

Galanthus

Galanthus (from Ancient Greek γάλα, (gála, "milk") + ἄνθος (ánthos, "flower")), or snowdrop, is a small genus of approximately 20 species of bulbous perennial herbaceous plants in the family Amaryllidaceae. The plants have two linear leaves and a single small white drooping bell-shaped flower with six petal-like (petaloid) tepals in two circles (whorls). The smaller inner petals have green markings.

Snowdrops have been known since the earliest times under various names, but were named Galanthus in 1753. As the number of recognised species increased, various attempts were made to divide the species into subgroups, usually on the basis of the pattern of the emerging leaves (vernation). In the era of molecular phylogenetics this characteristic has been shown to be unreliable and now seven molecularly defined clades are recognised that correspond to the biogeographical distribution of species. New species continue to be discovered.

Most species flower in winter, before the vernal equinox (20 or 21 March in the Northern Hemisphere), but some flower in early spring and late autumn. Sometimes snowdrops are confused with the two related genera within the tribe Galantheae, snowflakes *Leucojum* and *Acis*.

All species of *Galanthus* are perennial petaloid herbaceous bulbous (growing from bulbs) monocot plants. The genus is characterised by the presence of two leaves, pendulous white flowers with six free perianth segments in two whorls. The inner whorl is smaller than the outer whorl and has green markings.[2]

These are basal, emerging from the bulb initially enclosed in a tubular membranous sheath of cataphylls. Generally, these are two (sometimes three) in number and linear, strap-shaped, or oblanceolate. Vernation, the arrangement of the emerging leaves relative to each other, varies among species. These may be applanate (flat), supervolute (conduplicate), or explicative (pleated). In applanate vernation, the two leaf blades are pressed flat to each other within the bud and as they emerge; explicative leaves are also pressed flat against each other, but the edges of the leaves are folded back (externally recurved) or sometimes rolled; in supervolute plants, one leaf is tightly clasped around the other within the bud and generally remains at the point where the leaves emerge from the soil[3] (for illustration, see Stearn[4] and Davis[5]). In the past, this feature has been used to distinguish between species and to determine the parentage of hybrids, but now has been shown to be homoplasious, and not useful in this regard.

The scape (flowering stalk) is erect, leafless, terete, or compressed.[6]

At the top of the scape is a pair of bract-like spathes (valves) usually fused down one side and joined by a papery membrane, appearing monophyllous (single). From between the spathes emerges a solitary (rarely two), pendulous, nodding, bell-shaped white flower, held on a slender pedicel. The flower bears six free perianth segments (tepals) rather than true petals, arranged in two whorls of three, the outer whorl being larger and more convex than the inner whorl. The outer tepals are acute to more or less obtuse, spathulate or oblanceolate

to narrowly obovate or linear, shortly clawed, and erect spreading. The inner tepals are much shorter (half to two thirds as long), oblong, spatulate or oblanceolate, somewhat unguiculate (claw like); tapering to the base and erect. These tepals also bear green markings at the base, the apex, or both, that when at the apex, are bridge-shaped over the small sinus (notch) at the tip of each tepal, which are emarginate. Occasionally, the markings are either green-yellow, yellow, or absent, and the shape and size varies by species.[7][6]

The six stamens are inserted at the base of the perianth, and are very short (shorter than the inner perianth segments), the anthers basifixed (attached at their bases) with filaments much shorter than the anthers; they dehisce (open) by terminal pores or short slits.[6]

The inferior ovary is three-celled. The style is slender and longer than the anthers; the stigma is minutely capitate. The ovary ripens into a three-celled capsule fruit. This fruit is fleshy, ellipsoid or almost spherical, opening by three flaps, with seeds that are light brown to white and oblong with a small appendage or tail (elaiosome) containing substances attractive to ants, which distribute the seeds.[6][8]

The chromosome number is $2n=24$.[9][7]

Floral formula:

■

P

3
+
3

A

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G

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)

$$\star \setminus ; P_{\{3+3\}} \setminus ; A_{\{3+3\}} \setminus ; G_{\{\overline{\{3\}}\}}$$

The genus *Galanthus* is native to Europe and the Middle East, from the Spanish and French Pyrenees in the west through to the Caucasus and Iran in the east, and south to Sicily, the Peloponnese, the Aegean, Turkey, Lebanon, and Syria. The northern limit is uncertain because *G. nivalis* has been widely introduced and cultivated throughout Europe.[2] *G. nivalis* and some other species valued as ornamentals have become widely naturalised in Europe, North America, and other regions.[1] In the Udmurt republic of Russia, *Galanthus* are found even above the 56th parallel.[citation needed]

Galanthus nivalis is the best-known and most widespread representative of the genus *Galanthus*. It is native to a large area of Europe, stretching from the Pyrenees in the west, through France and Germany to Poland in the north, Italy, northern Greece, Bulgaria, Romania, Ukraine, and European Turkey. It has been introduced and is widely naturalised elsewhere.[10] Although it is often thought of as a British native wild flower, or to have been brought to the British Isles by the Romans, it most likely was introduced around the early sixteenth century, and is currently not a protected species in the UK.[11] It was first recorded as naturalised in the UK in Worcestershire and Gloucestershire in 1770.[12] Most other *Galanthus* species are from the eastern Mediterranean, while several are found in the Caucasus, in southern Russia, Georgia, Armenia, and Azerbaijan.[13] *Galanthus fosteri* is found in Jordan, Lebanon, Syria, Turkey, and, perhaps, Palestine.[14]

Most *Galanthus* species grow best in woodland, in acid or alkaline soil,[6] although some are grassland or mountain species.

Snowdrops have been known since early times, being described by the classical Greek author Theophrastus, in the fourth century BCE, in his *Περὶ φυτῶν ἱστορίαι* (Latin: *Historia plantarum*, Enquiry into plants). He gave it, and similar plants, the name *λευκόνιον* (*λευκος*, *leukos* "white" and *ἰόν*, *ion* "violet") from which the later name *Leucojum* was derived. He described the plant as "*πέποιθες γὰρ χρομασί λευκὰ καὶ ὁ λεπυρίδης*" (in colour white and bulbs without scales)[15] and of their habits "*ἴνθ' ἴνθ' τὸ μὲν πρῶτον κῆφαίνεται τὸ λευκόνιον, τοῦ μὲν ἰσχυρὰ μαλακώτερος ἐσθλὸς τὸ χειμῶνος, τοῦ δὲ σκληρώτερος ἰσχυρόν, νιαχοῦ τὸ πρῶτον*" (Of the flowers, the first to appear is the white violet. Where the climate is mild, it appears with the first sign of winter, but in more severe climates, later in spring)[16]

Rembert Dodoens, a Flemish botanist, described and illustrated this plant in 1583 as did Gerard in England in 1597 (probably using much of Dodoens' material), calling it *Leucojum bulbosum praecox* (Early bulbous violet). Gerard refers to Theophrastus's description as *Viola alba* or *Viola bulbosa*, using Pliny's translation, and comments that the plant had originated in Italy and had "taken possession" in England "many years past".[17] The genus was formally named *Galanthus* and described by Carl Linnaeus in 1753,[18] with the single species, *Galanthus nivalis*, which is the type species. Consequently, Linnaeus is granted the botanical authority. In doing so, he distinguished this genus and species from *Leucojum* (*Leucojum bulbosum trifolium minus*), a name by which it previously had been

known.[1][19][20]

In 1763 Michel Adanson began a system of arranging genera in families. Using the synonym *Acrocorydon* (also spelt *Akrokorydon*),[21] he placed *Galanthus* in the family Liliaceae, section *Narcissi*. [22] Lamarck provided a description of the genus in his encyclopedia (1786), [23] and later, *Illustrations des genres* (1793). [24] In 1789 de Jussieu, who is credited with the modern concept of genera organised in families, placed *Galanthus* and related genera within a division of Monocotyledons, using a modified form of Linnaeus' sexual classification, but with the respective topography of stamens to carpels rather than just their numbers. In doing so, he restored the name *Galanthus* and retained their placement under *Narcissi*, this time as a family (known as *Ordo*, at that time) and referred to the French vernacular name, *Perce-neige* [25] (Snow-pierce), based on the plants tendency to push through early spring snow (see Ecology for illustration). [26] The modern family of Amaryllidaceae, in which *Galanthus* is placed, dates to Jaume Saint-Hilaire (1805) who replaced Jussieu's *Narcissi* with *Amaryllidées*. [27] In 1810, Brown proposed that a subgroup of Liliaceae be distinguished on the basis of the position of the ovaries and be referred to as *Amaryllideae*, [28] and in 1813, de Candolle separated them by describing *Liliacées* Juss. and *Amaryllidées* Brown as two quite separate families. [29] However, in his comprehensive survey of the Flora of France (*Flore française*, 1805–1815) he divided Liliaceae into a series of *Ordres*, and placed *Galanthus* into the *Narcissi* *Ordre*. [30] This relationship of *Galanthus* to either liliaceous or amaryllidaceous taxa (see Taxonomy of Liliaceae) was to last for another two centuries until the two were formally divided at the end of the twentieth century. [31] Lindley (1830) followed this general pattern, placing *Galanthus* and related genera such as *Amaryllis* and *Narcissus* in his *Amaryllideae* (which he called The *Narcissus* Tribe in English). [32] By 1853, the number of known plants was increasing considerably and he revised his schema in his last work, placing *Galanthus* together, and the other two genera in the modern *Galantheae* in tribe *Amarylleae*, order *Amaryllidaceae*, alliance *Narcissales*. [33] These three genera have been treated together taxonomically by most authors, on the basis of an inferior ovary. As the number of plant species increased, so did the taxonomic complexity. By the time Bentham and Hooker published their *Genera plantarum* (1862–1883) [34] *ordo Amaryllideae* [35] contained five tribes, and tribe *Amarylleae* [36] three subtribes (see Bentham & Hooker system). They placed *Galanthus* in subtribe *Genuinae* and included three species. [37]

Galanthus

Acis

Leucojum

Galanthus is one of three closely related genera making up the tribe *Galantheae* within subfamily *Amaryllidoideae* (family *Amaryllidaceae*). Sometimes snowdrops are confused with the other two genera, *Leucojum* and *Acis* (both called snowflakes). *Leucojum* species are much larger and flower in spring (or early summer, depending on the species), with all six tepals in the flower being the same size, although some "poculiform" (goblet- or cup-shaped) *Galanthus* species may have inner segments similar in shape and length to the outer ones. *Galantheae* are likely to have arisen in the Caucasus. [38]

Galanthus has approximately 20 species, but new species continue to be described. [1] *G. trojanus* was identified in Turkey in 2001. [39][40] *G. panjutinii* (Panjutin's snowdrop) [41] was discovered in 2012 in five locations in a small area (estimated at 20 km² (7.7 sq mi)) of the northern Colchis area (western Transcaucasus) of Georgia and Russia. [42][43] *G.*

samoethracicus was identified in Greece in 2014. Since it has not been subjected to genetic sequencing, it remains unplaced. It resembles *G. nivalis*, but is outside the distribution of that species.[44][45]

Many species are difficult to identify, however, and traditional infrageneric classification based on plant morphology alone, such as those of Stern (1956),[46] Traub (1963)[47] and Davis[48] (1999, 2001),[49][50][6] has not reflected what is known about its evolutionary history, due to the morphological similarities among the species and relative lack of easily discernible distinguishing characteristics.[51][52][53] Stern divided the genus into three series according to leaf vernation (the way the leaves are folded in the bud, when viewed in transverse section, see Description);[46]

Stern further utilised characteristics such as the markings of the inner segments, length of the pedicels in relation to the spathe, and the colour and shape of the leaves in identifying and classifying species

Traub considered them as subgenera;

By contrast Davis, with much more information and specimens, included biogeography in addition to vernation, forming two series. He used somewhat different terminology for vernation, namely applanate (flat), explicative (plicate), and supervolute (convolute). He merged *Nivalis* and *Plicati* into series *Galanthus*, and divided *Latifolii* into two subseries, *Glauciaefolii* (Kem.-Nath) A.P.Davis and *Viridifolii* (Kem.-Nath) A.P.Davis.[49]

Early molecular phylogenetic studies confirmed the genus was monophyletic and suggested four clades, which were labelled as series, and showed that Davis' subseries were not monophyletic.[52][53] An expanded study in 2013 demonstrated seven major clades, corresponding to biogeographical distribution. This study used nuclear encoded nrITS (Nuclear ribosomal internal transcribed spacer), and plastid encoded genes *matK* (Maturase K), *trnL-F*, *ndhF*, and *psbK-psbI*, and examined all species recognised at the time, as well as two naturally occurring putative hybrids. The morphological characteristic of vernation that earlier authors had mainly relied on was shown to be highly homoplasious. A number of species, such as *G. nivalis* and *G. elwesii* demonstrated intraspecific biogeographical clades, indicating problems with speciation and there may be a need for recircumscription. These clades were assigned names, partly according to Davis' previous groupings. In this model clade, the group containing *G. platyphyllus* is sister to the rest of the genus.[2]

By contrast, another study performed at the same time, using both nuclear and chloroplast DNA, but limited to the 14 species found in Turkey, largely confirmed Davis' series and subseries, and with biogeographical correlation. Series *Galanthus* in this study corresponded to clade *nivalis*, subseries *Glauciaefolii* with clade *Elwesii* and subseries *Viridifolii* with clades *Woronowii* and *Alpinus*. However, the model did not provide complete resolution.[54]

Platyphyllus

Trojanus

Ikariae

Elwesii

Nivalis

Woronowii

Alpinus

sensu Ronsted et al. 2013[2]

Viridifolii

Glaucifolii

Galanthus

Galanthus is derived from the Greek γάλα (gala), meaning "milk" and άνθος (anthos) meaning "flower", alluding to the colour of the flowers. The epithet nivalis is derived from the Latin, meaning "of the snow".[56][57] The word "Snowdrop" may be derived from the German Schneetropfen (snow-drop), the tear drop shaped pearl earrings popular in the sixteenth and seventeenth centuries. Other, earlier, common names include Candlemas bells, Fair maids of February, and White ladies (see Symbols).[20]

Snowdrops are hardy herbaceous plants that perennate by underground bulbs. They are among the earliest spring bulbs to bloom, although a few forms of *G. nivalis* are autumn flowering.[8][58] In colder climates, they will emerge through snow (see illustration). They naturalise relatively easily forming large drifts. These are often sterile,[59] found near human habitation, and also former monastic sites.[58] The leaves die back a few weeks after the flowers have faded. Galanthus plants are relatively vigorous and may spread rapidly by forming bulb offsets. They also spread by dispersal of seed, animals disturbing bulbs, and water if disturbed by floods.[58][20]

Some snowdrop species are threatened in their wild habitats, due to habitat destruction, illegal collecting, and climate change.[2] In most countries collecting bulbs from the wild is now illegal. Under CITES regulations, international trade in any quantity of Galanthus, whether bulbs, live plants, or even dead ones, is illegal without a CITES permit.[60] This applies to hybrids and named cultivars, as well as species. CITES lists all species, but allows a limited trade in wild-collected bulbs of just three species (*G. nivalis*, *G. elwesii*, and *G. woronowii*) from Turkey and Georgia.[61] A number of species are on the IUCN Red List of threatened species, with the conservation status being *G. trojanus* as critically endangered,[62] four species vulnerable, *G. nivalis* is near threatened[63] and several species show decreasing populations.[2] *G. panjutinii* is considered endangered. One of its five known sites, at Sochi, was destroyed by preparations for the 2014 Winter Olympics.[42]

Galanthus species and cultivars are extremely popular as symbols of spring and are traded more than any other wild-source ornamental bulb genus. Millions of bulbs are exported annually from Turkey and Georgia.[2] For instance export quotas for 2016 for *G. elwesii* were 7 million for Turkey.[64] Quotas for *G. woronowii* were 5 million for Turkey and 15 million for Georgia.[65] These figures include both wild-taken and artificially propagated bulbs.

Celebrated as a sign of spring, snowdrops may form impressive carpets of white in areas where they are native or have been naturalised. These displays may attract large numbers of sightseers.[58] There are a number of snowdrop gardens in England, Wales, Scotland, and

Ireland.[66] Several gardens open specially in February for visitors to admire the flowers. Sixty gardens took part in Scotland's first Snowdrop Festival (1 Feb–11 March 2007).[67] Several gardens in England open during snowdrop season for the National Gardens Scheme (NGS) and in Scotland for Scotland's Gardens. Colesbourne Park in Gloucestershire is one of the best known of the English snowdrop gardens, being the home of Henry John Elwes, a collector of *Galanthus* specimens, and after whom *Galanthus elwesii* is named.[68][69]

Numerous single- and double-flowered cultivars of *Galanthus nivalis* are known, and also of several other *Galanthus* species, particularly *G. plicatus* and *G. elwesii*. Also, many hybrids between these and other species exist (more than 500 cultivars are described in Bishop, Davis, and Grimshaw's book, plus lists of many cultivars that have now been lost, and others not seen by the authors). They differ particularly in the size, shape, and markings of the flower, the period of flowering, and other characteristics, mainly of interest to the keen (even fanatical) snowdrop collectors, known as "galanthophiles", who hold meetings where the scarcer cultivars change hands.[70] Double-flowered cultivars and forms, such as the extremely common *Galanthus nivalis* f. *pleniflorus* 'Flore Pleno', may be less attractive to some people, but they can have greater visual impact in a garden setting. Cultivars with yellow markings and ovaries rather than the usual green are also grown, such as 'Wendy's Gold'.[71] Many hybrids have also occurred in cultivation.[6]

As of July 2017[update], the following have gained the Royal Horticultural Society's Award of Garden Merit:[72]

Propagation is by offset bulbs, either by careful division of clumps in full growth ("in the green"), or removed when the plants are dormant, immediately after the leaves have withered; or by seeds sown either when ripe, or in spring. Professional growers and keen amateurs also use such methods as "twin-scaling" to increase the stock of choice cultivars quickly.

Snowdrops contain an active lectin or agglutinin named GNA for *Galanthus nivalis* agglutinin.[98]

In 1983, Andreas Plaitakis and Roger Duvoisin suggested that the mysterious magical herb, moly, that appears in Homer's *Odyssey* is the snowdrop. One of the active principles present in the snowdrop is the alkaloid galantamine, which, as an acetylcholinesterase inhibitor, could have acted as an antidote to Circe's poisons.[99] Further supporting this notion are notes made during the fourth century BC by the Greek scholar Theophrastus who wrote in *Historia plantarum* that moly was "used as an antidote against poisons" although which specific poisons it was effective against remains unclear.[100] Galantamine (or galanthamine) may be helpful in the treatment of Alzheimer's disease, although it is not a cure;[101] the substance also occurs naturally in daffodils and other narcissi.[102]

low, northern wind; fall snow;
And thou—my loved and dear,
See, in this waste of burthened cloud
How Spring is near!

Walter de la Mare (1950)[103]

Snowdrops figure prominently in art and literature,[104] often as a symbol in poetry of spring, purity, and religion (see Symbols), such as Walter de la Mare's poem *The Snowdrop*

(1929).[105] In this poem, he likened the triple tepals in each whorl ("A triplet of green-pencilled snow") to the Holy Trinity.[58] He used snowdrop imagery several times in his poetry, such as *Blow, Northern Wind* (1950) – see Box.[103] Another instance is the poem *The Snowdrop*. by Letitia Elizabeth Landon in which she asks "Thou fairy gift from summer, Why art thou blooming now?"

Early names refer to the association with the religious feast of Candlemas (February 2) – the optimum flowering time of the plant – at which young women, robed in white, would walk in solemn procession in commemoration of the Purification of the Virgin, an alternative name for the feast day. The French name of *violette de la chandaleur* refers to Candlemas, while an Italian name, *fiore della purificazione*, refers to purification. The German name of *Schneeglöckchen* (little snow bells) invokes the symbol of bells.[20][58]

In the language of flowers, the snowdrop is synonymous with 'hope' (and the goddess Persephone's/Proserpina's return from Hades), as it blooms in early springtime, just before the vernal equinox, and so, is seen as 'heralding' the new spring and new year.

In more recent times, the snowdrop was adopted as a symbol of sorrow and of hope following the Dunblane massacre in Scotland, and lent its name to the subsequent campaign to restrict the legal ownership of handguns in the UK.[107][108]

