

Iran supports a great share of biodiversity and floristic endemism for *Fritillaria* spp. (Liliaceae): A review



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ABSTRACT

Iran supports a great share of exotic and/or endemic plant genera and species. The genus *Fritillaria* (Liliaceae) is a precious part of this botanical richness with 19 species, of which 10 are endemic to the country. However, signs are mounting that the country is truly at a crossroads when it comes to preservation of this national wealth. In this regard, an effective conservation strategy should thoroughly consider the classification of *Fritillaria*, as conservation practices are compromised by knowledge gaps in systematics and taxonomy. As published studies on *Fritillaria* in Iran have been sporadic and limited in scope, the aim of this review is to provide information necessary to help bridge these information gaps. Our objective is to facilitate increased understanding of the geographic, taxonomic, cytogenetic and phylogenetic status of Iranian *Fritillaria*, which is vital to meeting the goal of sustainable conservation of the genus in Iran and neighboring areas.

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1. Irano-Anatolian biodiversity hotspot

The Middle East enjoys a wealth of biological diversity encompassing a variety of ecosystems and associated habitats, including high- to low-density forests, deserts, plains, rangelands, savannas, oases, and mountains. Three of the world's 34 biodiversity hotspots, the Irano-Anatolian region, the Mediterranean forest region, and the Horn of Africa region, are located in the Middle East and West Asia regions (Hanson et al., 2009). The Irano-Anatolian region

hotspot covers an area of about 899,773 km², a considerable share of which is found in northern through western Iran, and is a World Heritage Site known for its rich biodiversity with about 6000 plant species. The Irano-Anatolian region also includes parts of Turkey, Iraq, Georgia, Azerbaijan, Armenia and Turkmenistan (Fig. 1, Left).

2. Geographic and ecosystem features of Iran

Iran is a vast country in Southwest Asia occupying an area of over 1.64 million square km; an area nearly as large as Italy, France, Spain and the British Isles combined (Firouz et al., 1970). The natural ecosystems of Iran cover about 80% of the country's surface area (Salahi et al., 2008), with 90 million ha of rangeland (nearly 54.8%) (Kharazipour, 2009), 12.4 million ha of forest (nearly 7.5%), and about 33 million ha of desert (about 20%).

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Fig. 1. Left, Irano-Anatolian hotspot region; Right, an estimation of geographic distribution for *Fritillaria* spp. throughout Iran.

Iran is a land of extremes; altitudes range from 5604 m on Mount Damavand's summit (Kharazipour, 2009) to 28 m below sea-level on the shores of the Caspian Sea (Akhani and Ghorbanli, 1993). The cold climates of the Zagros range, running from the northwest to the south, are replaced by the hot desert climates to the center and east. Mean January temperatures range from 20 °C along the Persian Gulf in Hormozgan province to about –11 °C in Chaharmahal & Bakhtiari (C & B) province. Dry lands of the interior areas change suddenly to the wet and moderate coastal climates of the Caspian coastal areas; the lush Caspian forest may receive an annual rainfall of 1950 mm, whereas lifeless sand-dunes of the 'Lut' remain arid (~30 mm annual rainfall).

Iran supports a great share of plant species and countless natural habitats characterized by many unique plants and centers of local endemism (Khourang et al., 2014). Up to 8200 plant species are recognized throughout the country, of which almost 1900 are endemic (Kharazipour, 2009). The genus *Fritillaria*, with a variety of species that grow naturally across different areas, is a major component of this botanical richness. However, signs are mounting that the country is truly at a crossroads when it comes to preservation of this national wealth.

Taxonomy and species conservation are often assumed to be interdependent activities; a shortage of taxonomic information and skills causes problems for conservation practitioners (Mace, 2004). From this point of view, dealing with the genus *Fritillaria* is a tricky effort, as the accepted units of diversity in the genus are hard to define and the exact habitat range of the species is hard to estimate. The existence of intermediate forms and continuous ranges of variation within this group of plants, which are phenomena generally caused by frequent hybridization at the species and subspecies level, accounts for the extreme difficulty in identifying many doubtful species. Furthermore, many of the species are native to remote uninhabited areas, where access to the habitats is extremely difficult. To make this even more complicated, members of the genus in Iran exhibit a wide range of variation in their morphological features (Sharifi-Tehrani and Advay, 2015) and physiological responses to the environment (Khourang et al., 2014). Thus, it is not surprising that among the large number of *Fritillaria* species known to occur in Iran, the majority of species are little known. Despite the necessity of an accessible comprehensive source of data to set practical conservation strategies, studies on *Fritillaria* in Iran have been quite sporadic and limited in scope. Following a comparative approach, here, we present a review of

detailed basic information necessary for understanding the geographic, taxonomic, cytogenetic and phylogenetic status of Iranian *Fritillaria*, which seem to be vital to meeting the goal of sustainable conservation of *Fritillaria* in Iran and neighboring areas.

3. Genus *Fritillaria* (L.)

The name *Fritillaria* is said to come from either the Latin term *fritillus* (the chequered Roman dice tower) (Kiani, 2015) or more likely the Latin root *frittullo* (the chess-board) (Gerard, 1995); both terms, however, denote the checkerboard pattern of the petals in *Fritillaria meleagris* L., the type species of the genus. *Fritillaria* is also the scientific name for butterflies in the family *Nymphalidae*, again referring to their patterned wings (Dunford and Sims, 2008).

Fritillaria (L.) is one of the most complex genera recognized in the family Liliaceae (Li et al., 2009). According to Rix (2001), the genus embraces about 140 species (165 taxa) of geophytic perennials, indigenous to the temperate climatic regions of the Northern Hemisphere (Rønsted et al., 2005) between latitudes 32° and 62°, especially throughout Europe, the Northern part of Africa bordering the Mediterranean Sea, the Mediterranean basin, the Middle East, Northern Asia and as far south as Iran, Afghanistan, the Himalayas, China, Korea and Japan. In North America *Fritillaria* occurs in Canada and in a narrow coastal strip from the Aleutian Islands to northern Mexico, extending inland to 16 states of the United States, especially California and Oregon (Beetle, 1944; Tekşen and Aytaç, 2011; Tomović et al., 2007). The genus has undergone marked species radiations in the Middle East, Southwest Asia and the eastern Mediterranean regions (Zaharof, 1988), particularly in Turkey and Iran. While Turkey, with 35 species and 6 subspecies (Tekşen and Aytaç, 2011), supports the greatest share of the world's *Fritillaria* resources, the significance of Iran rather lies in having a greater representation of different subgenera than any other country. Thus, the main center of the genetic diversity of the genus probably is Iran, where subgenera from Caucasus, central Asia and the Mediterranean meet (Rix, 1977). To date, 19 species (including at least 1 variety and 3 subspecies) are reported in Iran, of which at least 10 are endemic to the country (Table 1) (Advay et al., 2015; Bakhshi Khaniki, 1997a, 1997b; Reching, 1990; Rix, 1977, 2001).

Interestingly, the pattern of distribution of Iranian fritillaries largely corresponds to those parts of the country belonging to the Irano-Anatolian biodiversity hotspot (Fig. 1, Right). Fritillaries are quite hardy and occur over a wide range of climates and habitats

Table 1Nineteen *Fritillaria* species known to occur in Iran.

Genus <i>Fritillaria</i>	Species
Subgenus <i>Petilium</i>	<i>Fritillaria imperialis</i> (also <i>F. imperialis</i> var. <i>lutea</i> , the yellow form of the species), <i>F. raddeana</i> ^a
Subgenus <i>Theresia</i>	<i>F. persica</i>
Subgenus <i>Rhinopetalum</i>	<i>F. gibbosa</i> , <i>F. Ariana</i>
Subgenus <i>Fritillaria</i>	
Section <i>Fritillaria</i>	
Group <i>F. kotschyana</i>	<i>F. kotschyana</i> (ssp. <i>kotschyana</i> ^a & ssp. <i>grandiflora</i> ^a), <i>F. olivieri</i> ^a
Group <i>F. crassifolia</i>	<i>F. crassifolia</i> ssp. <i>kurdica</i> , <i>F. poluninii</i> , <i>F. reuteri</i> ^a , <i>F. straussii</i> ^a
Section <i>Olostyleae</i>	
Group <i>F. caucasica</i>	<i>F. caucasica</i> , <i>F. uva-vulpis</i> , <i>F. assyriaca</i> , <i>F. zagrica</i> ^a , <i>F. chlorantha</i> ^a , <i>F. chlororhabdota</i> ^a , <i>F. atrolineata</i> ^a , <i>F. avromanica</i> ^a

^a Endemic to Iran.

(Beetle, 1944). Most of the Iranian species are well-adapted to the uplands, foothills and associated plains of the Zagros range (Badfar-Chaleshtori et al., 2012), characterized by very rocky and sloping areas, wetlands, riparian zones, and different types of rangelands. The remaining species typically occur either on the northern slopes of the Mountain Elburz (also spelled Alborz) along the Caspian Sea in North Iran (Khaniki and Persson, 1997) or in flat and arid areas of the central parts of the country (Rix and Zarrei, 2007b). Iranian fritillaries mainly inhabit montane to alpine zones (1000–3600 m), but some species e.g. *Fritillaria raddeana*, at least in some parts, inhabit lowlands too (Khourang et al., 2014). With the exception of *Fritillaria imperialis* and *F. persica*, which are more southerly species, from the northern borders of the Zagros chain downwards, the geographical distribution of most of the Iranian species gradually decreases (Sharifi-Tehrani et al., 2015). The Zagros highlands at the border of Kordestan and Kermanshah provinces support the highest level of species richness in Iran (Wallis and Wallis, 2009), while the number of species in the southerly C & B province decreases to only four (Sharifi-Tehrani et al., 2015).

The typical bulb of *Fritillaria* species consists of a few fleshy, tightly packed scales and a thin, translucent tunic, which usually disappears as the bulb increases in size. Some *Fritillaria* species have naked bulbs consisting of many scales, which resemble those of *Lilium*; these species also have numerous bulbils, loosely attached (Rønsted et al., 2005). In the genus *Fritillaria*, flowers are usually pendant, solitary (sometimes in umbels or many-flowered racemes) and have a campanulate and typical tulip-like perianth (Zych and Stpiczyńska, 2012). Fritillaries generally bear actinomorphic flowers (Khaniki and Persson, 1997), except for members of subgenus *Rhinopetalum*, in which flowers are usually zygomorphic (Tamura, 1998). Nectaries are often flattish, usually linear, lanceolate or ovate, sometimes circular, and pollen grains are usually faveolate to reticulate (Khaniki, 2003). Species range from <10 to over 120 cm in height. Although fritillaries can be seen in nearly every color, white-yellow, orange-red and purplish-brown are most common among the Iranian species (Kiani, 2015). *F. imperialis* is well known for its unpleasant foxy odor (Helsper et al., 2006), emanated by all parts of the plant, which is thought to be a way for repelling herbivores. The majority of the species with green or brown, broadly campanulate, flowers have what is often called a “spermatoc scent”, associated only with the flowers and presumably related to the attraction of pollinators.

Fritillaries generally produce bisexual flowers (Shimizu et al., 1998); however, a few other mating systems like androdioecy (in *F. persica*, *F. involucrate* All., *F. messanensis* Raf. and *F. montana* Hoppe ex W.D.J.Koch) and andromonoecy (in *F. montana*) have also been documented (Peruzzi, 2012). The breeding systems vary from self-compatible to self-incompatible, demonstrating various degrees of out-crossing. *Fritillaria* species are probably pollinated by insects, especially Hymenoptera (mostly various species of bees and wasps), Diptera, Lepidoptera and Coleoptera (Zych and

Stpiczyńska, 2012), and even birds, as in the case of *F. imperialis* (Burquez, 1989; Peters et al., 1995).

Although variable based on the climatic conditions, species reported as commonly co-occurring with *Fritillaria* in Iran include *Artemisia* L. spp., *Gagea robusta* Zarrei & Wilkin, *Tulipa* L. spp., *Astragalus* L. sp., *Geranium* L. sp., *Prunus scoparia* (Spach) C.K.Schneid., *Rumex acetocella* L., *Kelussia odoratissima* Mozaff., *Daphne mucronata* Royle, *Gundelia tournefortii* L., *Rosa canina* L., *Glycyrrhiza glabra* L., *Anchusa* L. sp., *Anthemis* L. sp., *Quercus* L. sp., *Ranunculus* L. sp. and *Echinops* L. sp. (Babaei, 2014; Bakhshi, 2000; Khourang et al., 2014), many of which are endemic and of ethnopharmacological value and importance. Furthermore, different species of the genus *Fritillaria* may occur in same habitat (Khourang et al., 2014).

4. Phylogenetic relationship

The morphological classification of *Fritillaria* at the infrageneric level has been reviewed by several authors (Baker, 1874; Bentham and Hooker, 1883; Boissier, 1854; Turrill et al., 1980). According to the last revision by Rix (2001), the genus is subdivided into eight subgenera including *Fritillaria* [with two sections: *Olostyleae* Boiss. (six series) and *Fritillaria* (10 series)], *Rhinopetalum* Fisch., *Japonica* Rix, *Theresia* K. Koch, *Petilium* (L.) Endl., *Liliorhiza* (Kellogg) Benth. & Hook.f. (three series), *Davidii* Rix and *Korolkowia* Rix (Mucciarelli et al., 2016). Although the current classification of the genus is supported by molecular phylogenetic studies (e.g. Rønsted et al., 2005; Day et al., 2014) at the subgeneric level, relationships among species remain incompletely resolved, especially within subgenus *Fritillaria*.

Up to now, 19 species belonging to four subgenera are recorded in Iran; subgenus I) *Petilium* consists of four morphologically similar species, *F. imperialis*, *F. raddeana*, *F. chitralensis* (auct.) B. Mathew (also treated as *F. imperialis* var. *chitralensis* auct.) and *F. eduardii* A.Regel ex Regel (Wietsma et al., 2015); the first two species have been found in Iran. *F. persica* is the only species recognized in the monotypic subgenus II) *Theresia* (Türktaş et al., 2012).

Fritillaria gibbosa, *F. ariana*, *F. karelinii*, *F. stenantha* Rgl. and *F. bucharica* Rgl. are five morphologically similar species recognized in the subgenus III) *Rhinopetalum* (Rix and Zarrei, 2007b), of which the occurrence of the first two has been confirmed in Iran; historically, a separate genus closely related to *Fritillaria*, called *Rhinopetalum* Fisch. ex Alexand. was described in 1830 (Mathew, 2005). Several authors used the genus *Rhinopetalum* subsequently, but others such as Boissier (1846) and Baker (1874) opted to place these species in a distinct subgenus in the genus *Fritillaria*. Recent molecular studies of *Fritillaria* (Rønsted et al., 2005; Day et al., 2014) have confirmed that members of *Rhinopetalum* are nested in *Fritillaria*; so the incorporation of *Rhinopetalum* into *Fritillaria* is justified.

The largest subgenus of the genus, IV) *Fritillaria*, is morphologically classified into six complexes, namely *Fritillaria crassifolia*, *Fritillaria kotschyana*, *Fritillaria caucasica*, *Fritillaria graeca*, *F. meleagris* and *Fritillaria cirrhosa* groups (Rix, 2001), of which members of the first three complexes are reported in Iran. No member of the *F. meleagris* group has yet been recorded in Iran, but a representative of the group (*Fritillaria latifolia*) is found in neighboring areas of Turkey and the Caucasus, and is very likely to be found in northwest Iran (Rix, 1977).

Following the classification proposed by Rix (2001), data in Fig. 2 confirm the monophyly of all subgenera within the genus, except subgenus *Fritillaria*, which resolves into two phylogenetically distant clades. On the basis of molecular evidence, members of the group *Fritillaria* A (a large predominantly European, Middle Eastern and North African clade) are distantly related to the group *Fritillaria* B (a small clade of mainly Chinese and Central Asian species). This result supports recognition of the clade *Fritillaria* B as a new subgenus, yet to be formally named.

In Iran, phylogenetic research of *Fritillaria* is limited to few studies (e.g. Khourang et al., 2014; Sharifi-Tehrani and Advay, 2015). Although the findings of Khourang et al. (2014) reconfirmed most results of the previous phylogenetic studies of *Fritillaria* (e.g. Rønsted et al., 2005; Day et al., 2014), they suggested a new phylogenetic arrangement within the genus in some cases. In comparison to Day et al. (2014), the most comprehensive phylogenetic study of the genus, Khourang et al. (2014) used nine species (*F. imperialis*, *F. imperialis* var. *lutea* [the yellow form of the species], *F. persica*, *F. crassifolia*, *F. straussii*, *F. zagrica*, *F. kotschyana*, *F. gibbosa*, *F. reuteri* and *F. raddeana*), on which no information has been released on molecular phylogeny of *F. imperialis* var. *lutea* and *F. straussii* in the literature. Therefore, based on molecular evidence, the status of these taxa within the genus *Fritillaria* has remained undefined. Their results confirmed that *F. straussii* falls into the Middle Eastern group of subgenus *Fritillaria* (*Fritillaria* A). Furthermore, they claimed that red- and yellow-colored crown imperials are closely related, and both belong to subgenus *Petilium*.

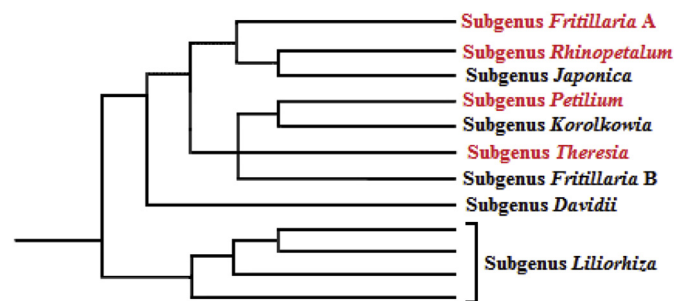


Fig. 2. Subgeneric classification of *Fritillaria* as adapted from Day et al. (2014); members of the subgenera highlighted in red occur in Iran.

Table 2
Chromosome number of some species of *Fritillaria* including Iranian species.

2x			3x		4x
x = 9	x = 11	x = 12	x = 13	x = 12	
<i>F. tenella</i>	<i>F. japonica</i>	Most of the examined species, including the Iranian taxa ^b	<i>F. pudica</i>	<i>F. lanceolata</i> ^a	<i>F. imperialis</i> var. <i>maxima lutea</i>
<i>F. montana</i>	<i>F. amabilis</i>		<i>F. glauca</i>	<i>F. camschatcensis</i> ^a	<i>F. imperialis</i> var. <i>maxima rubra</i>
<i>F. ussuriensis</i>	<i>F. ussuriensis</i>				<i>F. assyriaca</i> ^a
<i>F. ruthenica</i>					

^a Karyo-ecotypes (2x & 3x taxa) reported.

^b The status of the Iranian *F. avromanica* is unknown.

5. Karyology and cytogenetic characteristics

The genus *Fritillaria* has been used as a cytogenetic model for the study of chromosomal structure and cell division (meiosis & mitosis) processes, due to its exceptionally huge genome size (Darlington and La Cour, 1941); the tetraploid *Fritillaria assyriaca* is known to be the largest plant genome so far reported with 254.8 pg, nearly 800 times the size of the *Arabidopsis thaliana* genome (Zonneveld, 2010). Therefore, species of the genus have long held a special place in plant biology (Ambrožová et al., 2010). Chromosome numbers have been reported for over 50 species of *Fritillaria*; with a few exceptions (Kiran and Gedik, 2014; Matsuura, 1934; Marchant and Macfarlane, 1980; Noda, 1975; La Cour, 1978; Li and Shang, 1989), most of the species within the genus have a basic chromosome number $x = 12$ (Table 2).

In addition, *Fritillaria* is a genus with frequent variations in the chromosome structure, ascribed to polyploidy as well as fusion and fragmentation of some chromosomes. Although tetraploidy in fritillaries has been documented in few cases (Table 2), polyploidy within the genus is almost limited to triploid plants, which are frequently found (Ambrožová et al., 2010). Karyo-ecotypes are reported among *Fritillaria* species, as some taxa growing in different geographical-environmental conditions show various levels of ploidy, which directly affect their reproductive behavior, ecological tolerance, and distribution range (Marchant and Macfarlane, 1980).

Cytogenetic and karyotypic characteristics are available for all of the Iranian species, except *Fritillaria avromanica* which has just recently been reported (Khaniki, 2002e, 2002f, 2002g; Advay et al., 2015). All of the Iranian species are diploid ($2n = 2x = 24$), showing a variety of karyotype formulas; in the majority of the species, the presence of 1–4 pairs of satellites has been confirmed (Advay et al., 2015; Ahmadi-Roshan et al., 2016; Bakhshi, 2000; Bakhshi and Persson, 2002; Bakhshi Khaniki, 1997a, 1997b; Jafari et al., 2014; Khaniki, 2002e, 2002f, 2002g), mostly located on the long arms (Ahmadi-Roshan et al., 2016; Jafari et al., 2014); this may be evaluated as an indicator for chromosomal evolution or possible ways for structural differentiation. Khaniki (2002b) reported the presence of accessory B chromosomes (also known as supernumerary chromosomes) for *F. zagrica*, whereas Ahmadi-Roshan et al. (2016) and Jafari et al. (2014) found no accessory chromosomes in their assessments. From an evolutionary point of view, this would be considered quite normal, since it seems unlikely that accessories would persist in a species unless there was some significant adaptive advantage.

Different chromosome types have been reported in *Fritillaria*. In accordance with Peruzzi et al. (2009), Jafari et al. (2014) and Ahmadi-Roshan et al. (2016), four chromosome types have been confirmed to include 'm', 'sm', 'st' and 'T' in nine species (*F. imperialis*, *F. persica*, *F. raddeana*, *F. crassifolia* ssp. *kurdica*, *F. zagrica*, *F. kotschyana* ssp. *kotschyana*, *F. gibbosa*, *F. reuteri* and *F. straussii*), with the 'st' and 'sm' types appearing at the highest and the lowest frequencies. The 'T' chromosome type has been reported for the first time in *F. imperialis*, *F. imperialis* var. *lutea*, *F. raddeana*, *F. persica*, *F. crassifolia*, *F. zagrica* and *F. gibbosa* (Jafari et al., 2014; Ahmadi-Roshan et al., 2016); the

presence of the 'T' type chromosome in the karyotype of species directly correlates with the chromosomal asymmetry inferring the level of the species evolution. According to [Stebbins's classification \(1971\)](#), karyotypes of different species of Iranian *Fritillaria* can be classified as relatively asymmetric and/or evolved chromosomal structures ([Jafari et al., 2014](#)).

Fritillaries are quite different in the geometry of the chromosome structure, which directly affects their cross-compatibility and the fertility of the offspring. Compatible taxa generally show high degrees of chromosomal homology, making them potentially suitable for fertile interbreeding. Accordingly, a set of cross-compatible species, including *F. imperialis* × *F. imperialis* var. *lutea*, *F. persica* × *F. straussii*, *F. kotschyana* × *F. crassifolia*, *F. imperialis* × *F. crassifolia*, *F. imperialis* × *F. gibbosa*, *F. gibbosa* × *F. raddeana*, *F. reuteri* × *F. zagrica*, have been proposed by [Ahmadi-Roshan et al. \(2016\)](#) and [Jafari et al. \(2014\)](#), each of which are expected to make normal chromosome pairing and probably produce the most fertile hybrids when crossed to each other. The specific objectives of *Fritillaria* cytogenetics may be essentially diverse, but such knowledge is extremely useful, particularly in commercial improvement of cultivars through hybridization and/or identification of doubtful specimens via guestimating potential parents when several taxa inhabit in a given area.

6. Morphology and geographic distribution

In the following sections, detailed morphological characters and distribution ranges of the genus *Fritillaria* in Iran (including 19 species and 3 subspecies) are discussed. Keys to these taxa are also provided.

1. Flowers in an umbel, surmounted by numerous bracts (subgenus *Petilium*)
 2. Leaves shiny green, inflorescence umbella, perianth segments 40–55 mm, orange to red rarely yellow, nectary ca. 5 mm in diameter – *F. imperialis*
 2. Flowers yellowish–greenish, nectary 2–3 mm in diameter – *F. raddeana*
1. Flowers in a raceme or solitary, not surmounted by numerous bracts
 3. Flowers zygomorphic, the nectary of the upper perianth segment larger than that of the rest, forming a curved protuberance on the back of the segment (subgenus *Rhinopetalum*)
 4. Flowers tessellated, stem papillose throughout – *F. gibbosa*
 4. Flowers not tessellated, stem papillose only at the leaf bases (at the nodes) and below the lowest leaves – *F. ariana*
 3. Flowers actinomorphic, the nectaries all equal, not forming protuberances on the back of the perianth segments
 5. Leaves glaucous, stem smooth, inflorescence raceme, 7–20 flowers per stem, perianth segments 15–20 mm, pale yellow, style glabrous, undivided (subgenus *Theresia*) – *F. persica*
 5. Flowers usually solitary or 2–3 per stem (rarely up to 8–12), style papillose or bifid (subgenus *Fritillaria*)
 6. Perianth broadly campanulate, the nectary at the point of inflection of the segment, ca. 5 mm above its base, style glabrous, usually divided for 1/4–1/2
 7. Nectary ovate to lanceolate, less than half as long as the limb of the perianth segment (*F. kotschyana* group)

8. Perianth not or faintly tessellated, stem usually papillose at the ground level, leaves 7–10 times as long as wide – *F. olivieri*
8. Perianth heavily tessellated, stem glabrous, leaves 2–4 times as long as wide – *F. kotschyana*
7. Nectary linear, more than half as long as the limb of the perianth segment (*F. crassifolia* group)
9. Stem with 2 leaves at the base of each pedicel – *F. reuteri*
9. Stem with one leaf at the base of each pedicel, or leaves in a whorl of three below the flower
 10. Lower leaves usually trifoliolate or opposite, upper usually trifoliolate, perianth segments tessellated, without fascia – *F. straussii*
 10. Tepal with warty cells or smooth, perianth segments with/without fascia/tessellation, obtuse or acute.
 11. Tepal with warty cells, perianth segments with fascia and tessellated, obtuse – *F. crassifolia* ssp. *kurdica*
 11. Tepal smooth, perianth segments without fascia and not tessellated, acute – *F. poluninii*
6. Perianth narrowly campanulate; the nectary at the base or up to 2 mm above the base of the perianth segment (*F. caucasica* group)
12. Style stout, undivided
 13. Leaves usually 5–6 per stem, glaucous, linear, canal-iculated; stem often papillose at ground level; style undivided; stigma clavate – *F. assyriaca*
 13. Leaves 3–4 or 4–7 per stem, shiny green or glaucous, lanceolate or oblanceolate
 14. Leaves usually 4 per stem, not glaucous, lanceolate, flat; stem smooth – *F. uva-vulpis*
 14. Leaves usually 4–7 per stem, glaucous, oblanceolate – *F. chlororhabdota*
12. Style slender, sometimes 3-lobed at apex
 15. Leaves 3–4; style 9–17 mm – *F. caucasica*
 15. Leaves 4–10; style 5–10 mm
 16. Leaves green, not glaucous; perianth segments usually green – *F. chlorantha*
 16. Leaves usually glaucous
 17. Perianth segments striped, without yellow tips – *F. avromanica*
 17. Perianth segments purple with yellow tips, or yellow-greenish to green, nectary green-purplish or black
 18. Tepal purple, apex thoroughly bright yellow, nectary green-purplish – *F. zagrica*
 18. Tepal yellow-greenish to green, nectary black – *F. atrolineata*

6.1. Subgenus *Petilium* (L.) Baker

Subgenus *Petilium* comprises a small group of larger and sturdier species, distributed in Turkey, Iraq, Turkmenistan, Iran, Pakistan, Afghanistan, and the western Himalayas ([Rønsted et al., 2005](#)). They differ from the other subgenera of *Fritillaria* in the top half of the robust stem being leafless with a clear tuft of bract leaves above an umbel of 4–8 hanging flowers. The bulbs are much larger than those of most *Fritillaria* species are, and consist of a few, large, erect, imbricate, fleshy scales ([Rønsted et al., 2005](#)). The bulbs typically have a big hole in the top center where last year's stem grew, causing

a considerable decrease in the density of the bulb. This subgenus is also characterized by having white to yellowish, broadly triangular-ovate to circular nectaries, which are positioned very close to the base of the perianth segments. The style is 3-fid and the capsules are winged (Rønsted et al., 2005). Two well-known Iranian species, *F. imperialis* and *F. raddeana*, are discussed here.

6.1.1. *Fritillaria imperialis* L.

Crown imperial (*Fritillaria imperialis* L.) is known to be among the most widely grown species of the genus (Fig. 3). The predominant habitats of crown imperials in Iran are high elevations of the alpine Zagros region (Badfar-Chaleshtori et al., 2012) and neighboring areas (Table 3).

Bulb: up to 10 cm diameter, globose-ovoid; tunica thin and papery, without bulbils or stolons. **Stem:** 50–100 cm, rarely up to 110 cm, erect, smooth, papillae absent. **Leaves:** 20–30(–50), glossy, sessile, lanceolate, only adorn the lower part of the stem, arranged in 3–4 whorls of 4–8, the lowest 7–18 × 5–10 cm; bract leaves 6–12 × 0.5–1.5 cm, in a group of 10–20. **Flowers:** 1–12 (usually

4–7), broadly campanulate, whorled; perianth segments 4–6 cm long, red to orange, rarely yellow, broadly lanceolate, acute, all alike. **Nectaries:** 5 mm diameter, circular, white, at the base of the perianth segment. **Filaments:** 25–45 mm, glabrous; anthers 8–12 mm after dehiscence. **Style:** 30–45 mm, 3-fid to 1–4 mm, papillose towards apex. **Capsule:** up to 20 mm long, 30 mm diameter, winged. Flowers April to May.

Distribution: Iraq, Turkey, across the plateau of Iran to Afghanistan, Pakistan and the western Himalayan foothills.

Flowers in the crown imperial (in Persian *Taaj-e Khosro*) are at the top of the stem, topped by a crown of small bract leaves, hence the name. In Iran, crown imperial is also commonly known under the local name of '*Ashk-e Maryam*' meaning 'Tears of Mary' (Badfar-Chaleshtori et al., 2012), which refers to the drops of nectar (200–350 µl) that regularly appear at the petal base through the flowering stage, replaceable in less than a day upon extraction. It is also called '*Gel-e Begeriv*' (Weepy flower) amongst local 'Lor' people of C & B and Kohgiluyeh & Boyerahmad (K & B) provinces, two provinces with a remarkable share of the distribution.



Fig. 3. Left, red- and yellow-colored crown imperials naturally co-exist in the same habitats (photo by Hadi Jafari); Right, crown imperials surrounded by giant *Rumex acetosella* bushes (photo by Abbas Mohamadi).

Table 3
Distribution range and habitat type for members of subgenera *Petilium* and *Theresia*.

Species	Distribution range	Habitat
<i>F. imperialis</i> & <i>F. imperialis</i> var. <i>lutea</i>	<i>Golestan:</i> Khoshyeylaq. <i>West/East Azarbaijan.</i> <i>Kordestan:</i> Marivan; Uramanat; Eight-Frit Mountain. <i>Kermanshah:</i> Sarmil. <i>Lorestan:</i> Dorud; Azna; Aligudarz; Ushtran-Kuh. <i>Hamedan:</i> Malayer. <i>Ilam.</i> <i>C & B:</i> Chelgerd; Fakhir Abad; Sabze Kooh; Abkaseh Khoriyeh Mt.; Garganak; Beno-estaki; Qalatak; Maleh Zardeh. <i>Isfahan:</i> Golpaygan (Hende); Alvand-e Khomeyn protected area; Kuh-e Darabshah; Khansar; Fereydunshahr; Fareydan; Booein; Miandasht; Afus; Dehaqan; Semirom; Shahreza; Darreh-Bid. <i>K & B:</i> Pol-e Qarah towards Yasuj; Sisakht; around Pataveh; Yasuj towards Nurabad-e Mamasani. <i>Fars:</i> Sedeh; Tang-e Abdui; east of Kazerun; west of Dasht-e Arjan; around Nurabad-e Mamasani.	Western elevations of the alpine Zagros region and neighboring areas; edge of fields, rocky slopes, stony places, scrub (1000–3000 m).
<i>F. raddeana</i>	<i>Golestan:</i> within and close to the Golestan National Park; Almeh valley near Gorgan; Cheshmehy-e Khan. <i>Northern Khorassan:</i> Khombi & Sara Mt. in Garmeh region; Cheshmey-e Eshgh; Dasht intersection; Bahar & Saluk Mt.; Palang & Bozdaghi Mt.; Jowzak and western sides of Aladagh Mt. in Maneh & Samalghan region; Takal-e Qouz Mt. in Raz & Jargalan region; Spidan village; Asadli highlands in Bojnourd region.	Sloping and/or rocky areas, and in dense evergreen forests covered by tangled shrubs and thorny bushes; from near sea level (around the coastal range of the Golestan province) to about 1000 m (throughout the Northern Khorassan province).
<i>F. persica</i>	Northwest through southwest Iran especially in <i>East/West Azarbaijan:</i> Urmia; <i>Markazi:</i> Sefidkhani Mountain; <i>Kordestan:</i> Sanandaj; Marivan; Sanandaj to Hamedan. <i>Hamedan:</i> Kabudar Ahang. <i>Lorestan:</i> Khorram Abad; Nurabad; Azna; Ushtran Kuh. <i>Kordestan:</i> Eight-Frit Mountain. <i>Kermanshah:</i> Sarmil; Kuh-e Nova. <i>Ilam:</i> Abdanan. <i>C & B:</i> Along the main road towards Chelgerd; across Koohrang crown imperial plain. <i>K & B.</i> <i>Isfahan:</i> Road between Damaneh-Khansar; <i>Golestan-Kuh.</i> <i>Fars:</i> Between Kazerun-Shiraz; Sepidan as far as Yasuj.	Mountainous oak woodlands; single and/or small colonies can be seen at the borders of roads, plains, hills and valleys, edge of fields, rocky slopes, stony places (1500–2000 m).

Although various colors ranging from nearly a true scarlet through orange–yellow are found in crown imperials, they are regularly classified as red- and yellow-colored forms (Alp and Koyuncu, 2009; Kiani, 2015). In comparison to the red-colored form, the yellow-colored (known as *F. imperialis* var. *lutea*) individuals are rare in Iran and are considered a critically endangered variety. These are two different forms of the species that naturally co-exist in the same habitats (Khourang et al., 2014). It is worth noting that the yellow form is not a hybrid (Alp and Koyuncu, 2009). Despite the color difference, they show a high level of morphological similarity. The color of the main upright stem is variable based on the flower color; the stem of the red-colored form normally ranges black to dark brownish/purplish, while bright green is the commonest stem color for the yellow-colored individuals (Kiani et al., 2015b).

Crown imperial is mostly an out-crossing species, morphologically best suited to be pollinated by birds; although it may be visited by a variety of insects (Burquez, 1989). Crown imperials usually release a distinctly foxy odor unpleasant to some people, caused by a single sulphurous terpene component identified as 3-methyl-2-butene-1-thiol (Helsper et al., 2006). The odoriferous nature of the bulbs, leaves, and flowers may have evolved as a way to repel herbivores. Like other members of Liliaceae, *F. imperialis* is susceptible to depredation by the lily beetle *Lilioceris* Reitter spp. (Salahi Ardakani, 2014).

Crown imperial is among a few species in the genus with the ability to form extraordinarily huge colonies. At least three huge crown imperial colonies are recognized in Iran; 1) Aligodarz (Dalani) crown imperial plain (~2900 ha), 2) Khansar (Golestan-Kuh) crown imperial plain (~15 ha), and 3) Koohrang (Chelgerd) crown imperial plain (Fig. 12, left), among which the latter, occupying an area of over 3600 ha, is of high national/international importance to tourism.

Crown imperials, including both red- and yellow-flowered forms, often grow in association with a variety of other species, namely *Allium hirtifolium* Boiss., *Tulipa* L. spp., *Ixiolirion tataricum* (Pall.) Schult. & Schult. f., *Asperugo procumbens* L., *Astragalus brachybotrys* Bunge, *Astragalus angustiflorus* K. Koch., *Bromus tectorum* L., *Geranium persicum* Schönb.-Tem., *Prunus scoparia*, *Amygdalus elaeagnifolia* Spach, *Rumex acetocella*, *Kelussia odoratissima*, *Daphne mucronata*, *Euphorbia microsciadia* Boiss., and *Tragopogon gramini-folius* DC. Interestingly, in the Koohrang crown imperial plain, in which huge colonies of the species exist, *Rumex acetosella* is the primary co-occurring species, with very few others present (Kiani et al., 2015b).

6.1.2. *Fritillaria raddeana* Rgl.

Gorgan lily (*Fritillaria raddeana* Rgl.) (Fig. 4, Right) is an endemic species native to the semi-humid climate condition and lower elevations of north and northeast Iran. The species is found scattered primarily in Golestan province (Table 3).

Bulb: up to 8 cm diameter, globose (4–5 × 4–5 cm), fleshy, without bulbils or stolons. **Stem:** 50–90 cm, smooth. **Leaves:** numerous, long, not glaucous, lanceolate or elliptic, acute-acuminate, sessile, only adorn the lower part of the stem, arranged in 3–4 loose whorls of 4–8; the lowest up to 7–18 × 5–10 cm, lanceolate, acuminate; bracts leaves, 6–12 × 0.5–2.0 cm, linear-lanceolate, in a group of 8–25, 1–2 per flower. **Flowers:** 3–10(–20), pendant, whorled, campanulate, pale yellow, green-tinged, rarely pinkish; each flower umbel is topped by an erect crest of bracts; perianth segments 3–3.67 cm, broadly lanceolate, acute, yellowish to greenish; the outer 1.2 cm wide, the inner 1.5 cm wide. **Nectaries:** 2 mm diameter, broadly ovate to almost circular, placed nearly at the base of the perianth segment and/or 1 mm above the base, slightly impressed at the base, green-yellowish. **Filaments:** 22 mm, glabrous; anthers 8 mm after dehiscence. **Style:** 25 mm, 3-fid for 2 mm, papillose towards apex. **Capsule:** proportionally large, 20–30 × 20–30 mm, 20–30 mm diameter, ovoid, winged. Flowers March to April.

Distribution: Iran, Turkmenistan.

F. raddeana closely resembles the yellow-colored form of crown imperials. *F. raddeana* is easily distinguished from them by the larger number of flowers in the umbel, the more narrowly campanulate flowers, and much smaller and more angular nectaries (Rix, 1977).

As with crown imperial, *F. raddeana* is a species with the ability to form huge populations in its normal range. Such colonies are primarily centered in the Khombi and Sara Mountains in Garmeh region (Northern Khorassan province), where at least three plains covered by *F. raddeana* occupy a total area of over 18 ha (Kiani, 2015).

6.2. Subgenus *Theresia* (K. Koch) Baker

Fritillaria persica is the sole member of the monotypic subgenus *Theresia*. The species has a bulb consisting of only one massive fleshy scale, second in size only to *F. imperialis*, and numerous flowers on a tall stem. The nectary color largely depends on that of the flower, so that in some populations the nectaries are not very noticeable. Given its striking appearance and geometry, the species can be easily distinguished from other species.



Fig. 4. Left, *F. persica* (photo by Vendelbo, 1980); Right, *F. raddeana*, (photo by Robert B. Wallis).

6.2.1. *Fritillaria persica* L.

The distribution of Persian bells (*Fritillaria persica* L.) (Fig. 4, Left) across Iran is restricted to northwest through southwest areas (Table 3), relatively similar to those of *F. imperialis*, but at slightly lower elevations (1500–2000 m). In general, *F. persica* is a species of wider distribution, but of much lower number of plants in comparison to crown imperials (Kiani, 2015).

Bulb: up to 6 cm high, 3–5 cm diameter, solid, fleshy, ovoid or ellipsoid with/without a tunica formed by the scarios remains of the scales of previous year(s). **Stem:** 60–120 cm, smooth. **Leaves:** 9–25, 15 × 3 cm, lanceolate, acute, all alternate. **Flowers:** 10–50, campanulate, rarely dark purple, usually greenish, gray or yellowish, usually yellowish inside; perianth segments 15–20 × 6–7 mm, oblanceolate, oblong-obovate and obtuse, outer and inner similar. **Nectaries:** triangular-narrowly ovate, slightly depressed, placed 0.5–1 mm above the base of the perianth segments, surrounding lobes or rims absent, often green-yellowish. **Filaments:** 5–6 mm, glabrous, at first pressed back against the perianth segment, coming forward at dehiscence; anthers 4 mm. **Style:** 6–8 mm, entire, slender, glabrous. **Capsule:** 1–3 cm long, 1.2 cm in diameter, winged. Flowers April to May.

Distribution: Iran, Turkey, Syria, Lebanon, Palestine, Jordan, Cyprus.

F. persica is very variable, especially in flower color, leaf width and in presence or absence of bract leaves in the inflorescence. A variety of flower colors from white to deep purple is known; indeed, pale flowers are in great abundance in Iran (Kiani, 2015). Three forms, *F. eggeri*, *F. libanotica* and *F. arabica*, have been described as separate species, but there is much overlap between them and none seem to merit recognition at even subspecific level (Rix, 1977).

Androdioecy is a rare mating system in plants and *F. persica* is one of a few plant taxa in which androdioecious reproduction is reported (Mancuso and Peruzzi, 2010). Stem diameter and number of flowers are believed to be higher in the hermaphrodite plants compared with the males (Mancuso and Peruzzi, 2010). Each flowering stem bears numerous basal leaves as well as a terminal pyramidal raceme composed by many small nodding flowers of the same sexual morphology; either male or hermaphrodite. Apparently, flowers open gradually from the bottom of the raceme upwards. Likewise, those species in the Central Asian clade (Fig. 2), have the flowers arranged in a raceme, and open their flowers from the bottom upwards (e.g. *F. verticillata*, *F. olgae*).

6.3. Subgenus *Fritillaria* (L.)

Subgenus *Fritillaria* is the largest subgenus of the genus *Fritillaria*, comprising more than half of the species, including the type

species, *F. meleagris*. The species in this subgenus are widely distributed from Western Europe and the Mediterranean region to eastern Asia. These are characterized by having the typical *Fritillaria* bulb; the bulb usually consists of 2 (sometimes 3–4 if one or both of the scales from the previous year have persisted into a second season) subglobose and fleshy scales with/without a tunica, formed by the scarios remains of the scales of the previous year or years. The stem bears usually 1, sometimes 2–3 flowers, rarely up to 8 flowers as in *F. olgae* Vved. and *F. camschatcensis* or up to 12 flowers as in *F. pluriflora* Torr. ex Benth. (Khaniki and Persson, 1997). Subgenus *Fritillaria* is normally subdivided into two sections based on the style; species with a clearly 3-fid style are included in section *Fritillaria*, whereas species with an undivided style or a style that is only shortly trilobulate at the apex are placed in section *Olostyleae* (Rønsted et al., 2005). Rix (2001) subdivided section *Olostyleae* into 6 series and section *Fritillaria* into 10.

6.3.1. *F. crassifolia* group

This group consists of a complex of species and subspecies close to *Fritillaria crassifolia* Boiss. & Reut., with a distribution centered in eastern Anatolia and northern Zagros. The main species in this group is *F. crassifolia* comprising three dwarf subspecies (Rix, 2000b), of which only ssp. *kurdica* has been recorded in Iran (Bakhshi Khaniki, 2001a; Wallis and Wallis, 2009). The most widespread member of the complex is *F. crassifolia* ssp. *crassifolia*, which occurs in Turkey. Subspecies *kurdica* is frequent in alpine steppe throughout northwest Iran (Azarbaijan), east Turkey and northeastern Iraq; ssp. *hakkarensis* is scattered in Turkey and northeastern Iraq. In addition to this typical species, a) *F. reuteri*, b) *F. straussii* (Kiani et al., 2015a), and c) *F. poluninii* (Wallis and Wallis, 2009) are three morphologically distinct species of this group which occur in Iran. They all have usually broadly campanulate flowers pendant at maturity, and rather large linear nectaries, 5–10 × 1.5–2 mm (half or more as long as the perianth segments, placed 3–5 mm above the base), which are usually black-purplish at the base. All members of this complex, except *F. poluninii* and *F. reuteri*, have groups of warts or similar processes scattered on the surface of the tepal (Khaniki and Persson, 1997).

6.3.1.1. *Fritillaria crassifolia* ssp. *kurdica* (Boiss. & Noe) Rix. *Fritillaria crassifolia* ssp. *kurdica* (Boiss. & Noe) Rix (Fig. 5, Left) is a common plant from Zagros Mountains mainly reported along a relatively narrow border strip, bordering Turkey and Iraq in West and Northwest Iran (Rix, 1977).

Bulb: up to 3 cm in diameter, sometimes with bulbils. **Stem:** up to 10 cm high. **Leaves:** 4 (5–7), glaucous, lanceolate or linear lanceolate, all alternate; the lowest is wider than the rest, 3–5 cm long, 6–15 mm wide. **Flowers:** 1–2 (–4), campanulate, pendant at



Fig. 5. Left, *F. crassifolia* ssp. *kurdica*; Right, *F. poluninii* (photos by Robert B. Wallis).

maturity, yellowish or green, stippled and tessellated inside and out, sometimes on a greenish or yellowish background, with a green stripe along the center of each perianth segment; perianth segments, obovate to oblanceolate, obtuse. *Nectaries*: linear, about 8–10 × 1.5–2 mm, usually with a raised ridges on each side, more blackish at the base. *Capsule*: 4–4.5 cm long, obovoid, narrowly tapering at base, truncate at apex, not winged. Flowers April to July.

Distribution: Iran, Turkey, Iraq.

The species is rather diminutive, very variable especially in overall size and flower color, ranging from greenish, brownish to yellowish (or combinations thereof), often heavily tessellated, brown or purple inside and outside, often with green fascia. Subspecies *kurdica* is distinguishable from *ssp. crassifolia* in relatively very narrower basal leaves that are also higher in number; subspecies *crassifolia* usually has only 4 leaves, whereas *ssp. kurdica* bears 5–6 (Rix, 1977). It also differs in its more clearly defined fascia and the raised ridge on the inner side of the perianth segment, which forms the nectary. On the other hand, *F. poluninii* differs from *F. crassifolia ssp. kurdica* mainly in narrower perianth segments, smaller flowers and absence of the swollen nectary ridge.

6.3.1.2. *Fritillaria poluninii* (Rix) Bakhshi Khaniki & K. Persson. *Fritillaria poluninii* (Rix) Bakhshi Khaniki & K. Persson (Fig. 5, Right) is the rarest and smallest of four closely related species or subspecies, being recognized by its short stem (Rix, 2006).

Bulb: large for the size of the top growth, up to 2 cm in diameter, without bulbils and stolons. *Stem*: 4–8 cm, smooth. *Leaves*: 6–8, usually 6, the lowest narrowly lanceolate 4–7 × 8–10 mm, usually 5–7 times as long as wide, all alternate or subopposite, shiny green. *Flowers*: usually 1 or 2, rarely 3, nodding or horizontal, broadly campanulate or cup-shaped, pale purple to greyish, not or vaguely tessellated but lined with wavy green or brownish-purple veins, without fascia; tepals smooth, entirely lacking warty cells or other processes, usually spreading and not overlapping, acute, 11.5–14 mm long, the outer 4 mm wide narrowly ovate, the inner slightly wider, obovate. *Nectaries*: green, linear, 3.5–5 mm long, 1–1.5 mm wide, 3–5 mm above the tepal base. *Filaments*: ca. 6 mm, sparsely papillose. *Style*: 4–5 mm, the branches 2–3 mm, reflexed, slender, smooth. *Capsule*: ca. 35 mm long, cylindrical, tapering towards the base, not winged. Flowers April to May.

Distribution: West Iran and adjacent part of northeastern Iraq in Sulaimaniyah.

Fritillaria poluninii was previously treated as a subspecies of *F. crassifolia*, but later Khaniki and Persson (1997) raised this to the rank of species, because of several distinctive characteristics. It is differentiated from the other members of the *F. crassifolia* complex in the narrower leaves, smooth tepal surface without warty cells,

much shorter/narrower nectaries, the absence of the swollen nectary ridge and the absence of a dark spot at the base of the nectaries. As opposed to the other subspecies of *F. crassifolia* that have more oblanceolate tepals, in *F. poluninii* tepals are usually acute. The flowers are not tessellated (sometimes vaguely tessellated), but lined with green or brownish-purple veins; the veins are distinctly wavy, and can be confused with tessellation. Given these striking features, elevating *F. crassifolia ssp. poluninii* to a specific level is fully justified.

6.3.1.3. *Fritillaria straussii* Bornm. *Fritillaria straussii* Bornm (Fig. 6, Left) is a species restricted to northern Zagros Mountains (Rix, 1974).

Bulb: up to 2.5 cm in diameter, bulbils or stolons unknown. *Stem*: up to 30 cm, papillae absent. *Leaves*: 5–10, not glaucous; the lower 40–80 × 10–35 mm, broadly lanceolate to ovate, opposite or in a whorl of 3; the middle usually opposite; the upper up to 5 cm, linear, in a whorl of three or opposite. *Flowers*: 1–2 (–4), broadly campanulate; perianth segments greenish when young, often maturing to dark reddish-brown, tessellated all over, fascia obscure, oblanceolate, obtuse, the outer 25–27 × 8–9 mm, the inner 9–12 mm wide, obtuse. *Nectaries*: 10 × 2 mm, linear, greenish, ca. 5 mm above the base of the segment, distinctly depressed at the base. *Filaments*: ca. 10 mm, slender, papillose; anthers 3–4 mm after dehiscence. *Style*: ca. 8 mm, papillose, 3-fid to half or 3/4 of its length; style arms slender, reflexed. *Capsule*: 3–4.5 × 2.5 cm, obovoid, tapering towards the base, not winged. Flowers May to June.

Distribution: Endemic to Iran.

F. straussii is unique in that the flowers open green, and then mature to dark brown until before fading (Khaniki, 2002d). This is also unlike other species in its combination of a linear nectary and leaves opposite or in whorls (Rix, 1977).

6.3.1.4. *Fritillaria reuteri* Boiss. *Fritillaria reuteri* Boiss (Fig. 6, Right) is restricted to the mountains north and west of Esfahan (east of Shahr-e Kord) (Khaniki, 2002c), where it occurs in a few places, but in great quantities (Rix, 1977).

Bulb: up to 2 cm in diameter, without bulbil or stolons. *Stem*: 15–25 cm, papillae absent. *Leaves*: 3–8, all alternate; the lower 6–10 cm, linear lanceolate, at the base of the stem; the upper 3–7 cm, linear, 2 at the base of each pedicle, the intervening stem usually leafless. *Flowers*: 1–8, usually 2 broadly campanulate, nodding at maturity; perianth segments reddish-purple with a glaucous bloom, always with distinctive yellow tips, and often yellow inside, not tessellated; the outer 16–28 × 5–8 mm, oblanceolate, acute; the inner 8–13 mm wide, often obtuse. *Nectaries*: ca. 10 mm, linear, green, slightly raised and placed

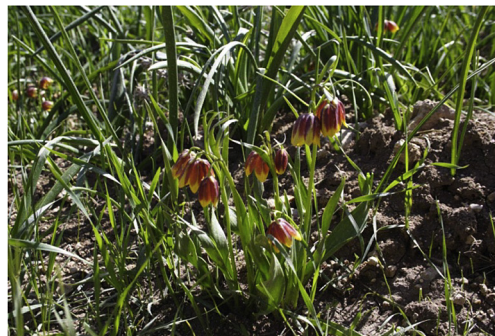


Fig. 6. Left, *F. straussii*; Right, *F. reuteri* (photos by Robert B. Wallis).

above the tepal base. *Filaments*: ca. 10 mm, slender, sparsely papillose; anthers 8 mm after dehiscence. *Style*: 1.3 cm, minutely papillose, 3-fid for 3 mm. *Capsule*: 35–45 mm long, cylindrical-obvoid, tapering towards the base, not winged. Flowers May to June.

Distribution: Endemic to Iran.

A pure yellow-flowered form has been recorded on several occasions, but otherwise the species is relatively invariable (Rix, 1977).

6.3.2. *Fritillaria kotschyana* group

In *Fritillaria kotschyana* group flowers are nodding and broadly campanulate (Khaniki, 2002b). The nectary is ovate or lanceolate, and always shorter than half the length of the limb of the perianth segment, located at the inflection of the bell (Khaniki and Persson, 1997; Rix, 1977). Two species of this group are restricted to small areas of high elevations; 1) *F. olivieri* Baker is found in the northern Zagros Range, while 2) *F. whittallii* Baker is scattered in southwest Anatolia; 3) *F. kotschyana* is very variable in color (ranging from pure green with little tessellation to brown) and flower size.

Fritillaria kotschyana ssp. *kotschyana* has been found mainly along upper slopes of the Elburz and Talysh Mountains as well as at the southern end of the Talysh, as far south as Khalkhal, where it inhabits a variety of habitats including sparse meadowland, unstable screes, rock crevices and among roots of small shrubs (Wallis and Wallis, 2009). Khourang et al. (2014) also reported this subspecies in meadows and sloping areas near Mianeh (East Azarbaijan); *F. kotschyana* ssp. *grandiflora* is only collected from the northern Talysh; 4) *F. hermonis* is only found in S. Syria and Lebanon (Lebanon, Chouf and Antilebanon ranges), while 5) *F. amana*, which was previously treated as a subspecies of *F. hermonis*, is limited to Turkey and NW Syria (Amanus and Nusairiah Ranges).

6.3.2.1. *Fritillaria kotschyana* Herb. ssp. *kotschyana*. *F. kotschyana* ssp. *kotschyana* (Fig. 7, Left) is primarily scattered along the Elburz Mountains (Table 4) (Wallis and Wallis, 2009).

Bulb: up to 3 cm in diameter, bulbils and stolons sometimes present. **Stem**: 8–25 cm, papillae absent. **Leaves**: 4–8, usually 5–6, green glaucous, all alternate; the lowest 7–10 cm, ovate to broadly lanceolate, 2–4 times as long as wide, the uppermost lanceolate, 1–3.5 cm long. **Flowers**: 1–2, brown-purplish or wholly green, usually on a green background, pendant, broadly campanulate, tessellated, inside and out, usually with green fascia; perianth segments 2.8–4.8 cm, the outer perianth segments 2.5–3.5 × 1.5–2 cm, broadly oblanceolate and obtuse, the inner

somewhat wider. **Nectaries**: ovate to ovate-triangular, ca. 5 mm in diameter, green and then mature to basally dark purplish, at the point of inflection of the bell. **Filaments**: 7–9 mm, papillose or rarely glabrous; anthers ca. 5 mm after dehiscence. **Style**: 7–9 mm, 3-fid for 1/4 to 1/2 its length. **Capsule**: 16–22 mm long, ovoid, tapering towards the base, not winged. Flowers April to July.

Distribution: Endemic to Iran.

6.3.2.2. *F. kotschyana* ssp. *grandiflora* (Gross.) Rix. *Fritillaria kotschyana* ssp. *grandiflora* (Fig. 7, Center) differs from ssp. *kotschyana* mainly in narrower leaves that resembles those of *F. olivieri* in shape and size, absence of fascia, narrower and longer nectaries (Khaniki and Persson, 1997), and size difference (Rix, 1977); larger specimens in ssp. *kotschyana* approach ssp. *grandiflora* in size.

Bulb: up to 3 cm in diameter, bulbils and stolons unknown. **Stem**: 30–50 cm. **Leaves**: 5–10, usually 7–8, lanceolate, all alternate; the lowest 10–23 mm wide, 6–8 times as long as wide. **Flowers**: 1–3 broadly campanulate, dark purplish or green, obscurely tessellated, without fascia; perianth segments 3.5–5.2 cm, oblong, triangular acute at apex; the outer 1–2 cm, usually oblong sometimes acute; the inner 2–3 cm wide. **Nectaries**: 7 × 2 mm, ovate-oblong, all over black-purple. **Filaments**: ca. 10 mm, papillose; anthers 6–7 mm. **Style**: ca. 10 mm, 3-fid for 1/10 to 1/2. **Capsule**: not known. Flowers April to May.

Distribution: Endemic to Iran.

6.3.2.3. *Fritillaria olivieri* Baker. *Fritillaria olivieri* Baker (Fig. 7, Right) is almost restricted to the area around Hamedan, being frequent on Mt. Alvand, where it grows in damp ground by streams (Table 4).

Bulb: up to 3 cm in diameter, solid, button-shaped, with few bulbils. **Stem**: 15–40 cm, sparsely papillose around ground level. **Leaves**: 5–10, usually 6–8, all alternate, narrowly lanceolate or oblong, acute, the lowest 7–14 cm long, 5–10 times as long as wide; the uppermost 3–6 cm, linear, usually not glaucous. **Flowers**: 1(–3), broadly campanulate; perianth segments 25–35 mm, green, pale yellow-green, shaded reddish-brown, untessellated (sometimes lightly tessellated), not tuberculate; the outer ca. 12 mm wide, obovate, obtuse; the inner somewhat wider. **Nectaries**: ca. 5 mm, dark green, narrowly-acutely lanceolate to linear-lanceolate; 7–9 mm above the base of segment. **Filaments**: ca. 12 mm, sparsely papillose; anthers ca. 5 mm. **Style**: 7–9 mm, 3-fid for 1/3 to 1/4, glabrous. **Capsule**: 4 cm long, obvoid, narrowly tapering towards the base, not winged. Flowers May to June.

Distribution: Endemic to Iran.



Fig. 7. Left, *F. kotschyana* ssp. *kotschyana*; Center, *F. kotschyana* ssp. *grandiflora* (photos by Marijn Van den Brink); Right, *F. olivieri* (photo by Robert B. Wallis).

Table 4
Distribution range and habitat type for members of subgenera *Fritillaria* and *Rhinopetalum*.

Species/Subspecies	Distribution range	Habitat
<i>F. crassifolia</i> ssp. <i>kurdica</i>	<i>Azərbaycan</i> : near Baku south to Kordestan near Marivan; Marand, Khoi to Tabriz road; north of Urmia; Kuh-e Sahand; S. foothills of Kuh-e Savalan; W. of Ardabil, pass between Ahar to Tabriz; SW. of Ahar; Bozqush. <i>Kordestan</i> : As far south as Sanandaj extending inland as far as Zanjan; between Marivan and Sanandaj; Dezli	Cliffs and stony banks along rivers, rocky plateau, slopes and ledges or sometimes on screes (but not the loose mobile screes that are the characteristic habitat of ssp. <i>crassifolia</i>); foothills and mountain steppes (1500–3500 m).
<i>F. poluninii</i>	<i>West Azərbaycan</i> : Mah Mt.; Qasemlu valley, near Urmia; a pass between Daraki and Nowsud; Hawraman Mt. <i>Kermanshah</i> : Eight-Frit Mountain. <i>Kordestan</i> : Sarv Abad; Seline village; Bandul village; Kale Tang	Limestone screes and grows well in deep soils by late snow patches at high altitudes (2200–2600 m).
<i>F. reuteri</i>	<i>C & B</i> : Cheshmeh Kuhrang, Sabze Kuh, Shahr-e Kord valley at foot of Zard Kuh. <i>Esfahan</i> : west of Esfahan, Chehel-Dokhtran Kuh, north-west Daran towards Arak, near Golestan Kuh (south of Khansar).	Boggy banks, wet rocky meadows and mountainous or hilly stony terrains (2500–3000 m)
<i>F. straussii</i>	<i>Kermanshah</i> : Kuh-e Sefid; Eight-Frit Mountain. <i>Kordestan</i> : Marivan; Dezli, all the way along the border with Iraq.	Shady places, rangelands of heavy soils and/or loose slopes dominated by <i>Quercus</i> spp. and large Apiaceae (1500–2100 m)
<i>F. kotschyana</i> ssp. <i>kotschyana</i>	<i>Tehran</i> : Mt. Alborz; Dizin pass. <i>Guilan</i> : Talysh; Massuleh; Rasht. <i>Mazandaran</i> : Chalus; Gachsar; Kandovan pass; Haraz valley. <i>Golestan</i> . <i>E. Azərbaycan</i> : Mianeh; Bozqush. <i>Ardabil</i> : Khalkhal. <i>Kordestan</i> : Saral	Stony soils often under bushes, rocky slopes and screes (2000–4000 m).
<i>F. kotschyana</i> ssp. <i>grandiflora</i>	Along Mt. Alborz scattered in <i>Guilan</i> : Talysh; Massuleh. <i>Golestan</i> : NW. side of the Jahan Nama protected area.	The same as <i>F. kotschyana</i> ssp. <i>kotschyana</i> (about 2200 m).
<i>F. olivieri</i>	<i>Hamedan</i> : Mt. Alvand; Ganjnameh; SW. of Hamedan. <i>Kordestan</i> : E. of Sanandaj. <i>Lorestan</i> : Khorramabad; Dorud. <i>E. Azərbaycan</i> : Tabriz	Damp meadows (2000–4000 m).
<i>F. caucasica</i>	<i>East Azərbaycan</i> : Tabriz; near Ahar	Subalpine meadows, stony areas of coniferous/oak forests or closed grasslands, grassy slopes, and shady, moist, peaty rock ledges on limestone in drier areas (1700–2900 m).
<i>F. assyriaca</i>	Throughout Zagros in <i>W. Azərbaycan</i> : Urmia; Sir kuh. <i>Kermanshah</i> : Eight-Frit Mountain. <i>Kordestan</i> : Sanandaj towards Hamedan. <i>Lorestan</i> : Khorram Abad; Azna; Dorud; Oshtoran Kuh. <i>Fars</i> : Kazerun to Behbahan; valley of Sepidan; Shiraz. <i>Tehran</i> .	Cultivated fields, mountain steppe, rocky slopes and stony hillsides/grounds (1000–2500 m). It is usually found in open habitats and has normal growth either in hot and dry or cool conditions.
<i>F. uva-vulpis</i>	Restricted to W. and NW. Iran: <i>W. Azərbaycan</i> : Urmia, 20 km SE. of Mahabad. <i>Kordestan</i> : Eight-Frit Mountain; Mahabad.	Zagrosian <i>Quercus</i> forest zone: crop fields and damp or marshy meadows (1000–2500 m).
<i>F. avromanica</i>	<i>Kordestan</i> : Marivan to Paveh (Hawraman area), Seline village; Abdalan Mt., 30 km to Sanandaj; Eight-Frit Mountain.	Rocky terrains and gravelly lands (1300–2100 m).
<i>F. atrolineata</i>	One locality in <i>W. Azərbaycan</i> province	Moist areas below cliffs (1500–1800 m).
<i>F. chlorantha</i>	<i>Kordestan</i> : Marivan. <i>Hamedan</i> : Alvand. <i>Lorestan</i> : Khorramabad, Gahar, Ushtran Kuh.	Mountain steppe among stones, and rocky and stony hillsides (1800–2000 m).
<i>F. zagrica</i>	From south Urmia Lake all the way down along Zagros chains: <i>W. Azərbaycan</i> : Takht-e Soleyman. <i>Markazi</i> : Arak to Golpaygan, 40 km, SE. of Arak; near Arak in Soltanabad village. <i>Hamedan</i> : Alvand Mt., Hamedan to Qazvin, 32 km from Hamedan; Asad Abad pass 23 km W. of Hamedan; Khorram Abad, 40 km S. of Arak. <i>Lorestan</i> : 23 km NE. of Azna. <i>Kordestan</i> : Salavat Abad valley, along the main road towards Sanandaj; Sanandaj to Hamedan, 12 km E. of Sanandaj. <i>Esfahan</i> : Kuh-e Darreh; Golpayegan to Damaneh, Kuh-e Darrebid; Khansar crown imperial plain	Mountain steppe, often by late snow patches (1800–3000 m).
<i>F. chlororhabdota</i>	<i>W. Azərbaycan</i> : Urmia-Salmas; Akhordarreh; Sir Kuh. <i>Kordestan</i> : Sanandaj, Salavat Abad valley. <i>Lorestan</i> : Azna; Dorud; Oshtoran Kuh; Khorram Abad	Widespread across Zagros ranges on grassy slopes, sometimes clumps, mountain steppes, stony hills, alpine pastures, rocky and grassy ledges, mainly associated with <i>Euphorbia</i> , <i>Geranium</i> , <i>Thymus</i> , <i>Tulipa</i> , <i>Anthemis</i> , <i>Gagea</i> , <i>Stipa barbata</i> , and grasses (1600–2000).
<i>F. gibbosa</i>	Widespread from northeast through northwest, east, center and southwest of Iran, along Zagros chain in <i>W. Azərbaycan</i> : Urmia; Khoi. <i>E. Azərbaycan</i> : Tabriz, 70 km NW Zanjan. <i>Alborz</i> : Karaj elevations. <i>Tehran</i> : Alborz, W side of the road from Tehran-Qom. <i>Qazvin</i> : Between Qazvin-Rasht. <i>Markazi</i> : SE. of Arak; Arak-Golpaygan. <i>Semnan</i> : Miami. <i>Hamedan</i> : NE. of Hamedan, 100 km north of Hamedan; Razan. <i>Kordestan</i> : 60 km east of Bijar. <i>Lorestan</i> : Khorram Abad; SW. of Dorud. <i>C & B</i> : Tangeye Sayyad. <i>Razavi Khorassan</i> : 17 km north of Torbate Heydarieh, on the road to Mashhad; 24 km north of Quchan; Kopet Daq; Between Kashmar and Rivash; Kuh-e Sorkh. <i>Northern Khorassan</i> : Around west of Bojnurd; near Almeh valley. <i>Southern Khorassan</i> . <i>Fars</i> : Niriz; near Marvdasht; Persepolis. <i>Golestan</i> : Gorgan, at the eastern end of the Caspian Sea	Adapted to arid and hot climates; usually associated with <i>Artemisia</i> ; open stony or sandy places, steppes, scrubs, rocky screes (1000–2000 m).
<i>F. ariana</i>	Confined to east and northeastern Iran in the parts of <i>Razavi Khorassan</i> province, adjacent to the border of Afghanistan: Mash'had; Hari Rud valley, on the Iranian side of frontier; near Sarakhs as far south as Taybad.	Deserted areas, on mobile sand dunes and sandy hills and plains, with a mixture of small annuals, which usually flower and set seed very quickly before the arrival of the dry summer (500–1000 m).

6.3.3. *Fritillaria caucasica* group

Fritillaria caucasica is the most diverse group within subgenus *Fritillaria* in Iran. All Iranian species belonging to *F. caucasica* group i.e., *F. caucasica*, *F. chlorantha*, *F. zagrica*, *F. uva-vulpis*,

F. assyriaca, *F. chlororhabdota*, *Fritillaria atrolineata* and *F. avromanica*, are distributed along the Zagros chain (Bakhshi Khaniki, 1997a, 1997b; Reching, 1990; Rix, 1977). Within this group, the species have comparatively small and narrowly

campanulate, narrowly lanceolate flowers, without tessellation. The small nectaries (not or only slightly depressed) are placed 0.5–1 mm above the base of tepals (Khaniki and Persson, 1997). Some species of this group e.g., *F. atrolineata*, *F. armena*, *F. zagrica* and *F. chlorantha*, have warts or warty cells scattered on the tepal surface.

6.3.3.1. *Fritillaria caucasica* Adam. Caucasian lily (*Fritillaria caucasica* Adam) (Fig. 8, Left) has only been found in two localities in northwestern Iran. The localities in Iran represent the southernmost extension of its range (Table 4). It differs from other Iranian species in its longer slender style and filaments.

Bulb: up to 2 cm in diameter, usually without bulbils, stolon unknown. **Stem:** 10–30 cm, papillae absent. **Leaves:** 3–4(-6), all alternate, broadly lanceolate to lanceolate, acute, the lowest 3–10 × 0.8–2.0 cm. **Flowers:** 1(-2), narrowly campanulate, sometimes constricted at mouth, somewhat reflexed at apex; perianth segments 22–30 mm, dark purplish-black, usually with a waxy bloom outside, sometimes paler inside, not tessellated; the outer 5–12 mm wide, usually acute; the inner 6–14 mm wide, acute or obtuse. **Nectaries:** 4.5–5 × 1 mm, linear-lanceolate to lanceolate, at the base of the segment, dark greenish. **Filaments:** 10–18 mm, slender, glabrous or papillose; anthers 4–8 mm. **Style:** 9–17 mm, slender, undivided, glabrous or papillose. **Capsule:** 4–6 cm long, cylindrical, tapering towards the base, not winged. Flowers April to June.

Distribution: Iran, southern Caucasus, northeast Turkey.

6.3.3.2. *Fritillaria uva-vulpis* Rix & *Fritillaria assyriaca* Baker. *Fritillaria assyriaca* Baker (Fig. 8, Center) is one of the most widespread (Table 4) and variable species in the genus and seems to have a quite diverse appearance in Iran (Wallis and Wallis, 2009).

Bulb: up to 3 cm in diameter, often with stolons or bulbils. **Stem:** 4–20 cm (elongating to 35 cm in fruit), often papillose near the base. **Leaves:** 4–6(-12), the lowest, 3–9 × 0.3–1.9 cm, sometimes opposite, ovate-lanceolate, the rest shorter, alternate, usually channeled, especially when young, linear, glaucous. **Flowers:** 1–2(-5), narrowly campanulate; perianth segments very variable in color, greenish, reddish or purplish brown, often with green fascia, yellowish inside, sometimes reflexed towards the tip; the outer 15–25 × 4–5 mm, narrowly oblong; the inner, 5–10 mm wide, usually obtuse. **Nectaries:** 2–4 × 1 mm, linear-lanceolate, ca. 1 mm above the base of the segment. **Filaments:** 5–9 mm, swollen, papillose; anthers 4–6 mm. **Style:** 5–10 mm, usually 7–8 mm long,

1.5–2 mm in diameter, not or slightly lobed at apex. **Capsule:** ca. 26 mm long, cylindrical, not winged. Flowers March to May.

Distribution: Iran, Iraq, Turkey.

The name ‘Fox’s grape’ was first invented by Rix (2000a) after the folkloric Kurdish name “*Tarai Raiwi*” for *Fritillaria uva-vulpis* Rix (Fig. 8, Right). *F. uva-vulpis* has been one of the most successful species in cultivation, because they produce many bulbils and grow vigorously (Rix, 2000a).

Bulb: up to 3 cm in diameter, usually with bulbils, without stolons. **Stem:** 10–20 cm, papillae absent. **Leaves:** 3–5, usually 4, shiny green, all alternate, the lowest 8–12 × 1–2 cm, narrowly lanceolate, acute, the upper ones smaller. **Flowers:** 1 (rarely 2), narrowly campanulate, usually rounded, narrowed at the mouth; perianth segments outside dusky purplish-gray, glaucous, with yellow tips outside, inside yellowish, obtuse, the outer 20–28 × 6–7 mm, ovate or ovate-lanceolate, obtuse or acute, the inner 6–12 mm wide, obovate, obtuse. **Nectaries:** 4 × 1.3 mm, narrowly ovate, 1 mm above the base of the segment, green. **Filaments:** 6–9 mm, papillose, swollen; anthers 7–9 mm before dehiscence. **Style:** 5–7 mm, thick, papillose, undivided. **Capsule:** ca. 35 mm long, obvoid, narrowly tapering towards the base, truncate at apex, not winged. Flowers March to April.

Distribution: Iran, Turkey, Iraq.

F. uva-vulpis is morphologically distinct; it has usually four flat, lanceolate, shiny green leaves spaced evenly up the stem; the radical leaves are narrowly lanceolate. *F. assyriaca* is widespread and very variable, especially in width of the leaf; it has 4–6 glaucous, narrow and canaliculate leaves, mainly placed on the upper half of the stem; the radical leaves are broadly ovate. *F. assyriaca* also has narrowly tubular-campanulate flowers with a more greenish tinge and a slightly flaring mouth, while the flowers of *F. uva-vulpis* are usually more rounded.

6.3.3.3. *Fritillaria zagrica* Stapf. Zagrosian lily (*Fritillaria zagrica* Stapf.) (Fig. 9, Left) is a comparatively dwarf species, native to the Zagros range (Table 4) (Bakhshi Khaniki, 2001b) where it grows as a snowmelt species at very high altitudes (1800–3000 m).

Bulb: up to 2 cm in diameter, ovoid, sometimes with few bulbils, without stolons. **Stem:** 4–10 cm, rarely over 10 cm, papillae sometimes present, lowest leaves with a wavy edge. **Leaves:** 4–7, usually 5–6, smooth, somewhat glaucous, all alternate or the lowest sub-opposite, lanceolate, 3–9 × 0.6–1.6 cm, the lowest narrowly oblanceolate to elliptic-oblong, 5–11 × 1.5–2 cm, usually folded at fruiting time, the uppermost, linear-narrowly lanceolate, 2–5 cm long, acute. **Flowers:** 1–2(-3), narrowly campanulate, with



Fig. 8. Left, Caucasian lily (*F. caucasica*); Center, *F. assyriaca*; Right, *F. cf. uva-vulpis* (photos by Robert B. Wallis).



Fig. 9. Left, *F. zagrica*; Right, *F. atrolineata* (photos by Robert B. Wallis).

few warts on the tepal surface; perianth segments 12–18 mm, outside and inside dark purplish-brown with a yellowish tip, and a waxy bloom outside, the outer segments, 12–18 × 4–7 mm, elliptic-lanceolate, acute, the inner 6.5–8 mm wide, lanceolate, obtuse. *Nectaries*: 3.5–5 × 1–1.5 mm, broadly lanceolate to narrowly elliptic, 1 mm above the base of the segments, green-purplish. *Filaments*: 8 mm, somewhat swollen, papillose; anthers 3–4 mm. *Style*: 8–9 mm, slender, papillose or subglobose. *Capsule*: cylindrical, 2.5–3.5 × 1.5–5 cm, obovoid, obtuse, tapering towards the base, not winged. Flowers March to May.

Distribution: Endemic to Iran.

Tekşen and Aytaç (2011), in a revision of the genus in Turkey, lumped *Fritillaria zagrica* with *F. pinardii*, but they are quite distinct. *F. zagrica* normally has the little yellow tips to the segments, while *F. pinardii* sometimes has a yellow distal margin, but if present, this always is a continuous margin on the distal edge. On the other hand, the *F. zagrica* that Tekşen and Aytaç used as a comparator is not the type specimen, but one from Turkey that is a significant outlier from the normal range of *F. zagrica*.

6.3.3.4. *Fritillaria atrolineata* Bakhshi Khaniki. *Fritillaria atrolineata* Bakhshi Khaniki (Fig. 9, Right) has been reported only from one locality in West Azarbaijan province (Table 4) by Bakhshi Khaniki (1997a).

Bulb: 7–11 × 7–10 mm, globose-subglobose, without bulbils or stolons. *Stem*: 20–25 cm above the bulb, longer in fruit, smooth. *Leaves*: 4–5, glaucous, the lowest 2–3 usually in a subternate (subverticillate) or subopposite position, the rest alternate, the lowest 9 × 1–1.5 cm, usually 8–9 times as long as wide, oblanceolate, the uppermost (bract leaves) 8.5 × 0.3 cm, linear to narrowly oblanceolate, acute. *Flower*: 1 (2), narrowly campanulate; perianth segments usually yellowish-green to green, outside more

yellowish towards margins, sometimes sparsely brown-dotted, inside tinged or sparsely dotted, pale reddish-brown towards margins, outer segments 20 × 6 mm, oblanceolate, obtuse, inner ones 8 mm wide, oblanceolate, obtuse, fascia obscure. *Nectaries*: linear, 4–6 × 0.5–1 mm, placed 0.5–1 mm above the base of tepals, black. *Filaments*: 7 mm, yellow, densely papillose in upper part. *Style*: 5–7 mm, stout, greenish-yellow, densely papillose, entire or very slightly 3-lobed, apex of stigma lobes papillose and with a central hole. *Capsule*: 2.5–3 × 1.5 cm, obovoid, obtuse, tapering towards the base, not winged. Flowers April.

Distribution: Endemic to Iran.

In the type description, Bakhshi Khaniki (1997a) referred to the black nectaries of *Fritillaria atrolineata*, hence the name. Bakhshi Khaniki classified the species in subgenus *Fritillaria* (*F. caucasica* group) based on its comparatively small overall size, geometry, position and color of the nectaries as well as narrowly campanulate flowers.

6.3.3.5. *Fritillaria chlorantha* Hausskn. & Bornm. *Fritillaria chlorantha* Hausskn. & Bornm (Fig. 10, Left) is a dwarf species confined to Zagros Chains (Table 4) (Rix, 1977).

Bulb: up to 2 cm in diameter, bulbils few, without stolons. *Stem*: 4–10 cm, papillae absent. *Leaves*: 4–10, usually 5, broad, shiny green, not glaucous, all alternate, the lowest ovate broadly lanceolate, 6–10 × 1.2–5 cm, the upper linear-lanceolate ca. 5 cm long. *Flowers*: 1–2, narrowly campanulate; perianth segments green outside, yellowish sometimes with purple markings inside and on the inner segments, rarely purple outside, the outer 15–25 × 3–4 mm, the inner somewhat wider. *Nectaries*: 3 × 1 mm, lanceolate, 1 mm above the base of the segment, green. *Filaments*: 6–7 mm, swollen, densely papillose; anthers 6–7 mm. *Style*:



Fig. 10. Left, *F. chlorantha* (photo by Robert B. Wallis); Right, *F. avromanica* (photo by Mahfuz Advay).

5–10 mm, usually 8 mm, rather stout, 3-fid at apex for 1–2 mm. *Capsule*: cylindrical, not winged. Flowers April to May.

Fritillaria chlorantha seems to be related to *F. atrolineata*, primarily on account of the flower color. There are, however, striking differences separating them: *F. atrolineata* has glaucous, long and narrowly oblanceolate leaves with the lowest ones sometimes two or three in subopposite or subverticillate (subternate) position; a comparatively long stem; small, narrowly campanulate flowers; dark, elongate linear nectaries, and entire styles. The foveolate exine of pollen grains, and slightly trilobulate styles are also typical of the species. By contrast, *F. chlorantha* has short stems; short, wide, shiny green leaves, all alternate; comparatively big tubular flowers; green, lanceolate nectaries, and styles 3-fid at apex (Bakhshi Khaniki, 1997a; Khaniki, 2002a).

6.3.3.6. *Fritillaria avromanica* M. Advay & M. Teksen. Avroman lily (*Fritillaria avromanica* M. Advay & M. Teksen) (Fig. 10, Right) has lately been reported only from Hawraman (also spelled Avroman) area in west Iran (Table 4) (Advay et al., 2015). It forms small, few-numbered populations of less than twenty individuals.

Bulb: up to 2.5 cm in diameter, globose, with 1–3 bulblets; tunica yellowish, thin, papery. *Stem*: erect, 7–20 cm, smooth. *Leaves*: 3–6(–9), sessile, glaucous, the lowest 3.4–11.0 × 2.0–4.5 cm, subopposite or alternate, ovate, obovate or lanceolate, acute, median leaves 2.5–7.5 × 0.4–3.0 cm, subopposite or alternate, obovate-linear, acute; bract leaves 2–3(–6), 1.5–3.9 × 0.1–0.5 cm, subopposite or alternate, linear, acuminate. *Flowers*: 1–3, narrowly campanulate; perianth segments purplish-brown with green or yellow stripes, outer 13.6–28.2 × 3.3–6.8 mm, lanceolate, acute, ciliate-tufted at apex, inner 17.9–20.0 × 4.5–6.5 mm, oblanceolate, obtuse, ciliate-tufted at apex. *Nectaries*: 3.0–3.8 × 1.5 mm, linear, linear-lanceolate, placed 1 mm above the tepal base, green. *Filaments*: 5.2–7.0 mm, papillose, enlarged to base, yellow; anthers 5.2–8.4 mm, oblong, apiculate, yellow during early anthesis but then blackish, basifixed. *Style*: 5.7–9.0 mm, 3-lobed, papillose. *Capsule*: 25–47 × 15–21 mm, cylindrical, truncate at apex, cunate at base, not winged. Flowers February to March.

Distribution: Endemic to Iran.

Advay et al. (2015) argued that *Fritillaria avromanica* and *F. assyriaca* are closely related based on floral traits, but these species clearly show very little morphological resemblance since the leaves are a completely different shape. Robert B. Wallis believes *F. avromanica* is much more similar to *F. chlorantha*, particularly in its ovate lanceolate lower leaves, and the former may just be a variant of the latter species (Personal communication). However, they are distinct in flower color and to some degree in leaf texture/arrangement. *F. chlorantha* is relatively invariable, but some

collections have perianth segments marked with purple, which may be a sign of hybridization with *F. zagrica* or *F. assyriaca*, both of which occur in the same area (Rix, 1977). On the other hand, the patterned coloration of the petals in *F. avromanica* do not seem to be a sign of variation or random hybridization in *F. chlorantha*. As in the case of taxonomic status of *Rhinopetalum* (See Section 4), molecular phylogenetic studies should help shed light on this challenging issue.

The species is mostly accompanied by *Bongardia chrysogonum* Boiss., *Ferula haussknechtii* H. Wolff ex Rech.f., *Smyrniopsis aucheri* Boiss., *Muscari neglectum* Ten., *Gagea graminifolia* Vved., *Anemone* L. spp. and *Astragalus* L. spp. (Advay et al., 2015).

6.3.3.7. *Fritillaria chlororhabdota* Bakhshi Khan. *Fritillaria chlororhabdota* Bakhshi Khan. (Fig. 11, Left) was reported in Iran for the first time by Bakhshi Khaniki (1997b), and all information available on this species is restricted to this report (Table 4).

Bulb: 1.5 cm in diameter, ovoid, without bulbils or stolons. *Stem*: 15–51 cm, 12–3(–45) cm above ground, smooth. *Leaves*: 4–7, somewhat glaucous, all alternate, the lowest 5–11 × 1.5–2 cm, narrowly oblanceolate to elliptic-oblong, usually folded at fruiting time; bract leaves 2–5 cm long, linear to narrowly lanceolate, acute. *Flowers*: 1–2, narrowly campanulate; perianth segments purplish outside, paler inside with median yellowish-green bands extending to apices, sometimes tinged or sparsely green-dotted towards margins, outer segments 12 × 16–46 mm, elliptic-narrowly oblong, obtuse, inner segments 6.5–8 mm wide, lanceolate obtuse. *Nectaries*: broadly lanceolate to narrowly elliptic, 2.5–4 mm long placed 0.5–1 mm above base of tepals, green. *Filaments*: 7–8 mm, yellow-brown, stout, glabrous to sparsely papillose at base, densely papillose in upper part; anthers 5–7 mm long before dehiscence, ellipsoid, brown-purplish, basifixed. *Style*: 6–8 mm, entire, stout, greenish-yellow, densely papillose. *Capsule*: 2.5–3.5 × 1.5–2 cm, obovoid, obtuse, tapering towards the base, not winged. Flowers April to May.

Distribution: Endemic to Iran.

Among the species belonging to the *Caucasica* group, *Fritillaria chlororhabdota* seems to be closest to *F. caucasica*, by phyllotaxy (position and number of the leaves) as well as shape and its external purplish color of the tepals. However, the species can be distinguished from *F. caucasica* by several characters, e.g., folded leaves at fruiting time, narrowly campanulate flowers, obtuse tepals with a median green stripe on the inside, wide lanceolate nectaries, shorter filaments, rough pollen exine with big luminae and an entire stout style. In contrast, *F. caucasica* has flat leaves during the whole of vegetative period, acute tepals (sometimes inner ones obtuse) that are paler purple inside (sometimes greenish) and without a green stripe along the whole of their length, linear-lanceolate nectaries, longer filaments, smooth pollen



Fig. 11. Left, *F. chlororhabdota* (photo by Mahfuz Advay); Center, *F. gibbosa* (Photo by Mehdi Zarrei); Right, *F. ariana* (Photo by Paul Christian).

exine (knobs are absent) with very small luminae (foveolate sculpturing type), and longer tribulate styles.

6.4. Subgenus *Rhinopetalum* (Fisch. ex Alexand.) Baker

The five members of subgenus *Rhinopetalum* (*F. gibbosa*, *F. karelinii* (Fisch. ex D. Don) Baker, *F. stenantha* Rgl., *F. bucharica* Rgl., *F. ariana*) all have rather flat, pink and distinctive starry flowers different in shape compared with other subgenera and species of the genus. They are inhabitants of the mountains and steppes of central and western Asia, from the Caspian sea and Iran, to Afghanistan and the dry hills of western Pakistan; two members of this subgenus, *F. gibbosa* and *F. ariana*, occur in Iran (Rix and Strange, 2017).

The filament movement is only found in members of *Rhinopetalum* and *Theresia* (*F. persica*); the stamens bend back against the tepals before dehiscence of the anthers, and then bend forward at dehiscence. The nectary structure in members of this subgenus clearly differ from all other species; the nectaries are deeply impressed and the nectary orifice is slit-like which is bordered by two lobes, and appears densely hairy, at least in the lower part (Rix and Zarrei, 2007a, 2007b). As against other subgenera, *F. gibbosa* and *F. ariana* are unique in that the flowers are zygomorphic, as the nectary lobes are rather fringed and broad, and the nectary on the uppermost tepal is more depressed than the others. In the other subgenera, the nectaries are less depressed (often flattish), and usually linear to lanceolate or ovate, except in subgenus *Petiliium* having usually circular nectaries. Following a morphological approach, the unique structure of the nectaries and other distinctive floral characters in all species of this subgenus imply that subgenus *Rhinopetalum* does not seem to be more than distantly related to the genus *Fritillaria*, and may probably merit formal recognition as a distinct genus (*Rhinopetalum* Fisch. ex Alexand.). We have discussed this uncertainty earlier through Section 4 based on molecular evidence.

6.4.1. *Fritillaria gibbosa* Boiss

Gibbous lily (*Fritillaria gibbosa* Boiss.) (Fig. 11, Center) has been claimed (Rix, 1977) to be geographically the most widespread species of the genus in Iran (Table 4). Normally, *F. gibbosa* is a species adapted to arid climates. Flowering begins very early, from March through May, on arid steppes, often among *Artemisia* L. spp., *Rosa persica* Michx. ex Juss., *Lactuca orientalis* (Boiss.) Boiss. and *Poa bulbosa* L. In east and southeast Iran where the summers are dry, it is very easy to grow this species.

Bulb: up to 3 cm diameter, without bulbils or stolons. **Stem:** 6–16 cm, densely papillose, especially below. **Leaves:** 4–10, twisted, the lower 30–70 × 13–18 mm, lanceolate to ovate, usually opposite, the rest linear, grayish; bract leaves linear, 2 at the base of each pedicle. **Flowers:** 1–7(–15), flat, horizontal at maturity; perianth segments about 15 × 10 mm, the outer somewhat narrower than the inner, all pinkish spotted and marked towards the apex, dark towards the base. **Nectaries:** about 4 mm, deeply impressed, the upper larger than the others, with papillose ridge inside. **Filaments:** 9–10 mm, papillose, especially below, sometimes purple; anthers about 2 mm, spherical after dehiscence. **Style:** 8–10 mm, entire, slender, glabrous. **Capsule:** 14 mm long, with 6 about 4 mm teeth. Flowers March to May.

Distribution: Iran, Uzbekistan, Turkmenistan, Armenia, Afghanistan, Pakistan (Baluchistan).

The species is highly variable, especially in the number and color of the flowers (Kiani, 2015). Flower color is usually pink, but ranges from white, orange-yellowish or purplish. The nectaries of *F. gibbosa* are very complex; the nectary on the topmost outer tepal is the largest (slightly however), and the inner one opposite it, is the

smallest. All have two papillose ridges running down their middle, pressed together and concealing the nectar. On the outer part of the ridges, the papillae become flattened yellow lamellae, giving the appearance of an irregular crest. As with *F. imperialis*, the nectaries may exude drops of nectar in early mornings. The area around the nectaries is yellowish-green, heavily marked with blackish-purple. It differs from *F. karelinii* in that all the tepals, which are relatively broader, have nectaries, though some are larger than others; in *F. karelinii* only the uppermost nectary is enlarged and the rest seem to be vestigial, and do not produce nectar (Rix and Zarrei, 2007b).

6.4.2. *Fritillaria ariana* (Losinsk. & Vved.) Rix

Pink star (*Fritillaria ariana* (Losinsk. & Vved.) Rix) (Fig. 11, Right) in Iran occurs nowhere in great abundance, but rather in very small populations mainly in northeastern Iran (Table 4) (Rix, 1977). It requires generally the same climatic conditions as were described for *F. gibbosa*. The geographical distribution of these two species is quite different; *F. gibbosa* is widespread in center and, northeast through northwest, all the way down along Zagros chain (Rix, 1977), but *F. ariana* is very rare in Iran (Sharifi-Tehrani et al., 2015) and is categorized as a critically endangered species. On the other hand, *F. ariana* grows primarily in sandy deserts, while *F. gibbosa* prefers clay steppes or rocky slopes (Rix and Strange, 2017).

Bulb: up to 3 cm diameter, without bulbils or stolons. **Stem:** 10–30 cm (–50 cm in fruit), glabrous or papillose only below the lowest leaves and at the nodes. **Leaves:** 8–12, long, the lowest pair considerably longer up to 120 × 12 mm, linear-lanceolate, opposite, the rest linear, scattered; bract leaves 20–40 × 2 mm, linear, 2 at the base of each pedicle. **Flowers:** 2–14, usually 6, flat, horizontal at maturity; perianth segments pink-reddish, unspotted or sometimes slightly mottled, marked with brown around the nectaries; the outer 25 × 10 mm, obovate, acute; the inner somewhat wider. **Nectaries:** about 4 mm long, deeply impressed, the uppermost largest, the outer larger than the inner. **Filaments:** 6–7 mm, slender, papillose or glabrous only near the base; anthers about 5 mm before, 2 mm after dehiscence. **Style:** 5–7 mm, entire, slender, glabrous. **Capsule:** 15 mm, not winged, but toothed at the upper corners. Flowers March to early April.

Distribution: Northeastern Iran, northwestern Afghanistan, southern Turkmenistan.

Fritillaria ariana is very similar to *F. gibbosa*, but they are separated by several characters; *F. ariana* is usually a much taller plant with narrower basal leaves, and more numerous flowers nearly always unspotted. The distinction between the broad basal leaves and narrower stem leaves of *F. gibbosa*, and the narrow basal and stem leaves of *F. ariana* is usually obvious. The stems of *F. gibbosa* are usually papillose all over, while those of *F. ariana* are glabrous or papillose only at the leaf bases (at the nodes) and below the lowest leaves (Rix, 1977; Rix and Zarrei, 2007b; Rix and Strange, 2017).

7. Eight-Frit Mountain

The Iraqi border is truly a paradise for those in search of fritillaries; within this region lies a range of mountains which has been christened “Eight-Frit Mountain” (Wallis and Wallis, 2009), as it is home to at least eight different species of the genus, each of which is growing in its own ecological niche. This location is south of Marivan in Kordestan province southwards on the road to Nowsud and on the border with Kermanshah Province. It is very close to the border with Iraq and includes a pass at about 2500 m (Fig. 12, Right).

The place is a habitat of a strange-looking form of *F. uva-vulpis* growing together with *Zagrosia persica* (Hauskn.) Speta. and *Bellevalia paradoxa* (Fisch. & C.A.Mey.) Boiss. There are also



Fig. 12. Left, Koohrang crown imperial plain (photo by Hossein Hasanzadeh); Right, Eight-Frit Mountain (Photo by Robert B. Wallis).

populations of *F. straussii* on the north side of the slope; *F. imperialis* on the top of the ridge and a very large *F. crassifolia* ssp. *kurdica* on the south-facing side of the slope; *F. avromanica* grows in the spiny bushes on the west-facing slope below the road on the south side of the cleft; *F. poluninii* grows in rock crevices in several parts of the pass; *F. assyriaca* can be found in several places on the slopes on both sides of the pass but a little lower down; *F. persica* populations are spread on the slopes while descending from the pass on the road towards Nowsud. Such a rich habitat, where members of the four subgenera known to occur in Iran coexist, is believed to be unique in the world (Wallis and Wallis, 2009).

8. Systematics serves conservation

In general, the large number of species (over 160 taxa), extensive polyploidy and highly polymorphic nature of several species of the genus *Fritillaria* indicate a genus near its peak of speciation (Beetle, 1944). As stated earlier, the occurrence of four different subgenera of the genus (including 19 species and 3 subspecies) has been confirmed in Iran. This makes the country an important area for diversification and evolution of new species, as species diversity itself could be a driver of further species diversification (Emerson and Kolm, 2005). Increasing species diversity may lead to greater genetic makeup complexity, which has been suggested as an evolutionary force driving speciation. This happens in a variety of ways, among which hybridization has played an especially important role in the evolution of the genus. Frequent hybridization can result in morphologically intermediate specimens and increased confusion in identification of *Fritillaria* species (Beck, 1947), which in turn increases the difficulty of making decisions related to conservation. Setting conservation priorities in taxonomically complex taxa is an essential but especially complicated process. Incomplete understanding of taxonomy can have disastrous impacts on conservation, since a given threatened species may not be readily distinguishable from a more frequent species.

Although the current classification of the genus proposed by Rix (2001) is supported by molecular phylogenetic studies at the subgeneric level (Rønsted et al., 2005; Day et al., 2014), the whole genus still raises important evolutionary and systematic questions, and many taxa recognized within different species belonging to subgenera *Fritillaria*, *Rhinopetalum* and *Petilium* present taxonomic problems. In the following sections, we provide a brief overview of the possible uncertainties that may easily mislead conservation activities.

8.1. Subgenus *Fritillaria*

Taxonomic uncertainties are most frequent in taxa belonging to subgenus *Fritillaria*. One such problem has been already

encountered in the case of *F. uva-vulpis* and *F. assyriaca*, which are known as two species of high similarity in general morphological characters. Although the name *F. assyriaca* has often been used for *F. uva-vulpis*, detailed examinations reveal their distinctiveness (Rix, 2000b). *F. assyriaca* is rather more widespread and is a common species in Iran, whereas *F. uva-vulpis* is considered as an endangered species. To make the case even more complicated, these two are among the most variable species in the genus and have quite diverse morphologies in Iran. In the most confusing case, Wallis and Wallis (2009) recorded a strange-looking *F. uva-vulpis* in the Eight-Frit Mountain area that is quite different from the description of the species. On the other hand, *F. kotschyana* subsp. *kotschyana* has been confused with *F. crassifolia*, all the subspecies of which are more dwarfed and have linear nectaries (Rix, 1977). In another instance, the name *F. kotschyana* has been used for dwarf *F. latifolia* from northern Turkey, a very different species that has never been recorded in Iran. At least two unknown taxa have been recorded in Kordestan, very close to the Iraq border, which seemed to be *F. crassifolia*, but did not fit any of the known subspecies (Wallis and Wallis, 2009). *F. pinardii* and *F. zagrica* are two taxa frequently mixed up in the literature (see Section 6.3.3.3), once again, for extreme resemblance in their morphological characters. For this reason, although, it has been recently a single report of *F. pinardii* in West Azarbaijan province (Sharifi-Tehrani and Advay, 2015), the inclusion of this species within Iranian flora awaits further studies. In short, there is a variety of similar cases mainly due to crossing compatibility of different taxa and/or morphological similarities (e.g. Beck, 1947; Rix, 1974, 1975; Bakhshi Khaniki, 1997b; Wallis and Wallis, 2009; Tekşen and Aytaç, 2011).

8.2. Subgenus *Rhinopetalum*

As with subgenus *Fritillaria*, identification errors are frequent and easily occur in subgenus *Rhinopetalum* mainly due to morphological similarities. For example, the red-listed *F. ariana* can be easily confused with *F. gibbosa*, which is widely distributed across Iran (Rix and Zarrei, 2007a). Moreover, *F. pterocarpa* Stocks, which is native to Baluchistan (Pakistan), is probably identical to *F. gibbosa* (Rix and Zarrei, 2007a). Although *F. karelinii* Fisch. ex D. Don has been claimed to occur in Iran on 31st May 1964 by Paul Furse (Rix and Zarrei, 2007b), we strongly believe this is an identification error; when Furse reported this record, the whole genus was poorly known. In addition, *F. karelinii* normally flowers very early in March; at this late date (31st May), it is very likely to have been in fruit and not in flower, making identification nearly impossible. Furse reported his record in Northern Khorassan (80 km west of Bojnurd, arid plains, yellow fine soil with stones and scattered *Artemisia*, scrub, 1800 m), where *F. gibbosa* is recorded 20 km from here in *Artemisia* steppe at 1300 m. Considering the normal range of

F. karelinii, described from steppe in Southern Urals north of the Caspian Sea, as far south as Koppe Dag, this is likely not *F. karelinii*.

8.3. Subgenus *Petilium*

In a similar case from subgenus *Petilium*, the abundance of *F. imperialis* var. *imperialis*, the most frequent species in Iran, is quite different from its very close relative, *F. imperialis* var. *lutea*, which is seriously on the brink of extinction (Khourang et al., 2014). Although the endemic *F. raddeana* is also reported in Kashmir (Ali, 2007), Pakistan is not within the normal range of the species. This record is doubtful and presumably is correctly assigned to either *F. chitralensis*, native to the Chitral District of northern Pakistan, or to *F. imperialis* var. *lutea*.

8.4. Subgenus *Theresia*

General morphological characters of *F. persica*, the sole member of subgenus *Theresia*, are clear-cut with no indication of intergressions or intermediates in Iran. This is the only species of the genus in Iran with numerous flowers arranged in a raceme, so that it can be easily distinguished from other species. Thus, in contrast to the above-mentioned cases, there is no identification concern about this species in Iran.

9. Conclusion

Implementation of conservation frameworks is negatively affected by a lack of basic information on taxonomy and biology of fritillaries in Iran, as taxonomy provides the foundation for conservation practices and sustainable management of the world's remaining resources. Studies carried out on the genus *Fritillaria* through the last four decades in Iran have been technically sound efforts, but quite sporadic and limited in scope. These studies give a fairly good overview of different aspects of Iranian *Fritillaria*, yet provide little information relevant to conservation, which remains relatively poorly understood. By describing geographical and ecological features of Iranian *Fritillaria* along with an intensive look into biodiversity of the genus with respect to its taxonomic status, a much clearer understanding of the essential elements of conservation strategies can be provided for all involved practitioners. Information described in this review may serve as a stepping-stone for setting conservation priorities, hopefully in the near future, in Iran and neighboring centers of biodiversity of the genus *Fritillaria*.

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