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RESEARCH ARTICLE

Oncocyclus irises: phylogeny, evolutionary history and revised taxonomy based on complete chloroplast genome sequences

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ABSTRACT

Although *Iris* sect. *Oncocyclus* has a long history of recognition as a separate taxon within the genus, its phylogeny and evolution are still poorly understood. In this study, we used plastid genomic data to reconstruct the phylogeny of *Oncocyclus*, to exam its relationships with other sections of the genus and to shed light on its infrageneric phylogeny, place of origin and evolution. The whole chloroplast genome-based phylogenetic tree constructed for 39 of approximately 43 species and subspecies currently recognized in sect. *Oncocyclus* resolved sect. *Oncocyclus* as monophyletic and most closely related to sect. *Hexapogon* and sect. *Regelia*. None of the species with infraspecific taxa included in our analysis was monophyletic, casting doubt on the current infrasectional taxonomy. The place of origin of *Oncocyclus* was found to be Iran, to where its ancestor apparently migrated from an area embracing Central Asia and Afghanistan. The evolutionary line leading to *Oncocyclus* from the closely related to it *Regelia* and *Hexapogon* was associated with a general reduction in number of flowers to one per stem with a concomitant increase in flower size. There were two major migration/expansion routes of *Oncocyclus* from Iran, namely to the Caucasus and Turkey. Next expansion of *Oncocyclus* was from southeastern Turkey to Levant. The above strategy of producing large solitary flowers turned out to be very successful in the rocky high elevation and foothill sides of north-western Iran, southeastern Turkey and the Caucasus, but, when they migrated to Levant, also in the deserts and sand dunes of the latter, which led to the rapid colonization of the region and the highest species richness for *Oncocyclus* among the regions that this group occupies. Based on the phylogenetic tree, a new section, *Khorassania*, is established and the taxonomic status of many species of *Oncocyclus* is clarified. In particular, four lower taxa have been elevated to species rank. Four species were treated as unresolved. Three new species from Iran must be established based on living material collected by Frédéric Depalle and maintained in his unique collection.

Key words: biogeography, plastome, speciation, *Iris*, homoploid hybridization

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Introduction

Iris L. (Iridaceae) comprises ca. 260 herbaceous, geophytic species distributed in temperate climatic zone of the Northern Hemisphere, mostly in Eurasia and North America, grouped into six subgenera and twelve sections based on species morphology and caryology (Mathew 1989). This infrageneric classification, however, is not uniformly accepted and systematic position of many species and species groups is unclear. There have been attempts to resolve the phylogenetic relationships within the genus, its subgenera and sections using chloroplast genes and spacers (Wilson 2003, 2004, 2009, 2011, 2017; Mavrodiev *et al.* 2014; Wilson *et al.* 2016). Unfortunately, the *Iris* chloroplast genome has a low level of variability and although commonly used chloroplast markers such as *matK*, *trnK*, *ndhF*, *petL-psbE*, *trnL-trnF* and *psbM-trnD* were useful in distinguishing large clades within *Iris*, they demonstrated limited utility in resolving species relationships within sections. A solution was to try to use whole plastid genomes obtained through next-generation sequencing (NGS) technologies to reconstruct the phylogeny.

Among the currently recognized 12 sections of *Iris*, *Oncocyclus* (Siemss.) Baker is one of the largest (30 to 65 species) and most distinct. It belongs to *Iris* s.str. (bearded irises or pogon irises), a group of rhizomatous taxa with a 'beard' of hairs on the falls or on both falls and standards. About 110 species of this group are in Europe, Asia and North Africa. This group, beside *Oncocyclus*, includes four monophyletic and well defined morphologically sections, *I.* sect. *Iris*, *I.* sect. *Psammiris*, *I.* sect. *Regelia*, and *I.* sect. *Pseudoregelia* (Crespo *et al.* 2015). A position of the fifth group, *I.* sect. *Hexapogon*, was not fully resolved in the molecular analyses (Crespo *et al.* 2015). All these sections except for sect. *Iris* have an aril on their seeds. For this reason, *Oncocyclus*, *Psammiris*, *Regelia*, *Pseudoregelia* and *Hexapogon* were placed by Rodionenko (2009) in the separate subgenus *Arillosae*, but this group was not recovered as monophyletic (Mavrodiev *et al.* 2014).

Section *Oncocyclus* is confined to southwestern Asia, and, according to the latest phylogenetic studies (Mavrodiev *et al.* 2014; Crespo et al. 2015; Wilson 2017) is most closely related to two sections in Central Asia: *Hexapogon* and *Regelia*. Plants of *Oncocyclus* have unifacial and falcate, to some degree, basal leaves, a conspicuous large aril on the seed, unbranched stems carrying a single large flower, tepals showing a rich veining color pattern, and a prominent signal spot that is distal to a relatively sparse non-linear beard that does not extend to the midpoint of the sepal. The chromosome number of these species is n = 10 (Avishai & Zohary, 1977). These species generally have small populations scattered across open landscapes (steppes, deserts, dunes and rocky hillsides) from the north Caucasus south to Iran, Turkey and the eastern Mediterranean countries. Most of the species are narrow endemics with very limited ranges that do not overlap. In terms of ecological specialization (climatically-edaphic and insect pollination), this is one of the most advanced groups of *Iris*. The thick rhizomes allow the plants to survive the dry and prolonged summers and persist in open landscapes with xeric Mediterranean and desert climate and in different types of soils, including limestone, basalt, loess and sand. Extreme reduction in flower number, each stalk bearing a single flower, is accompanied by a remarkable increase in flower size to attract large insect pollinators, mostly solitary bees. The flowers have triple 'pollination tunnels' with a 'landing platform' on the fall often marked with a signal spot. A tunnel directs the visiting insects to an anther covered with large amounts of large and sticky pollen grains. Upon entering, the visitor's back is dusted with pollen. During a visit to the next flower, the pollen on the insect's back is scraped by the overhanging and down-curled stigmatic surface, ensuring a high probability of pollination.

Oncocyclus has a long history of recognition as a separate taxon within *Iris*, either

as a subgenus (Spach 1846; Alefeld 1863; Baker 1877, 1892), section (Lynch 1904; Dykes 1912; Diels 1930; Mathew 1989; Rodionenko 2009) or subsection (Lawrence 1953; Rodionenko 1961; Pax 1988). Within *Oncocyclus*, there were two attempts of subdivision into smaller groups. Avishai & Zohary (1980) subdivided the group into seven morphological clusters or aggregates based on flower divergence. This subdivision, however, was not supported by molecular studies (Wilson et al. 2016; Volis *et al.* 2023). Gavrilenko (1986), also using floral characters, circumscribed three series: *Acutilobae* Gav. with petals and sepals narrowed distally, ser. *Paradoxae* Gav. with reduced sepals, and ser. *Ibericae* Gav. having rounded petals and sepals. This subdivision also failed to get molecular support (Wilson *et al.* 2016).

In our research, we addressed the following questions: (1) Is *Oncocyclus* monophyletic?; (2) Which sections are sister to *Oncocyclus*?; (3) Do disjunct populations of currently recognized species of *Oncocyclus* represent independent evolutionary lineages?; and (4) What is the ancestral area and most probable migration/expansion route for section *Oncocyclus*?

Materials and Methods

Sampling

Sampling was designed to embrace as many currently recognized species of *Oncocyclus* as possible, with several samples per species from different countries whenever possible. The taxa included 39 of approximately the 43 species and subspecies currently recognized in sect. *Oncocyclus* (ca. 91% of the overall diversity) plus two undescribed species and 12 outgroup species representing the species closest to *Oncocyclus* (Mavrodiev *et al.* 2014) sections *Hexapogon*, *Regelia*, *Pseudoregelia* and *Iris* (Suppl. Table). Representatives of sect. *Psammiris* were not included because no material was available. It should be noted that *Oncocyclus* irises can be studied satisfactorily only from living specimens because in herbaria, the species of this section seldom can be be recognized with certainty. Therefore the present work is based on the living plants in their natural habitat (focused as far as possible to plants from the type locations) as well as under cultivation in FD collection.

DNA was extracted from silica preserved leaf samples following the protocol of Doyle & Doyle (1987). The samples were checked by agarose gel (1.3%) electrophoresis with a DNA ladder (Thermo Scientific, Waltham, MA, U.S.A). DNA quality and concentration were checked with a spectrophotometer NanoDrop 2000 (Thermo Scientific, USA).

DNA was sheared to construct a 350 bp (insert size) sequence library with the Genomic DNA Sample Prep Kit (Illumina) according to the manufacturer's protocol and sequenced using 150 paired-end reads on the Illumina HiSeq 4000 at Beijing Novogene Bioinformatics Technology Co., Ltd, China. The Next Generation Sequencing (NGS) QC Tool Kit (Patel and Jain 2012) with default settings was used for raw data processing. The resulting clean reads were assembled in NovoPlasty version 3.8.3 (Dierckxsens *et al.* 2017). The plastid genomes were assembled from filtered reads by NovoPlasty v.3.3 (Dierckxsens *et al.* 2017) and Geneious 7.2.8 (Kearse *et al.* 2012) using as a reference *Iris gatesii* (GenBank ID: NC_024936.1). Multiple-sequence alignment of complete chloroplast genomes was performed with MAFFT (Katoh *et al.* 2002) and manually edited when necessary. Gene annotation was performed in Geneious v.10.0.2 by the reference. Gene nomenclature follows the Chloroplast Genome Database (http://chloroplast.cbio.psu.edu). The generated chloroplast genome annotation files were converted into feature table files with GB2squine (Lehwark and Greiner 2019) and submitted to GenBank via BankIt.

Phylogenetic analysis

For analyses, a model of nucleotide substitution was selected based on the Bayesian Information Criterion (BIC) using MrModelTest 2 (Nylander 2004). Maximum Likelihood (ML) analysis with a T92 substitution model was performed in MEGA version 11 (Tamura *et al.* 2013). The percentage of replicate trees in which the associated taxa clustered together in these analyses was estimated by bootstrapping with 1000 replicates. The plastid genome analysis also employed Bayesian inference conducted using MrBayes, version 3.2.1 (Ronquist *et al.* 2012) with 1,000,000 generations on four incrementally heated chains starting with random trees sampled every 100 generations. The average standard deviation of the split frequencies approached 0.01, indicating that all runs had converged to a stationary distribution. After discarding the first 25% of trees as burn-in, a 50% majority-rule consensus tree was constructed from the remaining trees to estimate posterior probabilities (PP). Internodes with posterior probabilities > 95% were considered statistically significant.

Analysis of species richness and endemism

After we mapped all verified species of *Oncocyclus* from occurrence records (Fig. 1), we calculated species richness (SR), endemism (E), weighted endemism (WE) and corrected weighted endemism (CWE) for equal area square grid cells of 200 × 200, 400 × 400 and 600 × 600 km using the software Biodiverse (version 4.3) (Laffan *et al.* 2010). The use of the unified grid cells, when each species contributes only once to each cell allows avoiding a problem of uneven sampling effort. WE is species richness inversely weighted by species ranges. CWE is species richness inversely weighted by species ranges and divided by the total number of species in a grid cell to partially account for high species richness. Thus, cells with high CWE are those with a high proportion of species with restricted ranges even if they are species-poor. The distribution pattern of SR, E, WE and CWE was visualized in ArcGIS 10.2.

Historical biogeographical analysis

Analysis of potential ancestral distribution areas at internal nodes was conducted using the Bayesian Binary Method implemented in RASP v.2.1b (Yu *et al.* 2010, Yu *et al.* 2013), which allows inferring geographic distributions at ancestral nodes using a full hierarchical Bayesian approach. The input file for RASP consisted of the 21,000 postburn-in trees from the plastome dataset analysis with MrBayes. Relative frequencies of ancestral areas reconstructed for each node were recorded and plotted onto the majority-rule consensus tree. Four areas of endemism were defined in the biogeographic analysis based on the extant distribution of the section: A, Levant including Jordan, Israel, Lebanon and Syria; B, Turkey; C, Caucasus including Armenia, Azerbaijan, Georgia and the Caucasian part of Russia; D, Iran; and E, Central Asia and Afghanistan.

Ecological niche modeling

We used species distribution modeling to predict the climatically suitable range for *I. demawendica*, the basal species of *Oncocyclus* in the phylogenetic tree. A rational for this analysis was that *I. demawendica* is the closest to the ancestor of *Oncocyclus* and therefore its environmental requirements should be closest to the ancestor requirements among the extant species of *Oncocyclus*. The 19 climatic variables summarizing temperature and precipitation dimensions of the environment were obtained for the relevant geographic area from WorldClim 1.4 (Hijmans *et al.* 2005) with a resolution of 30″ latitude/longitude (ca. 1km^2 at ground level). In addition to the current climate, we modeled species distribution using data for the mid-Holocene (~6 ka), Last Glacial Maximum (~21 ka) and the Last Interglacial (~120-140 ka).

To predict the species potential niche we used MAXENT v3.3.3 (Phillips *et al.* 2006; Phillips & Dudik 2008), which generates

estimates of probability of presence of a species that varies from 0 to 1, where 0 being the lowest and 1 the highest probability. In the analyses, we set the number of iterations to 1000 and used ten replicates under the 'crossvalidate' option. The accuracy of model predictions was tested by calculating the area under the 'Receiver Operating Characteristic (ROC) Curve' (AUC). The summary maps were generated by averaging Maxent outputs. Model predictions in ASCII grid layer format were loaded into ArcGIS 10.2 to produce the species predicted distribution maps with suitability values ranging from 0 to 1.

Results

Plastome features

Complete plastomes were recovered for all samples. The size of the plastome of the species of *Oncocyclus* ranged from 153,122 (*I. yebrudii*) to 153,493 (*I. petrana*) nucleotides. The plastomes of the species of *Oncocyclus* were identical in their structural organization, gene content, and gene arrangement. The gene sets were identical, each with 4 unique rRNA genes, 30 unique tRNA genes, and 79 unique protein coding genes. Each plastome contained 133 complete coding regions including duplicated genes in the IR and open reading frames (ORFs).

Phylogenetic analysis

The total length of the aligned data matrix with outgroups was 155,235 characters, of which 1729 (1.114%) were parsimony informative. The Bayesian and ML analyses produced trees with identical topology and strong node support (Fig. 2). Section *Oncocyclus* was resolved as monophyletic and well separated from the outgroup species. *Iris longiscapa* Ledeb., representing sect. *Hexapogon*, was the most closely related species to the taxa of *Oncocyclus*. The next closest species to *Oncocyclus* were *I. ferdowsii* Joharchi & Memariani, *I. afghanica* Wendelbo, *I. korolkowii* Regel, *I. stolonifera* Maxim. and *I. hoogiana* Dykes from sect. *Regelia*. The latter four were clustered together, while *I. ferdowsii* was apart and had an intermediate position between this clade and the *Oncocyclus* + *Hexapogon* clade. Three species from sect. *Iris*, *I. alberti* Regel, *I. imbricata* Lindl. and *I. lutescens* Lam., formed a clade sister to the clade *Oncocyclus* + *Hexapogon* + *Regelia*. Most dissimilar with *Oncocyclus* were *I. goniocarpa* Baker, *I. pandurata* Maxim. and *I. sichuanensis* Y.T.Zhao from sect. *Pseudoregelia*. The oldest species of *Oncocyclus* was *I. demawendica* (Bornm.) Dykes, which had a separate position on the tree. The two basal clades comprised *I. meda* Stapf, *I. camillae* Grossh., *I. iberica* Steven, different subspecies of *I. paradoxa* Steven and *I. acutiloba* Meyer and an undescribed species from Iran. The next by age were two clades, *I. pseudomeda* Salimbahrami & Saeidi and *I. urmiensis* Hoog.

Some clades exhibited polytomy due to high similarity of the plastomes of the comprising species.

Analysis of species richness and endemism

The species richness scores calculated per cell 200 × 200, 400 × 400 and 600 × 600 km did not accede 11, 12 and 15, respectively; the endemism scores (i.e. number of species not occurring anywhere outside the cell) did not accede 5, 7 and 13, respectively. The largest number of cells with the maximum endemism scores under resolution of 200 × 200 km was in Levant, and under resolution of 400 × 400 and 600 × 600 km was in the areas of Levant and the Caucasus plus adjacent areas of northeastern Turkey and northwestern Iran (Fig. 3). The same pattern showed spatial distribution of the WE scores. The spatial distribution of the CWE and SR scores revealed additional areas of high endemism and species richness in Turkey and Iran (Fig. 3).

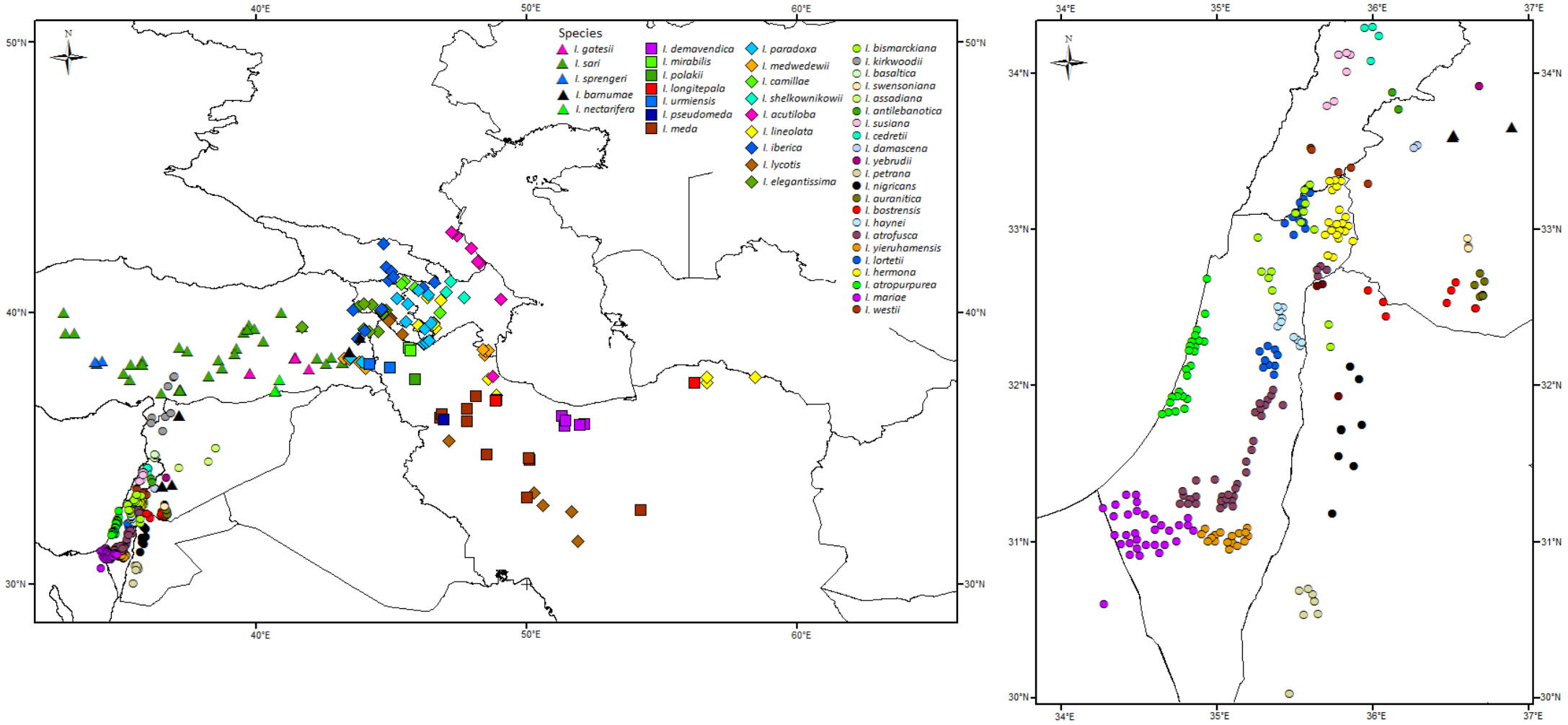


Figure 1. Left panel. A general map of spatial distribution of the *Oncocyclus* species. Right panel. The *Oncocyclus* distribution in Levant.

Figure 2. Phylogenetic tree derived from maximum likelihood (ML) and Bayesian inference (BI) for 56 *Oncocyclus* plastomes plus ten outgroup plastomes from the other sections. ML bootstrap proportion values and Bayesian posterior probabilities are shown next to the nodes. The scale bar represents the expected substitutions per site.

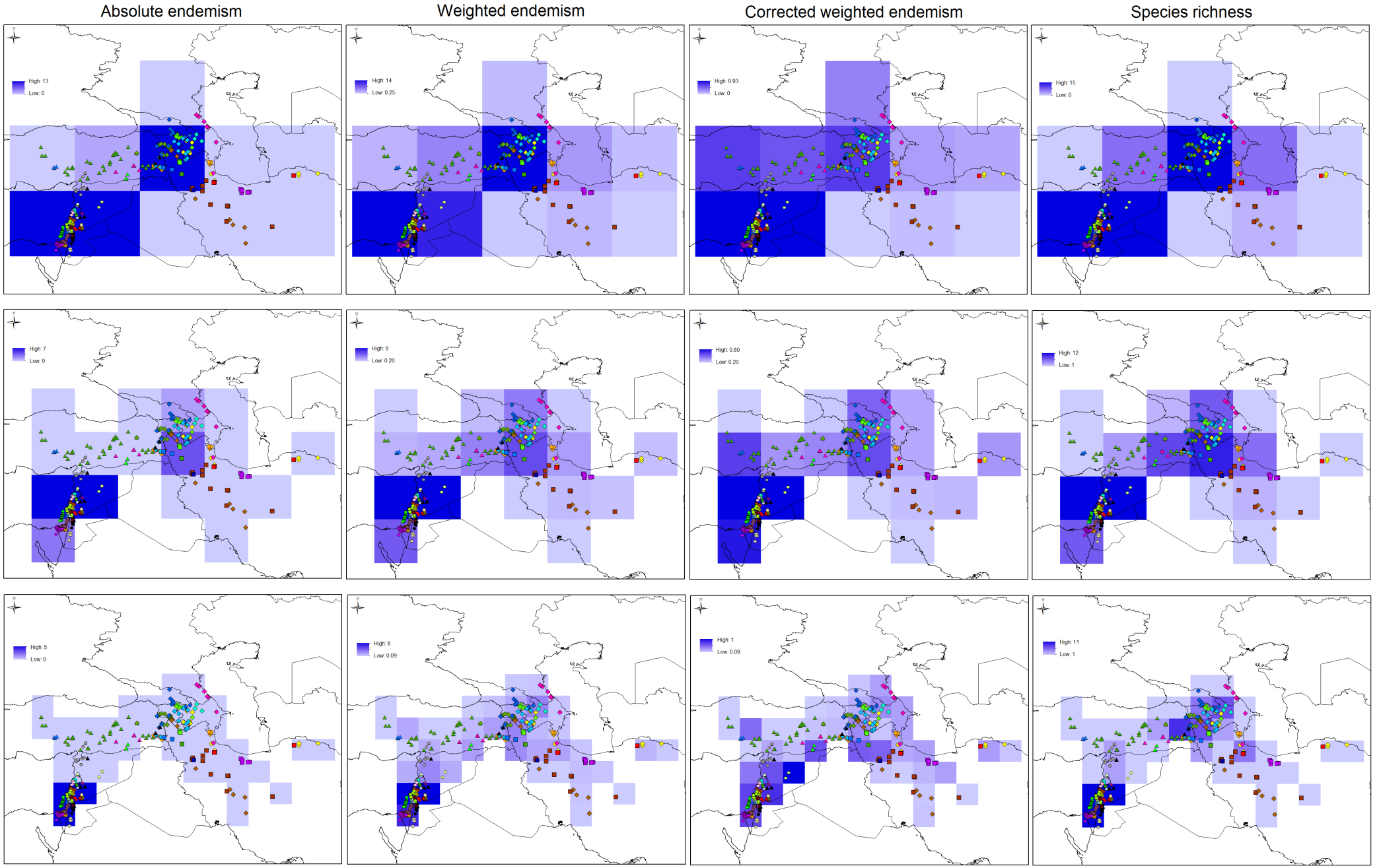


Figure 3. The spatial patterns of the four diversity metrics for sect. *Oncocyclus* using grid cells 600 x 600, 400 x 400 and 200 x 200 km (from top to bottom).

Historical biogeographical analysis

Results estimate that Iran is the most likely ancestral area for sect. *Oncocyclus* (99.4% probability). In contrast, a probability that any of the other four regions is the ancestral area for sect. *Oncocyclus* is very low (<0.01% for Levant and Turkey, 6.5% for the Caucasus and 1.5% for Central Asia/Afghanistan) (Fig. 4). Iran was also the most likely ancestral area for sect. *Hexapogon* , while Central Asia/Afghanistan was the most likely ancestral area for sect. *Regelia* (Fig. 4).

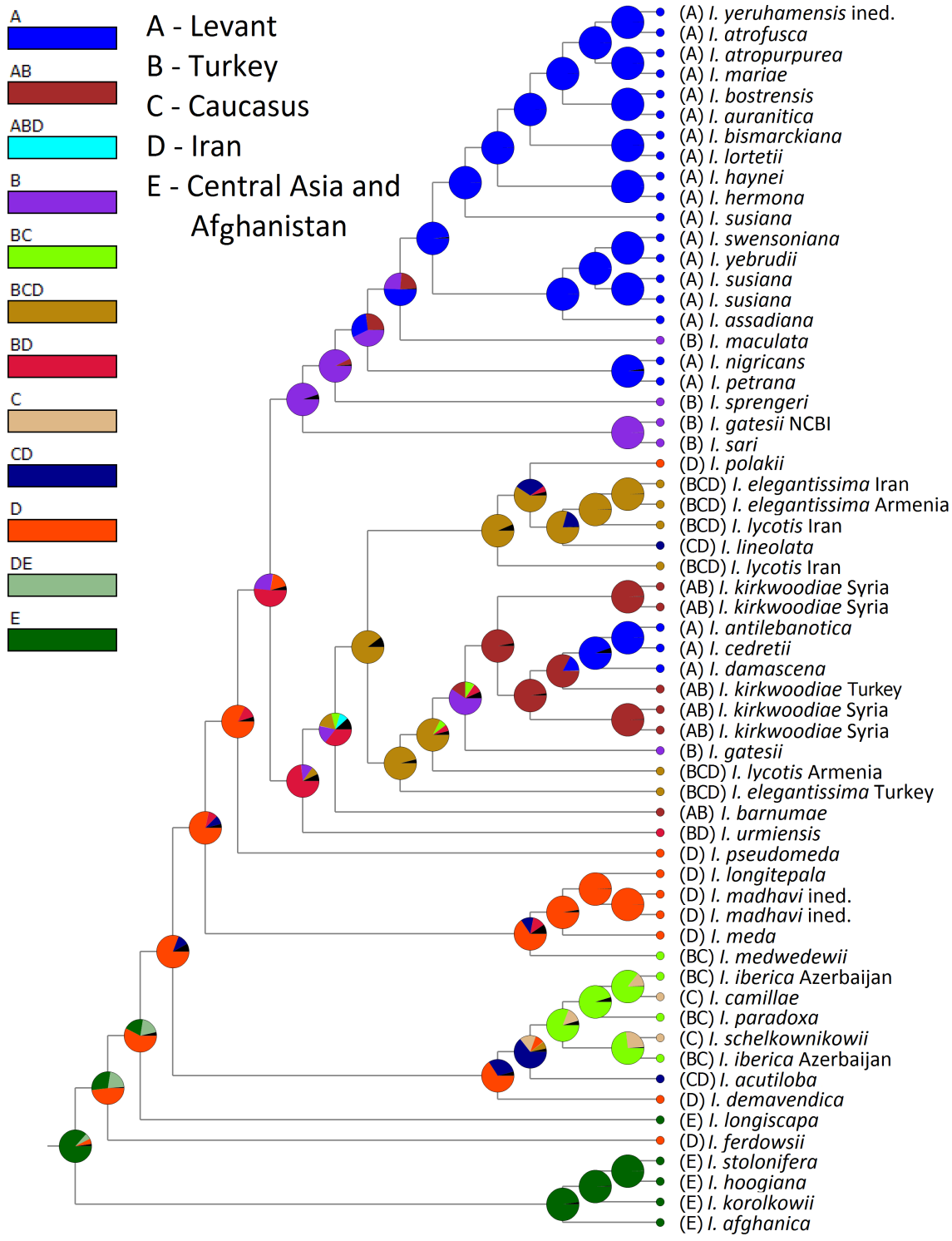


Figure 4. Biogeographic tree based on plastome data with five presumed ancestral areas. Most likely ancestral for a given clade states are reconstructed for key internal nodes.

Ecological niche modeling

The results of SDM for *I. demawendica* (Bornm.) Dykes showed that the suitable range for the habitat of this species under the current climate is almost identical to the habitat predicted to be suitable in the mid-Holocene (~6 ka) (Fig. 5). However, the predicted suitable habitat range for the last interglacial (~120-140 ka) was much lower, and for last glacial maximum (~21 ka) was much larger than the range predicted under the current climate (Fig. 5).

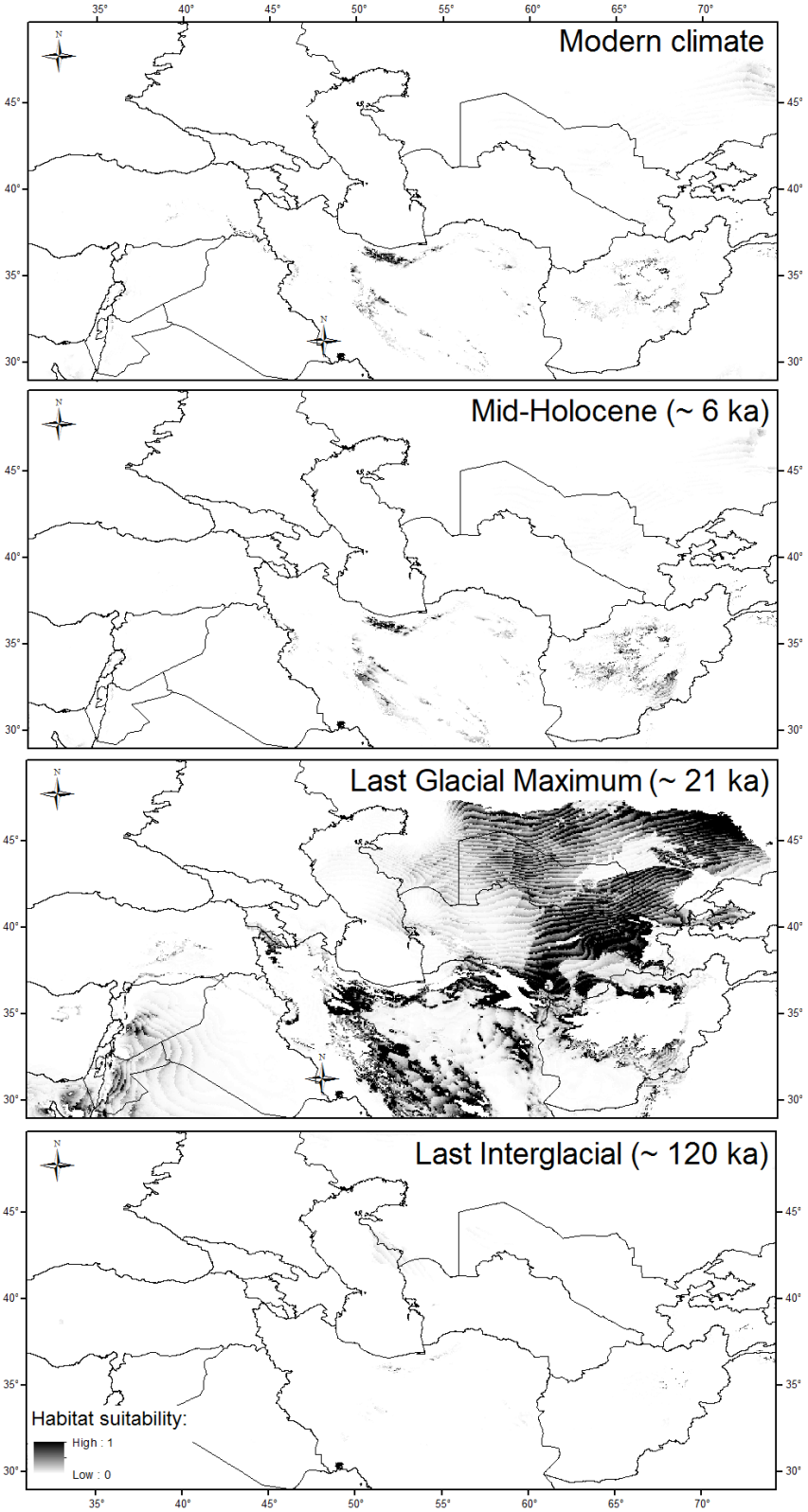


Figure 5. Predicted suitable ranges for *I. demawendica* for the four points in time

Discussion

Phylogenetic relationship with the other sections within subg. *Iris*

The section closest to section *Oncocyclus* was *Hexapogon*, represented in our study by *I. longiscapa*. Earlier, the close relationship of *Oncocyclus* and *Hexapogon* was reported by several authors (Mavrodiev *et al.* 2014; Wilson *et al.* 2016; Wilson 2017). However, in contrast to the above studies, in our phylogenetic tree *I. longiscapa* was not embedded in the *Oncocyclus* clade, but was sister to it. *Regelia* was found to be the second and *Iris* the third closest sections, confirming previous findings of Mavrodiev *et al.* (2014) and Wilson (2017). The section most dissimilar to *Oncocyclus* from the sections included in our study was sect. *Pseudoregelia*. All these sections formed distinct monophyletic clades in the tree. It should be noted that while sections *Hexapogon* and *Regelia* genetically differed little from *Oncocyclus*, sect. *Iris* and especially sect. *Pseudoregelia* differed greatly, indicating their old history as separate clades.

The two representatives of sect. *Hexapogon*, *I. falcifolia*, which occurs from northwestern Pakistan north to the Caucasus through Central Asia and northeastern Iran, and *I. longiscapa*, which is confined to Central Asia, are unique among the species of *Iris* in their chromosome number (2n = 18) (Randolph & Mitra 1961; Zakharyeva 1985). Species of *Regelia* in Central Asia and Afghanistan are not uniform in their chromosome number due to polyploidy (e.g. *I. stolonifera* and *I. hoogiana* have 2n = 44), but their basic chromosome number is 22 (Randolph & Mitra 1961; Bochantseva 1969). The caryological similarity of sect. *Hexapogon* and sect. *Regelia* to sect. *Oncocyclus* (2n = 20) agrees very well with the detected similarity of their respected plastomes. In the more distantly related sect. *Iris*, the species have a wide range of chromosome numbers, from 24 to 48 (Mitra 1956; Randolph & Mitra 1961). Evolution of *Oncocyclus* apparently involved reduction in chromosome number from 24 (sect. *Iris*) to 22 (sect. *Regelia*) and then from the common ancestor of *Oncocyclus* and *Hexapogon* species to 20 (sect. *Oncocyclus*) and 18 (sect. *Hexapogon*).

Morphologically, sect. *Hexapogon* is similar to sect. *Oncocyclus* in having knobby rhizomes and few (two or three) flowers in an inflorescence (Sennikov *et al.* 2023). However, plants of *Hexapogon* have long, narrow leaves and (together with *Regelia*) the distinct and unique feature within subg. *Iris* feature of a linear beard on each petal in addition to a linear beard on each sepal (which occurs in plants of sections *Pseudoregelia*, *Psammiris* and *Iris*). The *Regelia* group is also morphologically close to sect. *Oncocyclus*, from which it differs by the usually 2-flowered inflorescences and a more conspicuous linear band of hairs on all six perigone segments (falls and standards). Two of species of *Regelia*, *I. kuschkensis* and the recently described *I. ferdowsii* (Memariani & Joharchi 2017) from northeastern Iran have the combination of *Regelia* and *Oncocyclus* features (all six perigone segments bearded and solitary flowers, respectively), confirming the close relationship of these two sections. Sect. *Iris* is similar to *Oncocyclus* in such traits as thick rhizomes and broad, linear beards on the falls, but comprises many species with branched stems. *Pseudoregelia*, characterized by small vertical tuber-like rhizomes, narrower standards with blunt edges, and a dense beard of club shaped hairs only on the falls, is sister to all previous sections.

Carpology shows the high similarity of seeds of *Oncocyclus* with *Regelia* and *Hexapogon* in having a prominent aril and with *Regelia*, *Hexapogon* and *Iris* in having the surface of the testa reticulate-wrinkled. Seeds of *Pseudoregelia* and *Psammiris* are less similar to those of *Oncocyclus* in shape and surface structure, although they have a small and inconspicuous aril.

Phylogenetic relationship of species within sect. *Oncocyclus*

The plastome phylogenetic tree suggests that the early-diverged *Oncocyclus* lineages are associated with the Caucasus and Iran, and include mostly plants with short stems and relatively small flowers. The most basal position in the tree has *I. demawendica* (Bornm.) Dykes which taxonomic status as a species now cannot be questioned. This species is most closely related not to *I. barnumiae* to which it was assigned as a subspecies by Mathew & Wendelbo, but to the looking very different from this species *I. iberica*, *I. paradoxa*, *I. acutiloba*, *I. camillae* and *I. schelkownikowii*. Morphologically, the latter five species represent four distinct groups described by Avishai & Zohary 1980) as aggregates, Iberica (*I. iberica*), Paradoxa (*I. paradoxa*), Acutiloba (*I. acutiloba*) and Maculata (*I. camillae* and *I. schelkownikowii*). These four groups differ not only from *I. demawendica* but also from each other in shape, size and coloration of their standards and falls, as well as vein and beard pattern. The fact that the species comprising these groups are clustered together despite their great morphological differences suggests that diversification of flower types was a rapid and relatively recent process. On the other hand, known genetic compatibility of all species of *Oncocyclus* and reports of numerous natural hybrids suggest that natural hybridization strongly contributed to the detected incomplete lineage sorting. For example, Gavrilenko 1975) reported of extreme variability of virtually all Caucasian species in flower size, shape and coloration of petals and sepals, with numerous forms of such species as *I. iberica* (20), *I. camillae* (24), *I. elegantissima* (8), *I. acutiloba* (5), *I. schelkownikowii* (4), *I. ewbankiana* (5) and *I. lycotis* (9) described in the Soviet botanical literature. Prior to the well known artificial interspecific hybridization experiments done by Michael Avishai in the 1970s (Avishai 1977; Avishai & Zohary 1980), analogous experiments were conducted, using Caucasian species, by the Soviet botanists with successful seed production in 65-100% cases, and with the percentage of fertile pollen grains produced by the interspecific hybrids as high as 98-99% (Gavrilenko 1975). Gavrilenko concluded that the major factor explaining high number of species of *Oncocyclus* and their very high intraspecific variation was a frequently occurring hybridization process. One important note of Gavrilenko (1975) was that in western Azerbaijan, the richest in the Caucasus *Oncocyclus* diversity area having the most favorable for *Oncocyclus* conditions, the available for iris plants habitats were reduced by agricultural development in this area to the most inaccessible hillslopes and ravines. As the situation in other countries is not better, we can suspect that many more species, subspecies and variants, including their intermediate forms, existed until recently, but went extinct during historical times. This extinction is advancing rapidly today and, in many countries, once existing species cannot be found in locations from which they were described.

The remaining species of *Oncocyclus* were clustered in the phylogenetic tree into a large clade having three sub-clades. The oldest sub-clade comprised only the species from Iran and Azerbaijan. The first of the other two sister sub-clades comprised the species from Iran, Turkey, Syria and one species from Lebanon. The second sub-clade included the species from Turkey, Syria, Lebanon and Israel. Majority of the species in these two sub-clades have large flowers and differ mostly in coloration of standards and falls. With a very few exceptions these species are of Susiana, Iberica, Lortetii and Haynei type (*sensu* Avishai & Zohary 1980), i.e. with large or very large flowers, and falls and standards subequal or equally sized, orbicular or obovate. Within the latter sub-clade, the youngest compact group comprise exclusively Eastern Mediterranean species (i.e. from Lebanon, Syria, Jordan and Israel).

Neither of the species with infraspecific taxa included in our analysis was monophyletic confirming previous findings of Wilson et al. (2016). All the subspecies of *I. acutiloba*, *I. iberica* and *I. paradoxa* turned out to be genetically distinct and clustered separately. Moreover, we found that populations of the same

species in different areas that are indistinguishable morphologically can represent different species. For example, as we reported earlier (Volis *et al.* 2022), *I. petrana* from Israel sometimes referred to as *I. yeruhamensis* was very different genetically from its conspecific from Jordan. Similarly, *I. lycotis* from Iran and Armenia, and *I. gatesii* from two locations of Turkey separated by hundreds of kilometers were the members of different clades in the phylogenetic tree.

It should be noted that many clades of the phylogenetic tree exhibited polytomy despite great morphological dissimilarity and spatial isolation of the comprising them species. This indicates a very rapid speciation process when multiple speciation events happened at the same time. As a result, many daughter lineages are equally closely related to one another.

Centers of diversity, ancestral area and migration routes

The Caucasus and the eastern Mediterranean are the two presumed centers of *Oncocyclus* diversification and speciation (Rodionenko 2009). The Caucasus is the mountainous area bordered by the Black and Caspian Seas and including the entire countries of Georgia, Armenia and Azerbaijan, as well as the most southern part of Russia, the northeastern part of Turkey and the northwestern portion of Iran (Schatz *et al.* 2014). This biodiversity hotspot (Myers *et al.* 2000) is known as a corridor for the past species migrations between Asia and Europe, and also an area where many taxa evolved and radiated. The main *Oncocyclus* habitat (high elevation steppe and rocky scree slopes) in the Caucasus is rich in endemic or sub-endemic species. The eastern Mediterranean is also rich and diverse in species of *Oncocyclus*, with many of them endemic, but unlike in the Caucasus, species from other sections of subg. *Iris* do not occur in this region. In our study, point-to-grid analysis of species distribution confirmed that the Levant and the Caucasus and adjacent areas of northeastern Turkey and northwestern Iran, are two centers of species richness and endemism in *Oncocyclus*. Especially high species richness and endemism is in the Levant, i.e. an area embracing Israel, Lebanon, Jordan and Syria.

In several previous studies, the Caucasus was suggested as an area of early evolution in sect. *Oncocyclus* (Gavrilenko 1975; Rodionenko 2009) and its likely ancestral area (Wilson *et al.* 2016). Our findings do not support those views. The results of our biogeographic analysis undoubtedly suggest that the ancestral area of sect. *Oncocyclus* is Iran. Some of the early-diverged taxa within *Oncocyclus* either have their entire range confined to Iran (*I. demawendica*, *I. meda*, *I. pseudomeda*, *I. longitepala*), or have part or their range in Iran (*I. paradoxa*, *I. iberica* and *I. acutiloba*). The *Oncocyclus* ancestor apparently migrated from an area embracing Central Asia and Afghanistan. The ancestor was closely related to sect. *Regelia* and sect. *Hexapogon* and was similar to *I. ferdowsii*, which exhibits a unique combination of traits characterizing these sections: falcate leaves, short stems and solitary flowers (sect. *Oncocyclus*), but with all six perigone segments bearded (sect. *Regelia* and *Hexapogon*). The distribution of *I. ferdowsii* (northern Iran) and all of section *Hexapogon* (Central Asia, Iran and Afghanistan) gives us a clue to the most likely migration route of the ancestral taxa of *Oncocyclus*. The evolutionary line leading from the *Regelia-Hexapogon* ancestor to *Oncocyclus* was associated with a general reduction in number of flowers to a single flower per stem with a concomitant increase in flower size, high intensity of color and diversity of petal coloration to attract insect pollinators. There were two major migration/expansion routes of species of *Oncocyclus* from Iran, namely to the Caucasus and to Turkey. The next step in the expansion of *Oncocyclus* was from southeastern Turkey to the Levant, as was earlier suggested by Chaudhary *et al.* 1976). The above strategy of producing large solitary flowers turned out to be successful not only in rocky, high elevation and foothill sites in northwestern Iran, southeastern Turkey and the Caucasus, but

after migrating to the Levant, also in deserts and sand dunes of the latter, which led to rapid colonization the region and the greatest species richness in *Oncocyclus* among the regions that the group occupies.

On the other hand, the SDM analysis for *I. demawendica*, the closest species to the presumed ancestor of section *Oncocyclus*, showed that the range of its suitable habitat was maximal during the last glacial maximum (i.e. around 21 ka), embracing vast territories of Iran, Afghanistan and Central Asia, and meaning that the period of glacier advance was a time when *Oncocyclus* expansion to the west occurred as a result of climate cooling. The predicted range of the ancestral species was much smaller for the period preceding or following this cooler period. Thus, the evolution of species of *Oncocyclus* was tightly correlated with the climatic changes that occurred during periods of glacial advance and retreat, and the current small and isolated ranges of many species of *Oncocyclus* are a consequence of the general aridification in Western Asia that occurred during at least the last 10,000 years. Of course, humans also contributed to the shrinking of the *Oncocyclus* species ranges, but their activities only exacerbated the general trend.

Evolutionary forces that shaped *Oncocyclus* distribution

Previously, analyzing the evolutionary forces that shaped the distribution of section *Oncocyclus* in Israel we came to the conclusion that three evolutionary forces contributed to speciation in the section: local selection, geographic isolation and homoploid hybridization (Volis *et al.* 2022, 2023). Local adaptation was assumed by Avishai and Zohary (1980) to play a major role in the group speciation process, but experiments revealed that reproductive isolation in the form of post-zygotic selection against hybrids had a limited extent and could be detected in only two of the eight species studied that occupy very specific environments; coastal sand dunes and basaltic soil (Volis *et al.* 2023). The limited gene flow due to short seed dispersal distance, narrow specialization of flowers for insect pollination and presence of vegetative propagation via fragmentation of rhizomes was found to be more important in the evolution of *Oncocyclus*, leading to creation of a spatial structure of genetically differentiated clusters (Volis *et al.* 2022, 2023). The clusters underwent environment-specific selection, which for some differed strongly but for many others only a little (Dorman *et al.* 2009; Volis *et al.* 2019, 2021, 2023). The importance of local adaptation in other parts of the range of distribution of *Oncocyclus* is not known, but the fertility of interspecific hybrids reported by Avishai & Zohary 1980) for all species of *Oncocyclus* suggests its minor role in the evolution of the section. The presence of distinct lineages within the currently recognized species strongly suggests the importance of spatial isolation in shaping the distribution of *Oncocyclus*. However, spatial isolation cannot explain the pattern when accessions of the same species sampled within the same country not just differ to some extant from each other but are members of different clades in the phylogenetic tree. The most probable explanation for this pattern is homoploid hybridization. Involvement of homoploid hybridization in the evolution of *Oncocyclus* was inferred earlier from the interspecific historical gene flow detected with AFLP markers and complete fertility of interspecific hybrids (Volis *et al.* 2022, 2023). Those conclusions, limited to *Oncocyclus* in Israel, can now be generalized to the whole section. The importance of homoploid hybridization in the evolution of the section stems from observations and experiments conducted in the Caucasus. Natural hybridization among species of *Oncocyclus* has been commonly observed in that region (Grossheim 1940; Gavrilenko, 1975), and the natural hybrid *I.* × *grossheimii* was experimentally recreated by crossing *I. ewbankiana* (= *I. acutiloba*) and *I. lycotis* (Gavrilenko, 1975). Apparently, many species of *Oncocyclus* from other regions are also homoploid hybrids. Only homoploid

hybridization can explain why accessions of the same species (e.g. accessions of *I. gatesii* and *I. lycotis*) were not clustered together in the phylogenetic tree, but were members of different clades whose other members comprised different species.

Homoploid hybridization within sect. *Oncocyclus* has clear taxonomic implications. *I. schelkownikowii* Fomin was earlier hypothesized (Rix *et al.* 2015) to be a homoploid hybrid species whose possible parents could be *I. paradoxa*, *I. acutiloba* and *I. iberica*. Our results provided strong support for this assertion, as all these species were closely related. Moreover, *I. camillae*, highly similar to *I. schelkownikowii*, also appears to be a hybrid. It seems quite possible that hybridization first occurred between *I. acutiloba* and *I. iberica*, which resulted in *I. schelkownikowii* and then proceeded (through hybridization with *I. paradoxa*) in the creation of *I. camillae*. Additionally, as *I. iberica* from Azerbaijan was found to comprise genetically distinct entities, it may also be of a complicated hybrid origin. In general, many currently recognized species of *Oncocyclus* appear to be homoploid hybrids of unknown parentage.

Conservation implications

Virtually all species of *Oncocyclus* are represented by small, isolated and declining populations. For this reason, in many countries where *Oncocyclus* occurs the species are regarded as being in need of conservation actions to stop their rapid decline and even extinction (Shmida & Pollak 2007; Saad *et al.* 2009; Solomon *et al.* 2014; Memariani & Joharchi 2017; Salimbahrami *et al.* 2021). The results of our study suggest the importance of all existing populations of the currently recognized species for conservation, as many of them can be genetically unique. Historically, the major threat to species of *Oncocyclus* was over collecting; the more recent direct threat is through destruction of the habitat by plowing, construction and overgrazing (Cohen & Avishai 2000). Safeguarding the existence of these species cannot rely solely on existing or new protected areas, but should utilize a more proactive approach via creation of new populations in areas with suitable environmental conditions. This option has proven to be a viable strategy for irises (Volis *et al.* 2010, Volis & Blecher 2021). The limited species dispersal ability, intensive collecting in the previous few centuries and the wide-range anthropogenic destruction of the natural habitat in the last century suggest that the potential ranges for the species of *Oncocyclus* are much broader than those currently occupied or those predicted by modeling based on the present occurrence of the species.

Revised section taxonomy

Although the taxonomy of the section can not be revised in full, some updates are deemed necessary based on new genetic data. Below is the proposed classification of subgenus *Iris*, *pro parte* focusing on sect. *Oncocyclus*.

Conspectus of subgenus ***Iris***, *pro parte* (= subgen. ***Arillosae*** Rodionenko)

Sect. ***Hexapogon*** (Bunge) Baker in Gard. Chron., n.s., 5: 527 (1876) — *Iris [unranked]Hexapogon* Bunge, Beitr. Fl. Russl.: 329 (1852) — *Iris* subg. *Hexapogon (*Bunge) Alef. in Bot. Zeit. (Berlin) 21: 296 (1863) — *Iris* subsect. *Hexapogon* (Bunge) Benth. in Bentham & Hooker, Gen. Pl. 3: 687 (1882). Type: *Iris falcifolia* Bunge.

1. Iris falcifolia Bunge, Beitr. Fl. Russl.: 329 (1852).
Type: Uzbekistan. “In deserto sterili inter Buchara et Kermine [Karmana]”, 26.03.1842, A. Lehmann (lectotype P01846412, designated by Boltenkov (2017: 293); isolectotypes G-BOIS00330791, K000499038, LE01017929–LE01017933, LECB00000939, P01846413, P01846414).
Herbs, 50 cm tall. Rhizome creeping, abbreviated, consisting of nutlike fragments, one such fragment developing each year, forming

dense tussocks; roots numerous, thick, covered with fibrous vestiges of leaf sheaths. Leaves subradical, falcate, 3–5 mm wide, two leaves at the base of each stem translucent, vaginate, short, three upper ones falcate, filiform-linear from a sheathing base. Spathe valves 4, scabrous, membranous-margined, the outer entire, the fourth valve minute. Flowers 2 or 3, lilac-violet. Falls with the broadly ovate claw separated from the lamina by a constriction, the upper 1/3 of the lamina horizontally spreading or reflexed. Standards spatulate-oblong, about as long as the falls, the lower 2/3 bearded with yellowish hairs. Style branches pale lilac.
Distribution: Iran, Afghanistan, Pakistan, Central Asia (deserts).


Photo by Y. Yilek

2. Iris longiscapa Ledeb., Fl. Ross. 4: 93 (1852).
Type: Uzbekistan. From Tashkent to Karak-Ata [Karakatta], 11.04.1873, Korolkow & Krause (neotype LE00050370, designated by Boltenkov (2017: 293); isoneotypes K01193734, LE00050369, LE00050371, LE00050372) = *Iris filifolia* Bunge, Beitr. Fl. Russl.: 330 (1852), non Boiss. (1842), nom. illeg.
Type: Uzbekistan. 1842, A. Lehmann (lectotype LE01017925, designated by Boltenkov (2017: 293).
Herbs, 50–75 cm tall. Rhizome creeping, abbreviated, consisting of nutlike fragments, one such fragment developing each year, forming dense tussocks; roots numerous, thick, densely covered with fibrous leaf vestiges. Leaves all radical, narrowly filiform, not falcate, 2–3 mm wide. Spathe valves 3, thinner, sometimes almost hyaline throughout or at least the margin broadly hyaline. Flowers 2 or 3, lilac-violet. Falls oblong, bearded, hairs at the middle of the beard clavate, yellow, those at the margins slender and paler. Standards narrowly spatulate, with few clavate hairs on the claw or sometimes glabrous throughout; capsule 3-angled, pointed.
Distribution: Central Asia.


Photo by N. Beshko


Photo by Z. Umarov

Sect. ***Regelia*** (Foster) Foster in Garden 43: 131 (1893) — *Iris [unranked] Regelia* Foster in Gardener's Chron., ser. 3, 4: 36 (1888) — *Iris* subg. *Regelia* (Foster) Baker, Handb. Irideae: 20 (1892). Type*: Iris korolkowii* Regel

1. Iris stolonifera Maxim., Bull. Acad. Imp. Sci. Saint-Pétersbouhrg 2: 535 (1880).
Type: Uzbekistan. Zarafshan valley, Sangy-Dzhuman canyon, 25.05.1869, O. Fedtschenko (lectotype LE 00050109; isolectotypes 00050108, 00050110 designated by Sennikov et al., PDCA : 26 (2023).= *Iris leichtlinii* Regel in Trudy Imp. S.-Peterburgsk. Bot. Sada 8: 680 (1884). Type: ["Buchara"] Plants cultivated in the private garden of M. Leichtlin, 03.1884, M. Leichtlin (holotype LE 00050074).
= *Iris vaga* Foster in Gartenflora 36: 204, tab. 1244, fig. 7 (1887).
Type: [Cultivated plants, originally sent by N.I. Korolkov from Turkestan] *Iris vaga* Foster in Gartenflora 36: 204, tab. 1244, fig. 7 (1887) (lectotype designated by Sennikov et al., PDCA 3: 26 (2023).
Herbs, 30–60 cm tall. Rhizomes very short, with long fleshy root fibers; long fleshy stolons arising from the collar through the sheaths of old leaves. Stems erect, 2 or 3- flowered. Radical leaves obsolete; cauline leaves broadly linear, 5–11 mm wide, up to 50 cm long, gradually attenuate toward apex; uppermost stem leaf not reaching the base of spathe. Lower spathe valves obtusish, the inner shorter and narrower than the outer. Falls obovate, obtuse, the base of the lamina and the claw bearded with pale violet to whitish hairs, lamina lilac with a broad bronze-colored margin, the lower part whitish or yellowish-ferruginous. Standards slightly narrower and shorter than the falls, pale lilac, undulate, the margin crisped. Style-branches pale lilac. Capsule elongate acuminate; seeds pyriform, with a milky white aril.
Distribution: Central Asia (Pamir-Alai).


Photo by A. Ebel

Photo by F. Depalle

2. Iris afghanica Wendelbo, Notes Roy. Bot. Gard. Edinburgh 31(2): 338 (1972).
Type: In declivibus borealibus jugi Salang, Hedge, Wendelbo, Ekberg (holotype GB; isotype E, W-75611).
Herbs, 13–35 cm tall. Rhizomes with short thin branches. Leaves several, falcate, green with membranous margins. Stem 1–2 flowered. Spathe 6–7 cm long. Perianth tube 2 cm long. Falls 6–9 cm elliptic oblong to elliptic-lanceolate, acute, ground color cream to white, heavily veined, purple with large dark purple blotch, with central beard of long dark hairs. Standards 6–7.5 × 1.8–2.2 cm, narrowly obovate to elliptic-obovate, subacute, pale yellow to nearly white on inner side of lower half with a central beard of rather long greenish hairs. Anthers 1.2–1.6 cm long. Style-branches 3–3.5 × 1.6–1.8 cm, obovate, adpressed to falls, with lobes 0.5 cm, rounded, spotted grey-brown. Capsule 5.5 cm long, ellipsoid, with long beak.
Distribution: NE Afghanistan.

Photo by F. Depalle

3. Iris korolkowii Regel, Trudy Imp. S.-Peterburgsk. Bot. Sada 2: 432 (1873).
Type: [Uzbekistan. Presumably near Tashkent:] “Ex horto bot. Petropolitano, [18]73, sem. m. Korolkoff” (holotype LE 00050067).
Herbs, 40–60 cm tall. Rhizome short, firm; stem 30–40 cm long, erect, branched at the end. Leaves glaucescent, the cauline ones progressively decreasing in size, linear-ensiform, slightly acuminate, nearly straight. Spathe valves herbaceous, slightly ribbed, broadly lanceolate, membranous and translucid only at apex. Flowers 2, very close to each other. Perianth tube sub cylindric, rather short. Falls lamina elliptic, abruptly narrowed into the claw, spreading, emarginate, dingy white with purple veins, claw blackish-brown within, beard hidden. Standards nearly identical to the falls; filaments blackish-brown. Style-branches oblong, brown; crests acute, bearded at the margin.
Distribution: Afghanistan, Central Asia (Tien Shan, Pamir-Alai).


Photo by A. Gaziyev


Photo by K. Walker


Photo by A. Gaziyev

4. Iris darwasica Regel in Trudy Imp. S.-Peterburgsk. Bot. Sada 8: 679 (1884).
Type: Tajikistan. "In monte Ala-Kisrak ad orientem urbis Kuljab", 7000, 06.1883, A. Regel (holotype LE).
= *Iris hoogiana* Dykes, Gard. Chron. ser. 3, 60: 216 (1916).
Type: [Cultivated plants received from "Turkestan"] *Iris hoogiana* Dykes in Gard. Chron., ser. 3, 60: 216, fig. 84 (1916) (lectotype designated by Sennikov et al., PDCA 3: 25 (2023).
= *Iris karategina* B.Fedtsch. in Komarov, Fl. USSR 4: 542 (1935), nom. inval.
Herbs, 40–60 cm tall. Rhizome short, long stolons emerging through the sheaths of old leaves and spreading in different directions. Stems 20–70 cm long, erect; radical leaves obsolete; cauline leaves broadly linear, attenuate toward apex, acuminate, the upper third membranous, tinged with red; pedicels short. Flowers 2 or 3, entirely blue or lilac-violet or sometimes whitish. Perianth tube 2.5 cm, purple-tinged. Falls obovate, gradually narrowed into the claw, the beard prominent, yellow, spreading partly onto the lamina and not confined to the claw, gradually enlarged from base. Standards with dark beards, similar in size and shape to the falls. Style-branches not differing in color from perianth segments. Capsule elongated, pointed at the top. Seeds pyriform, brown, with a milky white aril.
Distribution: Afghanistan, Central Asia.


Photo by F. Depalle

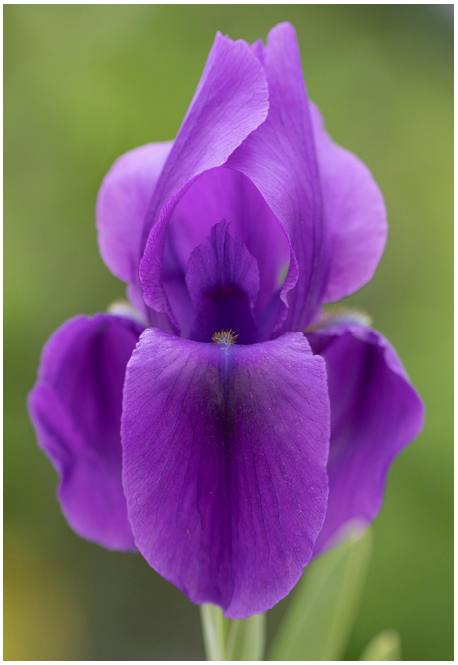


Photo by F. Depalle

5. Iris suworowii Regel in Trudy Imp. S.-Peterburgsk. Bot. Sada 9: 619 (1886); Regel in Gartenflora 35: 397 (1886).
Type: Tajikistan. “In montibus Kuh-i-Frusch”, “1883”, “A Regel” (lectotype LE 00050118, designated by Sennikov et al., PDCA 3: 27 (2023).
= *Iris lineata* Foster ex Regel in Gartenflora 36: 202 (1887).
Type: [Cultivated plants] *Iris lineata* in Gartenflora 36: 201, tab. 1244, fig. 1–6 (1887) (lectotype designated by Sennikov et al., PDCA: 27 (2023).
Herbs, 20–40 cm tall. Rhizome short, often giving rise to short stolons. Stems erect,
bearing 2 or 3 terminal flowers, surrounded at base with fibrous vestiges of old leaves. Leaves nearly all cauline, broadly linear, attenuate toward apex, slightly recurved, ca. 15–20 × 0.5 cm. Spathe valves carinate, acuminate, the upper one-third membranous; pedicels short. Perianth tube 2.5–4 cm long. Falls lamina obovate, gradually narrowed into the claw, intensely brownish-violet or brown as a whole, with brown or bluish-violet veins, the beard spreading onto the lamina, bluish-violet (in violet forms) or white (in brown forms). Standards the same color as the falls, rather abruptly narrowed into a very narrow claw. Style-branches not differing in color from perianth segments; crests lanceolate, long-acuminate.
Distribution: Afghanistan, Central Asia.


Photo by A. Ebel


Photo by O. Fragman-Sapir

5. Iris heweri Grey-Wilson & B.Mathew in Kew Bull. 29: 67 (1974).
Type: Afghanistan, Kattaghan, Khinjan Grey-Wilson, Hewer 769 (K, isotypes E. GB, W).
Herbs, 15–20 cm tall. Rhizomes brown, stoloniferous. Leaves 4–7, falcate with membranous margins, pale to mid green. Scape 4–10 cm long. Spathe 3–7 cm long. Flowers 5 cm in diam. Perianth tube 1.5 cm long. Falls 3.5–4.5 × 1.25–1.5 cm, half whitish, veined deep purple blue, blade deep purple-blue. Standards erect, deep or mid blue-purple, with a little pale whitish purple beard in the lower half. Style-branches mid or pale purple-blue. Stamens, filaments pale purple-blue; anthers white. Capsule 3.5 × 1.5 cm.
Distribution: NE Afghanistan.

Sect. ***Khorassanica*** Volis & F.O.Khass. sect. nova.
Plants in dense tufts. Rhizome short, horizontally creeping with fibrous remains of leaf sheaths. Stem 1-flowered. Falls with dense central beard of many long white and yellowish-tipped hairs reaching from base to the middle. Standards with hairs near the base not reaching to the middle.
Type: *Iris ferdowsii* Joharchi & Memariani.

1. Iris ferdowsii Joharchi & Memariani in Phytotaxa 291(3): 193 (2017).
Type: Iran, Razavi Khorassan: N Mashhad, south of Sandoq-Shekan pass, Gol-Khow, 1783 m, 5 May 2014, n. 45170 Joharchi (holotype FUMH!; isotype W!).
Herbs, (8–)10–20(–25) cm tall, forming small dense tufts. Rhizome short, horizontally creeping with fibrous remains of leaf sheaths. Leaves (4–)5(–6), basal, ± falcate, 6–10(–20) × 0.3–0.6(–0.8) cm, green to greyish-green, glabrous. Stem (3–)5–10(–15) cm, erect, 1-flowered. Spathe with 2 valves, 4.5–5.5(–7) cm, acuminate, green suffused with purple, membranous-chartaceous, with narrow hyaline margin, glabrous. Perigone tube 2.5–3.5 cm. Falls 4–5 × 1.7–2.2 cm, elliptic-oblong, sharply reflexed, cream-colored, heavily veined purple with a large dark-purple blotch in the upper half, bearing a dense central beard of many long white and yellowish-tipped hairs reaching from base to the middle. Standards 4.5–5 × 2.5–3 cm, obovate to spatulate, purplish with darker veins, with a distinct narrow claw up to 1.2 cm long, bearing a central beard of hairs near the base not reaching to the middle. Anthers 1.2–1.5 cm long, whitish. Filaments 1.2 cm long, whitish, purplish at base. Styles 3.5–4 × 1.3–1.5 cm, obovate, cream-colored purplish-tinged, obovate, with lobes ca. 1 cm x 0.8–0.9 cm. Capsules 3.5–5.5 × 1.3–1.5 cm wide, provided with an apical and short (up to 2 mm long) beak. Seeds 5–6(–8) × 3(–4) mm, ovoid, shiny brown, with rugose testa surface, topped with a distinct ring-shaped and cream-colored aril.
Distribution: Iran (Khorassan province).


Photo by F. Depalle

2. Iris kuschkensis Grey-Wilson & B.Mathew, Kew Bull. 29(1): 67 (1974).
Type: Afghanistan, Herat province, 34.5 miles N

of Herat, road to Kusck, 4100 ft, damp soil, 16.04.1971, Grey-Wilson & Hewer (K000464980, isotyoes E!, GB!, W!).
Herbs, 20–35 cm tall. Rhizomes in clumps, 30–40 cm across. Leaves upright, pale green. Scape 1-flowered. Spathe pale green. Falls 5 cm long, red purple with a purple beard. Standards 4–4.4 cm long, reddish-purple, with a purple beard, in the lower half. Style-branches pale purple. Anthers pale purplish-white. Capsule 5.5 cm long.
Distribution: NW Afghanistan.
Note: This species can be treated as in-between this newly described section and section *Regelia*.

Sect. ***Oncocyclus*** (Siemssen) Baker in Gard. Chron., ser. 3, 5: 787 (1876) = *Oncocyclus* Siemssen in Bot. Zeitung (Berlin) 4: 706 (1846) = *Iris* subg. *Oncocyclus* (Siemssen) Alefeld in Bot. Zeit. 21: 296 (1863) = *Iris* ser. *Acutilobae* Gavr., Zametki Sist. Geogr. Rast. 41: 74 (1986) = sect. *Sofaria* Chaudhary Bot. Not. 128(4): 401 (1975) nom. inval. = sect. *Bostris* Chaudhary, Bot. Not. 128(4): 401 (1975) nom. inval.
Type: *Iris paradoxa* Stev. (lectotype designated by Lawrence (1953: 355).

1. Iris demawendica (Bornm.) (Bornm.) Dykes, Gen. Iris 123 (1913) = *Iris acutiloba* subsp. *demawendica* (Bornm.) Bornm., Repert. Spec. Nov. Regni Veg. 47: 74 (1939) = *Iris barnumiae* subsp. *demawendica* (Bornm.) B.Mathew & Wendelbo, Fl. Iranica 112: 35 (1975).
Type: Persia borealis, m. Elburz, jugo Ladd, 250-2600 m, 04.06.1902, n. 8279, Bornmuller (holotype K 000464993).
Leaves 0.3–0.7 cm long, erect. Falls 3.4–7 × 2–3.8 cm. Standards 4–4.8 × 2.2–4.8 cm. Style-branches 3–5.6 × 1–1.2 cm.
Distribution: Iran.


Photo by F. Depalle

Photo by F. Depalle

2. Iris acutiloba C.A.Mey. in Verz. Pfl. Casp. Meer.: 32 (1831) = *Iris fominii* Woronow ex Grossh. Fl. Kavkaza 1: 285 (1928).
Type: In collibus siccis prope Baku, n. 74, 07.04.1830 (holotype LE!).
Herbs, 8–25 cm tall. Rhizomes small, thick and compressed, with many branches; in clumps. Leaves 10 × 0.2–0.6 cm, narrow, slender, curved or falcate, glaucous, grey green. Stem 1-flowered. Spathes 5–8 cm long. Perianth tube 1.5–2 cm long. Flower 5–8 cm long, cream, creamy white, whitish, pale brown, light grey, to pale violet, streaked or heavily veined with brown, brown black, grey, purple, or purple-brown. Falls reflexed, pointed or lanceolate, 4–7 cm long, marked with large dark red-brown, blackish, purple-violet or dark purplish-brown spots or deep purple signal patch, in the middle with sparse row of short brown beard hairs. Standards acute, pointed, larger than the falls, 4–8 cm long, unspotted. Style-branch 2–5 cm long, with brown spots.

Distribution: Caucasus (Azerbaijan, Dagestan).

Photos by F. Depalle

3. Iris lineolata (Trautv.) Grossh., Fl. Kavkaza, ed. 2, 2: 221 (1940) = *Iris acutiloba subsp. lineolata* (Trautv.) B.Mathew & Wendelbo in Rechinger Fl. Iranica 112: 32 (1975) = *Iris acutiloba* var. *lineolata* Trautv. in Trudy Imp. S.-Peterburgsk. Bot. Sada 1: 24 (1870).
Type: Azerbaijan. "Prope Diabar", 05.1870, G. Radde (holotype LE).
= *Iris ewbankiana* Foster in Gardener's Chron., ser. 3, 29: 397, fig. 152 (1901).
Type: Described from the Kopetdag Mts. on the border of Iran and Turkmenistan ("from the mountain range which separates Persia from Trans-Caucasia, 120 versts to the west of Askabad") not designated.
= *Iris grossheimii* Woronow ex Grossh. in Fl. Kavkaza 1: 255 (1928).
Type: Province Nachitschevan, prope pagum Sojuh, culta in sect. Cauc. 30.04.1925. E. Koenig (lectotype TBI designated by Gabryelan 2011: 133).
Distribution: Caucasus (Nachitschevan).
= *Iris helenae* C.Koch in Wochenschr. Gartn. Pflanzenk. 13: 179 (1870), "Helena" = *Oncocyclus helenae* C. Koch in Linnaea 21: 639 (1848), nom. inval.
Type: "Helena". Described from Azerbaijan ("Helenendorf" = Göygöl) destroyed at B.
Herbs, 20–35 cm tall. Rhizome short, creeping. Stem 1-flowered. Leaves narrowly linear, subfalcate, not exceeding the stem. Spathe valves to 15 mm, cylindric. Falls lanceolate, acuminate, distinctly veined with brownish-purple on a milky white ground, the limb horizontal and not reflexed as in related species. Standards obovate-lanceolate, veined with brownish-purple on a milky white ground, the claw sometimes covered with few yellow brown-tipped hairs. Style-branches short, chocolate-brown; crests quadrate, with slender brownish-purple veins. filaments brownish-purple. Capsule cylindric, narrowed at both ends.
Distribution: Azerbajan, ?Turkey, Iran, Central Asia (Kopetdag).


Photo by S. Banketov


Photo by F. Depalle

4. Iris longitepala (B.Mathew & Zarrei) Volis & F.O.Khass. comb. nov. Basionym *Iris acutiloba subsp. longitepala* B.Mathew & Zarrei in Bull. Brit. Iris Soc. Spec. Group 2008/9: 23 (plates 10-11) (2009).
Type: Iran, on the road from Manjil towards Zanjan, after Gilvan, Sorkeh Dizaj mountains, 1753 m, 05.11.2005, Zarrei et al. s.n. (tuh-e bot. exp.) (holotype TUH!).
Herbs, 18–22 cm tall. Rhizome slender, branching to produce compact, tufted plants. Leaves 4–5, 3–4 mm wide, falcate to suberect, greyish-green with a membranous margin. Stem 10–15 cm long. Spathe valves 8.0–8.5 cm long, pinkish-tinged. Flowers with a creamy-white ground color overlaid with brown veining; perianth tube 2.0–2.5 mm long. Fall 8.5–9.0 × 2.0–2.2 cm, oblong-lanceolate, acute, with a sparse central beard of long cream-colored hairs tipped brown and a central reddish-brown or purplish-brown signal patch. Standards 8.0–9.0 × 2.0–25 cm, oblanceolate, acute with a short narrow claw at the base. Style-branches 3.4–4.0 × 1.5 cm wide, elliptic-oblong, bilobed at apex, lobes crenulated, 7–8 × 7–8 mm. Stigma bilobed, finely crenulated.
Distribution: NW Iran.


Photo by Zein et Carlo


Photo by F. Depalle

5. Iris iberica M. Bieb., Fl. Taur.-Caucas. 1: 30 (1808).
Type (lectotype, designated by Kuthatheladze 1971: 16 as “type”):—GEORGIA. *Iris iberica* Stev. Iberia, [fl.], [April 1805], [Steven] s.n. Herb. Hoffmann No. 414 (MW0021788!).
Herbs, 15–20 cm tall. Rhizome slender, creeping, not stoloniferous. Stem 1-flowered. Leaves 4–6, glaucescent, narrowly linear, subfalcate, not exceeding the stem. Spathe valves lanceolate, acute, carinate, herbaceous-membranous. Flowers 10–15 cm long. Perianth tube cylindric, 2–3.5 cm long. Falls 3.5–6.5 × 2.7–6.5 cm, at first horizontal, finally recurved, spoon-shaped or obovate, distinctly concave, the limb orbicular to rounded-oblong, the limb with a triangular purplish-black patch on a whitish-yellow ground, the margin densely netted-veined with purple, the

claw broad, beard hairs, purplish-black. Standards 4.5–10 cm long, often narrower than falls, connivent, much lighter in color than the outer segments, the limb orbicular, the claw short. Style-branches as long as the fall, recurved, strongly convex, dark purplish-brown at base, fading toward apex to almost milky white with brownish-purple veins. Filaments pale purple; anthers milky. Capsule 7–9 x 2–2.5 cm, 3-angled ellipsoid.
Distribution: Georgia, Azerbaijan, Armenia, Turkey.

Photo by F. Depalle

Photos by F. Depalle

6. Iris paradoxa Steven in Mém. Soc. Imp. Naturalistes Moscou 5: 355 (1817) = *Iris annae* Grossh. in Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 13: 4 (1950).
= *Oncocyclus paradoxus* (Stev.) Siemss. in Bot. Zeit. 4: 705 (1846).
Type: (lectotype, first step of designation made by Fedtschenko 1935: 539, second step by Wendelbo & Mathew 1975: 30):—GEORGIA. *Iris paradoxa* m., in Iberia, [fl.], [1805], [Steven] s.n. (H1051971 [the specimen under No. 1051971; Fig. 6]).
= *Iris paradoxa* f. *choschab* (Hoog) B.Mathew & Wendelbo in Fl. Iranica 112: 31 (1975) = *Iris paradoxa* subsp. *choschab* (Hoog) Güner in e-Fl. Turkey, (Iris): 66 (2021).
Herbs, 10–40 cm tall. Rhizome compact, not stoloniferous. Leaves 4–6, falcate, greyish-green, 0.2–0.5 cm wide. Perianth tube 1.5–3 cm. Falls oblong, 2.5–4 × 1–1.5 cm, truncate at apex, with revolute margins, upper surface almost entirely covered with a dense blackish-purple, or violet, rarely golden-brown beard, ground color usually dark purple or violet, with a pale V-shaped mark in center and white marks at apex, sometimes also on margins. Standards broadly obovate, 5–9 × 3.3–6 cm, brown-purple, often strongly veined, deep violet, apex emarginate. Style-branches whitish to golden-yellow spotted brown, or dark purple, 2.1–3 × 1.1–1.5 cm with short crenulate erect lobes, 0.3–0.4 × 0.4–0.6 cm.
Distribution: Iran, Azerbaijan, Georgia.

Photos by F. Depalle


Photo by F. Depalle

7. Iris medwedewii Fomin in Věstn. Tiflissk. Bot. Sada 14: 43 (1909).
Type (lectotype, designated by Boltenkov & Guner Phytotaxa 468 (1) 2020: 050): — AZERBAIJAN. [Lerik Rayon], *Iris medwedewii* Fomin. Prov. Baku, distr. Lenkoran, prope pag. Kosmaljan, Suvant [Zuvand District], [fl.], 15 May 1908, Schelkownikow s.n. (TBI1025368! E00373764 [photo!]).
= *Iris paradoxa* var. *choschab* Hoog, Gard. Chron., ser.3,29:104 (1901).
Herbs, 30–45 cm tall. Rhizome short, creeping. Stem erect, bearing a solitary terminal flower. Leaves several, narrowly linear, subfalcate, not exceeding the stem. Spathe valves lanceolate, acute, carinate, herbaceous-membranous. Perianth tube slightly shorter than ovary. Falls linear, horizontally spreading, the claw densely covered with blackish-purple hairs, its margin veined blackish-purple, the rather small suborbicular blackish-purple limb often point-tipped. Standards much larger than the falls, subtruncate, irregularly toothed-margined, white, densely veined azure-violet, concave within, carinate outside, with scattered hairs at base. Anthers pale yellow. Style-branches shorter than the outer perianth segments, brown, spotted cinnamon-brown, the margins revolute. Style crests short, rounded.
Distribution: Azerbaijan (Lenkoran), Iran,Turkey.
Note: *I. medwedewii* was proved to be a separate species closer to *I. meda* than to *I. paradoxa*.

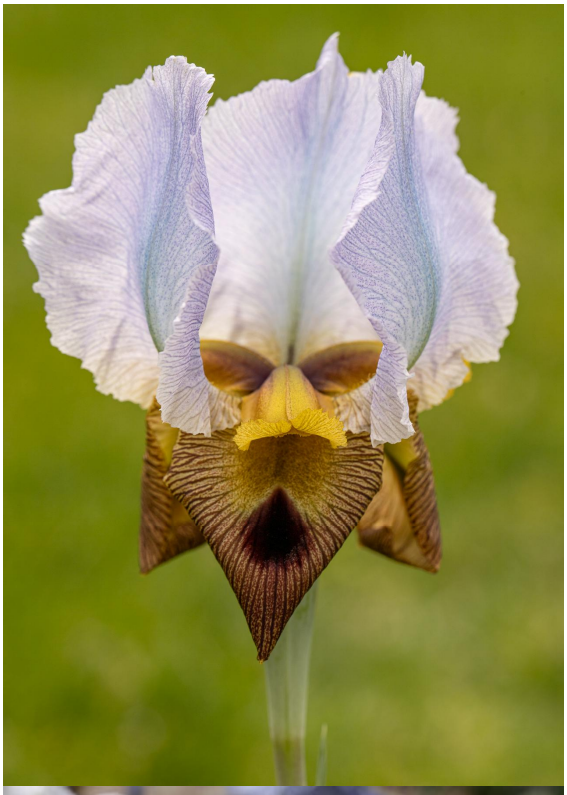

Photo by F. Depalle

Photo by F. Depalle

8. Iris × camillae Grossh., Grossheim & Schischkin, Sched. Pl. Or. Exsicc. Fasc. 40: 40 (1928).
Type: Lake Kazangel, Grossheim (holotype LE!).
Herbs, 20–40 cm tall. Rhizome short, creeping. Stem 1-flowered. Leaves 20–40 cm, narrowly linear, subfalcate, not exceeding the stem. Spathe valves lanceolate, acute, carinate, herbaceous-membranous. Flowers 6–9 cm. Perianth tube slightly longer than ovary. Falls short-ligulate, broadly obovate, deflexed, slightly narrowed at apex, pale yellow or azure-violet, sometimes with a violet patch; hairs of claw yellow. Standards the same size as but slightly broader than and same color as falls, erect. Style-branches recurved.
Distribution: Lesser Caucasus (Azerbaijan).

Photo by Y. Pirogov

Photo by F. Depalle



Photos by F. Depalle

9. Iris × schelkownikowii (Fomin) Fomin in A.V.Fomin & G.J.N.Woronow, Opred. Rast. Kavk. 1: 299 (1907).

Type: Habitat in collibus aridis Karadzha-dagh prope jugum Bos-Dagh, Trancaucasia orientalis secum ripam sinistrum Cyri, Schelkovnikov, 27.03.1909 (holotype TBI!, isotype LE!).

Herbs, 20–35 cm tall in small clumps. Rhizome short, creeping. Stem erect, bearing a solitary terminal flower. Leaves narrowly linear, subfalcate, not exceeding the stem. Spathe valves lanceolate, acute, carinate, herbaceous-membranous. Flowers 8–10 cm long. Perianth tube rather long. Falls reddish-purple blotch, or purple signal patch, oblong-lanceolate, acute, much smaller than standards, brown, with a round purple patch at center and purplish-lilac veins, the hairs of the claw yellow. Standards oval-oblong, acutish, violet or bluish-violet, with slender dark veins. Style-branches, brown.

Distribution: Azerbaijan.

Photos by F. Depalle

10. Iris meda Stapf in Denkschr. Kaiserl. Akad. Wiss., Wien. Math.-Naturwiss. Kl. 50: 20 (1885) = *Iris fibrosa* Freyn in Bull. Herb. Boissier 4: 182 (1896).

Type: In collibus ad Kabutarschan, 16.05.1882 (holotype WU!).

Herbs, 5–15 cm tall. Rhizomes stout, compact. Leaves 4–7, 0.15–0.4 cm wide, falcate to erect, grayish green with a narrow, inconspicuous membranous margins. Spathe valves 4–7 cm long, greenish. Perianth usually cream or whitish, rarely very pale, or yellowish, veined and edged, brown or brown-lilac. Perianth tube 2–3 cm long. Falls 3.2–5 × 1.5–2.1 cm, obovate, obtuse, often revolute at apex, with a large brown or brown-purplish spot in center, claw with a dense rather narrow beard of long usually yellow hairs rarely tipped with purple or brown along center. Standards 3–6 × 1.1–2.5 cm, obovate, obtuse, rounded at apex, narrowed to a short claw, at base, margin usually undulate. Anthers 1–1.4 cm; filaments 0.8–1 cm. Style-branches 2–3 × 0.9–1.5 cm, obovate to oblong, elliptic with reflexed, crenulate lobes 0.5–1.1 × 0.5–1 cm, stigma entire, shallowly bilobed.

Distribution: Iran.

Photos by F. Depalle

11. Iris pseudomeda Salimb. & H.Saeidi in Phytotaxa 527: 76 (2021).

Type: IRAN. Kurdistan province: Divandarreh, Zarrineh rural district, 2140 m, 26 May 2019, Saeidi & Salimbahrami 23404 (holotype HUI!; isotypes HUI!).

Herbs, 8–15 cm tall, forming small bunches sitting very close together. Rhizomes short and knobby, creeping horizontally with very slender roots. Leaves 4, basal with transparent leaf sheaths, straight but nearly curved only in longer ones, 0.2–0.3 cm wide, greyish green, glabrous, with shiny hyaline and smooth margin. Stem (5–)7–9(–10) cm long, erect, 1-flowered. Spathe with 2 valves, green, swollen, 4–5.5 cm, acuminate, glabrous, membranous at the edge and broadly membranous at the tip. Flower 3–5 cm, brownish. Perianth tube 1–3 cm. Falls 3.5–4 × 0.8–1.5 cm, blunt elliptic, minutely crenulate, reflexed at the inconspicuous wing-like parts, brown at the upper half and shiny yellow at lower half, heavily veined by darker brown with purple

signal blotch downright above the beard (purplish patch spread on upper half and amalgamated by the ground color), bearing long white hairs in a bushy form at the middle of falls to the base. Standards 3.5–4 cm long, 0.5–1 cm wide, oblong to spatulate with almost the same ground color in upper and lower parts as falls, strongly veined darker brown, both crenate and undulate. Anthers 1.3–1.5 cm, whitish. Filaments 1.3–1.5 cm, whitish. Style-branches 1.5–2 × 0.8–1.5 cm, obovate, crenate, golden yellow intensely dotty (in a way seen as brownish inside). Stigma crenate, narrowly reflexed at the highest edges, with rounded crests and superficially bilobate. Immature capsule spindle-shaped, 2 cm long.
Distribution: Iran.
Note: In protologue it was mentioned that the species is most similar to *I. meda*, but genetically it is most close to *I. urmiensis*.

Photos by F. Depalle

12. Iris urmiensis Jekyll & E.T.Cook in Garden (London, 1871-1927) 57: 471 (1900) = *Iris barnumiae* f. *urmiensis* (Jekyll & E.T.Cook) B.Mathew & Wendelbo in Fl. Iranica 112: 34 (1975).

Type (neotype, designated by Boltenkov & Guner Phytotaxa 468 (1) 2020: 052): — TURKEY. Hakkari Province, Yüksekova, Esendere, north sides, steppe, metamorphic hillsides, 1750–1850 m, [fl.], 31 May 1978, A. Güner 1716 [originally in Turkish] (HUB004501! [Fig. 5], isoneotypes AEF!, ANK!, GAZI!, K001291624!).

= *Iris chrysantha* Baker in Bot. Mag. 127: t. 7784 (1901).

Type: "Native of Persia?". Type (lectotype, designated by Boltenkov & Guner Phytotaxa 468 (1) 2020: 045):—[icon] "*Iris chrysantha*" in Baker, Bot. Mag. 127: t. 7784 (1901).

Note: Close to *I. barnumae* differing in perianth pale to deep yellow and beard of falls with yellow hairs.

Distribution: Iran, Turkey

Photo by C. Russell

Photos by F. Depalle

13. Iris barnumiae Foster & Baker in Gard. Chron., ser. 3, 4: 182 (1888) = *Iris barnumiae* f. *protonyma* (Stapf) B.Mathew & Wendelbo in Fl. Iran. 112: 34 (1975)

= *Iris polakii* f. *barnumiae* (Baker & Foster) Stapf in Bot. Mag. 155: t. 9279 (1932). Type (lectotype, designated by Wendelbo & Mathew 1975: 34, as "typus"):—[Specimen from a cultivated plant], [Label handwritten by M. Foster]: Iris Barnumi sp. n. mihi; [handwritten on the sheet]: Iris Barnumi M. Foster. Type specimen of Bot. Mag. t. 7050! Armenia, Van. From Prof. Michael Foster, [fl.], 1 June 1888, s.coll. s.n. (K000464997!).

Herbs, 10–30 cm tall. Leaves 4–6, falcate, erect, 0.1–0.5 cm wide. Flowers deep purple-violet, or yellow, not markedly veined. Perianth tube 1–3.5 cm long. Falls elliptic, to obovate, 3.5–6.5 × 1.3–5 cm, rounded to obtuse, or subacute, with a narrow median beard of yellow or cream sometimes tipped purple. Standards obovate, to elliptic or orbicular 4.3–8 × 2.5–5 cm. Style-branches elliptic-oblong, 2.7–4 × 1.5–2.4 cm with expanded crenulate lobes, 0.8–1.2 × 1 cm. Capsule ellipsoid 5.7–7cm long.

Distribution: Turkey.

Photo by O. Peri

14. Iris lycotis Woronow in Izv. Kavkazsk. Muz. 9: 35 (1915) = *Iris iberica* subsp. *lycotis* (Woronow) Takht. in A.L.Takhtajan & A.A.Fedorov, Fl. Erevana: 330 (1972).
Type: Type (lectotype designated by Wendelbo & Mathew 1975: 29 as "Typus"):—Azerbaijan. [Nakhchivan Autonomous Republic], *Iris lycotis* n. sp. Prov. Erivan, distr. Nachičevan, Montes Darry-dagh, [fl.], 23 May 1914, G. Woronow s.n. Exs. No. 13764 (LE01010445! [E00373767! & K! – photos], isolectotypes BAK No. 57898!, BM000832606!, ERE0000421!, ERE0000422!, LE01010444!, TGM No. 205 [E00373766! & K! – photos], TGM No. 206 [E00373765! – photo], TGM No. 8669, TGM No. 8670).
Herbs, 15–30 cm tall. Rhizome compact, not stoloniferous. Leaves 4–6, falcate, greyish-green, 0.2–0.6 cm wide. Perianth tube 2–3.5 cm long. Falls broadly elliptic to orbicular, 2.7-3.5–8.5 x 2.7-6.5 cm, often emarginate, strongly veined, and heavily spotted, brownish-purple on a white ground, with an orbicular blackish or dark brown signal spot in center and sparsely to densely bearded on claw, with a wide band of long purplish-brown hairs. Standards orbicular 4.5–11 × 3.5–8.4 cm pure white or heavily veined and spotted, pure white or brown or purple sometimes densely as falls. Style-branches 3.5–7 × 1.2–2.5 cm, with erect or reflexed crenulate lobes. 0.8–2.5 × 0.7–2 cm. Capsule fusiform 7–9 × 2–2.5 cm.
Distribution: Iran, Azerbaijan, Armenia, Turkey.
Note: The previously considered closely related or synonymous to this species *I. iberica* Steven was found to be genetically very different species.

Photos by F. Depalle

15. Iris polakii Stapf in Denkschr. Kaiserl. Akad. Wiss., Wien. Math.-Naturwiss. Kl. 50: 20 (1885) = *Iris barnumiae* f. *protonyma* (Stapf) B.Mathew & Wendelbo in Fl. Iranica 112: 34 (1975) nom. inval. Type (neotype, designated by Boltenkov & Guner Phytotaxa 468 (1) 2020: 051): —[Specimen from a cultivated plant]. [Label handwritten by O. Stapf]: *Iris polakii protonyma*, Stapf. Exper. Ground, Kew, Bot. Mag. t. 9279, [fl.], 24 May 1929, s.coll. s.n. (K000464994!).
Distribution: Iran.

16. Iris elegantissima Sosn. in Věstn. Tiflissk. Bot. Sada 36: 2 (1915) = *Iris iberica* subsp. *elegantissima* (Sosn.) Fed. & Takht., Fl. Erevana ed. 2, 331 (1972).
Type (lectotype designated by Wendelbo & Mathew 1975: 30 as “Typus”):—TURKEY, [Erzurum Province], [Information handwritten by E. Koenig]: Prov. Kars. Prope pag. Olty in rupestribus, [fr.], 4 June 1904, E. Koenig s.n.; Information handwritten by D. Sosnowsky]: *Iris elegantissima* Sosn. (TBI1039016!). Syntypes:—TURKEY. [Erzurum Province], [Printed label handwritten by D. Sosnowsky]: *Iris elegantissima* m., [Prov. Kars. Distr. Olty], Inter p. Tedžerek et Toprach-Kala, in collibus siccis argillosis, [fl.], 29 May 1912, D. Sosnowsky s.n., [Label handwritten by E. Gabrielian]: [Lectotypus], 9 November 1997, E. Gabrielian (TBI1025357!); [Printed label handwritten by D. Sosnowsky]: *Iris elegantissima* m., [Prov. Kars, Distr. Olty], prope p. Olty, in collibus siccis, [fl.], 15 May 1912, D. Sosnowsky s.n. (TBI1039017!);

[Printed label handwritten by D. Sosnowsky]: *Iris elegantissima* m., [Prov. Kars, Distr. Olty], prope p. Katrys, in agris, [fl.], 25 May 1912, D. Sosnowsky s.n. (TBI1025358!).

Herbs, 15–30 cm tall. Rhizome compact, not stoloniferous. Leaves 4–6, falcate, greyish-green, 02–06 cm wide. Perianth tube 2–3.5 cm long. Falls broadly elliptic to orbicular, 2.7-3.5–8.5 × 2.7–6.5 cm, often emarginate, strongly veined, and heavily spotted, brownish-purple on a white ground, with an orbicular blackish or dark brown signal spot in center and sparsely to densely bearded on claw, with a wide band of long purplish-brown hairs. Standards orbicular 4.5–11 × 3.5–8.4 cm pure white or slightly veined at the base, pure white or brown or purple sometimes densely as falls. Style-branches 3.5–7 × 1.2–2.5 cm, with erect or reflexed crenulate lobes. 0.8–2.5 × 0.7–2 cm. Capsule fusiform 7–9 × 2–2.5 cm. Seeds ca. 5 mm, with a wide large aril.

Distribution: Turkey, Armenia, Iran.

Note: DNA shows separate position of this species from *I. iberica*, moreover, samples from Iran also represent a different species to be described in the future.

Photos by F. Depalle

17. Iris gatesii Foster, J. Roy. Hort. Soc. 11: 144 (1889).
Type: (neotype, designated by Boltenkov & Guner Phytotaxa 468 (1) 2020: 046):—TURKEY. [Mardin Province], *Iris gatesii* Foster, Mardin, 5 km east of Mardin, around Bakırkır, north facing slopes, among vineyards, c. 1050 m, [fl.], 21 May 1978, A. Güner 1697 [originally in Turkish] (HUB004500! – two sheets [Fig. 1], isoneotypes AEF No. 7218!, K!).
Herbs, 40–50 cm tall. Rhizome stout, compact. Leaves 5–7, greyish-green, ca 1 cm wide. Perianth tube 3–6 cm long, segments minutely spotted, and finely veined, reddish-brown, brownish-purple, or nearly black on a whitish or creamy-yellow ground. Falls broadly obovate-elliptic, 8–11 × 4–8 cm, with a small median brown or blackish signal spot, bearded in lower half, with a broad band 2–2.5 cm wide of long yellowish or brown-purple hairs. Standards broadly obovate to orbiculate 8–9.5 × 5–9 cm. Style-branches 5–7 × 2 cm, with reflexed lobes, 1.5–2 × 1.5 cm. Capsule ellipsoid, acute, 7.5 × 2.5 cm, Seeds ca 1 cm, rugose, with a large white aril.
Distribution: Iraq, Turkey.

Photos by F. Depalle

18. Iris kirkwoodiae Chaudhary in Bot. Not. 125: 499 (1972).
Type: Type (holotype):—SYRIA. *Iris kirkwoodii* Chaudhary. North Syria, Bishmishly, [fl.], 19 April 1972, S. Chaudhary & Kirkwood 787 (BEI!).
Herbs, 50–60 cm tall. Rhizome stout, compact. Leaves 6–7, rather grassy-droopy, up to 1.5 cm wide, 30 cm long, pale green. Stem leaves one or two with one or two internodes showing through or above the basal leaves; peduncle length usually 25 cm or more. Flowers 15 cm tall, 8–10 cm wide; valves tightly clasping, not inflated, 11 cm. Perianth tube 2.5–3 cm. Falls 6–8 × 4–5 cm, ovate-orbiculate, often strongly recurved, embossed with dark purple veins and fine dots densely scattered on a pale greenish or white, clear ground, the spots larger and denser below and to the sides of the signal spot; the signal spot

orbicular, sometimes ovate, 1.5–2 × 1.5 cm; beard of long, maroon-purple or rusty-brown hairs. Standards 8.5 × 6–7.5 cm, orbicular-ovate, abruptly clawed with the claw channeled, 1 cm long. Standards with fine bluish-purple veins and dots on a clear pale blue ground, the dots and veins embossed only near the base and along the midrib. Anthers 2–3.5 cm, purple-backed; filaments 1.2–2 cm long, purple-dotted. Style-branches 7 cm long, including the lobes, 3-4 cm wide, dark maroon in the middle, dark purple to the sides, ridge keeled, the ridge prominent; the lobes minutely serrate, turned upwards; the width of the two lobes greater than the width of the style branches; lobes with fine embossed veins and very fine dots like the falls. Pods 9 cm, cylindrical, not lobed, the veins thick, prominent, raised above the surface or level with it. Ovary 3–5 cm long, almost terete or slightly trigonal with a stalk 0.5 cm long.
Distribution: Syria, Turkey.


Photo by F. Depalle

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19. Iris cedreti Dinsm. ex Chaudhary in Bot. Not. 125: 497 (1972).

Type: Lebanon, vicinity of Cedars of Lebanon, May 1972, Chaudhary, Chaudhary & Weymouth 789 (holotype BEI!).

Herbs, rarely exceeding 40 cm tall. Rhizome medium, compact, light yellow. Leaves 8 or 9, 1–2 cm wide, narrowed to the tip; stem leaf none or one. Flowers 18 cm from the base of the valves, up to 9 x 10 cm, reaching to the level of the falls, inflated, green. Perianth tube 2.5–3 cm long. Falls 6.5–9.5 × 4.5–5.5 cm, ovate, narrowed to the lip, finely crenate-irregularly serrate, the ground clear, white to lead-white; veins very fine, embossed, densely arranged (10–13 per cm), dark-maroon to maroon-purple; dots very fine, more embossed around the signal spot and the area above this level; dots on falls larger in darker biotypes, anastomosing so closely that dots form ground and ground appears as irregular white spots; signal spot orbiculate, 1.7–2 × 1.5 cm, nearly in middle of fall, dark maroonish purple; beard of sparse hairs, hairs rusty brown, pink, purple or mottled on pale green ground. Standards 8.5–11 × 6–6.5 cm, obovate, clawed, claw about 1.5 cm long, channeled; ground characteristically white to leaden white; veins very fine purplish dark maroon, rather embossed, parallelly densely arranged (13–20 per cm); dots fine, sparse near margin, larger and sparse in central area, finer and denser in lateral zones; inner and outer faces of standard with distinctly different shades; inner face dominated by white to leaden white ground, outer face dominated by purplish dark maroon. Stamens 3.5–4 cm long; anthers usually more than twice as long as filaments, creamy white or sometimes purple dorsally. Style branches 5.5–6 × 2 cm, strongly arched along arch of fall (the latter contributing only to floor of pollinator tunnel), strongly narrowly keeled, keel with small ridge, maroonish purple; lobes 1 × 1 cm, 2 lobes not wider than style branch; lobes upturned, veined and spotted like falls. Pod 8 cm long, inflated, lobed, narrowed towards both ends. Ovary 3.3 cm long, triangular, 6-lobed; ovary stalk 0.5 to 1 cm long.

Distribution: Lebanon

Photos by F. Depalle

20. Iris antilibanotica Dinsm., Post, Fl. Syria, Palest. & Sinai, ed. 2, 2: 599 (1933).
Type: Syria, above Bludan, May 19--. West (holotype, Dinsmore Herbarium?).
Herbs, 25–40 cm tall. Rhizome compact, up to 2 cm long, stoloniferous. Leaves 7 or 8, semi-evergreen, green, falcate (sickle shaped), 15–20 cm long, 1–1.5 cm wide, 2/3 of the stem. Stem slender or peduncle. Spathe inflated, 10 cm long. Perianth tube 4.5 cm long. Flowers are bicolored. Standards paler than the falls. The falls 4–8 × 5 cm, dark purple, or violet with darker veins. Signal small blackish, short hairs of yellow beard, sometimes purple tipped. Standards 6–10 × 8 cm wide, pale violet or purple, with dark veins. Style branches brown strongly keeled, similar color to the falls.
Distribution: Lebanon, Syria.


Photo by T. Fietz


Photos by F. Depalle

21. Iris damascena Mouterde, Nouv. Fl. Liban & Syrie 1: 318 (1966).
Type: Syria, Jabl Qasyoun, 1951, Pabot (holotype G).
Herbs, 30 cm tall. Rhizomes short, compact. Leaves 5–8, usually 7, arched-strongly recurved, 27 × 1 cm. Flowers 15 × 9 cm; base of valves often partly enclosed by upper one or two leaves; valves to 10 cm long, inflated, little colored with pale violet purple. Falls obovate-elliptic, to 8 × 5 cm, rather flat in basal area, droopy from immediately beyond beard area; ground creamy white, densely dotted and veined with dark brownish purple; dots and veins slightly embossed; signal spot small, elliptic, 1.5 × 1 cm, dark purple; beard of sparse purple hairs. Standards oval, 9 × 6 cm, ground creamy white, densely fine dotted and fine veined with purple, veins denser and embossed in basal area; narrowed into triangular area and then abruptly clawed, claw 1 cm with long, hairs purple; veins denser and embossed in basal area. Anthers 2.5 cm long; filaments 1.5 cm long. Style branches 4–5 cm long including lobes, narrowly ridged-keeled, strongly arching, hardly produced beyond spread of standards; lobes rather short, combined width of two lobes not wider than style branch; pollinator tunnel rather short.
Distribution: Syria.

Photos by F. Depalle

22. Iris sari Schott ex Baker in Gard. Chron., n.s., 5: 788 (1876).
= *Oncocyclus sarii* Klatt, Abh. Naturf. Ges. Halle 15: 373 (1882).
Type (holotype):—[Specimen from a cultivated plant], [Label handwritten by J.G. Baker], *Iris saarii* Schott, Herr Leichtlin, [fl.], May [18]76, s.coll. s.n. (K000464953!). Epitype (designated by Boltenkov & Guner Phytotaxa 468 (1) 2020: 057)): —TURKEY. [Gaziantep Province], *Iris saarii* Schott, Gaziantep, Zevkir [Durantaş Village], open rocky limestone hillside and in corn fields, 3300 ft., [fl.], 23 April 1934, E.K. Balls [& W.B. Gourlay] 821 (E00332859!, isoepitypes BM!, K! [two sheets]).
= *Iris lupina* Foster in Gard. Chron., ser. 3, 1: 738 (1887).
Type: (neotype, designated by Boltenkov & Guner Phytotaxa 468 (1) 2020: 047): —TURKEY. [Elâzığ Province], *Iris lupina* Foster, Kharput [Harpoot], Buslutasch, [fl.], 20 May 1888, P. Sintenis 450 (P02155089!, isoneotypes G!, K! [3 specimens], LE01043592!, P02155088!).
= *Iris manissadjianii* Freyn in Bull. Herb. Boissier 4: 180 (1896).
Type (lectotype, designated by Boltenkov & Guner Phytotaxa 468 (1) 2020: 047): —TURKEY. [Amasya Province], *Iris manissadjianii* Freyn. Karaman bei Amassia, [fl.], 15 May 1893, Manissadjian s.n. Exs. No. 1091 (M!).
Herbs, 10–40 cm tall. Rhizome stout, compact. Leaves 5–7, slightly curved, to strongly falcate, 0.3–0.9 cm long. Perianth tube 2–3 cm long. Falls elliptic, obtuse or rounded, 3.5–8 × 2.8–4.5 cm, undulate and serrate, veined reddish brown, purple or chocolate brown, on a creamy yellow or greenish yellow ground, with an irregular median blotch, of deep maroon, reddish brown or reddish purple, boarded in lower half with a dense beard (1 cm wide or less) of golden yellow or more rarely creamy hairs. Standards obovate, or suborbicular, 4–8.5 × 2.4–5.8 cm, crenate, and undulate, often darker than falls, with a creamy or yellow ground veined or suffused reddish or bluish purple. Style branches 3.5–5.5 × 1.3–2 cm, with erect, crenate lobes, 1–1.5 × 1–1.2 cm. Capsule fusiform, 5–6 × 1.5–2.3 cm.
Distribution: Turkey.

Photos by F. Depalle

23. Iris sprengeri Siehe in Gard. Chron., ser. 3, 36: 50 (1904).

Type (lectotype, designated by Boltenkov & Guner Phytotaxa 468 (1) 2020: 051)): —[icon] "Iris sprengeri" in Siehe, Gard. Chron. 36: f. 21 (1904a). Epitype (designated by Boltenkov & Guner Phytotaxa 468 (1) 2020: 051)):—TURKEY. [Konya Province], Karapinar, protected area, sandy steppe, 1002 m, [fl.], 1 May 2008, A. Güner 14744, Z. Aytaç, M.A.T. Johnson, M. Öztekin, M. Tekşen & M. Akbalık [originally in Turkish] (NGBB003628! [Fig. 4], isoepitype GAZI!).

= *Iris elisabethae* Siehe, Allg. Bot. Z. Syst. 11(7-8): 115 (-116) (1905).

= *Iris ewbankiana* var. *elisabethae* (Siehe) Dykes, Gen. Iris 112 (1913).

Type (neotype, designated by Boltenkov & Guner Phytotaxa 468 (1) 2020: 046): TURKEY. [Niğde Province], Iris Elisabethae Siehe n. sp. Oncocyclus Gruppe, ähnlich acutiloba, purpur, gestreift, Grundfarbe rosa, Steppen Cappadociens, im vulkan[ischen]. Sande, Östl[ich]. von Nigde [Niğde], [fl.], s.d., W. Siehe s.n. (LE00014039!, isoneotypes BM000958403!, E00332878!).

Herbs, 6–15 cm tall. Rhizome slender, with long stolons. Leaves 4 or 5, falcate, 0.3–0.5 cm wide. Perianth tube 1–1.5 cm long. Falls oblanceolate, acute 5–5.6 × 2–2.5 cm. heavily veined, reddish brown or purplish brown, on a white ground with a regular median dark purple blotch, bearded in a lower half with a sparse narrow band (0.5–0.8 cm wide) of yellow or cream colored hairs. Standards elliptic-oblanceolate, acute, 5.7–5.8 × 2.3–2.7 cm, crenate, prominently veined, purplish brown on a white ground and speckled along midvein. Style branches 2.5–3.5 × 1 cm, yellowish with brown spots, with short reflexed lobes, ca 0.5 × 0.4 cm. Capsule ellipsoid ca 3 × 1.5 cm.

Distribution: Turkey.

Photo by I. Güner

24. Iris petrana Dinsm. in G.E.Post, Fl. Syria, ed. 2, 2: 599 (1933).

Type: (Dinsmore Herbarium ?).

Herbs, 20–25 cm tall. Rhizome thin, stoloniferous. Stem 1-flowered. Leaves 6–10, 3–6 mm wide, ensiform, glaucous, strongly falcate, hardly ½ length of scape. Spathe 7.5 cm long. Flower 5–7 cm (exclude tube and ovary), mostly dark brown, sometimes varying in color (dark purple, violet, rarely Standards much lighter than falls). Falls 3.5–5.5 × 2.5–3 cm, recurved from

the middle, oblong-ovate, generally uniform in color; signal nearly black, hairs of beard mostly yellows, dark tipped, on a cream colored ground. Standards 5.5–6 × 3.5–4 cm, obovate-unguiculate, erect-incurved, nearly uniform, in color or with darker veins.
Distribution: Jordan.


Photo by F. Depalle

25. Iris nigricans Dinsm., Post, Fl. Syria, Palest. & Sinai, ed. 2, 2: 600 (1933).
Type: Jordan, Medaba, 25.04.1911, 770 m, Meyers, Fred S. & Dinsmore, J.E., n. M710 (holotype E 00345357).
Herbs, 30–40 cm tall. Rhizome stout, compact. Stem 1-flowered. Leaves 6–13, 8–9 cm wide, much shorter than scape and not reaching spathe, more or less falcate. Spathe ca 7 cm long. Flower 9–10 cm (exclude tube and ovary), dark brownish purple. Falls 6–7 × 3–4.5 cm, strongly recurved, from middle, oblong-ovate, dark brownish purple; signal black, beard of dark purple hairs on a cream colored to pale yellow ground. Standards 9–10 × 6–7 cm, obovate, unguiculate, erect recurved, slightly lighter in color than falls, with dark purple to dark violet veins and numerous and mostly coalescing dots on a paler ground. Style branches light chocolate colored.
Distribution: Jordan.


Photo by F. Depalle

27. Iris susiana L., Sp. Pl.: 38 (1753) = *Iris sofarana* Foster in Gard. Chron., ser. 3, 26: 389 (1899) = *Iris sofarana* subsp. *kasruwana* (Dinsm.) Chaudhary, G.Kirkw. & C.Weymouth in Bot. Not. 128: 392 (1976).
Type: Sweden, Uppsala (LINN-HL61-3).
Herbs, 30–40 cm tall. Rhizome short, compact, brown. Leaves 25 cm long, glaucous and slightly curved. Spathe slightly dilate at the base. Stem 1-flowered. Falls reflexed, ovate, 7 × 4 cm, strongly spotted with purple on a bluish-white base. Standards erect, with a color similar to or lighter than falls with white or purplish veins. Style branches 2–3 cm long.
Distribution: Lebanon.

Photos by F. Depalle

28. Iris assadiana Chaudhary, G.Kirkw. & C.Weymouth, Bot. Not. 128(4): 401 (1975) = *Iris barnumiae* var. *zenobiae* Mouterde in Nouv. Fl. Liban 1: 315 (1966).

Type: Syria, Sadad area, April 1974, Kirkwood 1312 (holotvpe, BEI).

Herbs, ca. 15 cm tall. Rhizomes at base of individual shoots small, buds at base only few and forming small clumps; stolons several, long, spindly or stout (of several nodes each) coming from base of each shoot constituting main rhizome; stolons ca. 12 cm long, becoming conical at base of single plantlet that develops from apical bud on each stolon. Leaves 6–8, usually falcate, strongly reflexed, 4–12 × 1 cm, usually single stem leaf or uppermost leaf longer than stem. Flowers odoriferous, 9.5–13 cm long; valves 5–7 cm long, inflated, keeled, pale green to yellowish pink on drying. Perianth tube 2 cm long. Falls 5–6.6 × 2.5–3.5 cm, uniformly dark maroon to dark purple to almost black with a few darker veins; signal spot velvety, darker, transversely oval, wider than long, notched, less than 1 × 1 cm or slightly more; beard of median band (0.5 cm wide) of long (1 cm) hairs; hairs on either side of median band short; long hairs bright yellow, either without purple tip or some with small purple tips or bright yellow masking purple tips; short hairs purple; ground below long hairs bright yellow, beard hairs in some biotypes completely lacking and only a yellow band on falls present. Standards 6–8 × 4–5 cm, obovate, gradually narrowed into claw; claw 1–1.5 cm long, channeled, channel with few yellow hairs, maroonish purple with darker veins, some biotypes dark purple. Anthers creamy white, 1.3–1.8 cm long; filaments 1.8–2 cm long. Style branches 4–5.5 cm long. including lobes, strongly arched, not keeled, if keeled then not ridged, pale orange streaked with purple, becoming darker towards center, with purple median streak; two lobes less than width of style branch; pollinator tunnel constituted mainly of style branch, fall forming only part of tunnel floor near very base; style branches often raised relatively high above falls and long beard hairs then laterally visible.

Pods 4 cm long, 1.25 cm wide, tapering. Ovary 2 cm long.
Distribution: Syria.


Photo by T. Fietz

29. Iris swensoniana Chaudhary, G.Kirkw. & C.Weymouth in Bot. Not. 128: 406 (1975).
Type: Syria, Tell Cbeban, April 1972, Chaudhary & Kirkwood 796 (holotype BEI!).
Herbs, 40 cm tall. Rhizomes small, compact, yellowish brown. Leaves 20 × 1 cm, up to 8, strongly recurved, even circinate. Flowers odoriferous, 12–19 × 7–8; valves more or less inflated, keeled, pale green to green. Perianth tube 2–4 cm long. Falls 6–7 × 3–3.5 cm, ovate-spatulate, narrowed or not into a baft, strongly recurved, often folded back; uniformly dark purple, almost black, with darker veins; signal spot orbiculate-reniform, notched, wider than long, 1–1.5 × 1.5–2 cm, velvety dark maroon-dark purple (almost black); beard of purple tipped bright yellow hairs (less than 0.5 cm long) in median region on yellow ground, hairs gradually becoming shorter toward sides where they are purple on a purple ground. Standards 6–8.5 × 3.5–5 cm, oblong, gradually or abruptly narrowed into claw; claw 1–1.5 cm long, channeled, channel with few purple and yellow hairs; limb uniformly purple or dark maroon, slightly lighter than falls. Stamens creamy white. Anthers 2–3.5 cm long; filaments1–1.5 cm long. Style branches 4–6 cm long including lobes, 2.5–3 cm wide, orange, strongly streaked with purple, becoming darker towards tip, ridge-keeled; lobes colored and veined like falls, triangular, crenate, recurved; lobes narrower than style branch; pollinator tunnel formed mainly by style branch, fall contributing only part of tunnel floor. Capsule 8–10 × 2.5 cm. Ovary 2–4 cm long, terete, broadly trigonal.
Distribution: Syria.


Photo by F. Depalle

30. Iris yebrudii Dinsm. ex Chaudhary in Bot. Not. 125: 259 (1972).
Type: Syria, Yebrud, May 1971. Chaudhary no. 786. (holotype BEI).

Herbs, 15–18 cm tall. Rhizomes small, compact. Stem 11-flowered, 5–25 cm long. Leaves falcate, 5 or 6, covering about 1/3–1/2 of stem; larger leaves 14–21 cm long. Spathe 1, close to the basal leaves. Bracts 2, keeled, the upper halves brownish purple and the lower halves dark brown; perianth tube 1.5 cm long. Flowers 8 cm long. Falls orbicular, recurved, 6.5 × 6 cm, closely finely dotted or veined with purple or brownish purple spots on clear white to yellowish white ground, middle veins distinctly yellow; signal patch about 0.7 × 1.3 cm, more or less diamond shaped, dark purple. Standards with short claw, orbiculate, 7 × 6 cm with fine purple veins towards periphery, major veins and those in central top end distinctly yellow; ground clear white towards periphery, yellow in middle and basal parts; dotted with purple or dark purple spots toward base and with few long, yellow hairs on median inner basal areas. Style branches 3.5 × 2 cm, sharply keeled, purple to dark purple; apices bilobed, lobes turned upwards and spotted and streaked like falls. Ovary 2.5 cm long, grooved.
Distribution: Syria.


Photo by F. Depalle

31. Iris bismarckiana E. Dammann & Sprenger in Nursery Cat. (Dammann) 51: 4 (1890).
Type: Northern Palestine c. 1890, G. Ecgers(?).
= *Iris nazarena* (Foster) Dinsm., Post, Fl. Syria, Palest. & Sinai, ed. 2 ii. 596 (1933)
= *Iris sari-nazarena* Foster ex Wulle in Gartenflora 42: 487 (1893).
Type: Israel, Nazareth, 20.03.1921, Meyers, Fred S. & Dinsmore, J.E., n. 9622 (holotype E 00332802).
Herbs, 30–50 cm tall. Rhizome medium - large, stoloniferous with long stolons. Leaves usually 8, spreading fan-like, rather obtuse, 2–3 cm wide, 25–40 × 2–3 cm, oblique, closely sheathing. Flowers often 15 cm long. Perianth tube 7 cm long. Falls 6–7 cm long, round-ovate; the ground creamy, thickly covered with oblong, embossed, red brown spots, veined with maroon or purple, often with a few small crimson or red brown spots; heard hairs dark purple; signal spot large, more or less orbicular, blackish red purple. Standards 7–8 cm long, orbicular, with a white ground except at the yellowish base; veins blue, dots dense, prominent, purple. Style branches relatively long, marked with reddish brown spots on a creamy ground.
Distribution: Lebanon, Israel, Jordan

Photos by F. Depalle

32. Iris mariae Barbey in Oesterr. Bot. Z. 41: 207 (1891) = *Iris helenae* Barbey ex Boiss., Fl. Orient. 5: 132 (1882) = *Iris barnumiae* var. *mariae* (Barbey) Dykes, Gen. Iris 116 (1913).
Type: Egypt, El Arisch. m 26.03.1880, Barbey, W., s.n. (holotype K 000363651).
Herbs, 20–30 cm tall, growing in clumps. Rhizomes stoloniferous; stolons 3–4 cm deep; roots reddish. Stem 1-flowered. Leaves 7–8, 4–6 mm wide, ensiform, strongly falcate, glaucous, 1/3–1/2 length of scape. Spathe longer than tube of perianth. Flower lilac to violet ca 7 cm (exclude tube and ovary). Falls 5 × 2.5–3 cm, oblong-ovate, recurved, darker than standards, violet with a dark velvety signals; hairs of beard nearly black. Standards 6–6.5 × 4 cm, lilac, erect-incurved with short claw.
Distribution: Sinai, Israel.

Photo by F. Depalle


Photo by F. Depalle

33. Iris maculata Baker in Gard. Chron., n.s., 6: 517 (1876).
Type (neotype, designated by Boltenkov & Guner Phytotaxa 468 (1) 2020: 048)): —TURKEY. [Elâzığ Province], *Iris lupina* Foster, Kharput [Harpoot], Buslutasch, [fl.], 20 May 1888, P. Sintenis 450 (P02155089!, isoneotypes G!, K! [3 specimens], LE01043592!, P02155088!).
= *Iris heylandiana* Boiss. & Reut. in P.E.Boissier, Fl. Orient. 5: 130 (1882)
Type: (lectotype, first step of designated by Chaudhary 1977: 25, second step designated by Boltenkov & Guner Phytotaxa 468 (1) 2020: 046)): [IRAQ]. [Label 1, handwritten]: Iris, Voyage d'Olivier en Orient, [fl.], s.d., [Olivier] s.n. Herb. Boissier; [Label 2]: *I. heylandiana* Boiss. et Reut. 1975, M. Awishari; [Label 3, printed]: If Mardin material is *I. gatesii*, then this (Olivier No.) from between 'Baghdad and Mossul' should be treated as the *I. heylandiana* Boiss. 15 June [19]75, S.F. Chaudhary (G00774785!, isolectotype G00774785a! "de Mossul a Bagdat").
= *Iris nectarifera* Güner in Notes Roy. Bot. Gard. Edinburgh 38: 413 (1980).
Type: Mardin, Kiziltepe, Senuart ile Tozan Karakolu arasi, sinir boyu, 500 m, 17.04.1979. Guner, 1858b (K 000464984).
Herbs, 35 cm tall. Rhizomes medium-small, short creeping stoloniferous. Leaves up to 9, less than 20 × 1 cm, strongly arched; stem leaf 1 or absent. Flowers 15 cm from base of valves, 7 cm wide; valves 7 cm long, more or less inflated, with brownish pink tinge. Falls obovate-cuneate, veined and spotted with brownish violet forming an open pattern on a whitish, clear ground, dark brown in throat (?); signal spot dark, narrow, elongate with distal edge irregular in outline; beard linear but spreading out laterally near base; beard hairs white, relatively sparse, of almost uniform length. Standards broader than falls, orbiculate-unguiculate, white with fine purplish brown veins and sparse dotting. Style branches horizontal-oblique, rather wide, orange (?); lobes short, crenate, two lobes less than width of style branch; pollinator tunnel mainly of style branch, fall contributing floor near base only, otherwise tunnel open on lower surface and linear beard laterally visible.
Distribution: Iraq, Turkey.


Photo by M. Balos


Photo by F. Depalle

Photo by F. Depalle

34. Iris hermona Dinsm., Post, Fl. Syria, Palest. & Sinai, ed. 2, 2: 596 (1933).
Type: Syria, S of Qunaitra April-May 19--, Dinsmore 1895 (holotype Dinsmore Herbarium ?).
Herbs, 30–50 cm tall. Rhizome rather stout, without stolons. Stem 1-flowered. Leaves 6–8, 1–1.5 cm wide, ensiform, erect or somewhat recurved, partly ever-green (on slopes of Mt. Hermon) appearing very early much shorter than scape and not reaching flower, narrower than in *I. bismarckiana*, glaucous. Spathe 10 cm long, often purplish. Flower bicolored. Falls 6.5–8.5 × 4.5–6.5 cm, obovate, recurved, with purple veins, many oblong purplish brown spots on a cream-colored ground; signal small, orbicular, almost black; claw short and broad; hairs of beard dark purple on a light ground. Standards 6.5–8.5 × 5.5–7.5 cm, suborbicular, erect-incurved, with fine purple veins, on white to pale lilac ground and nearly without dots. Lobes of style branches brown spotted, purplish brown, like falls; seeds numerous.
Distribution: Israel.

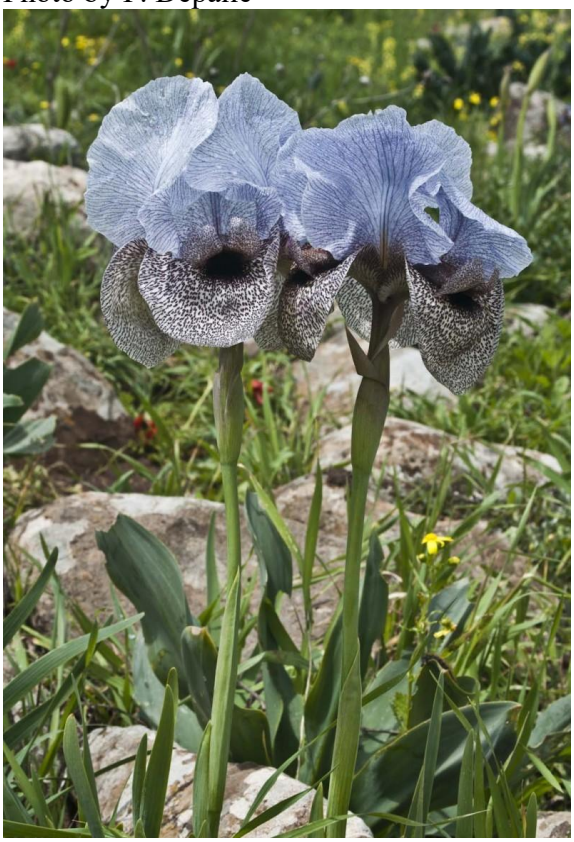
Photo by M. Yehuda

35. Iris lortetii Barbey in C.Barbey-Boissier & W.Barbey, Herbor. Levant: 178 (1882).
Type: Palestine (holotype G 00164488!).
Herbs, 30–50 cm tall. Rhizome stout, short, without stolons. Stem 1-flowered. Leaves 7 or 8, 1–2 cm wide, ensiform, erect, nearly reaching base of spathe, or of flower, glaucous. Spathe longer than perianth tube, 7.5–10 cm long. Flower bicolored. Falls 5–8 × 4.5 cm, oblong-ovate, recurved with numerous lilac to pink dots, and veins on cream or yellowish ground; signal rather small, brownish purple or red; beard with sparse brown hairs, on purple ground. Standards 9–11 × 7–8 cm, orbicular with distinct claw, erect-incurved, light colored with fine lilac veins, devoid of dots; margins irregularly crenate-dentate.
Distribution: Israel, Lebanon.


Photo by S. Gold

36. Iris westii Dinsm., Post, Fl. Syria, Palest. & Sinai, ed. 2, 2: 596 (1933).
Type: Lebanon, Tawmatun-Niha, May 1930, West 1896 (holotype Dinsmore Herbarium ?).
Herbs, up to 30 cm tall. Rhizome medium, compact. Leaves 6–8, 20 × 1 cm, falcate; stem leaf one or two. Flowers 12.5–15 cm long; valves about 11 cm long, slightly inflated. Perianth tube 3–4 cm long. Falls 5–8 × 5–5.5 cm, elliptic-obovate, veins and spots prominently embossed, brownish purple to purple, the spots dense; signal spot 1.5 cm long, located in middle of fall; beard of long, rather sparse purple hairs, rather wide, extending almost to edges of fall and almost to lower edge of signal spot. Standards 6–9 × 5–6 cm, obovate-cuneate, gradually narrowed into claw, 1 cm long; limb orbiculate; lilac blue veins and minute dots on pale lilac ground, dots becoming bigger and embossed towards base. Anthers 2 cm long; filaments 1.7 cm long. Style branches horizontal-oblique (apparently not arched downwards as seen in herbarium material), 6–6.5 × 3 cm, thickly dotted-streaked with brownish purple on ‘wine colored’ ground; lobes upturned, dotted and veined like falls; two lobes wider than style branch; pollinator tunnel apparently mostly open; fall and style branch meeting only toward basal area. Ovary 3–4.5 cm long, stalk 1 cm long.
Distribution: Lebanon, Syria, Israel.

Photos by F. Depalle

Photo by T. Fietz

Photo by A. Trail

37. Iris basaltica Dinsm., Post, Fl. Syria, Palest. & Sinai, ed. 2, 2: 597 (1933).
Type: Syria, Kalaat-ul Husn (Krak de Chevaliers) area, March-April, 19--, West (Dinsmore Herbarium?).
Herbs, 15–70 cm tall. Rhizomes dark brown, compact. Leaves 9–12, 24 cm long. Perianth tube is 2.8 cm long. Flowers 15 cm long. Falls of similar color with standards, ovate to lanceolate shaped, 9 × 5 cm; signal is rounded, dark, in the middle with sparse, short hairs of beard, which are brownish purple, or maroon or purple, tipped with dark yellow. Standards pale, orbicular, 8.5–10.5 × 7–7.5 cm with scattered purple hairs on claw. Style branches 8 cm long, with multiple maroon or purple spots. Ovary 2.5 cm long. Capsule 6–11 cm with 6 lobes.
Distribution: Lebanon, Syria.

38. Iris haynei Baker, Gard. Chron. n.s., 6: 710 (1876) = *Iris biggeri* Dinsm., Post, Fl. Syria, Palest. & Sinai, ed. 2. 2: 599 (1933).
Type: Israel, East of sea of Galilee, 700 m, 20.04.1921, Meyers, Fred S. & Dinsmore, J.E., n.1894 (holotype E 00332813).
= *Iris speciosissima* Filippov in Věstn. Tiflissk. Bot. Sada 13: 48 (1917).
Type (neotype, designated by Boltenkov & Guner Phytotaxa 468 (1) 2020: 051)): —TURKEY. [Iğdır Province], Prov. Erivan, distr. Surmalu, in monte Takältu [Tekelti Mountain, or Tekaltı Dağı], [fl.], 29–30 May 1914, I. Volčanetski s.n. Exs. No. 13494 (TGM No. 8607!, isolectotypes TGM No. 8605!, TGM No. 8608!).
Herbs, 40–50 cm tall, growing in clumps. Rhizome stout. Leaves 5–8, 1–1.5 cm wide, ensiform, erect, reaching spathe. Spathe 7–8.5 cm long. Flowers fragrant, 10–12 cm (exclude tube and ovary), distinctly longer than broad, mostly purple. Falls 7–8 × 4–6 cm, oblong-ovate, recurved from about the middle, dark purple to brownish-purple, very densely dotted, and veined; signal blackish, dark purple; beard on a yellowish or white ground, hairs varying in color, (dark purple, white or dark tipped yellow). Standards 9–10 × 6–7 cm, erect-incurved, obovate, purple veined, and densely purple dotted on a pale ground.
Distribution: Israel, Jordan.

Photos by F. Depalle

39. Iris auranitica Dinsm. in G.E.Post, Fl. Syria, ed. 2, 2: 601 (1933).
Type: Syria, Jabl Kulayb, May 1933, Dinsmore,13045 (Dinsmore Herbarium ?).
Herbs, 50 cm tall. Rhizome medium, compact, yellow. Leaves up to 9, 25 × 1 cm, erect or slightly arched, sheathing the stem almost to the top; stem leaves one or two. Flowers odorous,15 cm tall from base of the valves, valves rather tightly clasping, 8-9.5 cm, greenish-yellow. Perianth tube 2 cm long. Falls 7 × 4 cm, obovate, bronze, with very minute, uniformly and rather densely distributed purplish-red spots and very fine reddish-purple veins or without spots and with only faint venation; signal spot about 1.5 × 1.5 cm, orbiculate to pendulum-shaped, dark maroon or reddish-yellow; beard dense, the hairs bright yellow with very minute purple-red tips; the hairs longest in the middle (0.5 cm) and gradually becoming shorter towards the sides. Standards 8.5 × 5.5 cm, obovate, golden-yellow to bronze, with very fine purplish-red veins or without dots and with only faint veins; claw 1 cm, channeled, with golden yellow, dull brown tipped, dense hairs. Anthers 2.2–3 cm, tailed, creamy white to light yellow; filaments 1–2 cm, light yellow. Style-branches 4.7–5.5 cm including the lobes, 3 cm wide, golden yellow with very fine purple to brownish-purple dots, rather oblique and arched, ridge keeled, the ridge more prominent near the lobes; the lobes not wider than the width of the style branches, upturned, spotted and veined like the falls; the style branches forming a rather short pollinator tunnel with the falls near their bases, the tunnel open away from base. Pods 8 cm long, narrow. Ovary 4 × 1 cm, stalk 0.5 cm.
Distribution: Syria.

Photos by F. Depalle

40. Iris bostrensis Mouterde in Bull. Soc. Bot. France 101: 420 (1955).
Type: Syria, Hauran. Highwood, n.6 (G 00164504).
Herbs, 40–50 cm tall, growing in clumps. Rhizome staut. Stem 1-flowered. Leaves 5–8, 1–1.5 cm wide. Ensiform, erect, reaching spathe. Spathe 7–8.5 cm long. Flowers fragrant, 10–12 cm (exclude tube and ovary), distinctly longer than wide, mostly purple. Falls 7–8 × 4–6 cm, oblong-ovate, recurved from the middle, dark purple to brownish-purple, very densely dotted, and veined; signal blackish dark purple; beard on yellowish or white ground, of hairs varying in color (dark purple, white or dark yellow). Standards 9–10 × 6–7 cm, erect-incurved, obovate, purple-veined, and densely purple-dotted, on a pale ground.
Distribution: Syria, Jordan.

Photos by F. Depalle

41. Iris atrofusca Baker in Gard. Chron., ser. 3, 13: 384 (1893) = *Iris loessicola* Kushnir in Palestine J. Bot., Jerusalem Ser., 4: 231 (1949) = *Iris hauranensis* Dinsm. in G.E.Post, Fl. Syria, ed. 2, 2: 598 (1933).
Type: Israel, Jerusalem (East of) 14.04.1921, 780 m, Meyers, Fred S. & Dinsmore, J.E., n. B2502 (E 00332797).
= *Iris jordana* Dinsm., Post, Fl. Syria, ed. 2, 2: 598 (1933).
Type: Jordan Valley, near Baysan, April 1921, Dinsmore 1893 (holotype, Dinsmore Herbarium ?).
Herbs, 20–30 cm tall. Rhizome stout, compact. Stem 1-flowered. Leaves 5–8, 1 cm wide, ensiform, glaucous, erect or falcate, reaching and somewhat exceeding base of spathe. Spathe 7–8 cm long. Flowers fragrant, purplish-brown to dark purple. Falls 6–7.5 × 3–4.5 cm, obovate cuneate, recurved from the middle, dark-brown purple to nearly black; signal broad, brown-black, hairs of beard yellow, brown-tipped, on a crème color ground. Standards 7–9 × 4.5–7 cm, erect incurved, obovate-cuneate to suborbicular-cuneate, with dark purplish-brown to dark purple radiating veins and dense dots.
Distribution: Israel, Jordan.


Photo by F. Depalle


Photo by F. Depalle

42. Iris atropurpurea Baker in Gard. Chron., ser. 3, 5: 330 (1889) = *Iris eggeri* Tubergen, Wholesale Cat. Flowerroots 1901: 23 (1901).
Type: Described from plants collected in Syria by Mesiirs. Daraman & Co, of Naples.
Herbs, 25–35 cm tall, growing in clumps. Rhizomes stoloniferous, stolons less than 1 cm in thickness. Stem 1-flowered. Leaves 7–11, 5–8 mm wide, ensiform, glaucous, falcate, not reaching base of spathe, and often only about ½ as long as scape. Spathe up to 7 cm long. Tube somewhat longer than spathe. Perianth generally chestnut-brown, to dark purple, varying from reddish to nearly black purple. Falls 3.5–6 × 2.5–4 cm, oblong-ovate, recurved, uniform in color; signal semi-circular black, velvety; hairs of beard yellow, dark tipped, on a yellow ground. Standards 5.5–8 × 4.5–6 cm, suborbicular-unguiculate, erect-incurved, similar in color to falls, often slightly lighter with inconspicuous dark veins and devoid of dots.
Distribution: Israel.


Photo by S. Gold

43. Iris yeruhamensis ined.
Type: in HUJ. All specimens under the name of *I. petrana* collected in Israel and stored in HUJ represent this species.
Distribution: Israel
Note: This species is genetically close to *I. atrofusca* and differs sharply *from I. petrana* from Jordan.


Photo by F. Depalle

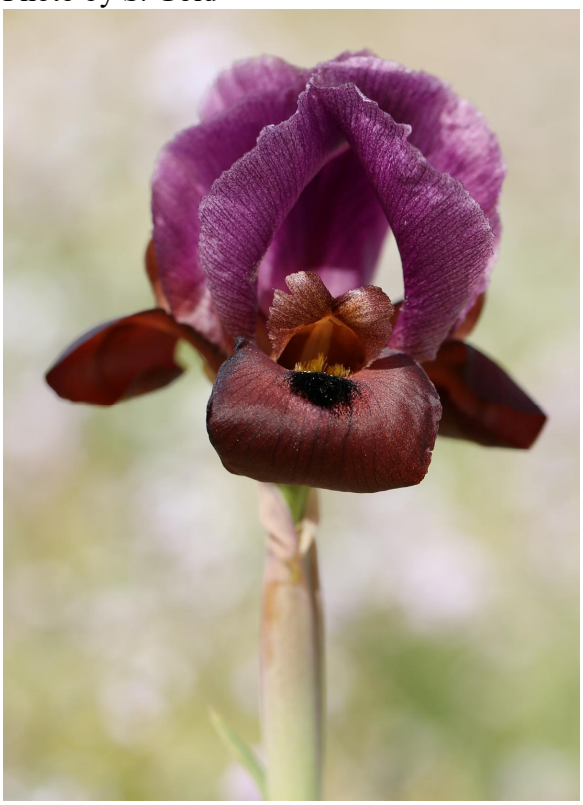
Photo by F. Depalle

44. Iris brianii ined.
Type: in a living collection of Frederic Depalle, is close or identical to *I. paradoxa* f. *mirabilius* Gavr. invalidly described without a type.
Distribution: Iran.

Photo by F. Depalle

45. Iris depallei ined.
Type: in a living collection of Frederic Depalle.
Distribution: Azerbaijan

46. Iris madhavi ined.
Type: in a living collection of Frederic Depalle. Named after Edris Madhavi who discovered this species.
Distribution: Iran.


Photo by F. Depalle

47. Iris selahii ined.
Type: in a living collection of Frederic Depalle. Known as "moleskin".
Distribution: Iran.

Unresolved species:

1. Iris straussii Leichtlin ex Micheli in Rev. Hort. (Paris) 71: 363 (1899).
Type: Iran (Persia), Arak, Markazī: cult., e Sultanabad (T. Strauss); described from Leichtlin collection (JE 00020010).
Distribution: Iran.
Note: There is only type specimen validly described.

2. Iris keredjensis Parsa in Kew Bull. 4: 33 (1949).
Type: Gazy, Kuh Dascht, prope Karadj, 20.05.1941, Parsa 49 (K 000464987).
Note: very close to *Iris polakii* Stapf.
Distribution: Iran.

3. Iris × sinistra Sosn., Soobshch. Akad. Nauk Gruzinsk. S.S.R. 2(7): 651 (-653) (1941).
Distribution: Azerbaijan.

4. Iris × brzhezitzky Grossh., Izv. Azerbaidzhansk. Fil. 10: 30 (1944) = *Iris* × *tatianae* Grossh., Izv. Azerbaidzhansk. Fil. 10: 30 (1944).
Distribution: Azerbaijan.

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Suppl. Table. Species identity, place of collecting, area of endemism and Genebank accession numbers for the analyzed samples.

Species names according to the proposed classification	Place of collecting	Area of endemism	Genebank accession number
I. lineolata (Trautv.) Grossh. (=*I. acutiloba* Mey. subsp. *lineolata* Mathew & Wendelbo)	Armenia	Caucasus and Iran	PP897863
I. longitepala (B.Mathew & Zarrei) Volis & F.O.Khass. comb. nov. (= *I. acutiloba* Mey. subsp. *longitepala* Mathew & Zarrei)	Iran	Iran	PP897875
I. acutiloba Mey. (=*I. acutiloba* subsp. *acutiloba* Mathew & Wendelbo)	Azerbaijan	Caucasus and Iran	PP897849
I. schelkownikowii Fomin (=*I. acutiloba* var. *schelkownikowii* Fomin)	Azerbaijan	Caucasus	PP897851
I. antilibanotica Dinsm.	Syria	Levant	PP897852
I. assadiana Chaudhary, Kirkw. & Weymouth	Syria	Levant	PP897867
I. atrofusca Baker	Israel	Levant	MW476735
I. atropurpurea Baker	Israel	Levant	MW476736
I. auranitica Dinsm.	Syria	Levant	PP897870
I. barnumiae Foster & Baker	Turkey	Turkey and Levant	PP897859
I. bismarckiana Regel	Israel	Levant	OR098703
I. bostrensis Mouterde	Syria	Levant	OR752431
I. camillae Grossh.	Azerbaijan	Caucasus	PP897850
I. cedretii Dinsm.	Lebanon	Levant	MW476737
I. damascena Mouterde	Syria	Levant	PP897853
I. demawendica (Bornm.) Dykes (=*I. barnumae* subsp. *demawendica* Mathew & Wendelbo)	Iran	Iran	PP897880
I. gatesii Foster	Turkey	Turkey	KM014691
I. haynei Baker	Israel	Levant	MW476738
I. hermona Dinsm.	Israel	Levant	OR098704
I. elegantissima Sosn. (=*I. iberica* subsp. *elegantissima* Fed. & Takht.)	Iran	Turkey, Caucasus & Iran	PP897862
I. elegantissima Sosn. (=*I. iberica* subsp. *elegantissima* Fed. & Takht.)	Armenia	Turkey, Caucasus & Iran	PP897861
I. elegantissima Sosn. (=*I. iberica* subsp. *elegantissima* Fed. & Takht.)	Turkey	Turkey, Caucasus & Iran	PP897860

I. iberica Hoffm.	Azerbaijan	Turkey and Caucasus	OR742345
I. lycotis (=*I. iberica* subsp. *lycotis* (Woronow) Takht.)	Armenia	Turkey, Caucasus & Iran	MW476739
I. lycotis (=*I. iberica* subsp. *lycotis* (Woronow) Takht.)	Iran	Turkey, Caucasus & Iran	OR742346
I. kirkwoodiae Chaudhary	Syria	Turkey and Levant	PP897854
I. kirkwoodiae Chaudhary	Syria	Turkey and Levant	PP897855
I. kirkwoodiae Chaudhary	Syria	Turkey and Levant	PP897856
I. kirkwoodiae Chaudhary	Syria	Turkey and Levant	PP897857
I. kirkwoodiae Chaudhary	Turkey	Turkey and Levant	PP897858
I. lortetii Barbey ex Boiss.	Israel	Levant	OR098705
I. mariae Barbey	Israel	Levant	MW476740
I. meda Stapf	Iran	Iran	PP897878
I. maculata Baker (=*Iris heylandiana* Boiss. & Reut. =*I. nectarifera* Güner)	Turkey	Turkey	PP897874
I. nigricans Dinsm.	Jordan	Levant	MW476741
I. paradoxa Steven	Armenia	Caucasus	OR789644
I. medwedewii Fomin (=*I. paradoxa* f. *choschab* (Hoog) Mathew & Wendelbo)	Azerbaijan	Caucasus	PP897879
I. yeruhamensis ined. (=*I. petrana* Dinsm.)	Israel	Levant	MW476743
I. petrana Dinsm.	Jordan	Levant	MW476742
I. polakii Stapf	Iran	Iran	
I. pseudomeda Salimbahrami & Saeidi	Iran	Iran	OR789642
I. sari Schott ex Baker	Turkey	Turkey	PP897866
I. susiana L. (=*I. sofarana* subsp. *kasruwana* (Dinsm.) Chaudhary)	Lebanon	Levant	PP897868
I. susiana L. (=*I. sofarana* subsp. *kasruwana* (Dinsm.) Chaudhary)	Lebanon	Levant	PP897871
I. susiana L. (=*I. sofarana* Foster)	Lebanon	Levant	PP897869
I. sprengeri Siehe	Turkey	Turkey	OR789639
I. swensoniana Chaudhary, Kirkw. & Weymouth	Syria	Levant	PP897873
I. yebrudii Dinsm. ex Chaudhary	Syria	Levant	PP897872
I. urmiensis Hoog	Iran	Turkey and Iran	PP897865
I. madhavi ined.	Iran	Iran	PP897877

I. madhavi ined.	Iran	Iran	PP897876
Outgroups			
I. longiscapa Ledeb. (sect. *Hexapogon*)	Uzbekistan	Central Asia	PP897881
I. afghanica Wendelbo (sect. *Regelia*)	Afghanistan	Afghanistan	OR098702
I. ferdowsii Joharchi & Memariani (sect. *Regelia*)	Iran	Iran	PP897884
I. hoogiana Dykes (sect. *Regelia*)	Tajikistan	Central Asia	OR774962
I. korolkowii Regel (sect. *Regelia*)	Uzbekistan	Central Asia, Afghanistan, Pakistan	PP897882
I. stolonifera Maxim. (sect. *Regelia*)	Uzbekistan	Central Asia	PP897883
I. imbricata Lindl. (sect. *Iris*)	Armenia	Caucasus and Iran	OR789640
I. alberti Regel (sect. *Iris*)	Uzbekistan	Central Asia	PP897885
I. lutescens Lam. (sect. *Iris*)	France	Europe	OR752430
I. goniocarpa Baker (sect. *Pseudoregelia*)	China	China, India, Burma and Bhutan	PP897886
I. pandurata Maxim. (= *Iris tigridia* Bunge and Ledeb.) (sect. *Pseudoregelia*)	China	Kazakhstan, Russia, Mongolia and China	OR774963
I. sichuanensis Y.T.Zhao (= *Iris leptophylla* Lingelsh. ex H.Limpr.) (sect. *Pseudoregelia*)	China	China	OR789643