Hyacinthus orientalis L.

Subjects: Horticulture

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Hyacinthus orientalis L., commonly known as hyacinth, is one of the most important cultivated plants around the world. The cultivars of this species are characterised by their flowers with strong fragrances and a wide range of attractive colours, which make them a beloved option among ornamentals. The chloroplast genomes of *Hyacinthus* cultivars ranged from 154,458 bp to 154,641 bp, while those of *Bellevalia paradoxa* and *Scilla siberica* were 154,020 bp and 154,943 bp, respectively. Each chloroplast genome was annotated with 133 genes, including 87 protein-coding genes, 38 transfer RNA genes and 8 ribosomal RNA genes.

Hyacinthus orientalis	hyacinth	Scilla siberica	Bellevalia paraxoda		chloroplast genome
cultivar phylogeny	geophytes	Asparagaceae	Scilloideae	Hyacinthaceae	

1. Taxonomy of Hyacinthus orientalis L.

1.1. Morphology

Hyacinthus orientalis L., commonly known as hyacinth, is one of the most important cultivated plants around the world ^{[1][2][3]}. The cultivars of this species are characterised by their flowers with strong fragrances ^{[1][4][5][6][7][8][9]} and a wide range of attractive colours ^{[1][4][5][7][10][11]}, which make them a beloved option among ornamentals ^{[7][8][9]}.

As a geophyte ^{[3][12]}, the hyacinth has a significant, globose bulb ^[5] (**Figure 1**A,E) which is modified from its stem and leaves ^{[13][14]}. Its stem is shrunken and flattened as the disc (**Figure 1**F), while the modified leaves become scale leaves ^{[13][14]} (<u>Figure S1</u>) acting as the storage of nutrients ^[7]. The bulb of the hyacinth is tunicate ^{[4][5]}, meaning that the outermost layers of scale leaves turn into a thin and dry cover called a tunic to protect the inner, fresh scale leaves ^{[13][15]}. The outer tunics of the hyacinth show different colours depending on cultivars ^[5], which can be generally classified into three major colours: dark purple, beige-to-white, and silvery purple.

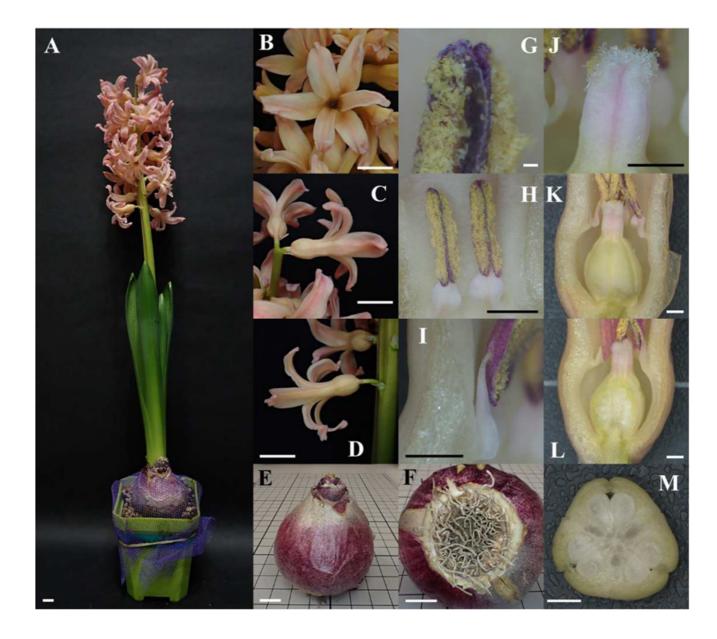


Figure 1. Overview and close-up photos of *Hyacinthus orientalis* L. 'Gipsy Queen'. (**A**) Overview of an individual of *Hyacinthus orientalis* L. 'Gipsy Queen' (scale bar = 1 cm). (**B**–**D**) The corolla (scale bar = 1 cm). (**B**) Front view. (**C**) Side view of corolla on the upper inflorescence. (**D**) Side view of corolla on the lower inflorescence. (**E**,**F**) The bulb (scale bar = 1 cm). (**E**) Side view of the bulb of which tunic is in slivery purple. (**F**) The disc with remnant roots. (**G**–**I**) Androecium. (**G**) Pollen sacs under microscopy (scale bar = 0.01 cm). (**H**) Stamens (scale bar = 0.1 cm). (**I**) Filaments of dorsifixed anthers (scale bar = 0.1 cm). (**J**–**M**) Gynoecium (scale bar = 0.1 cm). (**J**) Receptive papilla on the stigma. (**K**) Superior ovary. (**L**) Longitudinal section of the ovary showing axile placentation. (**M**) Cross section of the ovary showing ovules in three locules.

The inflorescence of the hyacinth is a raceme with 2 to 40 flowers on a single scape [1][5] (leafless stalk arising from ground level [13][15]). The number and density of flowers vary across cultivars. Wild populations of *Hyacinthus orientalis* blossom in comparatively looser scapes, bearing fewer flowers in a blue colour [5][16]. Cultivars of hyacinths have flowers in different colours [1][4][5][6][8][9][10][17][18][19], including red, pink, orange, yellow, white, blue and purple. The flower normally has six tepals arranged in two whorls (P₃₊₃) (**Figure 1**B), which are basally united

forming a perianth tube (**Figure 1**C,D) and constricted above the trilocular superior ovary $(G_{(3)})$ ^[5] with axile placentation (**Figure 1**L,M). The perianth lobes are oblong–spathulate in shape, spreading to recurved ^{[5][10]}. Stamens of the hyacinth are in the same number as tepals (A_{3+3}) and attached to the tepals while not reaching to the throat of the perianth tube ^[5]. The linear, longitudinally dehiscent dorsifixed anthers are longer than the filaments ^[5] (**Figure 1**H,I) and show different colours depending on the cultivars ^[19]. Different cultivars of hyacinths can either blossom with single or double flowers ^{[16][18][19][20]}.

Hyacinths originate from the Mediterranean region, including Turkey, Syria and Lebanon ^{[1][5][10][19][21]}. In Turkey, the species naturally inhabits rocky limestone slopes and scrubs ^[21]. The species is also found in Israel where it appears in small stands under the shade of maquis among rocks ^{[12][22]}.

1.2. Nomenclature

The scientific name *Hyacinthus orientalis* L. was first published by Carl Linnaeus in 1753 in *Species Plantarum* ^[23]. The species has an indispensable role in the nomenclature of related taxa. Being the type species of the genus *Hyacinthus* L., *Hyacinthus orientalis* L. also represented the family Hyacinthaceae Batsch ex Borkh. as *Hyacinthus* L. is the designated type genus ^{[24][25]}. The family was proposed by Borkhausen in 1797 ^[26] and has been recognised by several taxonomists and taxonomic systems including Dahlgren et al. in 1985 ^[27], Conran et al. in 2005 ^[10], the NCBI Taxonomy system ^[28] and the Angiosperm Phylogeny Group (APG) II system in 2003 ^[29]. However, since 2009, the APG system has adopted broader limits for organising the families in Asparagales ^{[30][31]}. The family Hyacinthaceae was included in the family Asparagaceae *sensu lato* and ranked as a subfamily ^{[30][31]}. ^[32]. According to the International Code for Nomenclature of Plants, Algae and Fungi (ICN), no conserved names are allowed for taxa below family level ^[33]. Since the subfamily name Hyacinthoideae (Link, 1829) ^[34] had been previously adopted, according to the priority of names in ICN, the subfamily name Scilloideae (Burnett, 1835) ^[35] was adopted for such inclusion ^[32].

2. Cultivation of Hyacinthus orientalis L.

2.1. History of Cultivation

The cultivation of hyacinth is long-standing with 460 years of history. The earliest record can be traced back to 1562, when the hyacinth was imported from Turkey to Eastern Europe ^[20]. At the end of sixteenth century, the hyacinth was introduced into England as a cultivated plant ^[36]. Cultivars of hyacinths were produced through either hybridisation or mutation ^{[7][11]}. The climax of hyacinth cultivation should be dated back to the 1760s, when over 2000 cultivars of hyacinths were recorded in the French Monograph *Des Jacintes de Leur Anatomie Reproduction et Culture* published by Saint Simon in 1768 ^[14]. However, most of these cultivars were unable to survive ^[20].

2.2. Nomenclatural Circumscription of Hyacinthus Cultivars

Homonyms and synonyms of cultivar epithets are serious issues in the nomenclature of *Hyacinthus* cultivars ^{[8][11]} ^{[16][20]}. Distinct cultivars have shared an identical cultivar epithet, causing the problem of homonyms. For example, three cultivars with single blue flowers from three different origins—Haarlem, Overveen and Hillegom—shared the epithet 'Queen of the Blues' ^[16]. Another cultivar epithet 'Grand Vainqueur' was severely abused, as almost all colours of flowers, regardless of single or double, were called this epithet ^[16]. In contrast, a single cultivar was given two or more cultivar epithet, causing the problem of synonyms. For example, the registered 'Orange Boven' was given the unaccepted epithet 'Salmonetta' ^[20]; the registered 'China Pink' was misapplied with the epithet 'Delft Pink' ^[19]; the registered 'Kroonprinses Margaretha' was given two misapplied epithets, 'Crownprincess Margareth' and 'Margareth' ^[19].

Since 1955, Koninklijke Algemeene Vereeniging voor Bloembollencultuur (KAVB) in the Netherlands was appointed as an International Cultivar Registration Authority (ICRA) for hyacinths by the International Society of Horticulture (ISHS) Commission for Nomenclature and Cultivar Registration ^{[37][38]}. In the *International Checklist for Hyacinths and Miscellaneous Bulbs* published by KAVB in 1991, there were 202 registered cultivars of hyacinths ^[19]. In 1993, about 50 cultivars were commercialised in floricultural production ^[7]. As of 1 January 2020, 368 registered cultivars of hyacinths were recorded in the database of KAVB ^[39]. According to the *International Code of Nomenclature for Cultivated Plants* (ICNCP), for the plants governed by ICRA, each cultivar can only be given one accepted name ^[38].

3. Recent Molecular Insight into Hyacinthus Cultivars and the Potentiality of Chloroplast Genomes for Cultivar Phylogeny

The compatibility of cross-fertilisation and phylogenetic relationships among the *Hyacinthus* cultivars have been studied by karyotypic ^{[8][11][20][40][41][42]} and molecular means ^{[9][43]}, respectively. The diversity of chromosomal karyotypes was characterised in *Hyacinthus* cultivars, which can be diploid, triploid, tetraploid and aneuploid ^{[8][20]} ^[40]. It is difficult to identify the authenticity of hybrid offspring in hyacinths ascribed by their richness of chromosomal ploidy variation and also the greater chances to obtain hybrid offspring from parents with higher ploidy ^{[8][20][42][43]}. As the hyacinth grows only in the right season and starts to blossom in the 2nd to 3rd year from seeds ^{[2][4]}, the cost of breeding a new cultivar can be greatly reduced by early identification and selection ^[43].

The research group of Hu et al. utilised twelve Inter-Simple Sequence Repeat (ISSR) molecular markers to analyse the phylogenetic relationships of 29 *Hyacinthus* cultivars ^[9]. In their unweighted pair group method with arithmetic mean (UPGMA) tree, cultivars with the same colour were mostly grouped into the same cluster. They concluded that the phylogenetic relationships among *Hyacinthus* cultivars had a correlation with the flower colours to a certain extent ^[9]. The research group continued to identify hyacinth hybrid progeny using the twelve ISSR molecular markers ^[43]. The authenticity of hybrid offspring was assured by the presence of parental bands and offspring-unique bands in the electrophoresis diagram of the ISSR analysis ^[43].

With recent technological advancements, the assembly of complete chloroplast genomes has become more feasible. Apart from resolving phylogenetic problems ^{[44][45][46][47]}, chloroplast genomes were recently applied in studying ornamental plants such as *Lilium* L. ^{[48][49]}, *Camellia* L. ^[50], *Lagerstroemia* L. ^[51], *Meconopsis* Vig. ^[52] and *Paeonia* L. ^[53]. The chloroplast genomes were utilised to reconstruct the phylogenetic relationship in horticultural species ^{[48][49][50]} and sometimes even up to the cultivar level ^{[51][54][55]}.

Currently, only six complete chloroplast genomes of Scilloideae are available, including three of *Barnardia japonica* (Thunb.) Schult. et Schult. f. (NC_035997 = KX822775, MH287351 ^[56] and MT319125 ^[57]), one of *Hyacinthoides non-scripta* (L.) Chouard ex Rothm. (NC_046498 = MN824434) ^[58], one of *Albuca kirkii* (Baker) Brenan (NC_032697 = KX931448) ^[59] and one of *Oziroe biflora* (Ruiz et Pav.) Speta (NC_032709 = KX931463) ^[59]. It a report to present the chloroplast genomes of the genus *Hyacinthus* L., *Bellevalia* Lapeyr. and *Scilla* L., which were members of Scilloideae of Asparagaceae *sensu* APG IV. In total, nine chloroplast genomes were sequenced and assembled using Illumina sequencing technology, providing important germplasm resources and insight for the cultivar breeding of the hyacinth and its relatives.

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