonhardi

templum, detexi, sicut etiam in loco Le Rose dicto'. Type: none cited. Neotype (**designated here**): ITALY. inter segetes prope Florentiam rara, 20.iv.1878, *E. Levier s.n.* (COI-00050858!). Note: This should be treated as *T. agenensis* 'Maleolens'.

Tulipa apula Guss. ex Ten., Fl. Neapol. Prodr. App. 5: 12 (1826). Neotype (**designated here**): GREECE. 'in campis ins. Chios', iii.1846, Heldreich s.n. (BM!).

Tulipa (N) praecox var. foxii Reboul, Antologia (Florence) 28(2): 291 (1827). Tulipa foxiana Reboul, Select. Sp. Tulip.: 2 (1838). Tulipa praecox var. foxiana (Reboul) Levier, Tulip. Eur.: 53 (1884). Tulipa praecox subsp. foxiana (Reboul) K.Richt., Pl. Eur. 1: 214 (1890). Tulipa strangwaysiana Reboul ex Baker, J. Linn. Soc., Bot. 14: 281 (1874), nom. inval. pro syn. Type: ITALY. San Niccolo, Fox Strangways (not located). Note: This is a white form of the species and should be treated as a cultivar: T. agenensis 'Foxii'.

Tulipa (N) lortetii Jord., Ann. Soc. Linn. Lyon, n.s., 5: 9 (1858). Tulipa oculus-solis var. lortetii (Jord.) Baker, J. Linn. Soc., Bot. 14: 278 (1874). Tulipa oculus-solis subsp. lortetii (Jord.) Nyman, Consp. Fl. Eur., Suppl. 2: 303 (1890). Tulipa praecox subsp. lortetii (Jord.) K.Richt., Pl. Eur. 1: 214 (1890). Lectotype (designated here): FRANCE. Bouches du Rhône: les terre a blé a Cassis près Marseille, iii.1860, L. C. Lortet s.n. (K!). Note: This should be treated as T. agenensis 'Lortetii'.

Tulipa boissieri Regel, Gartenflora 22: 296 (1873). Type: ISRAEL [Palaestina]. Ramlah, Roth s.n. (isotype: K-000844474!). Note: This is a synonym of T. agenensis 'Maleolens'.

Tulipa oculus-solis var. strangwaysii Regel, Trudy Imp. S.-Peterburgsk. Bot. Sada 2: 447 (1873). Holotype: Figure t. 1419 in Bot. Reg. 17 (1831): 'T. oculus solis praecox' of Strangways.

Tulipa heliophthalma St.-Lag., Ann. Soc. Bot. Lyon 7: 70 (1880), nom. inval. pro syn.

Tulipa elwesii Baker, Gard. Chron., n.s., 20: 789. 1883, nom. illeg. Holotype: CULTIVATED, from bulbs collected in Iran, Teheran, 8.iv.1880, Hort. Elwes s.n. (K-000844477!). Note: This specimen is accompanied by a hand-coloured illustration.

Tulipa hexagonata Borbás, Oesterr. Bot. Zeitschr. 33: 202 (1883). Tulipa praecox var. hexagonata (Borbás) Levier, Tulip. Eur.: 54 (1884). Type: none cited

Tulipa (N) martelliana Levier, Bull. Soc. Sci. Nat. Neuchâteloise 14: 245 (1884). Tulipa maleolens subsp. martelliana (Levier) Nyman, Consp. Fl. Eur., Suppl. 2: 303 (1890). Note: This is a synonym of *T. agenensis* 'Maleolens'.

Tulipa libanotica Regel, Gartenflora 37: 126 (1888). Holotype: CULTIVATED. From bulbs collected in Lebanon, ex Hort. Dammannensi, Naples (LE; illustration K!).

Tulipa dammannii Regel, Trudy Imp. S.-Peterburgsk. Bot. Sada 10: 688 (1889). Holotype: CULTIVATED. From bulbs collected in Lebanon, ex Hort. Dammannensi, Naples (LE; illustration K!).

Tulipa aximensis E.P.Perrier & Songeon, Bull. Herb. Boissier 2: 435 (1894). Ind. loc.: FRANCE, Aime (none cited). Neotype (**designated here**): FRANCE. Aimes. 'Les champs à Aime, Carentaise', 1843, Huguenin 229 (K-000518089! left hand specimen). Note: This should be treated as T. agenensis 'Aximensis'.

Tulipa sharonensis Dinsm. in G.E.Post, Fl. Syria, ed. 2, 2: 621 (1933). Tulipa agenensis subsp. sharonensis (Dinsm.) Feinbr., Fl. Palaestina 4: 41 (1986). Type: ISRAEL [Palestine]. Haifa: Binyamina, al Sarafand, Dinsmore s.n. fasc. 2 (BEI). Note: This is a synonym of T. agenensis 'Maleolens'.

Tulipa veneris A.D.Hall, J. Bot. 76: 317 (1939). Holotype: CULTIVATED. Grown from bulbs collected by M. T. Dawe on Cyprus, 1939, John Innes Hort. Inst. s.n. (K-000844479!). Note: this should be treated as T. agenensis 'Veneris'.

Notes: For most of its history, this species was known as *T. oculis-solis*, but the name *T. agenensis* has priority. Both names were based on a naturalized population in Agen, France. It is distinguished from garden tulips with 'eyed' tepals in having longer outer tepals and shorter inner ones. *Tulipa agenensis* 'Maleolens' has been described as a smaller version of this species. Some triploid taxa, such as *T. agenensis* 'Praecox' and *T. agenensis* 'Veneris', can be easily distinguished by their larger flowers, but fall within the variability of this species.

2. Tulipa (T) albanica Kit Tan & Shuka, Phytotaxa 10: 19 (2010)

Holotype: ALBANIA (northeast Albania). Kukësi district: 6 km from Kolshi village to Surroj, Nand W-facing open stony serpentine slopes of Ahmet Xhindit, 7.v.2009, Shuka 250 (TIR; isotypes C, LD).

Distribution: Northeastern Albania.

Note: A species belonging to the T. scardica complex.

Tulipa (T) alberti Regel, Gartenflora 26: 257, t. 912 (1877)

Lectotype (designated here): Illustration t. 912 in Gartenflora 26 (1877). Material collected by Regel in Turkestan, Kuiankus, 19.iv.1877, Regel s.n. Iter Turkestanicum 303 (BM!, K-000844498!, K-000844500!, P-00730915!) exists, but this material is not mentioned in the protologue, but may be useful as epitypes when such are needed.

Distribution: Kazakhstan, Kyrgyzstan.

4. Tulipa (T) aleppensis Boiss. ex Regel, Trudy Imp. S.-Peterburgsk. Bot. Sada 2: 450 (1873)

Lectotype (designated by Marais, 1984, as 'holotype'): SYRIA. 'prope Aleppo in agris', 5.iv.1865, Hausknecht s.n. (K-000844476!; isotypes: BM-001066497!, BM-001066498!).

Distribution: Southern Turkey, Syria.

Tulipa oculus-solis var. aleppica Baker, J. Linn. Soc., Bot. 14: 278 (1874). Holotype: SYRIA. 'prope Aleppo in agris', 5.iv.1865, Hausknecht s.n. (K-000844476!; isotypes: BM-001066497!, BM-001066498!).

Tulipa sintenisii Baker, Gard. Chron., III, 9: 330 (1891). Lectotype (**designated here**): CULTIVATED. Hort. Kew., 14.iii.1861, Baker s.n. (K-000844457!). Note: Bulbs were sent from Schuschnass [Şuşnaz] near Erzerum by Sintenis to Leichtlin, who sent bulbs to Kew, where they flowered and from which Baker made the description. Marais (1984) stated that no specimen was preserved, but the material cited here is original and annotated by the author. It is therefore selected here as lectotype.

Note: Tulipa sintenisii was accepted by Wilford (2006) and Marais (1984), but the latter stated that this may well be a clonal selection. Specimens from near Beirut (Hall, 1938, John Innes Hort. Inst. 22.iv.1933, K!) are a triploid form of T. agenensis (Feinbrun-Dothan, 1986), but Wilford (2006) stated that T. aleppensis may well be derived from T. agenensis; they are similar, differing only in plant size, petal shape and tunic hairiness. Tulipa aleppensis is maintained here with reservation.

5. Tulipa (T) altaica Pall. ex Spreng., Syst. Veg. 2: 63 (1825)

Ind. Loc.: 'Mons Imaus'. Type: Pallas s.n. (not located). Neotype (**designated here**): Ledebour, Ic. Pl. Ross. 2: t. 134 (1830).

Distribution: Altay and Kazakhstan to northwestern China.

Tulipa gesneriana var. lutea Regel, Bull. Soc. Imp. Naturalistes Moscou 41(1): 438 (1868). Syntypes: Kirghisenstppe des Flusses Ural, Borszczow (LE); Asiatische Kirghisensteppe bei Kopal, Ludwig (LE).

Tulipa tarbagataica D.Y.Tan & X.Wei, Acta Phytotax. Sin. 38: 302, fig. 1 (2000). Holotype: CHINA. Xinjiang: Tacheng, in bushes, 1200–1600 m, 13.v.1996, D. Y. Tan 9606 (XJA).

Note: Tulipa tarbagataica is compared with T. altaica in the original description, from which it differs only in minor characters of tunic texture and capsule shape. Based on cultivated plants, Van Raamsdonk & De Vries (1995) placed T. anisophylla, T. iliensis and

T. kolpakowskiana into synonymy. These are all rather similar and obviously closely related, but can be morphologically distinguished by characters that appear to be stable in wild populations. Further field work and population level studies are needed to resolve this species complex. There are no specimens in the Pallas Herbarium (BM), which is why the plate of Ledebour was selected as a neotype.

 Tulipa (T) anisophylla Vved., Byull. Sredne-Aziatsk. Gosud. Univ. 21: 147 (1935)

Holotype: TAJIKISTAN. Darwas: 'pr. Kuf in fl. Pändsch ripa dextra (Kalaichum)', iii.1883 *Mussa s.n.* (LE).

Distribution: Southern Tajikistan.

Tulipa kolpakowskiana var. humilis Regel, Trudy Imp. S.-Peterburgsk. Bot. Sada 8: 651 (1884). Holotype: TAJIKISTAN. 'In Bucharae orientalis chanato Darwas ad fluvium Pändsch', A. Regel s.n. (LE).

Tulipa korshinskyi Vved., Byull. Sredne-Aziatsk. Gosud. Univ. 21: 149 (1935). Holotype: TAJIKISTAN. 'Darvas', 17.vi.1897, *Korshinsky* 1713 (4928) (LE).

Note: A species similar to *T. altaica* and *T. kolpa-kowskiana* and may just be a dwarf form of the first. Field studies are needed to confirm its relationship.

7. *Tulipa* (T) *armena* Boiss., Diagn. Pl. Orient., II, 4: 99 (1859)

Holotype: TURKEY. 'Armenia, in montibus inter Erzeroum et Ispir, prope Setehanck ad radices Kog-Dagh', vi.1853, Huet du Pavillon (G?, not seen; isotypes: K-000844460!, K-000844461!, K!, both yellow- and red-flowered forms are preserved in the type collection).

Distribution: Northeastern Turkey, Transcaucasia to north-western Iran.

Tulipa gesneriana var. minor Boiss., Fl. Orient. 5: 194 (1884). Syntypes: TURKEY. Aucher-Eloy 5271; Huet s.n.; IRAN. Hausknecht s.n. (possibly in G, none seen). Note: It is possible that these specimens do not all belong to the same taxon. The reference to Huet most probably refers to the type of T. armena and thus this variety is placed here.

Tulipa lutea Freyn, Bull. Herb. Boissier 4: 185 (1896). Holotype: TURKEY. Galatia: Amasya, 'in planitie Sula Owa versus Mersiwan', 28.iii.1894, Manissadjian 1110a (BRNM!; isotype: M!).

Tulipa galatica Freyn, Bull. Herb. Boissier 4: 186 (1896). Tulipa armena forma galatica (Freyn) Raamsd., Pl. Syst. Evol. 195: 41 (1995). Tulipa armena var. galatica (Freyn) Eker, Türk. Bitkileri List.: 610 (2012). Holotype: TURKEY. Amasya: 'Galatien, auf der vassen Ebene Sülü-Owa, zwischen

Amasia und Mersiwan', 28.iii.1894, *Manissadjian 1110b* (BRNM!; isotype M!). Note: Material labelled under this name grown from bulbs originally distributed by Van Tubergen (Netherlands) may be this species (e.g. in BRNM, M, K), but some specimens cultivated under this name appear to be garden tulips belonging to the *T. ×gesneriana* complex. *Tulipa galatica* Freyn is, however, the yellow form of *T. armena*.

Tulipa willmottae Freyn, Mém. Herb. Boissier 1900(13): 29 (1900), as 'Willmottiae'. Holotype: TURKEY. Van: 'Waragh-Dagh', 1899, Kronenberg s.n., exsicc. C.G. van Tubergen (BRNM!).

Tulipa mucronata Fomin, Vestn. Tiflissk. Bot. Sada 9: 13 (1908). Holotype: TURKEY. Kars: 'Habitat in regione montana Armeniae rossicae, jugum Skaltutan, districtus Olty provinciae Kars', E. König s.n. (LE; photograph K!)

Tulipa karabachensis Grossh., Trudy Bot. Inst. (Baku) 2: 249 (1936). Holotype: AZERBAIJAN. Karabach, Schuscha, Lysogorsk, Dumi, Megry in Zangezur, Karyatnyi s.n. (BAK; photograph E!).

Tulipa confusa Gabrieljan, Novosti Sist. Vyssh. Rast. 1966: 38 (1966), nom. inval. pro syn.

Tulipa gumusanica Terzioğlu, Ann. Bot. Fenn. 39: 150 (2002). Holotype: TURKEY. A7 Gümüşane: Zigana Mountain, 11.vi.2000, Terzioğlu 13362 (KATO). The 'isotype' Coşkunçelebi 296 (KTUB) mentioned in the original publication is a different gathering from the same locality and is therefore a paratype.

Notes: A variable species with red- and yellow-flowered populations, with the yellow plants known as *Tulipa galatica*. *Tulipa gumusanica* is very similar in all characters to *T. galatica*, also being a yellow colour variant with differences only in stamen colour. *Tulipa armena* var. *lycica* (Baker) Marais appears to be an independent species (Türktaş *et al.*, 2013) and is therefore treated here under its older name *T. foliosa*.

8. Tulipa (T) banuensis Grey-Wilson, Kew Bull. 29: 76 (1974)

Holotype: AFGHANISTAN. Baghlan: Andarab valley, 27 km east of Banu, mountains to the north of the road, 2200–2500 m, 7.v.1971, Grey-Wilson & Hewer 791 (K-000844486!; isotypes E-00373862!, GB, K-000844487!, W).

Distribution: Northeastern Afghanistan (Andarab Valley).

Note: This species appears similar to *T. praestans*, but differs in the narrow upper leaves, stems always one-flowered, black basal blotch on the acuminate tepals and the black filaments that are as long as the anthers.

9. Tulipa (E) biflora Pall., Reise Russ. Reich. 3, 'anhang': 727 (1776)

Liriopogon biflorum (Pall.) Raf., Fl. Tellur. 2: 35 (1837). Orithyia biflora (Pall.) Kunth, Enum. Pl. 4: 227 (1843). Tulipa sylvestris var. biflora (Pall.) Ledeb., Fl. Ross. 4: 136 (1853). Podonix albiflora Raf., Fl. Tellur. 4: 28 (1838), nom. illeg. superfl.

Lectotype (designated here): RUSSIA. 'Habitat ad Wolgam locis desertis maxime argillosis, "Deserta Caspica"', Fischer s.n. (B-W-06559-010!); syntypes are present in BM (000528948!) and M.

Distribution: Macedonia, Caucasus, Turkey, eastern Egypt (Sinai), Levant, northern Saudi Arabia, Crimea, Ukraine, southern Russia, Kazakhstan, Kyrgyzstan, Turkmenistan, Uzbekistan, Afghanistan, Iran, Iraq, northern Pakistan, northwestern China.

Tulipa sogdiana Bunge, Beitr. Fl. Russl.: 338 (1852). Holotype: UZBEKISTAN. 'Inter Bukhara et Kermin', A. Lehmann s.n. (LE; isotype K-000844627!).

Tulipa buhseana Boiss., Diagn. Pl. Orient., II, 4: 98 (1859). Tulipa biflora var. buhseana (Boiss.) Regel, Trudy Imp. S.-Peterburgsk. Bot. Sada 2: 444 (1873). Type: IRAN. 'prope Yezd Persiae', Buhse s.n. (G).

Tulipa crispatula Boiss. & Buhse, Nouv. Mém. Soc. Imp. Naturalistes Moscou 12: 211 (1860). Tulipa humilis var. crispatula (Boiss. & Buhse) Boiss., Fl. Orient. 5: 200 (1882). Type: 'Bei Guleki zwischen Damgan und Rischm, auf einem Sandhügel', 28.iii.1849, Boissier 1203 (G).

Tulipa bucharica Merck. ex Boiss., Fl. Orient. 5: 193 (1882), nomen.

Tulipa biflora var. major Boiss., Fl. Orient. 5: 200 (1882). Holotype: IRAN. 'Hab. in apricis calcareis ad Khan Zenjun inter Persepolin et Schiraz', Hausknecht s.n. (G).

Tulipa polychroma Stapf, Denkschr. Kaiserl. Akad. Wiss. Wien., Math.-Naturwiss. Cl. 50(2): 18 (1885). Lectotype (**designated here**): IRAN. 'In montibus Karaghan ad Schurab, solo salso-gypsaceo', 11.v.1882, Polak s.n. (WU 0065316!; isolectotypes: WU-0033198!, K!; ex Hort. Vindob., Pichler 116, G-00176264!; WU-0065315!).

Tulipa androssowii Litv., Spisok Rast. Gerb. Russk. Fl. Bot. Muz. Imp. Akad. Nauk 6: 114 (1908). Lectotype (designated here): TURKMENISTAN 'Turkestania'. Balkan Province: 'Transkaspia': Türkmenbaşy Distr. 'Krassnowodsk', 'in arenosis pr. st. Perewal', 27.iii.1902 (fl.), 29.iv.1905 (fr), N. Androssow 1895 (H-12370805!: isolectotypes H!. Fl. LE. PRC-454343).

Tulipa koktebelica Junge, Trudy Bot. Muz. Imp. Akad. Nauk 16: 112 (1916). Holotype: UKRAINE. Crimea: 'Tauria, Koktebel', 14.iv.1914, 7.iii.1915, A. Junge s.n. (LE; photographs E!, K!).

Tulipa biflora var. grandiflora Grossh., Exsicc. (Pl. Orient.) 1928: 353 (1928). Type: AZERBAIJAN.

Gandzha: 'Krachkesaman', 13.iv.1928, A. Kolakovsky s.n. (isotype: K!).

Tulipa turcomanica B.Fedtsch. in B.A.Fedtschenko & al., Fl. Turkm. 1: 306 (1932). Holotype: TURK-MENISTAN. Kopet Dagh, I. Lipsky s.n. (LE).

Tulipa humilis var. ornata Bornm. & Gauba, Repert. Spec. Nov. Regni Veg. 47: 77 (1939). Holotype: IRAN. 'Keredj', D. E. Gauba 1164 (B?).

Tulipa halophila Bornm. & Gauba, Repert. Spec. Nov. Regni Veg. 47: 77 (1939). Holotype: IRAN. 'Persia borealis: Hügel von Raswandeh (Salzgebiete)', 15.iv.1935, D. E. Gauba 1162 (B-100365941!).

Tulipa mariannae Lindtner, Glasn. Skopsk. Naucn. Društva 20: 137 (1939). Lectotype (**designated here**): MACEDONIA. 'Serbia australis olim Macedonia, in aridis, ad basin m. Orlovo Brdo pt., Krivolak', 20.iii.1939, V. Lindtner s.n. (K!).

Tulipa binutans Vved., Bot. Mater. Gerb. Inst. Bot. Zool. Akad. Nauk Uzbeksk. S.S.R. 13: 33 (1952). Holotype: KYRGYZSTAN. 'Alatay', 1923, Vvedensky 264 (TASH).

Tulipa prolongata Vved., Opred. Rast. Sred. Azii 2: 319 (1971). Holotype: TAJIKISTAN. 17.v.1960, Botschantzev & Egorova 15 (LE).

Note: An extremely variable species across its range. Rechinger (1990) included the single-flowered T. polychroma Stapf in T. biflora and so did Wilford (2006). Zonneveld (2009) accepted T. polychroma, but this is inconsistent with his taxonomy: the two have similar genome sizes and we conclude, on the basis of morphology and genome size, that T. polychroma should be treated in synonymy. Tulipa prolongata Vved. is similar, falls within the distribution of the species and differs only in its slightly longer bulbs. Tulipa binutans was originally placed under T. bifloriformis, but its nodding flower buds are a character found in some forms of T. biflora, and it can therefore not be kept separate from that species (Wilford, 2006). Some Turkish populations of T. biflora are known to lack the filament hairs typical of subgenus Eriostemones (Marais, 1984), and this raises doubt about the distinctiveness of T. sogdiana, which differs from T. biflora only in having glabrous stamens. After revising the type of T. callieri Halácsy & Levier, we decided that this taxon is better placed under T. sylvestris subsp. australis.

10. Tulipa (E) bifloriformis Vved., Opred. Rast. Sred. Azii 2: 320 (1971)

Holotype: UZBEKISTAN. Tian-Schan occidentalis, in collibus argillosis circa urb. Taschkent, 19.iii.1923. M.G. Popov & A.I. Vvedensky 1036 (TASH; isotypes: BM!, H-1200916!; K!).

Distribution: Kazakhstan, Kyrgyzstan, Tajikistan, Uzbekistan.

Tulipa orthopoda Vved., Opred. Rast. Sred. Azii 2: 320 (1971). Holotype: KAZAKHSTAN. Turkestan, 5.iv.1930, Lipschitz & Pavlov 32 (TASH).

Note: This species is similar to *T. turkestanica*. *Tulipa* orthopoda is a dwarf form flowering earlier and having rounder petals (Wilford, 2006), which may warrant recognition, but it will require further field work to establish the variability of *T. bifloriformis* in the wild.

11. Tulipa (T) borszczowii Regel, Bull. Soc. Imp. Naturalistes Moscou 41(1): 438 (1868)

Holotype: KAZAKHSTAN. Steppe Kara-Kum am Aralsee, Borszczow 677 (LE; photograph K!).

Distribution: Kazakhstan.

Tulipa glaucophylla Fisch. ex Regel, Trudy Imp. S.-Peterburgsk. Bot. Sada 2: 448 (1873), nom. inval., pro syn.

Tulipa aurata Litv., Izv. Turkestansk. Otd. Imp. Russk. Geogr. Obshch. IV, 5: 35 (1905).

12. Tulipa (T) botschantzevae S.N.Abramova & Zakal., Novosti Sist. Vyssh. Rast. 10: 104 (1973) Holotype: TURKMENISTAN. 'Turkomania, pars centralis montium Kopet-Dag, mons Tagarev, ad austro-occidentem a statione viae ferreae Bacharden, in angustiis Almadzhik', 25.iv.1971, S. Abramova & L. Zakaliabina s.n. (LE).

Distribution: Kopet Dagh (south Turkmenistan, north-east Iran).

13. Tulipa (T) butkovii Botschantz., Bot. Mater. Gerb. Inst. Bot. Zool. Akad. Nauk Uzbeksk. S.S.R. 16: 8 (1961)

Holotype: UZBEKISTAN. 'Tian-Schan Occidentalis, in montibus Alatau Taschkendicis', 1959, *Botschantzeva* 3754 (TASH).

Distribution: Uzbekistan.

Note: This species is similar to *T. alberti* and could be placed there in synonymy (as was carried out by Van Raamsdonk & De Vries, 1995), but it has different anther dehiscence and is therefore maintained here, although the taxa are obviously closely related.

14. Tulipa (T) carinata Vved., Opred. Rast. Sred. Azii 2: 318 (1971)

Holotype: UZBEKISTAN. 'Pamiro-Alaj: ad declivia argilloso-saxosa humida in montibus Tschulbair supra pag. Sina', 23.v.1929, A. Vvedensky 551 (TASH; isotypes BM!, H-1200913!, K!).

Distribution: Pamir Mts. to northern Afghanistan (Tajikistan, Uzbekistan, Afghanistan).

15. *Tulipa* (E) *cinnabarina* K.Perss., New Plantsman 7: 200 (2000)

Holotype: TURKEY. Konya: between Ermenek and Hadım, 3.iv.1990, Kammerlander, Pasche, Persson & Zetterlund 90-37 (GB).

Distribution: South-central Turkey.

Tulipa karamanica Özhatay & Koçak in P.H.Davis (ed.), Fl. Turkey 11: 324 (2000 publ. 2001). Holotype: TURKEY. Karaman: Sarıveliler-Taşkent, 13 km from Sarıveliler, 18.v.1999, B. Koçak & S. Koçak s.n. (ISTE; isotype: K!).

Note: A species similar to T orphanidea and T humilis.

16. Tulipa (C) clusiana Redouté, Liliac. 1: t. 37 (1803)

Lectotype (designated here): Plate 37 in Redouté Liliac. 1: t. 37 (1803). Note: The original publication refers to an illustration in Clusius (1611), page 9: Curae Posteriores, 'Tulipa persica praecox', but this figure is actually printed on page 18. Marais (1984) erroneously designated the figure on page 9 as the lectotype. Reboul (1838) also cited this woodcut but erroneously listed page 19. All these are invalid typifications and basing a species on a woodcut often makes the species difficult to interpret. Moreover, it is not certain that this illustration represents this species, although it is depicted in Besler (1613) as 'Tulipa persica non aperta', and so it was in cultivation in Clusius' time. To avoid future confusion, we hereby designate the plate in Redouté (1803), which is original material and preserves the usage of the name.

Distribution: Northern Iraq and Iran to Afghanistan and the western Himalayas (Pakistan); naturalized in France, Greece, Italy, Portugal, Spain, Tunisia and Turkey.

Tulipa praecox Cav., Descr. Pl.: 448 (1802), nom. utriq. rej. prop. Holotype: SPAIN. 'In agris prope Atocha', iii.1790, anon. ex Herb. Cavanilles (MA-476450!).

Tulipa rubroalba Brot., Fl. Lusit. 1: 520 (1804). Tulipa clusiana var. rubroalba (Brot.) Nyman, Consp. Fl. Eur.: 724 (1882). Type: PORTUGAL. 'Marquesinhas, colitur in hortis', Brotero s.n. (LISU).

Tulipa stellata Hook., Bot. Mag. 54: t. 2762 (1827). Tulipa clusiana var. stellata (Hook.) Regel, Trudy Imp. S.-Peterburgsk. Bot. Sada 2: 54 (1873). Tulipa clusiana forma stellata (Hook.) S.Dasgupta & Deb, Candollea 40: 165 (1985). Lectotype (designated here): CULTIVATED. 'East Indies', s.coll. s.n. ex Herb. Hooker. (K-000844484!).

Tulipa hispanica Willd. ex Schult. & Schult.f. in J.J.Roemer & J.A.Schultes, Syst. Veg. 7: 380 (1829).

Holotype: SPAIN. 'Habitat in Hispania', anon. (B-W-06566-010!).

Liriactis albiflora Raf., Fl. Tellur. 2: 97 (1837). Type: none cited.

Tulipa undulata Jacquem. ex Baker, J. Linn. Soc., Bot. 14: 279 (1874), nom. inval. pro syn.

Tulipa leichtlinii Regel, Trudy Imp. S.-Peterburgsk. Bot. Sada 10: 366 (1887). Holotype: KASHMIR. 'Habitat in Kaschmiriae valle Scind', *Gammie s.n.* (LE?; isotype: CAL?).

Tulipa fernandezii Blatt., J. Bombay Nat. Hist. Soc. 27: 420 (1934). Tulipa clusiana forma fernandezii (Blatt.) S.Dasgupta & Deb, Candollea 40: 169 (1985). Holotype: PAKISTAN. Waziristan: on slope of Shuidar Peak from Datta Khil Fort, 18.iv.1930, Blatter & Fernandez 1526 (K-000844381!).

Tulipa porphyreochrysantha Blatt., J. Bombay Nat. Hist. Soc. 37: 421 (1934). Tulipa clusiana forma porphyreochrysantha (Blatt.) S.Dasgupta & Deb, Candollea 40: 168 (1985). Holotype: PAKISTAN. Waziristan: hillside near Anghm village, iv.1930, L. Meynell 999 (K-000844383!).

Tulipa aitchisonii A.D.Hall, J. Bot. 76: 313 (1938), as 'aitchesonii'. Lectotype (**designated here**): CULTIVATED. UK, Surrey, grown from bulbs collected at Chitral, Kashmir, John Innes Hort. Inst. (K-00084382!).

Tulipa aitchisonii subsp. cashmeriana A.D.Hall, J. Bot. 76: 315 (1938). Tulipa clusiana forma cashmeriana (A.D.Hall) Raamsd., Pl. Syst. Evol. 195: 37 (1995). Lectotype (**designated here**): CULTIVATED. UK, Surrey. Grown from bulbs collected at Ladakh, Kashmir, comm. T. Hay, 1939, John Innes Hort. Inst. (K-000844386!).

Tulipa hafisii Bornm. & Gauba, Repert. Spec. Nov. Regni Veg. 47: 77 (1939). Type: Fedde Rep. XLVII, tab. CCLXXXVI; photograph of specimen: IRAN. Cultivated in Bot. Gard. Keredj, from bulbs collected near Shiraz, D. E. Gauba 1160 (B?).

Tulipa chitralensis A.D.Hall, Gen. Tulipa: 85 (1940). Lectotype (**designated here**): CULTIVATED. UK, Surrey, grown from bulbs collected in the Swat Valley by Capt. Cobb, comm. W. Thompson-Glover, 1939, John Innes Hort. Inst. s.n. (K!). Note: This specimen is associated with a bulb collection also preserved at K, and the type includes a hand-coloured illustration of a live plant.

Tulipa stellata var. chrysantha A.D.Hall, Gen. Tulipa: 85 (1940). Tulipa clusiana var. chrysantha (A.D.Hall) Sealy, Bot. Mag. 165: t. 13 (1948). Lectotype (**designated here**): CULTIVATED. UK, Surrey, grown from bulbs collected by Thompson-Glover, 21.v.1940, John Innes Hort Inst. 5.35'/40 (K!).

Tulipa aitchisonii var. clusianoides Wendelbo, Biol. Skr. 10(3): 162 (1958). Tulipa clusiana forma clusianoides (Wendelbo) S.Dasgupta & Deb, Candollea

40: 169 (1985). Holotype: AFGHANISTAN. 'Karez Emir', $O.H.\ Volk\ 1466$ (W).

Tulipa oreophila Rech.f., in Fl. Iran. 165: 86 (1990). Holotype: AFGHANISTAN. Kabul: 25 km N Qasim Khel, 'in montibus aupra Pocala prope Azrow (Azre Darrah)', 24.vi.1964, Freitag 5840 (herb. Freitag; isotype W).

Tulipa greywilsonii Rech.f., in Fl. Iran. 165: 87 (1990). Holotype: AFGHANISTAN. Bamian: Band-i Amir, 9500 ft, 27.v.1971, Grey-Wilson & Hewer 955 (E-00373789!; isotypes: GB, K-000844488!, K-000844489!, W).

Tulipa clusiana forma diniae Raamsd., Pl. Syst. Evol. 195: 36 (1995). Holotype: CULTIVATED. Netherlands. IVT Wageningen acc. no. 68590, T. de Vries 1115 (WAG). Note: This is a synonym of T. clusiana 'Cynthia'.

Notes: Rechinger (1990) discussed the difficulty in distinguishing T. aitchisonii and T. stellata, both of which we synonymize here. Tulipa stellata is a white form of this species. Rechinger (1990) also stated that T. oreophila belongs in this complex but that it is morphologically separate. Because of the morphological variability of T. clusiana, it is included here. The differences between T. clusiana and T. greywilsonii are insignificant, based on tunic length and flower colour alone. Tulipa aichisonii was separated by Hall (1938) because it is the diploid form of T. clusiana. It is not usually included in the broad concept of T. clusiana (Wilford, 2006), but it belongs here and can be treated as a Cultivar Group if taxonomic recognition is needed. Tulipa praecox Cav. has priority over T. clusiana, but the name T. praecox has usually been treated in the concept of Tenore (= T. agenensis), and therefore T. praecox Cav. has been proposed for rejection (Christenhusz, Fay & Govaerts, 2013). Tulipa chrysantha Boiss. is often treated as the yellow form of T. clusiana, but the type specimens of this name clearly show it to be the yellow form of T. montana. The yellow form of T. clusiana was described by Hall as var. chrysantha and is perhaps better treated as a cultivar or Cultivar Group. The similarity of the names for these yellow forms has caused some confusion, although the plants themselves are different.

17. Tulipa (E) cretica Boiss. & Heldr. in P.E.Boissier, Diagn. Pl. Orient. 13: 19 (1854)

Tulipa sylvestris var. cretica (Boiss. & Heldr.) Regel, Trudy Imp. S.-Peterburgsk. Bot. Sada 2: 443 (1873). Holotype: GREECE. Crete: 'In montib. Laysiti Cretae', v.1846, T.H.H. von Heldreich s.n. (G; isotypes: BM-001066431!, H-1315637 left hand specimen!, K! (three sheets), P-02077499!, WAG-0004631!). Distribution: Crete.

18. Tulipa (T) cypria Stapf ex Turrill, Bot. Mag. 157: t. 9363 (1934)

Lectotype (designated here): CULTIVATED. UK. Surrey: Merton, 5.v.1931, John Innes Hort. Inst. s.n. (K-000844478!). Note: This specimen was used to make the illustration in the Botanical Magazine and was therefore chosen as the lectotype.

Distribution: Cyprus.

Note: This species is similar to *T. agenensis* and is possibly a geographical variant of it (Wilford, 2006). It is classified as Endangered B2ab(iii) following the IUCN criteria (Bilz, 2011).

19. Tulipa (E) dasystemon (Regel) Regel, Trudy Imp. S.-Peterburgsk. Bot. Sada 6: 507 (1879)

Orithyia dasystemon Regel, Trudy Imp. S.-Peterburgsk. Bot. Sada 5: 261 (1877).

Holotype: KAZAKHSTAN. 'In montibus prope Wernoje ad fluvium Almatinka', A. Regel (LE; isotype PRC-454341).

Distribution: Kazakhstan, Kyrgyzstan, Central Asia to northwestern China.

Tulipa dasystemonoides Vved., Byull. Sredne-Aziatsk. Gosud. Univ. 21: 147 (1935). Holotype: 'Altai Talac', 11.vi.1909, Minkwitz 1365 (LE).

Tulipa paradasystemon Vved. in V.L.Komarov (ed.), Fl. URSS 4: 362 (1935), nom. inval.

Tulipa neustruevae Pobed., Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 11: 62 (1949).

Note: Tulipa dasystemon of commerce is not this species, but T. urumiensis Stapf. Tulipa dasystemonoides Vved. appears to be identical to T. dasystemon, but was distinguished by Vvedensky (1935a) as having a leathery bulb tunic and occasionally two flowers per stem. Tulipa neustruevae may well be a low-elevation form, differing only in having glossy green leaves and brighter yellow flowers.

20. *Tulipa* (T) *dubia* Vved., Byull. Sredne-Aziatsk. Gosud. Univ. 21: 148 (1935)

Holotype: 'Chotan ruch'ya Kash-ka-su', 10.vi.1909, Minkwitz 617 (LE).

Distribution: Kazakhstan, Kyrgyzstan, Uzbekistan.

21. Tulipa (T) faribae Ghahr., Attar & Ghahrem.-Nejad, Novon 17: 437 (2007)

Holotype: IRAN. Kermanshah, between Paveh and Javanrud (Zagros Mts), 15.v.1980, A. Ghahreman 29931 (TUH; isotypes FAR, MO, TUH).

Distribution: Iran.

Note: This taxon is compared with *T. suaveolens* (as *T. schrenkii*) in the original description, but it does not overlap in distribution with this species. *Tulipa*

faribae has non-undulate leaf margins, erect, thicker stems and much larger tepals and longer anthers than *T. suaveolens*. To us, it seems more similar to the variable *T. systola*, which occurs sympatrically in Iran. They may belong to the same species, but further study in the field is needed to verify its status.

22. *Tulipa* (T) *ferganica* Vved., Byull. Sredne-Aziatsk. Gosud. Univ. 21: 148 (1935)

Tulipa altaica var. ferganica (Vved.) Raamsd., Pl. Syst. Evol. 195: 39 (1995).

Holotype: 'Kuragt Aubyekom', 23.viii.1933, Vvedensky 592 (TASH).

Distribution: Kyrgyzstan, Uzbekistan.

Note: A species similar to *T. altaica* and it may have to be united with it. Field work will be needed to study the variability of *T. altaica* throughout its geographical range.

23. Tulipa (T) foliosa Stapf, Denkschr. Kaiserl. Akad. Wiss. Wien., Math.-Naturwiss. Cl. 50(2): 80 (1885)

Lectotype (**designated here**): CULTIVATED. 'Cult. in hort. Vindob. e bulbo a Dre. Luschan in Nemrud Dagh prope Kiachta', *Luchan s.n.* (WU-0065317!; isolectotypes K-000844466!, WU-0065318!, WU-0065319!, WU-0065320!).

Distribution: Central and southern Turkey.

Tulipa oculus-solis var. lycica Baker, J. Linn. Soc., Bot. 14: 278 (1874). Tulipa armena Boiss. var. lycica (Baker) Marais, Kew Bull. 35: 258 (1980). Lectotype (designated here): TURKEY. 'Lycia prope Arsam', E. Forbes 624 (K-000844465!; isolectotype: K-000844464!).

Tulipa ciliatula Baker, Gard. Chron., III, 7: 640 (1890). Ind. typ.: 'Based on living material cultivated from material collected in Turkey, Anti-Taurus, by Mr. Whitall'. Lectotype (**designated here**): CULTI-VATED. Hort. Barr s.n. (K-000844469!).

Tulipa concinna Baker, Gard. Chron., III, 13: 538 (1893). Ind. typ.: 'Based on living material cultivated from material collected in Turkey, western Taurus, by Mr. Whittall'. Holotype: CULTIVATED. Hort. Barr s.n. (K-000844463!). Note: This specimen includes a hand-coloured illustration.

Tulipa heterochroa Freyn, Bull. Herb. Boissier 4: 184 (1896). Holotype: TURKEY. Amasya: 'Karaman pr. Amassia', 20.v.1893, A. Manissadjian 173b (BRNM!; isotypes: B-100367670!, B-100367671!, B-100367672!, FI, K-000844462!, LD-1408557!, M!, Z-000072931!).

Note: Türktaş et al. (2013) showed that T. armena var. lycica is not conspecific with T. armena var. armena.

Therefore, it is separated here and placed under its oldest name *T. foliosa*. The species differs from *T. armena* in having densely hairy tunics with long twisted soft hairs, instead of short bristly hairs around the base plate and neck and sparse in between.

24. Tulipa (T) fosteriana W.Irving, Gard. Chron. III, 39: 322 (1906)

Holotype: figure 130 in Gard. Chron. III, 39: 323 (1906).

Distribution: Pamir Mts, Tajikistan, Kyrgyzstan and Uzbekistan to Afghanistan.

Tulipa victoris Vved., Trudy Tashk. Univ, Bot. 187: 61 (1961), nom. inval.

Tulipa affinis Botschantz., Bot. Mater. Gerb. Inst. Bot. Zool. Akad. Nauk Uzbeksk. S.S.R. 16: 6 (1961). Holotype: "Turkestania, Pamiralaj', 1956, Botschantzeva 2190 (TASH).

Note: Tulipa affinis was distinguished on the basis of a taller stature, narrower leaves and smaller flowers, which fits within the natural variability of *T. fosteriana*.

25. Tulipa (T) ×gesneriana L., Sp. Pl.: 306 (1753). Tulipa coronaria Salisb., Prodr. Stirp. Chap. Allerton: 236 (1796), nom. superfl.

Lectotype (designated by Dasgupta & Deb in Candollea 40: 158. 1985): Herb. Linn. no. 425.2 (LINN!). [Fig. 3].

Distribution: A complex hybrid only known from cultivation, escaping and sometimes naturalizing in France, Italy, Norway, Russia, Spain, Switzerland and Turkey.

Note: Linnaeus included all known garden tulips under his species T. gesneriana. He named the species after the Swiss physician Conrad Gesner, the first European to describe and illustrate a tulip (Gesner, 1561). However, Gesner's illustration resembles T. suaveolens, rather than Linnaeus' tulip. The tulip preserved in the Linnean herbarium is a tall single tulip with broad leaves and probably yellow tepals. It matches some late flowering tulips used in the 18th and 19th centuries as stock for breeding flamed types. Few of these are still in cultivation, but they are the ancestors of the modern Darwin hybrids. The name T. gesneriana should not be applied to modern cultivars or any wild species.

Tulipa hortensis Gaertn., Fruct. Sem. Pl. 1: 64, t. 17, f. 2 (1788). Type: none cited; the figure shows fruits and seeds only.

Tulipa stricta Stokes, Bot. Mat. Med. 2: 239 (1812).

Tulipa pubescens Willd., Enum. Pl., Suppl.: 17 (1814). Holotype: Anon. (B-W-06565-010!). Note: This may be a garden hybrid between T. ×gesneriana and T. suaveolens.

Tulipa laciniata Fisch. ex Bellerm., Mag. Neuesten Entdeck. Gesammten Naturk. Ges. Naturf. Freunde Berlin 7: 67 (1816).

Tulipa campsopetala Delaun. ex Loisel., Herb. Gén. Amateur 3: t. 172 (1819). Holotype: Plate in Herb. Gén. Amateur 3: t. 172, fig. 2 (1819). Note: This is a broken garden tulip.

Tulipa (N) bonarotiana Reboul, Nonnul. Sp. Tulip. Not.: 7 (1822). Tulipa strangulata var. bonarotiana (Reboul) Reboul, Antologia (Florence) 28(2): 292 (1827). Tulipa scabriscapa var. bonarotiana (Reboul) Fox-Strangw., Edwards's Bot. Reg. 23: t. 1990, f. 3 (1837), as 'Buonarotiana'. Tulipa scabriscapa var. bonarotiana (Reboul) Nyman, Consp. Fl. Eur.: 723 (1882), nom. illeg. superfl. Tulipa strangulata var. bonarotiana (Reboul) Levier, Tulip. Eur.: 84 (1884), nom. illeg. superfl. Tulipa strangulata subsp. bonarotiana (Reboul) K.Richt., Pl. Eur. 1: 216 (1890). Neotype (designated here): ITALY. 'aux environs de Florence, dans le champs Alla Villa Buonarroti, a Settignano', iv.1846, Reboul s.n. (FI).

Tulipa (N) strangulata Reboul, Nonnul. Sp. Tulip. Not.: 6 (1822). Tulipa scabriscapa var. strangulata (Reboul) Fox-Strangw., Edwards's Bot. Reg. 23: t. 1990, f. 3 (1837). Tulipa strangulata var. princeps Reboul, Antologia (Florence) 28(2): 292 (1827), nom. inval. pro syn. Ind. loc.: 'Dirutam Divi Miniatis arcem inter et Divae Margaritae templum, detexi'. Type: not located.

Tulipa strangulata var. neglecta Reboul, Antologia (Florence) 28(2): 292 (1827). Tulipa neglecta (Reboul) Reboul, Select. Sp. Tulip.: 7 (1838). Tulipa scabriscapa var. neglecta (Reboul) Nyman, Consp. Fl. Eur.: 723 (1882). Type: ITALY. Bologna, 1826, Bertoloni, not located. Note: This is a yellow form.

Tulipa media C.Agardh ex Schult. & Schult.f. in J.J.Roemer & J.A.Schultes, Syst. Veg. 7: 379 (1829). Tulipa turcica var. media (C.Agardh ex Schult. & Schult.f.) Regel, Trudy Imp. S.-Peterburgsk. Bot. Sada 2: 457 (1873). Type: Agardh s.n. (LD?, not found).

Tulipa repens Fisch. ex Sweet, Brit. Fl. Gard. 4: t. 97 (1831).

Tulipa bicolor Raf., Atlantic J.: 153 (1833). Type: USA. Arkansas: herb. Rafinesque (not located). Note: A naturalized garden tulip.

Tulipa montana Raf., Atlantic J.: 153. 1833, nom. illeg., based on an illustration in Audubon (1809) from USA, Alleghany Mountains, not seen. Note: A naturalized garden tulip.

Tulipa scabriscapa Fox-Strangw., Edwards's Bot. Reg. 23: t. 1990 (1837). Note: Even though the descriptions are based on a variety of tulips found 'wild' around Florence, the accompanying illustration

shows a number of garden tulips, including the following two:

Tulipa scabriscapa var. *mixta* Fox-Strangw., Edwards's Bot. Reg. 23: t. 1990, f. 1 (1837). Note: A broken garden tulip.

Tulipa scabriscapa var. primulina Fox-Strangw., Edwards's Bot. Reg. 23: t. 1990, f. 4 (1837). Note: A yellow garden tulip.

Tulipa unguiculata Raf., Fl. Tellur. 2: 35 (1837). Type: none cited.

Tulipa serotina [Clusius] Reboul, Select. Sp. Tulip.: 6 (1838). Note: This is based on an illustration in Clusius (1601), Rar. Pl. Hist.: 144, 'T. serotina flava'. It represents a garden cultivar.

Tulipa variopicta Reboul, Select. Sp. Tulip.: 7 (1838). Tulipa scabriscapa subvar. variopicta (Reboul) Nyman, Consp. Fl. Eur.: 723 (1882). Tulipa strangulata var. variopicta (Reboul) Levier, Tulip. Eur.: 84 (1884). Tulipa strangulata subsp. variopicta (Reboul) K.Richt., Pl. Eur. 1: 215 (1890). Holotype: ITALY. San Niccolo, in fields near Florence, iv.1846, Reboul s.n. (FI).

Tulipa scabriscapa var. hawardeniana Bertol., Fl. Ital. 4: 86 (1839). Type: ITALY. Florence, 'Gamberaia', Reboul s.n., not located.

Tulipa scabriscapa var. rebouliana Bertol., Fl. Ital. 4: 86 (1839). Ind. loc.: 'legi Bononiae in collibus dell'Osservanza cum specie, et habui Florentia a Ricoboli', not located.

Tulipa (N) spathulata Bertol., Fl. Ital. 4: 85 (1839). Tulipa gesneriana var. spathulata (Bertol.) Nyman, Consp. Fl. Eur., Suppl. 2: 302 (1890). Type: ITALY. 'Habui ex agro Florentino in villa Antinoriana alle Rose', Reboul, not located. Note: This is sometimes in cultivation as a variety of T. gesneriana. It should be treated as T. Didieri Group 'Spathulata'.

Tulipa (N) didieri Jord., Observ. Pl. Nouv. 1: 34 (1846). Lectotype (designated here): FRANCE. Savoie: Saint Jean de Maurienne, 1846, *C. Jordan s.n.* (BM-001066427!; isolectotypes BM-001066426!, K!). Note: This should be treated as *T.* Didieri Group 'Didieri'.

Tulipa (N) fransoniana Parl., Nuov. Gen. Sp. Monocot.: 15 (1854). Holotype: ITALY. In campis prope Florentiam, F. Parlatore s.n. (FI, isotype PH-28529!). Note: this neo-tulipa belonging to the Didieri Group is no longer cultivated, but closely resembles T. 'Spathulata'.

Tulipa (N) platystigma Jord. in P.C.Billot, Annot. Fl. France Allemagne: 32 (1855). Tulipa didieri subsp. platystigma (Jord.) Nyman, Consp. Fl. Eur.: 724 (1882). Note: This differs from other naturalized tulips in its lilac-purple colour. It should be treated as T. Didieri Group 'Platystigma'.

Tulipa (N) billietiana Jord., Ann. Soc. Linn. Lyon, n.s., 5: 11 (1858). Tulipa didieri var. billietiana (Jord.) Baker, J. Linn. Soc., Bot. 14: 283 (1874). Tulipa

didieri subsp. billietiana (Jord.) Nyman, Consp. Fl. Eur., Suppl. 2: 303 (1890). Ind. loc.: 'Cette espèce croît spontanément dans les champs de la vallée de Maurienne, en Savoie, d'où je l'ai reçue de Mgr Billiet archevèque de Chambéry'. Type: none cited. Note: This yellow cultivar should be treated as T. Didieri Group 'Billietiana'.

Tulipa (N) mauritiana Jord., Ann. Soc. Linn. Lyon, n.s., 5: 12 (1858). Loc. ind.: 'Cette espèce croît spontanément dans les champs de la vallée de Maurienne en Savoie. J'en ai reçue de M. Didier'. Type: none cited. Note: this should be treated as T. Grengiolensis Group 'Mauritiana'. The cultivar 'Cindy' previously placed under this taxon also belongs to the Grengiolensis Group.

Tulipa (N) planifolia Jord., Ann. Soc. Linn. Lyon, n.s., 5: 13 (1858). Tulipa didieri var. planifolia (Jord.) Baker, J. Linn. Soc., Bot. 14: 283 (1874). Ind. Loc.: 'Cette espèce habite . . . la vallée de Maurienne en Savoie, d'où elle m'a été envoyée par M. Didier'. Type: none cited. Neotype (designated here): CULTI-VATED. UK, Surrey: Kew Gardens, 9.v.1896, s.coll. s.no. (K-000518092!). Note: this should be treated as T. Didieri Group 'Planifolia'.

Tulipa (N) mauriana Jord. & Fourr., Icon. Fl. Eur. 1: 9 (1866). Tulipa didieri var. mauriana (Jord. & Fourr.) Baker, J. Linn. Soc., Bot. 14: 283 (1874). Tulipa fransoniana subsp. mauriana (Jord. & Fourr.) Nyman, Consp. Fl. Eur., Suppl. 2: 303 (1890). Note: this should be treated as T. Didieri Group 'Mauriana'.

Tulipa retroflexa Baker, J. Linn. Soc., Bot. 14: 282 (1874). Lectotype (**designated here**): CULTIVATED. 14.v.1873, Hort. Barr s.n. (K-000844393!). Note: A hybrid of unknown parentage.

Tulipa acutiflora DC. ex Baker, J. Linn. Soc., Bot. 14: 283 (1874), nom. illeg.

Tulipa fulgens Baker, J. Linn. Soc., Bot. 14: 285 (1874). Lectotype (**designated here**): CULTIVATED. 3.v.1873, Hort. Barr. s.n. (K-000844394!). Note: this is a putative hybrid between T. ×gesneriana and T. suaveolens.

Tulipa (N) mauriannensis Didier, Bull. Soc. Dauphin. Échange Pl. 1875: 43 (1875). Ind. Loc.: FRANCE. Vallée de Maurienne, no specimen cited. Note: This belongs to the Didieri Group. The name is no longer in use.

Tulipa macrospeila Baker, Gard. Chron. n.s. 20: 11 (1883). Lectotype (**designated here**): CULTIVATED. South Kensington, v.1883, Hort. E. G. Loder s.n. (K-000844388!). Note: This cultivar belongs to the Didieri Group. The name is no longer in use.

Tulipa connivens Levier, Orig. Tulip. Sav. Ital.: 12 (1884), nom. inval. pro syn.

Tulipa lurida Levier, Orig. Tulip. Sav. Ital.: 15 (1884). Type: ITALY. Florence, Impruneta, Martelli (not located).

Tulipa sommieri Levier, Orig. Tulip. Sav. Ital.: 15 (1884). Tulipa scabriscapa var. sommieri (Levier) Nyman, Consp. Fl. Eur., Suppl. 2: 302 (1890). Holotype: ITALY. Villa Pratolino, 26.iv.1871, S. Sommier s.n. (FI).

Tulipa didieri var. flavicans Levier, Tulip. Eur.: 63 (1884). Tulipa didieri subsp. flavicans (Levier) K.Richt., Pl. Eur. 1: 214 (1890). Note: a yellow tulip belonging to the Didieri Group, probably representing T. 'Billietiana'.

Tulipa connivens var. luteoguttata Levier, Tulip. Eur.: 65 (1884). Tulipa connivens subsp. luteoguttata (Levier) K.Richt., Pl. Eur. 1: 214 (1890).

Tulipa connivens var. obtusata Levier, Tulip. Eur.: 65 (1884). Tulipa connivens subsp. obtusata (Levier) K.Richt., Pl. Eur. 1: 214 (1890).

Tulipa neglecta var. atroguttata Levier, Tulip. Eur.: 80 (1884). Tulipa neglecta subsp. atroguttata (Levier) K.Richt., Pl. Eur. 1: 215 (1890).

Tulipa strangulata var. obtusata Levier, Tulip. Eur.: 84 (1884). Tulipa strangulata subsp. obtusa K.Richt., Pl. Eur. 1: 215 (1890). Lectotype (**designated here**): ITALY. Toscana (Etruria): 'e loco adhui ignoto agriflorentini gustannis in emporium affertus et vilipretio venditatur', 26.iv.1886, E. Levier s.n. (K!).

Tulipa etrusca Levier, Bull. Soc. Sci. Nat. Neuchâtel 14: 262 (1884). Tulipa serotina var. etrusca (Levier) Nyman, Consp. Fl. Eur., Suppl. 2: 302 (1890).

Tulipa orientalis Levier, Bull. Soc. Sci. Nat. Neuchâtel 14: 263 (1884).

Tulipa (N) passeriniana Levier, Bull. Soc. Sci. Nat. Neuchâtel 14: 270 (1884). Tulipa suaveolens var. passeriniana (Levier) Nyman, Consp. Fl. Eur., Suppl. 2: 302 (1890). Note: this should be treated as T. Didieri Group 'Passeriniana'.

Tulipa viridiflora auct., Garden (London) 32: 514 (1887). Note: This forms the basis for the Viridiflora Group.

Tulipa vitellina auct., Garden (London) 36: 531 (1889).

Tulipa baldaccii Mattei, Malpighia 7: 56 (1893). Ind. typ.: Described from living plants bought by the author on the market of Bologna, 25.iv.1889. Type: none cited.

Tulipa (N) marjolettii E.P.Perrier & Songeon, Bull. Herb. Boissier 2: 432 (1894). Tulipa perrieri Marj. ex P.Fourn., Quatre Fl. France: 165 (1935), nom. superfl. Type: FRANCE. Aime, R.R. (not located). Neotype (designated here): CULTIVATED. 1903, ex Hort. E.A. Bowles (BM!). Note: This should be treated as T. Grengiolensis Group 'Marjolettii'.

Tulipa segusiana E.P.Perrier & Songeon, Bull. Herb. Boissier 2: 435 (1894). Ind. loc.: Italy, Suse. Type: not located.

Tulipa (N) saracenica E.P.Perrier, Bull. Herb. Boissier, II, 5: 507 (1905). Type: FRANCE. Savoie: Saint-

Jean-de-Maurienne, Mont-André, commune d'Hermillon, *E. Perrier de la Bathie* (not located). Note: This should be treated as *T.* Didieri Group 'Saracenica'.

Tulipa (N) grengiolensis Thommen, Bull. Murith. Soc. Valais. Sci. Nat. 63: 63 (1946). Note: This taxon is variable in the naturalized population in the Valais from where it was described, having flowers varying from red to pale yellow. The common one in cultivation with pale yellow flowers with red-feathered edges can be treated as T. Grengiolensis Group 'Grengiolensis'.

Tulipa (N) montisandrei J.Prudhomme, Monde Pl. 89: 22 (1994). Holotype: CULTIVATED. France. Savoie: 'vieille cultures de sainfoin tout près du hameau du Mont André, commune d'Hermillon, 11.v.1989, J. Prudhomme 765.21 (Herb. Prudhomme; isotypes: G, P). Holotype: FRANCE. Villefort. cultivated plant, 25.iv.2007, Lieser s.n. (P). Note: This should be treated as T. Didieri Group 'Montisandrei'.

Tulipa (N) rubidusa Lieser, Iris et Bulbeuses 158: 18 (2008). Holotype: FRANCE. Villefort. cultivated plant, 25.iv.2007, Lieser s.n. (P). Note: this belongs to the Didieri Group.

Tulipa sedunii Lieser, Iris et Bulbeuses 158: 19 (2008). Holotype: FRANCE. Villefort. cultivated plant, 14.v.2007, Lieser s.n. (P). Note: this is not a species, but better treated under its established cultivar name T. Grengiolensis Group 'Cindy'.

Tulipa norvegica Lieser, Iris et Bulbeuses 161: 66 (2011). Holotype: FRANCE. Florac. cultivated plant, 29.iv.2011, Lieser s.n. (P). Note: this is a garden escape of an old-fashioned Darwin Hybrid tulip (single late, pink), which will have an established cultivar name, possibly T. 'Pink Impression'. It should not be treated as a species.

Notes: Tulipa ×gesneriana is an early garden hybrid. The origin lies undoubtedly in Turkey, Persia or Central Asia, but it is uncertain from which species it is derived, but it most likely involved T. suaveolens. T. armena, T. hungarica, T. agenensis, T. kaufmanniana and possibly several others. The circumscription of the species has varied in the past; Linnaeus (1753), who did not want to separate all the garden forms as species, meant it to treat all garden tulips under a single species name. This can of course not be followed, because many garden hybrids have different parental origins. Hall (1940) described T. gesneriana as a tulip which is more like T. armena. Rechinger (1990) defined it as something similar to T. suaveolens, following the assumption that the type of it is Gesner's tulip (Mordak, 1990). Early cultivars have naturalized in many places in Europe, and it has been suggested that 'T. Didieri' represents the wild form of T. xgesneriana, but no truly wild populations are known. Many names of historical garden plants are

difficult to match with modern hybrids, and therefore these have been placed here under T. xgesneriana, a garden plant of which the typical form is no longer extant but descendents are found amoung our garden tulips. In principle, this name could be applied to most garden hybrids, but it is not in current horticultural tradition to do so. As it is a garden plant of unknown origin, it is better to refrain from using the name for modern cultivars because it does not give any additional information. We probably will never know what is the origin of T. xgesneriana, but the group can be defined as a classical garden tulip with cup-shaped flowers, with or without a blotch, and long, oblong to lanceolate leaves (Wilford, 2006). The associated neo-tulipae are placed in the Didieri Group, if unicolorous with basal blotches, and in the Grengiolensis Group, if having differently coloured margins. These should be treated as cultivars in their respective Groups.

There has been a confusion about the name *T. acuminata*. Bulbs offered in the trade under this name do not correspond with the type specimen of *T. acuminata* Vahl, which is a synonym of *T. agenensis*. The correct name for the horned tulip is *T.* 'Cornuta', a name under which this plant used to be known.

26. Tulipa (T) greigii Regel, Gartenflora 22: 290, t. 773 (1873)

Lectotype (designated here): Illustration t. 773 in Gartenflora 22 (1873). Several syntypes from 'Turkestania', collected by Sewerow, Fedschenko, Krause and Korolkow, are cited in the protologue, but none was traced. Possibly material is in existence in LE. A specimen collected by Regel ['Karagus, Kuratan', Regel 147 (G-00176266!, K-000844619!)] is not original material. The specimen Korolkow s.n. (K-000844620!) is this species, but was collected in 1877 after its description.

Distribution: Northeastern Iran, Kazakhstan, Kyrgyzstan, Tajikistan, Uzbekistan.

Tulipa altaica var. karatavica Regel, Bull. Soc. Imp. Naturalistes Moscou 41(1): 439 (1868). Tulipa karatavica (Regel) Vved. ex Lipsch., Izv. Bot. Sada Akad. Nauk S.S.S.R. 30: 733 (1931 publ. 1932). Holotype: KAZAKHSTAN. Im Kokanischem Karatau, Sewerzow s.n. (LE).

Tulipa greigii var. flava Regel, Trudy Imp. S.-Peterburgsk. Bot. Sada 2: 449 (1873). Type: none cited.

Tulipa krauseana Regel, Trudy Imp. S.-Peterburgsk. Bot. Sada 6: 508 (1879). Type: KAZAKHSTAN. 'In montibus Karatavicis', Krause (LE?)

Tulipa mogoltavica Popov & Vved., Opred. Rast. Sred. Azii 2: 318 (1971). Holotype: TAJIKISTAN. 'Tian-Shan Occidentalis: ad declivia saxosa montium

Mogoltau in angustiis fl. Schunluk', 22.iv.1927, *I. Granitov* 483 (TASH; isotypes: BM!, H-1200899!).

Notes: Tulipa greigii can be easily recognized by its dark leaf markings, almost unique in tulips, although also found in varieties of T. undulatifolia. Cultivars with such markings are often placed in the 'Greigii Group', but these are nearly always the result of hybridization with T. fosteriana and/or T. kaufmanniana and should therefore be placed in a Cultivar Group independent of a species. Maybe 'Greig Hybrids' would be a good Group name for such hybrid cultivars with striped leaves. Tulipa mogoltavica is a red colour form of T. greigii. Tulipa krauseana was placed by Regel in Orithyia, but it is described as having no pronounced style, spotted leaves and small yellow-white flowers, similar to T. greigii. It was accepted by Vvedensky (1935b) but, according to Hall (1940), this is a doubtful species. It was not accepted by Botschantzeva (1982), but it was not placed into synonymy by her. We have not seen original material, but it is likely to belong here.

27. Tulipa (C) harazensis Rech.f., in Fl. Iran. 165: 91 (1990)

Holotype: IRAN. Maz: east side of Haraz River, ridge east of Emarat, 16.iv.1959, Wendelbo 211 (BG; isotype: W).

Distribution: Northern Iran.

Note: This species is similar to the variable *T. montana*, but seems to be consistently different. It is maintained here tentatively, pending further study.

28. Tulipa (O) heteropetala Ledeb., Icon. Pl. 1: 21, t. 85 (1829)

Holotype: KAZAKHSTAN. 'Bukhtarminsk et Mont Kurtschum', Ledebour s.n. (LE).

Distribution: Altay to northern Kazakhstan.

Ornithogalum oxypetalum Ledeb., Fl. Altaic. 2: 27 (1830). Orithyia oxypetala (Ledeb.) D.Don in R.Sweet, Brit. Fl. Gard. 7: t. 336 (1835). Orithyia uniflora var. oxypetala (Ledeb.) Regel, Izv. Imp. Obsc. Ljubit. Estesv. Moskovsk. Univ. 21(2): 142 (1876). Holotype: RUSSIA. 'Altai', C.F. v. Ledebour s.n. (LE; isotypes: K-000844632!, PH-19923!).

29. *Tulipa* (O) *heterophylla* (Regel) Baker, J. Linn. Soc.. Bot. 14: 295 (1874)

Orithyia heterophylla Regel, Bull. Soc. Imp. Naturalistes Moscou 41(1): 440 (1868). Eduardoregelia heterophylla (Regel) Popov, Index Seminum (AA) 3: 9 (1936).

Holotype: CHINA. 'Tienshan: Trens Ui Ala Tau', Semenow s.n. (LE).

Distribution: Southern Kazakhstan, Kyrgyzstan, northwestern China.

30. *Tulipa* (T) *heweri* Raamsd., Nordic J. Bot. 18: 52 (1998)

Holotype: CULTIVATED. Grown from seeds collected in Afghanistan, Salang Pass, N of Kabul, v.1994, L.W.D. van Raamsdonk 7001 (WAG-0058097!; isotypes K, LE, WAG-0058098!).

Distribution: Afghanistan.

Note: A species similar to *T. praestans*, but with less ciliate leaf margins (Wilford, 2006).

31. Tulipa (T) hissarica Popov & Vved., Byull. Sredne-Aziatsk. Gosud. Univ. 21: 149 (1935)

Holotype: TAJIKISTAN. 'Gissarskii chrebet' [Hissar Mountains], Myra, 14.vi.1915, Popov 1063⁴ (TASH). Distribution: Tajikistan.

Note: A little known species, mainly propagated vegetatively in botanical gardens in Central Asia. It is a small, yellow-flowered species that is rather distinct, without close relatives according to Botschantzeva (1982), but Zonneveld (2009) placed it in section Kolpakowskianae.

32. *Tulipa* (T) *hoogiana* B.Fedtsch., Gard. Chron. III, 48: 53 (1910)

Lectotype (designated here): Supplementary illustration to Gard. Chron III, 48, July 23, 1910.

Distribution: Southern Turkmenistan to northern Iran.

Tulipa amabilis B.Fedtsch., Bot. Jahrb. Syst. 50(Suppl.): 612 (1914), nomen.

Tulipa ingens forma pallida B.Fedtsch., Fl. Turkm. 1: 303 (1932).

Tulipa sovietica A.D.Hall, Gen. Tulipa: 159 (1940). Lectotype (**designated here**): CULTIVATED. 1939, John Innes Hort. Inst. s.n. (K-000844615!; isotype: K-000844616!).

Note: This species belongs to the group of *T. ingens*, *T. fosteriana* and *T. lanata*. Even though they differ in minute characters, these species are geographically isolated and intermediates do not exist outside cultivation.

33. *Tulipa* (E) *humilis* Herb., Edwards's Bot. Reg. 30(Misc.): 30 (1844)

Neotype (designated here): IRAN. 'In solo schistoso m. Elbrus pr. Derbend', 6.v.1843, T. Kotschy, Pl. Pers. bor. 105 (K!). Note: Herbert (1844) wrote that he 'received it from Mr. Kotschy, who collected it on Mount Elburz. It flowered at Spofforth in April 1844'.

No cultivated specimen labelled by Herbert was found, and so the *Kotschy* specimen is the closest we have to original material.

Distribution: Southern and southeastern Turkey, Azerbaijan, Lebanon, Syria, northern Iraq, northern Iran.

Tulipa violacea Boiss. & Buhse, Nouv. Mém. Soc. Imp. Naturalistes Moscou 12: 211 (1860). Type: AZERBAIJAN. 'Talyschgebirge, an der Westseite oberhalb des Dorfes Chummes', 18.iv.1848, Boissier 953 (G). Note: This is generally treated as T. humilis Violacea Group, although not all cultivars currently placed in this Group belong here. Wild plants should be referred to as T. humilis var. violacea (Boiss. & Buhse) Christenh., comb. nov., whereas cultivars should be placed in T. humilis Violacea Group.

Tulipa sylvestris var. pulchella Fenzl ex Regel, Trudy Imp. S.-Peterburgsk. Bot. Sada 2: 443 (1873). Tulipa pulchella (Fenzl ex Regel) Baker, J. Linn. Soc., Bot. 14: 289 (1874). Holotype: TURKEY. 'Cilicicum in Tauri alpis Bulgar Dagh', 9.vii.1853, Kotschy exsicc. Tulipa 506 (LE; isotypes BM!, WAG-0002099!). Note: Wild plants should be treated as T. humilis var. pulchella (Fenzl ex Regel) Christenh., comb. nov., whearas cultivars are placed in T. humilis Pulchella Group.

Tulipa alpina J.Gay ex Baker, J. Linn. Soc., Bot. 14: 289 (1874), nom. inval. Lectotype (**designated here**): TURKEY. 'Region alpine du Taurus oriental, au-dessus de Boulgarmaden', vii.1855, J. Gay 152 (K!).

Tulipa lownei Baker, J. Linn. Soc., Bot. 14: 294 (1874). Lectotype (**designated here**): SYRIA. 'Southern Syria, top of Mt Hermon', 1863–1864, B. T. Lowne s.n.ex Herb. Hooker. (K!; isotypes BM!, ex Herb. Churchill. K!, ex Herb. Lowne K!).

Tulipa lownei var. haynei Baker, J. Linn. Soc., Bot. 14: 295 (1874). Holotype: LEBANON, Hayne s.n. (K!). Tulipa aucheriana Baker, Gard. Chron., n.s., 20: 168 (1883). Lectotype (designated here): IRAN. Ispahan, Aucher-Eloy 5372 (K!). Note: This should be treated as T. humilis var. aucheriana (Baker) Christenh., comb. nov.

Tulipa caucasica Lipsky, Vestn. Tiflissk. Bot. Sada 6(1): 85 (1905). Tulipa lipskyi Grossh., Fl. Kavkaza 1: 223 (1928), nom. superfl. Holotype: RUSSIA. Caucaus, 'prov. Kuban: fonts fl. Kuban, Uczkulan, in declivibus montium', 24.vi.1900, N. Desoulavy 942 (LE; isotypes: C!; H-1237832!; FI; K!; PRC-454342).

Tulipa narcissiodora Markgr., Gartenbauwissenschaft 22: 551 (1957). Ind. Typ.: 'Libanon: Boron-Zedern, Dr. Werckmeister, blühend im Botanischen Garten München, April 1957'. Holotype: LEBANON. Werckmeister (M!).

Tulipa kurdica Wendelbo, Bot. Not. 127: 276 (1974). Holotype: IRAQ. Arbil: 'In declivibus austrooccidentalibus Algurd Dagh (M. Helgurd)', 2400 m, 5.vi.1960, *Agnew & Hadač 2232* (PR; isotype E-00373785!, fruiting specimen). Note: This should be treated as *T. humilis* var. *kurdica* (Wendelbo) Christenh., **comb. nov.**

Tulipa humilis subsp. matinae Zojajifar & Sheidai, Iranian J. Bot. 9: 66 (2001). Holotype: IRAN. Hamadan: Kuh-e Alvand, near Ganjnameh, 23.iv.1999, Bidari 99130 (HSBU).

Notes: Tulipa humilis is a variable species in flower colour and size, even within a population, and its petal blotches vary from black to blue to yellow. Plants with violet or crimson flowers and black blotches were described as *T. humilis* var. *violacea*, but this does not always correspond to cultivars classified in the *T. humilis* Violacea Group.

Tulipa T. humilis var. aucheriana is essentially a geographical variant differing only in size and flower colour; in horticulture, it can be treated as a Cultivar Group. Rechinger (1990) accepted T. kurdica, but stated that it belongs to the morphological variability of T. humilis. Wilford (2006) also accepted T. kurdica, but included T. pulchella in T. humilis. Natural varieties with a geographical isolation should be treated at varietal rank, but when cultivars selected from these are best treated as Cultivar Groups. Tulipa pulchella was accepted in a morphometric study on Turkish Tulipa (Eker, Babaç & Koyuncu, in press), but this did not take the entire distribution of the species into account. It can be recognized as a regional variety or, when cultivated, as a Cultivar Group.

34. *Tulipa* (T) *hungarica* Borbás, Foldmiv. Erdek.: 561 (1882)

Lectotype (**designated here**): ROMANIA. Banat: 'in rupibus pendibus vallis Kazán ad Danibium inferiorem', 16.iv.1873, Borbás 1091 (BP-588426!).

Distribution: Southern Bulgaria (probably native), naturalized in Romania.

Tulipa urumoffii Hayek, Verh. K. K. Zool.-Bot. Ges. Wien 61: (110) (1911). Tulipa orientalis var. urumoffii (Hayek) Stoj. & Stef., Fl. Bulgar. 1: 240 (1924). Tulipa hungarica var. urumoffii (Hayek) Hayek, Repert. Spec. Nov. Regni Veg. Beih. 30(3): 69 (1933). Lectotype (designated here): BURGARIA. In graminosis siccis ad Belovo, 1910, I. K. Urumoff 176 (WU-0065328!; isotype: WU-0065329!).

Tulipa rhodopea (Velen.) Velen., Reliq. Mrkvic.: 28 (1922). Tulipa orientalis var. rhodopea Velen., Sitz. Ber. Böhm. Ges. Wiss. 40: 8 (1899). Tulipa hungarica subsp. rhodopea (Velen.) Raamsd., Pl. Syst. Evol. 195: 42 (1995). Holotype: BULGARIA. Plovdiv District: 'In submontanis ad Stanimaka' [Asenovgrad], 14.v.1899,

 $V.~St\check{r}ibny~s.n.~(PRC-451295~\&~451296~(specimen mounted on two sheets); isotype: H-1315685!).$

Tulipa (N) hungarica var. undulatifolia Roman, Stud. Cercet. Biol. (Bucharest), Ser. Biol. Veg. 23: 478 (1971). Tulipa hungarica subsp. undulatifolia (Roman) Roman & Beldie, Fl. Republ. Social. Român. 13: 52 (1976). Holotype: ROMANIA. 'in saxosis et lapidosis ad vallem Oglănic prope pagum Gura Văii (distr. Mehedinți)', 24.iv.1966, N. Roman s.n. (BUCA). Note: not to be confused with T. undulatifolia Boiss.

Tulipa aureolina Delip., Feddes Repert. 87: 1 (1976). Holotype: BULGARIA. Burgas distr.: 'in collis 'Kara bair'', 5.v.1971, S. Dimitrov & D. Delipavlov s.n. (SOA).

Note: This rounded yellow tulip is probably closely allied to *T.* ×*gesneriana* and may be one of the parents or may also be a hybrid. It is possible that this taxon escaped during Ottoman occupation of the area. Its origin is unknown and it is therefore often treated as a neo-tulipa, and, if done so, these taxa may be treated under a separate Cultivar Group. Material in cultivation as *T. hungarica* in the Netherlands is not this species, but a red-flowered member of the Didieri Group. Natural populations of this species are listed as Near Threatened by the IUCN redlist (Stevanović, 2011), but this may need to be revised because of the updated taxonomy of this species.

35. *Tulipa* (T) *iliensis* Regel, Gartenflora 28: 162, t. 975, fig. c, d (1879)

Lectotype (**designated here**): KYRGYZSTAN. 'Sarybulak', 23.iv.1878, A. Regel s.n. (P-00730916!; isolectotype BM!).

Distribution: Kazakhstan, Kyrgyzstan, northwestern Xinjiang (China).

Tulipa thianschanica Regel, Trudy Imp. S.-Peterburgsk. Bot. Sada 6: 508 (1879). Holotype: KYR-GYZSTAN. 'In montibus thianschanicis ad fluvium Agias', A. Regel s.n. (LE; isotypes: BM!, K-000844633!).

Tulipa thianschanica var. sailimuensis X.Wei & D.Y.Tan, Acta Phytotax. Sin. 38: 304 (2000). Holotype: CHINA. Xinjiang: Sailimuhu, 31.v.1999, D. Y. Tan & X. Wei 99036 (XJA).

Note: Regel (1879) placed *T. thianschanica* in subgenus *Orithyia*, but it belongs to subgenus *Tulipa* because there is no defined style, stamens are described as glabrous and specimens cannot be distinguished from *T. iliensis* according to Hall (1940). *Tulipa iliensis* appears to be a small form of *T. kolpakowskiana* and hence Van Raamsdonk & De Vries (1995) placed both under *T. altaica*, to which these taxa certainly are allied.

36. *Tulipa* (T) *ingens* Hoog, Gard. Chron., III, 32: 14 (1902)

Lectotype (designated here): figure 7 in Gard. Chron., III, 32: 14 (1902).

Distribution: Tajikistan, Uzbekistan.

Tulipa tubergeniana Hoog, Gard. Chron., III, 35: 358 (1904). Lectotype (**designated here**): Illustration in Supplement Gard. Chron., III, 35, 4.vi.1904.

Tulipa bactriana S.de Groot, nom. prov., in K. Tojibaev, Tulips of Uzbekistan ed. 2 (2013).

Note: Wilford (2006) accepted *T. tubergeniana* as separate from *T. ingens*, but they differ only in minor characters, mostly flower size. Zonneveld (2009) placed this species erroneously as a synonym of *T. tubergeniana*, but *T. ingens* has priority. *Tulipa bactriana* is a form with a longer bulb, longer leaves and a narrower flower (Tojibaev, 2013), but it fits within the general variability of this species.

37. *Tulipa* (T) *julia* K.Koch, Linnaea 22: 225 (1849) *Tulipa montana* var. *julia* (K.Koch) Baker, J. Linn. Soc., Bot. 14: 279 (1874).

Lectotype (designated here): GEORGIA. Shuragel [Arpa River plain], Koch s.n. (G-00176269!).

Distribution: Eastern Turkey, Transcaucasia, Lebanon, northern Iran.

Tulipa kaghyzmanica Fomin, Vestn. Tiflissk. Bot. Sada 9: 13 (1908). Holotype: TURKEY. Kars: 'Habitat in Armenia rossica regione montana montis Kurtlu, districtus Kaghysman', *Mikhailovskyi s.n.* (LE?, not located).

Note: A species similar to *T. systola*.

38. *Tulipa* (T) *kaufmanniana* Regel, Gartenflora 26: 194, t. 906 figs 6–11 (1877)

Type: UZBEKISTAN. [Chirchiq], 'In Turkestaniae montibus fluvium Tschirtschik adjacentibus', A. Regel (L.F.)

Distribution: Kazakhstan, Kyrgyzstan, Tajikistan, Uzbekistan.

Tulipa berkariensis Rukšāns, nom. provis., Buried Treasure: 174 (2007), as 'berkariense', nomen.

39. *Tulipa* (E) *kolbintsevii* Zonn., Plant Syst. Evol. 298: 1294. (2012)

Holotype: CULTIVATED. Grown in the Netherlands from material collected at Dzjungarian Ala-Tau, Taskora Valley, J.J. de Groot s.n. (L-0821329!).

Note: This species is similar to *T. regelii*, differing only in its narrower, non-plicate leaves.

40. Tulipa (T) kolpakowskiana Regel, Trudy Imp. S.-Peterburgsk. Bot. Sada 5: 266 (1877)

Holotype: KAZAKHSTAN. 'In Turkestania prope Wernoje et in valle fluvii Almatinka', A. Regel s.n. (LE; possible isotype K!).

Distribution: Kazakhstan, Kyrgyzstan, northeastern Afghanistan, northwestern Xinjiang.

Tulipa triphylla Regel, Trudy Imp. S.-Peterburgsk. Bot. Sada 5: 636 (1878). Holotype: CHINA. 'In collibus arenosis inter Kuldscha et lacum Sairam', A. Regel (LE).

Tulipa aristata Regel, Trudy Imp. S.-Peterburgsk. Bot. Sada 6: 506 (1879). Holotype: CHINA. 'Kur karaussu prope Schischo in China occidentali', *A. Regel* (LE).

Tulipa triphylla var. hoeltzeri Regel, Gartenflora 33: 34 (1884). Tulipa hoeltzeri (Regel) Dykes, Not. Tulip Sp.: 74 (1930). Tulipa dykesiana Vved. in V.L.Komarov (ed.), Fl. URSS 4: 348 (1935), nom. inval. pro syn. Type: tab. 1144 in Gartenflora 33 (1884).

Notes: A variable species throughout its range, but uniform in cultivation. It is certainly related to *T. altaica* and *T. iliensis* and maybe it should be merged with the former as Van Raamsdonk & De Vries (1995) suggested. The species hybridizes in the wild with *T. ostrowskiana*, increasing the variability in the field, further complicating the taxonomy of this group.

41. Tulipa (T) korolkowii Regel, Trudy Imp. S.-Peterburgsk. Bot. Sada 3(2): 295 (1875)

Holotype: UZBEKISTAN. 'Habitat in solo lutoso in desertis inter Turkestaniam et Khiwam prope Farisch', Korolkow et Krause s.n. (LE).

Distribution: Kazakhstan, Kyrgyzstan, Tajikistan, Uzbekistan.

Tulipa nitida Hoog, Gard. Chron., III, 31: 350 (1902). Lectotype (**designated here**): figure 19 in Gard. Chron., III, 31: 351 (1902).

Tulipa rosea Vved., Opred. Rast. Sred. Azii 2: 319 (1971). Tulipa korolkovii forma rosea (Vved.) Zonn., Plant Syst. Evol. 281: 244 (2009). Holotype: TAJIKISTAN. Pamir-alaj: 'in collibus siccissimis gypsaceis prope petroleas <<Santo>>', 16.iv.1923, M. Popov & A. Vvedensky s.n. (TASH; isotypes: BM!, H-1200897!, K!).

42. *Tulipa* (T) *kosovarica* Kit Tan, Shuka & Krasniqi, Phytotaxa 62: 2 (2011)

Holotype: KOSOVO. Rahoveci Province: Mirusha region, at foot of Mt. Kozniku, *Shuka 4578* (TIR; isotypes C, LD).

Distribution: Kosovo.

Note: A species belonging to the *T. scardica* complex.

43. *Tulipa* (E) *koyuncui* Eker & Babaç, Nordic J. Bot. 28: 325 (2010)

Holotype: TURKEY. B9 Van: between Van-Başkale, Güzeldere pass, 2738 m, 19.v.2006, $Eker\ 1565$ (AIBU; isotype AEF).

Distribution: Southeastern Turkey.

Note: Similar to *T. biflora*, from which it may not be separable. It has fewer flowers per stem that are completely yellow (tepals not white with yellow blotch) and has shorter filaments.

44. Tulipa (T) kuschkensis B.Fedtsch., Fl. Turkm.2: 302 (1932)

Lectotype (designated here): TURKMENISTAN. 'In valle Schur-Safed prope haud procul ab oppido Kuschka', I. Linczevski 5413 (H-1200903!; isolectotype BM!).

Distribution: Southern Turkmenistan, Iran, Afghanistan.

Note: There are two collections cited in the original publication, only the latter of which we could trace. The voucher selected here as lectotype is annotated by Fedtschenko. This species is similar to *T. hoogiana* and *T. undulatifolia*.

45. Tulipa (T) lanata Regel, Trudy Imp. S.-Peterburgsk. Bot. Sada 8: 647, t. 4. (1884)

Holotype: TAJIKISTAN. 'Pamir-Alaj, distr. Hissar, Chodscha-Balkata ad fluvium Kafirniga', *A. Regel s.n.* (LE; isotype K-000844618!).

Distribution: Tajikistan, Uzbekistan, Afghanistan, northern Pakistan, western Himalayas.

Note: A species similar to others in section *Eichleres* (e.g. *T. hoogiana*, *T. fosteriana*, *T. ingens*, *T. undulatifolia*), but can be easily distinguished by its fine, soft pubescence that covers all vegetative parts of the plants.

46. Tulipa (T) lehmanniana Merckl. in A.A. von Bunge, Beitr. Fl. Russl.: 337 (1852)

Lectotype (designated here): UZBEKISTAN. A. Lehmann s.n., Bunge Rel. Lehm. 337 (K-000844622!). Distribution: Eastern Iran, Kazakhstan, Kyrgyzstan, Turkmenistan, Tajikistan, Uzbekistan, Afghanistan.

Tulipa behmiana Regel, Trudy Imp. S.-Peterburgsk. Bot. Sada 6: 505 (1879). Holotype: KAZAKHSTAN. 'Prope Iliisk ad fluvium Ili', A. Regel (LE).

Tulipa zenaidae Vved., Byull. Sredne-Aziatsk. Gosud. Univ. 21: 150 (1935). Type: KYRGYZSTAN. 'Habitat in montibus Alexandricis (Tien-Shan)', 14.vi.1932 Vvedensky 280 (TASH).

Note: A species similar to *T. borszczowii* and *T. korolkowii* (Wilford & Zarrei, 2009), belonging to the complex surrounding *T. systola* and *T. julia*. *Tulipa zenaidae* is similar to *T. lehmanniana* and, in our opinion, does not warrant recognition.

47. Tulipa (T) lemmersii Zonn., Peterse & J.Groot, Pl. Syst. Evol. 298: 91 (2012)

Ind. loc.: Grown in the Netherlands from material collected in Kazakhstan.

Holotype: Chimkent: Mashad Pass, [2007], A. Peterse s.n. (L-0822655!).

Distribution: Kazakhstan.

Note: The label on the holotype specimen does not state that it was cultivated, or when it was collected, but, in the protologue, it is mentioned that the type was cultivated and collected in 2007. This is a species belonging to the *T. altaica* complex.

48. Tulipa (C) linifolia Regel, Trudy Imp. S.-Peterburgsk. Bot. Sada 8: 648, t. 5. (1884)

Holotype: TAJIKISTAN. Darvas: 'ad fl. Pandsch', iii.1883, Mussa s.n. (LE; isotypes: BM!, G-00176313!, K-000844623!, NY-319921!).

Distribution: Northeastern Iran, Tajikistan, Afghanistan.

Tulipa maximowiczii Regel, Trudy Imp. S.-Peterburgsk. Bot. Sada 10: 687 (1889). Ind. Loc.: 'Buchara orientalis', no specimen cited. Neotype (**designated here**): UZBEKISTAN. 'Diwalay ad orientem a Kulak, Buchara orient.', 27.iii.—8.iv.1883, Regel s.n. (K!).

Tulipa batalinii Regel, Trudy Imp. S.-Peterburgsk. Bot. Sada 10: 688 (1889). Ind. Loc.: Buchara, no specimen cited.

Tulipa afghanica Markgr., Gartenbauwissenschaft 22: 551. 1957. Ind. Loc: 'Afghanistan, leg: Frau Hermine Priemer, blühend im Botanischen Garten München, April 1957'. Holotype: CULTIVATED. Priemer (M!).

Note: Tulipa batalinii is the yellow form of the otherwise red T. linifolia; in horticulture, these are classified as T. linifolia Batalinii Group. Tulipa maximowiczii does not differ from typical T. linifolia (Dykes, 1925).

49. *Tulipa* (C) *montana* Lindl., Bot. Reg. 13: t. 1106 (1827), excluding figure

Neotype (designated here): IRAN. Khorassan: 80 km after Bojnourd towards Gordgan, 7 km to Chamanbid, 31.iii.2005, M. Zarrei & K. Golzarian 35242 (K!).

Distribution: Southern Turkmenistan to Iran.

Tulipa chrysantha Boiss. in C.G.T.Kotschy, Exsicc. (Pl. Pers. Bor.) 1846: 78 (1846). Tulipa montana var. chrysantha (Boiss.) Regel, Trudy Imp. S.-Peterburgsk. Bot. Sada 2: 454 (1873). Tulipa linifolia forma chrysantha (Boiss.) Raamsd., Pl. Syst. Evol. 195: 38 (1995). Holotype: IRAN. 'In solo schistoso Elburs, prope pagum Dareke', 25.iv.1843, T. Kotschy 78 (G; isotypes: BM!, H-1237840!, K-000844483!, P-00730899!, WAG-0004642!).

Tulipa biebersteiniana var. aurantiaca Baker, J. Linn. Soc., Bot. 14: 291 (1874). Holotype: IRAN. Ispahan, Aucher-Eloy 5373 (K-000844480!; isotype BM!).

Tulipa montana var. maculata Regel, Trudy Imp. S.-Peterburgsk. Bot. Sada 2: 454 (1873). Lectotype (designated here): TURKEY. Prope Erzerum, Aucher-Eloy, herb. d'Orient. 5375 (P-00730888!; isotype LE?). Syntype: IRAN. 'Inter Abuschir et Schiras', Kotschy (LE?).

Tulipa wilsoniana Hoog, Gard. Chron., III, 32: 50 (1902). Lectotype (designated here): figure 121 in Gard. Chron., III, 29: 327. 1901. Rechinger (1990) erroneously cited a specimen from Turkmenistan, I.A. Gubanov s.n. (LE), as the holotype, but this is not original material.

Tulipa giselae Bornm. & Gauba, Repert. Spec. Nov. Regni Veg. 47: 78 (1939). Holotype: IRAN. Elburs: 'Keredj, am Kuh Daschteh', 26.v.1936, *Gauba* (B, not located).

Notes: The illustration of this plant by Lindley (1827) is unlike the plants known in the wild under this name. No specimen is in existence, and a neotype is thus selected here to maintain taxonomic stability. For the same reason, Regel suggested the use of the name T. chrysantha Boiss. for this taxon instead. There has, however, been confusion about the application of that name; it had been uncertain whether that name should be applied to the yellow form of T. montana or the yellow form of T. clusiana. The isotypes studied of T. chrysantha Boiss. clearly place it as a synonym of T. montana. Tulipa wilsoniana was based on a plant identical to T. montana and is synonymized here. Kiani et al. (2012) applied T. wilsoniana to an accession in their molecular study of Iranian tulips and found that it is embedded in T. micheliana (a synonym of T. undulatifolia). Because the taxa belong to different subgenera, we believe that the specimen in that study may have been misidentified.

50. Tulipa (E) orithyioides Vved., Byull. Sredne-Aziatsk. Gosud. Univ. 21: 150 (1935)

Holotype: UZBEKISTAN. Tschulbair, 30.vi.1929, Vvedensky 423 (TASH).

Distribution: Tajikistan, Uzbekistan.

Tulipa subbiflora Vved., Opred. Rast. Sred. Azii 2: 320 (1971). Holotype: KYRGYZSTAN. Pamiro-Alai, 20.v.1966, Dshalalov (TASH).

Note: A species similar to *T. urumiensis*, differing in having a slightly pronounced style. It does not belong to subgenus *Orithya* because it has hairy stamens, placing it firmly in subgenus *Eriostemones*.

51. Tulipa (E) orphanidea Boiss. ex Heldr., Gartenflora 11: 309 (1862)

Tulipa sylvestris var. orphanidea (Boiss. ex Heldr.) Regel, Trudy Imp. S.-Peterburgsk. Bot. Sada 2: 443 (1873). Tulipa crocata Orph., Bull. Congr. Internl. Bot. Hort. St. Petersbourg 1869: 116 (1870), nom. inval. pro syn.

Holotype: GREECE. 'Am Berge Malevo (bei Hagios Petros und Xerokampi) in östlichen Laconien', Orphanides 843 (G). Note: Marais (1984) erroneously cited no. 834 as the type.

Distribution: Eastern Balkans, Bulgaria, Greece, Aegean Islands, Crete, western Turkey.

Tulipa turcica Griseb., Spic. Fl. Rumel. 2: 382 (1846), nom. illeg.

Tulipa atheniensis Orph., Bull. Congr. Internl. Bot. Hort. St. Petersbourg 1869: 116 (1870). nom. inval. pro syn. Type: GREECE. Attica: Mont Parnes near Athens, 1857, Orphanides (not located).

Tulipa bithynica Griseb. ex Baker, J. Linn. Soc., Bot. 14: 282 (1874). Lectotype (**designated here**): TURKEY. Bithynia, *Grisebach s.n. ex Herb. Hooker*. (K!); syntypes: TURKEY, E. Boissier (K!), Aucher-Eloy 2178 (BM!, K!).

Tulipa minervae et atheniensis Orph. ex Baker, J. Linn. Soc., Bot. 14: 294 (1874), nom. inval., polynom. Tulipa hageri Heldr., Gartenflora 23: 97 (1874). Holotype: GREECE. Pentelico, T. von Heldreich s.n. (G-00176268!; isotype: BM-001066432!). Note: This should be treated as Tulipa orphanidea Hageri Group.

Tulipa cruciata Baker, Gard. Chron., n.s., 20: 789. 1883. Lectotype (**designated here**): TURKEY. Bordagh, iv.1874, Elwes, ex Hort Kew, iv.1878, from Maw (K!).

Tulipa theophrasti Candargy, Bull. Soc. Bot. France 44: 143 (1897). Ind. loc.: GREECE. Lesbos. 'C. in reg. mont. Olympi fluvio Caryophytia'. Type: none cited. Note: This should be treated as *T. orphanidea* Theophrasti Group.

Tulipa hageri var. nitens H.B.May, Gard. Chron., III, 33: 302 (1903). Type: none cited.

Tulipa thracica Davidov, Sborn. B'lghar. Akad. Nauk 12: 118 (1915).

Tulipa doerfleri Gand., Fl. Cret. 102: 1814 (1916). Tulipa hageri var. doerfleri (Gand.) Hayek, Repert.

Spec. Nov. Regni Veg. Beih. 30(3): 70 (1932). Tulipa orphanidea subsp. doerfleri (Gand.) Zonn., Pl. Syst. Evol. 281: 244 (2009). Lectotype (designated here): GREECE. Crete: 'Hagios Vasilis, in montis Kedros', 28.iv.1904, I. Dörfler, Iter Creticum 182 Herbarium Normale 5338 (WU-0065331!; isotypes G-00176265, H-1315663!, LD-1029948!, P-02077482!, WU-0065330!).

Tulipa whittallii Elwes ex W.C.F.Newton, J. Linn. Soc. Bot. 47: 341 (1926), nomen. Tulipa whittallii A.D.Hall, Book Tulip: 70 (1929). Tulipa orphanidea var. whittallii (A.D.Hall) Dykes, Not. Tulip Sp.: 34 (1930). Tulipa orphanidea subsp. whittallii (A.D.Hall) Zonn., Pl. Syst. Evol. 281: 244 (2009). Type: none cited. Neotype (designated here): CULTIVATED. USA, NY, Ithaca, grown at hortorium garden from bulbs of J. A. Mars, Derreen, Haslemere, Surrey, UK, 20.v.1971, L.H. Bailey Hortorium 10412 (BM!). Note: This should be treated as T. orphanidea Whittallii Group.

Tulipa hellespontica Árpád, Magyar Bot. Lapok 32: 145 (1933). Type: TURKEY. 'Thracia orientalis: In lapidosis dumetosis humosis collinis ad pagum Dermenköj non procul a Čataldja', 1913, I. K. Urumoff s.n. (WU?, not located).

Tulipa hayatii O.Schwarz, Repert. Spec. Nov. Regni Veg. 36: 69 (1934). Lectotype (annotated by Persson in 2002, **designated here**): TURKEY. Izmir: Bornova, Yamanlardag supra Burnova, in agris montanis humidis, prope lacum "Kisgöl", 900 m, v.1932, O. Schwarz 241 (B-100365939!).

Tulipa goulimyi Sealy & Turrill, Kew Bull. 10: 59 (1955). Lectotype (**designated here**): GREECE. Island of Kythira, village of Potamos near Prophet Elias (cemetery), 4–7.iv.1954, *C. N. Goulimis 1011* (K-000400292!; isotype: K-000400293!).

Notes: A variable taxon with forms that are geographically isolated, but with typical plants spanning the range of the species. It has been shown that one population can include specimens matching several of the synonyms listed above (Marais, 1984). Names are usually maintained in horticulture because they describe different colour forms stable in cultivation (e.g. T. hageri, T. theophrasti, T. whittallii). These are better treated as Cultivar Groups (e.g. T. orphanidea Hageri Group, T. orphanidea Theophrasti Group, T. orphanidea Whittallii Group). Some Turkish populations of T. orphanidea are known to lack the filament hairs typical of subgenus Eriostemones (Marais, 1984). Tulipa thracica and T. hellespontica were segregated on the basis of their hairy ovaries (Árpád, 1933). The cultivar T. orphanidea Hageri Group 'Splendens' should not be confused with T. splendens Delip., which is a synonym of T. suaveolens.

52. Tulipa (T) ostrowskiana Regel, Gartenflora 33: 34 (1884)

Tulipa tetraphylla subsp. ostrowskiana (Regel) Raamsd., Pl. Syst. Evol. 195: 39 (1995).

Lectotype (designated here): KAZAKHSTAN. 'Iter Turkestanicum, Kl. Almaty Schlucht bei Werny', 2.iv.1879, A. Regel s.n. (K!).

Distribution: Kazakhstan, Kyrgyzstan.

Note: This species is similar to *T. kolpakowskiana* and T. korolkowii, with which it hybridizes in the wild, complicating the taxonomy of this group. Thorough taxonomic revision of wild populations is needed to resolve this species complex.

53. Tulipa (T) persica (Lindl.) Sweet, Hort. Brit., ed. 2: 536 (1830)

Tulipa oculus-solis var. persica Lindl., Bot. Reg. 14: t. 1143 (1828).

Holotype: Illustration t. 1143 in Lindley (1828).

Distribution: Northwestern Iran.

Notes: According to Lindley (1828), this is most closely related to T. agenensis, and it may have to be merged with that species; however is maintained here pending further research. It has larger, glaucous leaves and larger flowers, which are whitish on the outside. The name 'T. persica' has often been erroneously applied to T. celsiana, which is a form of T. sylvestris subsp. australis. Plants sold under the name T. eichleri 'Excelsa' are probably T. persica.

54. Tulipa (T) platystemon Vved., Byull. Sredne-Aziatsk. Gosud. Univ. 21: 150 (1935)

Holotype: KYRGYZSTAN. Sary-bija, 12.vi.1913, Knorring 154 (LE).

Distribution: Kyrgyzstan, only known from the type specimen. It seems similar to a yellow T. anisophylla with two flowers per stem.

55. Tulipa (T) praestans H.B.May, Gard. Chron., III, 33: 239 (1903)

Type: None cited. Neotype (**designated here**): TAJIKISTAN. 'Tadzhikistania Australis. Declive boreale montis saline Chodzha-Mumin, Schibliak', 17.iv.1976, A. P. Czukavina & N. M. Amanova 49 (H-1496422!).

Distribution: Tajikistan.

Tulipa subpraestans Vved., Opred. Rast. Sred. Azii 2: 318 (1971). Holotype: CULTIVATED. 'Planta e bulbis a V. Botschantzev in collibus saxosis prope pag. Tut-Kaul, ad ripas dexteras fl. Vachsch a 1933 lectis in Horto Botanico Universitatis Asiae Mediae enata', 23.iv.1935, A. Vvedensky 5420 (TASH; isotypes: BM!, H-1200896!, K!, US-00091878!).

Note: Tulipa praestans is variable in the field and includes several garden selections of wild origin, such as T. subpraestans and T. praestans 'Van Tubergen's Variety'.

56. Tulipa (E) regelii Krassn., Bot. Zap. 2: 21 (1887) Holotype: KAZAKHSTAN. 'Prope fauces fluminis Kurtu inter saxa non rara in montibus Andrakai rarior', iv.1886, A. Krassnow s.n. (LE).

Distribution: Southeastern and eastern Kazakhstan.

Note: A distinctive species with plicate leaves.

57. Tulipa (E) saxatilis Sieber ex Spreng., Syst. Veg. 2: 63 (1825)

Lectotype (designated here): GREECE. Creta, 1817, Sieber s.n. (HAL-0109614!; isotypes H-1000682!, K!, PRC-454332, M!, PRC-454333, PRC-454334, PRC-454335, PRC-454336).

Distribution: Southern Aegean Islands, Crete, western Turkey, naturalized in mainland Greece and Italy.

Tulipa beccariana Bicchi, Descr. Nuov. Sp. Tulip.: 2 (1860).

Tulipa chrysobasis Coustur. & Gand., Bull. Soc. Duffour 1914: 38 (1914). Holotype: GREECE. Crete, Kalamarka, 10.vi.1914, M. Gandoger 5880 (K!).

Tulipa bakeri A.D.Hall, J. Bot. 76: 316 (1938). Tulipa saxatilis subsp. bakeri (A.D.Hall) Zonn.. Pl. Syst. Evol. 281: 244 (2009). Holotype: CULTIVATED. Hillside, Oakhill Road, Kippington, Sevenoaks, 21.iv.1939, from bulbs collected in Crete, Amari Province, Asomatus, 25 km south of Retino, Mr. G. P. Baker s.n. (K-000400294!).

Note: Zonneveld (2009) maintained the diploid T. bakeri as a subspecies of the triploid T. saxatilis (see Hall, 1940), but the two are not geographically isolated and both diploid and triploid plants occur in mixed populations in the wild. Some of the collections sent by G. P. Baker to Kew are also mixed gatherings. The two are similar, differing only in flower and anther colour and the definition of the blotch, and they possibly differ in vigour. They are better treated as forms of the same species. Cultivars derived from T. bakeri should be listed as T. saxatilis Bakeri Group.

58. Tulipa (T) scardica Bornm., Repert. Spec. Nov. Regni Veg. 19: 199 (1923)

Lectotype (designated here): MACEDONIA. 'In declivitat, prope Raduše (inter Usküb et Totovo)', 28.iv.1918, J. Bornmüller 5002 (B-100365938!; isotype B-100365937!).

Distribution: Southern Kosovo to Macedonia.

Tulipa pavlovii Kitan., Izv. Bot. Inst. (Sofia) 2: 177 (1951). Type: MACEDONIA. Orlovo Brdo, 'inter urbem Štip et pagum Krivolak', 8.iv.1947, B. Kitanov s.n. (SOM). Note: The original publication includes a coloured plate.

Note: This species is one of a complex of species in the southern Balkans. It includes *T. albanica*, *T. kosovarica* and *T. serbica*, all rather similar species. They have sometimes erroneously been synonymized under *T. gesneriana* (e.g. The Plant List). They have affinity with *T. agenensis*, but are found in completely natural situations. The taxonomy is discussed by Mayer & Micevski (1970) and Shuka *et al.* (2010, 2012).

59. Tulipa (T) scharipovii Tojibaev, Linzer Biol. Beitr. 41: 1063 (2009)

Holotype: UZBEKISTAN. 'Tien-Shan Occidentalis, montes Kuramensis, prope pagum Uygursay', 20.iii.2009, Tojibaev s.n. (TASH).

Distribution: Uzbekistan.

60. Tulipa (T) schmidtii Fomin, Viestn. Tiflissk. Bot. Sada 14: 47 (1909)

Type: AZERBAIJAN. 'Habitat ad pagum Eschaktschi prov. Baku, distr. Lenkoran', 29.iv.1907, A.N. Kaznakov & A. B. Schelkovnikov s.n. (LE, TGM (two sheets); photographs K!).

Distribution: Southern Transcaucasia, northern Iran.

Note: A species similar to *T. hoogiana*, differing in hairiness of the tunic and greater number of leaves that are generally much narrower.

61. Tulipa (T) serbica Tatic & Krivošej, Bocconea 5: 733 (1997)

Holotype: SERBIA. Knjaževac: Mt Rogozna near Donja Kamenica, 900 m, on serpentine soil, *Tatic & Krivošej s.n.* (herb. Pristina).

Distribution: Northern Kosovo to southeastern Serbia.

Note: A species belonging to the T. scardica complex.

62. Tulipa (O) sinkiangensis Z.M.Mao, in Fl. Reipubl. Popul. Sin. 14: 282 (1980)

Holotype: CHINA. Xinjiang: Urumqi, 29.iv.1974, Z.M. Mao et al. 8909 (XJBI).

Distribution: North-western China.

Note: A species similar to or may be conspecific with *T. heterophylla*.

63. Tulipa (T) sosnowskyi Achv. & Mirzoeva, Trudy Bot. Inst. Akad. Nauk Armyansk. S.S.R. 7: 31 (1950) Type: Not located.

Distribution: Armenia, Azerbaijan.

Note: This species belongs to the complex surrounding *T. ingens* and *T. fosteriana*.

64. *Tulipa* (E) *sprengeri* Baker, Gard. Chron., III, 15: 716 (1894)

Holotype: CULTIVATED. From material originally collected in Asia Minor, Amasia, 8.v.1894, ex Hort. Dammann & Co. s.n. (K-000844459!).

Distribution: Amasya (Turkey).

Tulipa brachyanthera Freyn, Bull. Herb. Boissier 4: 187 (1896). Holotype: TURKEY. Amassia, Galatia, A. Manissadjian 1151 (BRNM!; isotypes: K-000844458!, LD-1404357!, P-00730904! Z-000072930!).

Note: Marais (1984) stated that *T. sprengeri* has all the characters of subgenus *Eriostemones*, except for the hairs at the base of the filaments. The bulbs from which the plant was grown were sent in 1892 by Mühlendorff from Amasya to the firm of Dammann near Naples. Thought to be extinct in the wild (Govaerts, 1998; Maunders et al., 2001; Wilford & Fay, 2007), it may have been refound (Sheasby, 2007: 137). It persists and self-seeds in gardens in Europe.

65. *Tulipa* (T) *suaveolens* Roth, Ann. Bot. (Usteri) 10: 44 (1794)

Type: None cited. Neotype (**designated here**): KAZAKHSTAN. 'Deserta Caspica', *Pallas s.n.* (BM!). *Distribution:* Crimea, Kazakhstan, Transcaucasia, Iran and adjacent Turkey.

Tulipa volgensis M.Bieb. ex Eichw., Pl. Nov.: 2 (1831). Tulipa hortulanorum Wender., Allg. Gartenzeitung 6: 71 (1838). Type: none cited. Note: this was based on living plants growing in Holland under the name 'Pottebakker', which may have been a 'Duc van Tol'

Tulipa odoratissima Vis., Orto Bot. Padova: 149 (1842).

Tulipa oxypetala Steven, Bull. Soc. Imp. Naturalistes Moscou 30(2): 81 (1857). Holotype: TURKEY. Tauria. s. coll. s.n. ex Herb. Steven (H-1315686!; isotype K!).

Tulipa schrenkii Regel, Gartenflora 22: 297 (1873). Tulipa gesneriana subsp. schrenkii (Regel) Nyman, Consp. Fl. Eur., Suppl. 2: 302 (1890). Holotype: KAZAKHSTAN. 'In desertis Songaricis', Bunge, reliq. Lehmann 1390 (LE; isotype: K!). Note: the K specimen is mounted on the same sheet with a Schrenk specimen from 1870, also collected in Songaria. An original Schrenk specimen is also present in BM, but these are not types.

tulip.

Tulipa suaveolens var. bicolor Regel, Acta Hort. Petrop. 8: 650 (1884). Holotype: UZBEKISTAN. Tashkent, iv.1882, A. Regel s.n. (LE; isotypes: K-000844621!, P-00730908!).

Tulipa turcarum Levier, Bull. Soc. Sci. Nat. Neuchâtel 14: 271 (1884).

Tulipa gesneriana var. acutiflora Pacz., Zap. Kiev. O-va Est. XI, I: 159 (1890).

Tulipa monticola E.Wulff, Fl. Taurica 1(3): 41 (1930).

Tulipa splendens Delip., Feddes Repert. 87: 3 (1976). Holotype: BULGARIA. Jambol distr.: Simeonovo, 3.v.1964, I. Česchmedjiev & D. Delipavlov s.n. (SOA).

Note: This species is generally known under the name of T. schrenkii, but the older name T. suaveolens has priority. It was originally believed that T. suaveolens was not based on a wild plant and therefore may have represented an old cultivar, such as one of the red and yellow Duc van Tol Group. In the Russian literature, it has been suggested to synonymize T. schrenkii under T. gesneriana (Mordak, 1990) because the tulip Gesner described was almost certainly this species. However, Linnaeus did not base his description on Gesner's account (even though he cited it), the lectotype specimen of T. ×gesneriana in the Linnean Herbarium is a cultivated garden hybrid and quite different from wild T. suaveolens. It has been suggested that the name T. schrenkii, which is based on a wild plant, should be used, and T. suaveolens treated as a cultivar, but this is contrary to the botanical and horticultural codes. Because there is no type mentioned in the original publication of Roth for T. suaveolens, we hereby lectotypify it with a wild-collected specimen, which fixes this name to a wild plant. Tulipa suaveolens undoubtedly figured in the creation of garden tulips, and many of the early flowering cultivars appear similar. However, the garden hybrids have a complex ancestry, and this name should therefore only be applied to plants of known wild origin.

66. Tulipa (T) subquinquefolia Vved., Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 9: 245 (1946)

Holotype: TAJIKISTAN. Distr. Kulab. 'Ad declivia prope p. Arzantschi', Divnogorskaja, 14.v.1910, *Vvedensky 360* (LE).

Distribution: Tajikistan.

67. Tulipa (E) sylvestris L., Sp. Pl.: 305 (1753). Liriopogon sylvestre (L.) Raf., Fl. Tellur. 2: 35 (1837)

Lectotype (designated by Van Raamsdonk in Wisskirchen et al., 1997): Herb. Linn. no. 425.1 (LINN!).

Distribution: Widely naturalized in northern and western Europe, Siberia, Belarus and the Ukraine, North Africa, Balkans, Turkey to Iran and North America. It is impossible to ascertain where this species is native; probably from southern Spain, throughout northern Africa, to Central Asia.

Notes: Marais (1984) stated correctly that the subspecies cannot be distinguished because many morphologically intermediate specimens are known. It is generally accepted that *T. australis* is the diploid form of T. sylvestris. The two overlap in distribution in North Africa (and the latter is naturalized across Europe, Turkey and North America), and it has also been suggested that the two should be treated at the species level. In that case, T. australis would have to be renamed *T. pumila* because that name has priority. We treat this species in its broadest sense, as we did for the related T. orphanidea and its numerous colour variants. Tulipa biebersteiniana is here synonymized under T. sylvestris subsp. australis, because the taxa are not distinguishable when the entire range is taken into account. Tulipa biebersteiniana has been used for plants with a more eastern distribution than Iberian and North African T. sylvestris subsp. australis, and occasionally has two flowers per stem. Three subspecies are here tentatively recognized, complying with the current usage of these names and maintaining a stable taxonomy for these taxa.

67a. Tulipa (E) sylvestris subsp. australis (Link) Pamp., Boll. Soc. Bot. Ital. 1914: 114 (1914)

Tulipa australis Link, J. Bot. (Schrader) 1799(2): 317 (1800). Tulipa gallica var. australis (Link) Hy, Bull. Soc. Bot. France 59: 384 (1912).

Ind. Loc.: 'Südlichen Europa', no specimen cited. Neotype (**designated here**): SPAIN. Extremadura; Cáceres, 27.iv.1994, J.J.F.E. de Wilde & R.W. de Wilde-Bakhuizen 11108 (WAG-16826!).

Distribution: Mediterranean Europe from Portugal to Greece and Turkey and North Africa from Morocco to Libya, Central Europe from Switzerland and France to Belarus, Russia and the Ukraine, Transcaucasia, Iran, Altai, Kazakhstan to northwestern Xinjiang. This subspecies is distributed nearly throughout the entire geographical range of the genus. There is considerable variability between populations, but these differences do not seem to warrant recognition at higher taxonomic levels.

Tulipa pumila Moench, Methodus: 301 (1794). Type: none cited. Note: This is a two- or three-flowered tulip with yellow and purple streaked flowers.

Tulipa celsiana Redouté, Liliac. 1: t. 38 (1803). Liriopogon celsianum (Redouté) Raf., Fl. Tellur. 2: 35 (1837). Tulipa australis var. celsiana (Redouté) Levier, Tulip. Eur.: 104 (1884). *Tulipa sylvestris* var. celsiana (Redouté) Levier, Bull. Soc. Neuchâteloise Sci. Nat. 14: 104 (1884). *Tulipa sylvestris* subsp. celsiana (Redouté) Hayek, Repert. Spec. Nov. Regni Veg. Beih. 30(3): 71 (1932). Lectotype (**designated here**): figure 38 in Redouté, Liliac. 1 (1803).

Tulipa breyniana Ker Gawl., Curtis's Bot. Mag. 19: t. 717 (1804), nom. illeg. Note: There was a confusion of this name with the unrelated *T. breyniana* L., which is *Moraea collina* Thunb. (Iridaceae).

Tulipa transtagana Brot., Fl. Lusit. 1: 519 (1804). Tulipa celsiana var. transtagana (Brot.) Nyman, Consp. Fl. Eur.: 723 (1882). Tulipa australis subsp. transtagana (Brot.) K.Richt., Pl. Eur. 1: 216 (1890). Tulipa australis var. campestris Willk. in M.Willkomm & J.M.C.Lange, Prodr. Fl. Hispan. 1: 219 (1862). Holotype: PORTUGAL. 'Trans Tagum in ericetis', Brotero s.n. [519] (B-W-06567-010!).

Tulipa sylvestris M.Bieb., Fl. Taur.-Caucas. 1: 270 (1808), nom. illeg. Tulipa biebersteiniana Schult. & Schult.f. in J.J.Roemer & J.A.Schultes, Syst. Veg. 7: 382 (1829). Tulipa sylvestris var. biebersteiniana (Schult. Schult.f.) Regel, Trudy S.-Peterburgsk. Bot. Sada 2: 442 (1873). Ind. Loc.: 'In hortis et vineis ad fluvium Terek inter Mosdok et Kisljar', April, Bieberstein s.n. (not found). Note: There is a fruiting specimen in LE (F. A. Marschall a. Bieberstein) labelled as the type, but Bieberstein and Schultes described flowering material; April is mentioned as the collection month, and so it is unlikely that this fruiting specimen is the type.

Tulipa brujniana Roxb., Hort. Bengal.: 24 (1814), nomen.

Tulipa maculata Roth, Nov. Pl. Sp.: 196 (1821). Tulipa celsiana var. maculata (Roth) Regel, Trudy Imp. S.-Peterburgsk. Bot. Sada 2: 445 (1873). Note: A replacement name for *T. breyniana* Ker Gawl., based on plants growing in the Hortus Botanicus of Amsterdam.

Tulipa celsiana J.Henning, Mém. Soc. Imp. Naturalistes Moscou 6: 70 (1823), nom. illeg. non Redouté.

Tulipa patens C.Agardh in J.Roemer & J.A.Schultes, Syst. Veg. 7: 384 (1829). Type: 'in Sibiria', Agardh (LD?, not found).

Tulipa pumila Tausch, Flora (Bot. Zeit.) 12(1 Erg.): 47 (1829), nom. illeg. Ind. loc.: Caucasia. Type: no specimen cited, but original material is present in PRC-454339.

Tulipa tricolor Ledeb., Icon. Pl. 2: 13 (1830). Tulipa sylvestris var. tricolor (Ledeb.) Ledeb., Fl. Ross. 4: 136 (1853). Holotype: RUSSIA. Altai, C.F. v. Ledebour s.n. (LE; isotypes: HAL-0109613!, K-000844490!, PH-28533!)

Tulipa sibirica Patrin ex Kunth, Enum. Pl. 4: 226 (1843).

Tulipa sylvestris var. montana Kunze, Flora (Bot. Zeit.) 29: 637 (1846). Tulipa australis var. montana (Kunze) Willk. in M.Willkomm & J.M.C.Lange, Prodr. Fl. Hispan. 1: 219 (1862). Tulipa australis subsp. montana (Kunze) K.Richt., Pl. Eur. 1: 216 (1890). Tulipa fragrans var. montana (Kunze) T.Durand & Schinz, Consp. Fl. Afric. 5: 408 (1894). Tulipa celsiana var. montana (Kunze) Batt. & Trab., Fl. Algérie, Monocot.: 168 (1895). Tulipa sylvestris forma montana (Kunze) Pamp., Boll. Soc. Bot. Ital. 1914: 116 (1914). Holotype: SPAIN. 'Sierra de Chiva in regione alpina, c. v. in declivitate orientali montis Santa Maria', June, Willkomm (LZ, destr.). Note: Willkomm specimens are present in COI (00050845!, 00050846!), but the localities of these specimens are not the same.

Tulipa thirkeana K.Koch, Linnaea 22: 226 (1849). Holotype: TURKEY. 'Bithynisches Olymp', Koch s.n. (B?; isotype G-00176263!).

 $Tulipa\ sylvestris\ var.\ minor\ Ledeb.,\ Fl.\ Ross.\ 4:\ 136\ (1853),\ nom.\ inval.\ pro\ syn.$

Tulipa sylvestris var. niphontiana Czern., Consp. plant. Charc. Ucr.: 64 (1859).

Tulipa australis var. parviflora Willk. in M.Willkomm & J.M.C.Lange, Prodr. Fl. Hispan. 1: 219 (1862). Type: T. sylvestris in Herb. Boutelou (SEV). Original Willkomm material (probably isotype) is present in COI-00050844!.

Tulipa fragrans Munby, Bull. Soc. Bot. France 13: 256 (1866). Tulipa australis var. fragrans (Munby) Levier, Tulip. Eur.: 103 (1884). Tulipa celsiana var. fragrans (Munby) Batt. & Trab., Fl. Algérie, Monocot.: 167 (1895). Tulipa sylvestris forma fragrans (Munby) Pamp., Boll. Soc. Bot. Ital. 1914: 116 (1914). Lectotype (designated here): ALGERIA. Oran, Munby s.n. (K-000365948!).

Tulipa alpestris Jord. & Fourr., Brev. Pl. Nov. 2: 120 (1868). Tulipa celsiana var. alpestris (Jord. & Fourr.) Nyman, Consp. Fl. Eur.: 723 (1882). Tulipa sylvestris var. alpestris (Jord. & Fourr.) O.Bolòs & Vigo, Fl. Països Catalans 4: 80 (2001).

Tulipa browniana H.Vilm., Fl. Pleine Terre, ed. 3: 1172 (1870).

Tulipa maculata Baker, J. Linn. Soc., Bot. 14: 289 (1874), nom. inval.

Tulipa microgyna Baker, J. Linn. Soc., Bot. 14: 292 (1874). Holotype: TURKEY. Mount Ida, Aucher-Eloy s.n. (G-DC).

Tulipa acrocarpa Jord. ex Baker, J. Linn. Soc., Bot. 14: 293 (1874), nom. inval., pro syn.

Tulipa caucasica Orph. ex Nyman, Consp. Fl. Eur.: 723 (1882), nom. inval., pro syn.

Tulipa australis var. transtagana Levier, Tulip. Eur.: 104 (1884).

Tulipa callieri Halácsy & Levier, Jahreskat. Wiener Bot. Tauschanst. 1897: 69 (1897). Holotype: UKRAINE. Hügel bei Sudak, iv.1896, *A. Callier 205* (PRC-454344 & 454345 (two sheets); isotypes: DS-422814!, E-00386980!, FI, K! (two sheets), STU!).

Tulipa bessarabica Zapal., Consp. Fl. Gallic. Crit. 1: 167 (1906).

Tulipa australis var. taurica Miscz., Trudy Byuro Prikl. Bot. 5: 51 (1912), nom. provis. in key.

Tulipa gallica forma armoricana Hy, Bull. Soc. Bot. France 59: 384 (1912). Ind. loc.: 'France. Tertre a Martigné-Ferchaud (Ille-et-Vilaine)'. Type: none cited.

Tulipa fragrans var. scappuccii Vacc., Bull. Soc. Toscana Ortic. 38: 217. 1913. Tulipa sylvestris forma scappuccii (Vacc.) Pamp., Boll. Soc. Bot. Ital. 1914: 116 (1914). Type: none cited.

Tulipa abatinoi var. aurea Borzì & Mattei, Boll. Reale Orto Bot. Palermo 11: 242 (1913). Tulipa sylvestris forma aurea (Borzì & Mattei) Pamp., Boll. Soc. Bot. Ital. 1914: 116 (1914). Type: LIBYA. Garian, iii.1913, Abatino s.n. (PAL?).

Tulipa sylvestris var. mediterranea Pamp., Boll. Soc. Bot. Ital. 1914: 115 (1914). Type: none cited.

Tulipa tchitounyi Azn., Magyar Bot. Lapok 16: 34 (1917 publ. 1918). Type: TURKEY. 'entre Assourouvank et la crête occidentale du Mont Varak', D. Tchitouny, Herb. Artist. exs. 3 (G).

Tulipa atlantica Pomel ex Batt., Contr. Fl. Atlantique: 87. 1919, nom. inval. pro syn. Original material cited: ALGERIA. Teniet-el-Had, 8.v.1860, A. N. Pomel s.n. (MPU-006840!).

Tulipa tenuiscapa Pomel ex Batt., Contr. Fl. Atlantique: 87. 1919. Type: none cited, but probably a *Pomel* specimen in MPU. Battandier (1919) stated this to be a dwarf variety of *T. sylvestris*.

Tulipa paschalis Sennen, Ann. Soc. Linn. Lyon, n.s., 70: 63 (1923 publ. 1924), nomen. Note: specimens associated with this name are preserved at MPU.

Tulipa australis subsp. mauritii Sennen, Cat. Fl. Rif Orient.: 121 (1933), nomen. Tulipa sylvestris var. mauritii Valdés, Lagascalia 18: 326 (1996). Holotype: MOROCCO. M. Tidiguin, Sennen s.n. (BC; isotype BM!).

Tulipa quercetorum Klokov & Zoz, Trudy Inst. Bot. Kharkivs'k. Derzhavn. Univ. 1: 63 (1935). Holotype: UKRAINE. Dnjepropetrovsk distr.: 'In querceto prope opp. Novomoskovsk', 19.iv.1930, M. Klokov s.n. (CWU).

Tulipa quercetorum var. tricolor Klokov & Zoz, Trudy Inst. Bot. Kharkivs'k. Derzhavn. Univ. 1: 63 (1935). Tulipa biebersteiniana var. tricolor (Klokov & Zoz) Knjaz., Kulikov & E.G.Philippov, Bot. Zhurn. (Moscow & Leningrad) 86(3): 116 (2001). Type: none cited.

 $Tulipa\ samarica\ Klokov\ \&\ Zoz,\ Trudy\ Inst.$ Bot. Kharkivs'k. Derzhavn. Univ. 1: 65 (1935), nom. provis.

Tulipa valerii Zoz & Klokov, Trudy Inst. Bot. Kharkivs'k. Derzhavn. Univ. 1: 65 (1935). Type: none cited.

Tulipa talijevii Klokov & Zoz, Trudy Inst. Bot. Kharkivs'k. Derzhavn. Univ. 1: 66 (1935), nom. inval. pro syn.

Tulipa hypanica Klokov & Zoz, Trudy Inst. Bot. Kharkivs'k. Derzhavn. Univ. 1: 66 (1935). Holotype: UKRAINE. 'Ukraina meridionalis, in decliviis steppaceis as fl. Inhul prope opp. Nikolajev', 22.iv.1928, *P. Oppermann* (CWU).

Tulipa sareptana Klokov & Zoz, Trudy Inst. Bot. Kharkivs'k. Derzhavn. Univ. 1: 66 (1935), nom. prov. Tulipa ophiophylla Klokov & Zoz, Trudy Inst. Bot. Kharkivs'k. Derzhavn. Univ. 1: 68 (1935).

Tulipa ophiophylla subsp. donetzica Klokov & Zoz, Trudy Inst. Bot. Kharkivs'k. Derzhavn. Univ. 1: 68 (1935). Holotype: UKRAINE. 'Ukraina orientalis. In decliviis lapidosis prope p. Tretja Rota (distr. Lisiczansk, prov. Donetzica)', 21.iv.1925, *I. Zoz* (CWU).

Tulipa ophiophylla subsp. graniticola Klokov & Zoz, Trudy Inst. Bot. Kharkivs'k. Derzhavn. Univ. 1: 68 (1935). Tulipa graniticola (Klokov & Zoz) Klokov, Visn. Rosl. URSR 11: 755 (1950). Holotype: UKRAINE. 'Ukraina meridionalis-orientalis. In graniticis monticulae Bestash ('Kamjani Mohyly'), 7 km S versus a p. Rosovka prov. Donetzicae', 30.iv.1927, s. coll., s.n. (CWU).

Tulipa ophiophylla subsp. bestashica Klokov & Zoz, Trudy Inst. Bot. Kharkivs'k. Derzhavn. Univ. 1: 69 (1935). Type: none cited.

Tulipa australis var. melillensis Sennen & Mauricio, Diagn. Nouv. Pl. Esp. Maroc: 167 (1936). Holotype: SPANISH MOROCCO. Melilla: Rostrogordo et Hidum, coteaux calcaires Melilla, 25.ii.1932, Mauricio 5839 ex Herb. Sennen (MPU!).

Tulipa sylvestris var. herbetei Sennen & Mauricio, Diagn. Nouv. Pl. Esp. Maroc: 243 (1936). Lectotype (designated here): MOROCCO. Djebel Kerker, garrigues, vers Puerta Abada, 22.iv.1934, Sennen & Mauricio 9583 (BM!).

Tulipa scythica Klokov & Zoz, Trudy Inst. Bot. Kharkivs'k. Derzhavn. Univ. 1: 69 (1936). Holotype: UKRAINE. 'Ukraina meridionalis. Ascania Nova. In ripis paludis steppae ('pod')', 26.iv.1926, s. coll., s.n. (CWU; isotype: Herb. Ascania-Nova).

Tulipa riparia Knjazev, Kulikov & E.G.Philippov, Bot. Zhurn. (Moscow & Leningrad) 86(3): 116 (2001). Holotype: RUSSIA. RSSA Baschkiria: 'Mons Jangantau ad ripam dextram fl. Jurjuzanj inter pag. Musatovo et Arkaulovo, in pratulis sub monte', 11.v.1985, M. Knjasev s.n. (LE).

Tulipa riparia var. lutea Knjaz., Kulikov & E.G.Philippov, Bot. Zhurn. (Moscow & Leningrad) 86(3): 117 (2001). Holotype: RUSSIA. 'Prov. Tscheljabinsk: fl. Sim ca. 10–15 km supra opp. Sim, ad ripam sinistram aliquanto infra ostium fl. Tankal', 30.v.1985, M. Knjasev s.n. (LE).

Note: A variable taxon of which *T. celsiana* is a late flowering form from North Africa known in cultivation for over four centuries (Wilford, 2006). *Tulipa biebersteiniana* has more flowers per stem, and the name has traditionally been applied to the taxa from southern Siberia and Central Asia. Numerous regional variants are described, but all integrate into each other and do not appear to warrant recognition. Zoz & Klokov (1935) treated the Ukrainian populations of this group in detail, but their taxa represent local genotypes that do not hold when the species is studied from the entire geographical area.

67b. Tulipa (E) sylvestris subsp. primulina (Baker) Maire & Weiller, in Fl. Afrique N. 5: 103 (1958)

Tulipa primulina Baker, Gard. Chron., n.s., 18: 8 (1882). Tulipa sylvestris var. primulina (Baker) Maire, Bull. Soc. Hist. Nat. Afrique N. 29: 454 (1938). Lectotype (designated here): CULTIVATED. 'From bulbs collected by H. J. Elwes in the Djibel Aures Mountains in Algeria', 17.iv.1883, Hort. Elwes s.n. (K-000365947!).

Distribution: Algeria, Morocco.

Tulipa cuspidata Regel, Gartenflora 33: 66 (1884). Tulipa sylvestris subsp. cuspidata (Regel) Maire & Weiller, in Fl. Afrique N. 5: 104 (1958).

Tulipa elwesii Regel, Gartenflora 33: t. 1147 (1884), nom. illeg.

Note: Battandier (1919) already stated that *T. cuspidata* is most likely the same plant as *T. primulina*. We agree with this observation.

67c. Tulipa (E) sylvestris subsp. sylvestris

Distribution: Italy, Sardinia, Sicily, northwestern Libya, introduced and naturalized elsewhere, extending north to Scotland, Finland and Sweden and North America.

Tulipa turcica Roth, Catal. Bot. 1: 45 (1797). Tulipa gallica Delaun. ex Loisel., Herb. Gén. Amateur 3: t. 160 (1829). Tulipa sylvestris var. gallica (Delaun. ex Loisel.) Kunze, Flora 29: 699 (1846). Tulipa australis var. gallica (Delaun. ex Loisel.) Levier, Tulip. Eur.: 103 (1884). Tulipa australis subsp. gallica (Delaun. ex Loisel.) K.Richt., Pl. Eur. 1: 216 (1890). Lectotype (designated here): plate t. 160 in Herb. Gén. Amateur 3 (1829).

Tulipa aurea Raf., Atlantic J.: 153 (1833). Ind. loc.: USA. Type: None cited, the description appears to refer to *T. sylvestris*, which is known to have naturalized in the eastern USA.

Tulipa grisebachiana Pant., Oesterr. Bot. Zeitschr. 23: 265 (1873). Tulipa sylvestris subsp. grisebachiana

(Pant.) Hayek, Repert. Spec. Nov. Regni Veg. Beih. 30(3): 71 (1932). In loc.: HERCEGOVINA. 'Hab. in rupestribus montis Gliva prope Trebinje'. Type: none cited

Tulipa florentina Baker, J. Linn. Soc., Bot. 14: 290 (1874), nom. inval., pro syn.

Tulipa marshalliana Andrz. ex Baker, J. Linn. Soc., Bot. 14: 290 (1874), nom. inval., pro syn.

Tulipa grisebachii [Pant.] Borbás, Oesterr. Bot. Zeitschr. 33: 202 (1883), nomen.

Tulipa balcanica Velen., Sitzungsber. Königl. Böhm. Ges. Wiss., Math.-Naturwiss. Cl. 1893(37): 65 (1893). Tulipa sylvestris subsp. balcanica (Velen.) Hayek, Repert. Spec. Nov. Regni Veg. Beih. 30(3): 71 (1932). Holotype: BULGARIA. Barmuk above Sliven, 1893, s. coll. s.n. (PRC-451981).

Lilium bononiense E.H.L.Krause in J.Sturm, Deutschl. Fl., ed. 2, 1: 91 (1906). Type: none cited.

Tulipa abatinoi Borzì & Mattei, Boll. Reale Orto Bot. Palermo 11: 241 (1912). Type: LYBYA. Garian, iii.1913, Abatino s.n. (PAL?).

Tulipa grandiflora Hy, Bull. Soc. Bot. France 59: 384 (1912). Tulipa sylvestris subsp. grandiflora (Hy) Hayek, Repert. Spec. Nov. Regni Veg. Beih. 30(3): 71 (1932). Syntypes: GREECE. Nymann. FRANCE. 'Galliae meridionalis', Loret. None located.

Tulipa gallica var. occidentalis Hy, Bull. Soc. Bot. France 59: 384 (1912). Ind. Loc.: FRANCE. 'In collibus Galliae occidentalis, per Andegaviam et Pictavium rara, certe spontanea'. Type: none cited.

68. Tulipa (T) systola Stapf, Denkschr. Kaiserl. Akad. Wiss., Wien. Math.-Naturwiss. Cl. 50(2): 17 (1885)

Holotype: IRAN. 'In agris ad Schurab in monte Karaghan', 12.v.1882, T. Pichler s.n. Iter Persicum, Dris. J. E. Polak. s.n. (WU-0065327!; isotype K!).

Distribution: Eastern Turkey, southern Transcaucasia, throughout the Levant south to the Sinai and east to western Iran.

Tulipa montana var. amblyophylla Post, Pl. Post. 1: 13 (1890). Tulipa amblyophylla (Post) Feinbr. in Eig, Zohary & Feinbr., Anal. Fl. Pal. 362 (1948), Tulipa montana subsp. amblyophylla (Post) Mout., Nouv. Fl. Liban Syrie 1: 231 (1966). Holotype: SYRIA. 'Jebel Aïn el-Wu'ûl', 7.iv.1890, G.E. Post 10 (BEI!; isotype K!).

Tulipa carrieri Sprenger, Bull. Soc. Tosc. Ortic. 19: 230 (1894).

Tulipa levieri Sprenger, Bull. Soc. Tosc. Ortic. 19: 230 (1894).

Tulipa sultanabadensis Sprenger, Bull. Soc. Tosc. Ortic. 19: 230 (1894).

Tulipa straussii Bornm., Mitt. Thüring. Bot. Vereins, n.f., 29: 43 (1912). Holotype: IRAN. 'In monte

Noa-Kuh ditionis oppidi Kerind', 14.v.1910, *T. Strauss* (not located).

Tulipa florenskyi Woronow, Bot. Mater. Gerb. Glavn. Bot. Sada RSFSR 5: 61 (1924). Holotype: CULTIVATED. 'Hort. Bot. Tiflisiene' [Tblisi], from bulbs collected by A. Florensky in 1915 in Sultanabad, northern Persia (LE).

Tulipa stapfii Turrill, Bot. Mag. 157: t. 9356 (1934). Tulipa cuspidata Stapf, Denkschr. Kaiserl. Akad. Wiss., Wien. Math.-Naturwiss. Cl. 50(2): 17 (1885), nom. illeg. Holotype: IRAN. Hamadan: 'In rupestribus prope Genjname' [Ganj Nameh], 19.iv.1882, T. Pichler, Iter Persicum Dris. J. E. Polak. s.n. (WU-0065326!).

Notes: This species is similar to T. julia. Wilford (2006) included T. stapfii in T. systola following Rechinger (1990), who stated that it is difficult to separate them on the basis of herbarium material. Zonneveld (2009) accepted these as separate on the basis of supposed different genome sizes. Typically, T. systola is a plant with narrow leaves, whereas T. stapfii has broad leaves. Tulipa sultanabadensis is a broad-leaved plant, and therefore that name will take priority over T. stapfii if this taxon is maintained distinct from T. systola, Tulipa florenskyi was compared with T. julia by Botschantzeva (1982), but we found this taxon to be more similar to T. systola, even though these taxa are all close and may need to be revised following further study. There are many intermediate forms, making it impossible to maintain many of these taxa.

69. *Tulipa* (T) *talassica* Lazkov, Turczaninowia 14(3): 11 (2011)

Holotype: KYRGYZSTAN. 'Jugi kirgisici declivum generale australe, praemontia adversus urbem Talas', 27.iv.2011, G.A. Lazkov s.n. (LE; isotypes ALTB, FRU, MW).

Note: Compared in the original description with *T. ostrowskiana*, *T. kolpakowskiana* and *T. thianschanica* (= *T. iliensis*). It was previously confused with the latter, but it has a different structure of the tunic. It belongs to the unresolved species complex surrounding *T. altaica* and is therefore maintained here tentatively. Thorough field studies are needed.

70. Tulipa (T) tetraphylla Regel, Trudy Imp. S.-Peterburgsk. Bot. Sada 3(2): 296 (1875)

Holotype: KYRGYZSTAN. Turkestaniae in valle Kotschkura, Kaulbars, Baro s.n. (LE, not located). Distribution: Kazakhstan, Kyrgyzstan, northwestern Xinjiang.

Tulipa kesselringii Regel, Trudy Imp. S.-Peterb. Bot. Sada. [Act. Hort. Petrop.] 5: 637 (1877). Ind typ.: 'Bulbos misit A. Regel e regionibus turkestanicis.

Dedicavi cultivatori eruditissima J. Kesselring' (LE?), not located.

Tulipa brachystemon Regel, Gartenflora 31: 323, t. 1099, f. 2,3 (1882). Lectotype (**designated here**): Illustration t. 1099, f. 2 in Gartenflora 31 (1882).

Tulipa corynestemon A.D.Hall, Gen. Tulipa: 138 (1940). Holotype: CULTIVATED, UK, Surrey: Merton, John Innes Hort. Inst. s.n. (K-000844493!).

Note: Tulipa kesselringii was established as a synonym of T. tetraphylla by Vvedensky (1935b). Tulipa corynestemon was synonymized under T. tetraphylla by Botschantzeva (1982), even though this species has peculiar filament shapes. This is a variable character in this species.

71. Tulipa (T) ×tschimganica Botschantz., Bot. Mater. Gerb. Inst. Bot. Zool. Akad. Nauk Uzbeksk. S.S.R. 16: 10 (1961)

Holotype: KYRGYZSTAN. 'Habitat in montibus Alatau Taschkendicis', 1959, Botschantzeva 99 (TASH). Distribution: Kyrgyzstan.

Tulipa anadroma Botschantz., Bot. Mater. Gerb. Inst. Bot. Zool. Akad. Nauk Uzbeksk. S.S.R. 16: 7 (1961).Holotype: KYRGYZSTAN. 'Tian-schan occidentalis, Tschatkal', 1953, Miryeov 1967 (LE).

Note: It has been suggested that this taxon is a natural hybrid (or species of hybrid origin) between *T. dubia* and *T. kaufmanniana* (Phillips & Rix, 1981). Populations are variable and span the range between the two parents, but can be distinguished by the large basal blotches inside the tepals. *Tulipa anadroma* is also suggested to be a hybrid between the same parents and is therefore synonymized here awaiting further field study.

72. Tulipa (E) turkestanica (Regel) Regel, Trudy Imp. S.-Peterburgsk. Bot. Sada 3(2): 296 (1875) Tulipa sylvestris var. turkestanica Regel, Trudy Imp. S.-Peterburgsk. Bot. Sada 2: 443 (1873). Syntypes: 'Habitat satis frequenter in Turkestaniae provinciis', Fedschenko, Korolkow, Krause, Kuschakewicz. Lectotype (designated here): 'Chiwa', Korolkow & Krause s.n. (COI-00050870!). Distribution: Kyrgyzstan, Tajikistan, Uzbekistan.

Note: A species closely related to *T. bifloriformis*.

73. *Tulipa* (T) *ulophylla* Wendelbo, Nytt Mag. Bot. 14: 99 (1967)

Holotype: IRAN. Maz: 'In valle Haraz supra Zardman (Siah Bisheh)', fl 26.iv.1959, fr 26.vii.1959, *P. Wendelbo 355* (BG).

Distribution: Iran.

Tulipa wendelboi Matin & Iranshahr, Iranian J. Bot. 7: 228 (1998). Holotype: IRAN. Mazandaran: 18 km to Marzan-abad, before Pol-e Owshan, 10.v.1996, Matin, Daneshpazhuh & Ghanbari 12974 (IRAN).

Note: Tulipa wendelboi is a variant differing little from T. ulophylla according to Wilford (2006), which is followed here. Matin & Iranshahr (1998) distinguished it from T. ulophylla because of its shorter stems, more leaves, a cordiform (instead of lanceolate) blotch, shorter filaments and purple instead of yellow anthers, all characters variable in T. ulophylla.

74. Tulipa (T) undulatifolia Boiss., Diagn. Pl. Orient. 5: 57 (1844)

Holotype: TURKEY. Izmir: 'in herbosis pinguibus ad pedem rupium in summo monte Tartali [Tahtali Da.] supra Smyrnam', 1842, Boissier s.n. (G; isotype P-00730876!).

Distribution: Southern Balkans, Greece, Lesbos, western Turkey, Transcaucasia.

Tulipa boeotica Boiss. & Heldr. in P.E.Boissier, Diagn. Pl. Orient., II, 4: 99 (1859). Lectotype (designated here): GREECE. 'in agris Boeoticae inter Oropo et Chalcidam', iii.1844, T.H.H. von Heldreich s.n. (H-1237831!; isotypes: K! (two sheets), P-02049054!).

Tulipa euanthiae Orph. in P.E.Boissier, Diagn. Pl. Orient., II, 4: 100 (1859). Tulipa boeotica subsp. euanthiae (Orph.) K.Richt., Pl. Eur. 1: 215 (1890). Type: GREECE. 'in regione media montis Malevo Laconiae prope Xerocampo', Orphanides (G?, not located).

Tulipa strangulata Heldr. ex Baker, J. Linn. Soc., Bot. 14: 286 (1874), nom. illeg.

Tulipa eichleri Regel, Gartenflora 23: 193 (1874). Lectotype (**designated here**): Illustration t. 799 in Gartenflora 23 (1874). Material from Azerbaijan, Schemacha [Şamaxı] (LE; photograph K!) has been cited as the holotype by Rechinger (1990), but this material is not mentioned in the protologue and therefore cannot be a type.

Tulipa micheliana Hoog, Gard. Chron. III, 31: 350 (1902). Tulipa eichleri var. micheliana (Hoog) Raamsd., Pl. Syst. Evol. 195: 40 (1995). Tulipa undulatifolia var. micheliana (Hoog) Wilford. Lectotype (designated by Wilford, 2013): figure 120, Gard. Chron. III, 31: 353 (1902). Note: Material from Turkey collected by Sintenis (BM!, MO!, K!) has been suggested as type material, but this is not listed in the protologue and thus cannot be the type.

Notes: Hall (1940) included *T. undulatifolia* erroneously under *T. praecox* Ten. (= *T. agenensis*), resulting in the name falling out of use. Plants known from cultivated fields in Transcaucasia are known as

T. eichleri, but are identical to the material from the Balkan Peninsula (Marais, 1984) and Turkey known as *T. undulatifolia*. *Tulipa micheliana* is a variety of this species with striped leaves and can be confused with the related *T. greigii*.

75. *Tulipa* (O) *uniflora* (L.) Besser ex Baker, J. Linn. Soc., Bot. 14: 295 (1874)

Ornithogalum uniflorum L., Mant. Pl.: 62 (1770). Gagea uniflora (L.) Schult. & Schult.f. in J.J.Roemer & J.A.Schultes, Syst. Veg. 7: 553 (1829). Orithyia uniflora (L.) D.Don in R.Sweet, Brit. Fl. Gard. 7: t. 336 (1836). Tulipa stylosa Fisch., Index Seminum (LE) 3: 28 (1837), nom. superfl.

Neotype (designated by Levichev, 1997): RUSSIA. 'In Siberiae montis Sini Sopka', E. Laxmann (LE; isoneotype K-000844631!).

Distribution: Siberia, Kazakhstan, northern China, Mongolia.

Orithyia nutans Trautv., Pl. Imag. Descr. Fl. Russ.: 15, table 10 (1844).

Tulipa mongolica Y.Z.Zhao, Novon 13: 277 (2003). Holotype: CHINA. Inner Mongolia: Xilin Gol Meng. Baiyinxile, 20.v.1979, Shu-run Liu 395 (HIMC; isotype HIMC).

Note: The type of subgenus *Orithyia*, which can be recognized by its defined style. This subgenus has been suggested to be intermediate between *Tulipa* and *Amana* (Phillips & Rix, 1981), but this is not the case; *Amana* is closer to *Erythronium* (Clennett *et al.*, 2012), whereas *Orithyia* belongs to *Tulipa*. It is the most eastern species of *Tulipa*.

76. *Tulipa* (E) *urumiensis* Stapf, Curtis's Bot. Mag. 155: t. 9288 (1932)

Type: CULTIVATED. Bulbs sent to Firma Van Tubergen, originally from Iran (Urmia), 1928. A preserved flower from the Van Tubergen garden and associated original illustration are labelled as presented by the Editor of the Botanical Magazine to the Kew Herbarium. This is **hereby designated** as the lectotype (K!).

Distribution: Northwestern Iran, Kazakhstan, Kyrgyzstan.

Tulipa tarda Stapf, Curtis's Bot. Mag. 156: t. 9321 (1933). Holotype: Plate 9321 in Curtis's Bot. Mag. 156 (1933).

Tulipa dasystemon auct., non Regel (1879).

Note: Zonneveld (2009) erroneously accepted *T. tarda* over the older name *T. urumiensis*. *Tulipa urumiensis* has yellow tepals, which is the only difference from the partly white tepals of *T. tarda*. The species is

common in cultivation in both colour forms. *Tulipa* dasystemon of commerce belongs to this species.

77. Tulipa (T) uzbekistanica Botschantz. & Sharipov, Novosti Sist. Vyssh. Rast. 8: 109 (1971) Holotype: UZBEKISTAN. 'Uzbekistania australis, promontoria ad meridiem a via Dechkananabad – Derbent, montes Kurukdagana, ad declive australe trajectus Tally', 19.v.1967, V. Botschantzev 134 (LE). Distribution: Uzbekistan.

Note: This species is similar to *T. fosteriana* and *T. ingens*, but differs in having a leathery tunic that is hairy only at the base and top.

78. Tulipa (T) vvedenskyi Botschantz., Bot. Mater. Gerb. Inst. Bot. Zool. Akad. Nauk Uzbeksk. S.S.R. 14: 3 (1954)

Holotype: TAJIKISTAN. 'In valle fl. Angren prope p. Tjurk', 1950, Botschantzeva s.n. (TASH).

Distribution: Tajikistan.

UNPLACED CULTIVARS

Some taxa described as species are actually cultivars and should be treated as such.

Tulipa 'Elegans'. Tulipa elegans Baker, J. Linn. Soc., Bot. 14: 286 (1874)

Lectotype (designated here): CULTIVATED. 3.v.1873, Hort. Barr s.n. (K-000844395!).

Note: It is indicated on the specimen label that this is a garden hybrid between T. pubescens and T. 'Cornuta'.

Tulipa 'Cornuta'. *Tulipa cornuta* Delile in P.J.Redouté, Liliac. 8: t. 445 (1815)

Holotype: figure 445 in Redouté, Liliac. 8 (1815).

Notes: This cultivar is offered in the trade under the name *T. acuminata*, but the type specimen of that species appears to belong to *T. agenensis*. These are plants with exceptionally narrow needle-like tepals, reminiscent of the horned tulips depicted in Ottoman art. It has been suggested to be an early hybrid of unknown parentage.

Synonym: Tulipa stenopetala Delaun. ex Loisel., Herb. Gén. Amateur 3: t. 171 (1819). Holotype: Plate in Herb. Gén. Amateur 3: t. 172, fig. 1 (1819).

CULTIVAR GROUPS OF NEO-TULIPAE

Tulipa Didieri Group

Neo-tulipae; selections from naturalized *T.* ×*gesneriana*, often early hybrids. Tepals of members of this Group are pointed, long and have a blotch at the

base. Cultivars currently in cultivation are: *Tulipa* 'Billietiana', 'Didieri', 'Fransoniana', 'Mauriana', 'Montisandrei', 'Passeriniana', 'Planifolia', 'Platystigma', 'Rubidusa', 'Saracenica', 'Spathulata' and 'Villarclément'.

Tulipa Grengiolensis Group

Neo-tulipae; selections from naturalized *T.* ×*gesneriana*, often early hybrids. Tepals of members of this group are pointed, broad, are generally pink, white or yellow, and have a margin that is tinged rose or red. Cultivars currently in cultivation are: *Tulipa* 'Cindy', 'Grengiolensis', 'Marjolettii' and 'Mauritiana'

UNPLACED NAMES

Tulipa boettgeri Regel, Trudy Imp. S.-Peterburgsk. Bot. Sada 10: 366 (1887). Ind. Loc.: 'In Bucharae orientalis provincia Baldschuan prope urbem Kangurt'. Type: none cited. Note: This is suggested to be similar to *T. praestans* H.B.May (Vvedensky, 1935b), but we have not found any original material to verify this. If the two taxa were to be combined, this name will have priority over *T. praestans*, causing nomenclatural instability in horticulture.

Tulipa kopetdaghensis B.Fedtsch. ex Czerniak., Izv. Glavn. Bot. Sada S.S.S.R. 26: 256 (1927). nomen. Tulipa kopetdaghensis B. Fedtsch. ex Czerniak., Fedde Repert. 27: 266 (1930), nomen. Note: this name was never validly published. Associated specimen: CULTIVATED. Originally from Kopet Dagh, Schlucht Tschuli, Fedtschenko (LE, not seen).

EXCLUDED NAMES

Tulipa anhuiensis X.S.Shen, Acta Bot. Yunnan. 23(1): 39 (2001), basionym = Amana anhuiensis (X.S.Shen) Christenh., comb. nov. Type: CHINA. Anhui: Qianshan Xian, Tianzhu Shan, 1.iv.1998, X.S. Shen 98006 (holotype PE!). Note: This recently described species clearly belongs to Amana. The combination for this species in that genus is provided here.

 $Tulipa\ breyniana\ L.,\ Sp.\ Pl.\ 1:\ 306\ (1753) = Moraea\ collina\ Thunb.\ (Iridaceae).$

Tulipa edulis (Miq.) Baker, J. Linn. Soc., Bot. 14: 295 (1874) = **Amana edulis** (Miq.) Honda.

Tulipa edulis var. latifolia Makino, Bot. Mag. (Tokyo) 16: 16 (1902) = **Amana erythronioides** (Baker) D.Y.Tan & D.Y.Hong.

Tulipa erythronioides Baker, J. Bot. 13: 292 (1875) = **Amana erythronioides** (Baker) D.Y.Tan & D.Y.Hong.

Tulipa graminifolia Baker ex S.Moore, J. Bot. 13: 230 (1875) = **Amana edulis** (Miq.) Honda.

 $\begin{array}{lll} \textit{Tulipa latifolia} & (\text{Makino}) & \text{Makino}, \text{ Bot. Mag. (Tokyo)} \\ 28: & 28 & (1914) = \textbf{\textit{Amana}} & \textbf{\textit{erythronioides}} & (\text{Baker}) \\ \text{D.Y.Tan & D.Y.Hong.} \end{array}$

Tulipa ornithogaloides Fisch. ex Besser, Flora 17(1 Beibl.): 25~(1834) = Gagea triflora~(Ledeb.) Schult. & Schult.f.

Tulipa pudica (Pursh) Raf. Atlantic J.: 153
(1833) = Fritillaria pudica (Pursh) Spreng.
Tulipa sibthorpiana Sm., Fl. Graec. Prod. 1: 229
(1809) = Fritillaria sibthorpiana (Sm.) Baker.
Tulipa section Stellaster (Heist. ex Fabr.) Baill.,
Hist. Pl. 12: 463 (1894). = Scilla L.