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All around the world at the moment there is sadness and distress at the Corona Virus pandemic. Flower shows, garden openings and all sorts of gatherings have been banned and travel is not only difficult but frowned upon. We hope we can contribute to the mitigation of the frustration many feel at the isolation they are experiencing by the wealth of resources provided by the SRGC in our website and forum and that IRG readers will be able to gain some respite from the daily worries by enjoying the articles presented here. This month we have a paper by Dr. Dimitri Zubov. The article considers the

species of the genus Galanthus L. distributed in the Caucasus, within a context of the newly established phylogenetic snowdrop clades - *Platyphyllus, Woronowii, Alpinus* and *Nivalis*. The ranges of snowdrop species distribution with the indication of tentative geographical and ecological races as well as the biotopes in which snowdrops grow in the Caucasus are described.

IRG cover photo: Galanthus plicatus subsp. plicatus - photo D. Zubov.

Further to their recent naming of a *Zephyranthes* species for daughter Sarah, John and Anita Watson recount their latest trip with Sarah to see "her" plant in nature in Chile. The new species named in the December IRG (Watson & Flores 2019), *Zephyranthes sarae*, flowers late in the season, so when Sarah visited them, they decided to take her to try to see it in flower.



Will Hembree is now working at the famous Longwood Gardens in Pennsylvania. He is well regarded in North American Rock Garden Society circles and we are pleased to be able to deliver here a brief tale of his cross-country botanising hike with his father on the Appalachian Trail. This article was first published in the NARGS Piedmont Chapter newsletter and Will has also offered the story of the hike in a very popular talk. At a time when even families are being separated by the virus busting regulations, it is somewhat poignant to read of this father and son adventure.

Will Hembree at the <u>J.C. Raulston Arboretum</u> for a <u>Piedmont</u> <u>Chapter</u> talk - photo Bobby J. Ward.

Corona Virus Crisis 2020

In the light of the Corona virus crisis, all Scottish Rock Garden Club events are cancelled up to the month of June 2020. SRGC will keep members updated with news of events due after that date as the situation becomes more clear in the coming weeks. The safety of our members and the public is our priority and we will be guided by the advice of the Scottish and UK governments. We hope that the spread and effects of the virus can be contained and that at least there will be the chance for us to enjoy our own gardens at this time and, with proper regard to safe distancing, to get outdoors to take some fresh air and enjoy nature.

Stay safe, everyone.

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----Genus Report----

Genus Galanthus L. in the Caucasus: Dr. Dimitri Zubov, Ukraine.

Summary. The article considers the species of the genus *Galanthus* L. distributed in the Caucasus (11 taxa discussed), within a context of the newly established phylogenetic snowdrop clades - *Platyphyllus, Woronowii, Alpinus* and *Nivalis*. The ranges of snowdrop species distribution with the indication of tentative geographical and ecological races as well as the biotopes in which snowdrops grow in the Caucasus are described. The complexity of the taxonomic treatment within clades was considered. The questions of occurrence of polyploidy patterns in the genus are also raised.

Key words: Caucasus, Colchis refugium, Hyrcan refugium, snowdrops, species aggregate, microspecies, autopoliploidy.

As is well known, the Caucasus region is a primary centre of speciation and biodiversity for the genus Galanthus L. [Refs. 4, 15, 73]. This Eurasian geographical region is located to south of East European Plain that covers the territory of Russian Federation (RF), Georgia (incl. Abkhazia, South Ossetia), Armenia and Azerbaijan. The Caucasus Mountains are bounded by the Black Sea to the west and the Caspian Sea to the east. According to physical-geographical zonation, the Caucasus is located within the Alpine-Himalayan orogenic belt with recent active tectonics and characterized by a diversity of the mountain relief. According to geological and geomorphological structure, the Caucasus includes four main orographic zones stretching from north to south and coinciding with the basic structural Caucasus elements, such as: Ciscaucasian Plain (Scythian platform), the Greater Caucasus Range mountain system (WNW-ESE direction), the Transcaucasian Depression (a system of intermontane basins), the Transcaucasian Highlands (the Lesser Caucasus) [21]. Also, three floristic regions are interrelated in the Caucasus: Circumboreal, Mediterranean and Irano-Turanian. The floristic districts of the Caucasus are provided by Y.L. Menitsky and represented as: Western and Eastern Ciscaucasia (or North Caucasus); Western, Central and Eastern Caucasus; North-Western, Western, Central, South-Western, Southern and Eastern Transcaucasia; and Talysh Mountains, a northwestern subrange of another mountain range mostly lying in Iran – the Alborz Mountains [50]. The Caucasus region harbors two western Palearctic glacial refugia: (1) Colchis - western coast of Black Sea and (2) Hyrcan – southern coast of Caspian Sea.

Of the currently proposed *Galanthus* clades, the following ones are distributed within the Caucasus: *Platyphyllus clade* (3 taxa), *Woronowii clade* (3 taxa), *Alpinus clade* (4 taxa) and *Nivalis clade* (1 taxon) with 11 taxa in total at the moment [55]. However, due to the diversity of natural biotopes in the Caucasus, it is difficult to reveal the geographic races of Caucasian plants, notably *Galanthus* species, and their ecologic transitions that have very likely arisen and evolved over the last 5.3 mya. A period of the Late Miocene, when the previously insular Greater Caucasus has become a peninsula of the Southwestern Asia with the genus *Galanthus* cradle – the Ancient Colchis refugium (a present-day Colchis Lowland territory) [71, 79].

In the Caucasus, snowdrops being mesic bulbous ephemeroids are growing in different plant formations, ranging from grassroots and foothill summer-green deciduous forests (lower montane zone, 150-900 m), like oak forests (W Ciscaucasia, NW Transcaucasia - Quercus petraea (Matt.) Liebl., *Q. pubescens* Willd., *Q. robur* L., *Q. hartwissiana* Steven [Galanthus plicatus M. Bieb. subsp. plicatus, Galanthus alpinus Sosn.], in W Transcaucasia (Colchis) - *Q. imeretina* Steven ex Woronow, in C and S Transcaucasia - *Q. iberica* Steven ex Bieb., *Q. macranthera* Fisch. & C.A. Mey. ex Hohen., in Talysh - *Q. castaneifolia* C.A. Mey.), ashen forests (*Fraxinus excelsior* L., in S Transcaucasia - *F. oxycarpa* Willd.), sweet chestnut forests (*Castanea sativa* Mill.), Caucasian elm forests (*Zelkova carpinifolia* (Pall.) K. Koch), hornbeam forests (*Carpinus betulus* L., *C. orientalis* Mill.); gorge mixed forests with *Tilia begoniifolia* Steven, *Acer pseudoplatanus* L., *A. campestre* L., *A. laetum* C.A. Mey. (in C and S Transcaucasia - *A. ibericum* M. Bieb., *A. hyrcanum* Fisch. & C.A.

Mey.), Alnus glutinosa (L.) Gaertn., A. barbata C.A. Mey., Buxus colchica Pojark. - [Galanthus rizehensis Stern, Galanthus woronowii Losinsk., G. alpinus].

Among the forests of *the lower montane zone* it should be allocated special *Colchis mixed forests with evergreen underbrush* [*G. rizehensis, G. alpinus, G. woronowii*], and *oak-Persian ironwood Hyrcan forests* (*Parrotia persica* (DC.) C.A. Mey., *Q. castaneifolia* C.A. Mey.) in the Talysh Mountains [*Galanthus transcaucasicus* Fomin], both bearing the features of the Tertiary relict phytocoenotic complex.

In higher altitudes the snowdrops grow in *the middle montane forest belt* (800-2000 m) with summergreen beech forests (*Fagus orientalis* Lipsky), dark coniferous Caucasian fir forests (*Abies nordmanniana* (Steven) Spach) - [*Galanthus krasnovii* Khokhr., *Galanthus panjutinii* Zubov & A.P. Davis, *Galanthus lagodechianus* Kem.-Nath., *G. alpinus*]; and the rock-forest complexes - [*G. panjutinii*, *G. alpinus*, *G. woronowii*]. Further they enter the subalpine crooked forest zone (1800-2200 m, *Rhododendron caucasicum* Pall., *Corylus avellana* L., *Sorbus caucasica* Zinserl., *Acer trautvetteri* Medw., *Betula litwinowii* Doluch., *Salix caucasica* Andersson, *Vaccinium arctostaphylos* L., etc.) – [*G. alpinus*, *G. panjutinii*, *G. lagodechianus*], and the area of alpine-meadow vegetation of nival zone with alpine carpets – it is the uppermost version of short grass alpine meadows on the border with snowfields (2000-2800 m, *Briza markowiczii* Woronow, *Carex micropodioides* V. Krecz., *Luzula pseudosudetica* V. Krecz., *Myosotis alpestris* F.W. Schmid, *Gnaphalium supinum* L., *Dichodon cerastoides* (L.) Britton, *Ranunculus brachyolobus* Boiss. & Hohen., *Campanula tridentata* Schreb., etc.) - [*Galanthus platyphyllus* Traub & Moldenke, *G. alpinus*, *G. transcaucasicus*] [31, 41, 83].

The range of soils and bedrock on which the Caucasian snowdrops subsist, is broad enough both in the latitudinal and altitudinal directions. These are forest brown, humus-carbonaceous and yellow soils developed on marl, schist, limestone and sandstone, also they grow on the subalpine montane-meadow soils and alpine montane-tundra and montane-meadow (acidic, leached) soils [75].

At the time, in the comprehensive study of Caucasian *Galanthus* species were engaged the following Russian, Armenian, Georgian and Soviet botanists and naturalists: F.J. Ruprecht, 1868 [56, 57], A.V. Fomin, 1909 [23], A.A. Grossheim, 1928-1949 [29, 32, 34], A.S. Losina-Losinskaya, 1935 [48], L.M. Kemularia-Nathadze, 1947, 1977 [36-38], Yu.I. Koss, 1951 [44], A.P. Khokhryakov, 1963, 1966 [39, 40], Z.T. Artjushenko, 1966, 1970 [2, 4], L.I. Sveshnikova, 1971 [69, 70], A.A. Kolakovsky, 1961-1986 [41-43], E.Ts. Gabrielian et al., 1982-2002 [24-27], I.N. Timukhin and B.S. Tuniev, 2002 [75], A.S. Zernov, 2000-2006 [81-83], Z.T. Artjushenko and E.V. Mordak, 2006 [3], A.P. Seregin and E.G. Suslova, 2007 [59].

The comprehensive systems and determination keys for the genus *Galanthus*, including Caucasian taxa, have also been developed by the British, European and American researchers – E. Boissier, 1884 [10], J.G. Baker, 1887-1891 [5-7], G. von M. Beck, 1894 [9], P. von Gottlieb-Tannenhain, 1904 [28], H.P. Traub and H.N. Moldenke, 1948 [76], F.C. Stern, 1956, 1963 [67, 68], O. Schwarz, 1963 [58], P. Wendelbo, 1970 [78], A.P. Davis, 1996-2001 [15-17], B. J. M. Zonneveld, 2003 [84], C. Brickell, 2006 [12], D.A. Zubov and A.P. Davis, 2012-2019 [55, 85-87].

The first complete and critically revised genus *Galanthus* system was presented in the monograph of Soviet botanist Zinaida Artjushenko *"Amaryllidaceae Jaume St.-Hilaire of USSR. Morphology, systematics and uses"*, 1970 [4]. The latest detailed and accurate monograph on the genus is of Aaron Davis *"The Genus Galanthus"*, 1999 [15] (Figs. 47, 48).

In 2013, a group of researchers headed by Nina Rønsted proposed a new phylogenetic system of *Galanthus*, based not only on morphological features, as earlier suggested in Artjushenko and Davis genus treatments, but on the molecular sequencing data matrices (phylogenetic assay), which allowed the allocation of seven comprehensive *Galanthus* clades: *Platyphyllus, Woronowii,*

Alpinus, Nivalis, Trojanus, Ikariae, and *Elwesii*. The species representatives of the first four clades are distributed within the Caucasian territory [55].

Nonetheless, the Caucasian representatives of the genus *Galanthus* are still poorly explored to date. It is almost impossible to determine some of the herbarium specimens, as well as the Caucasus backwoods with spring weather turmoil still inaccessible for conducting the full-scale field studies. Traditional genus systematics based on the morphological characters (leaf blade coloration, type of vernation, number of inner perianth segment marks, etc.) currently seems to be outdated and does not reflect the true phylogenetic relationship between plant populations native to a particular territory under exploration. For example, it is still not clear a question of delimitation of the polyploid *G. lagodechianus agg.* species complex (species aggregate), which apparently has a very large area from Ciscaucasia to S Transcaucasia and presumably Talysh Mountains; and mostly diploid *G. alpinus agg.* species complex (species aggregate) occupying the biotopes of Ciscaucasia, Caucasus and Transcaucasia.

Platyphyllus clade (*Galanthus krasnovii, G. platyphyllus, G. panjutinii*) [Western and Central Transcaucasia; Western and Central Caucasus – Russian Federation, Georgia, Turkey]. Figs. 1, 5-16.

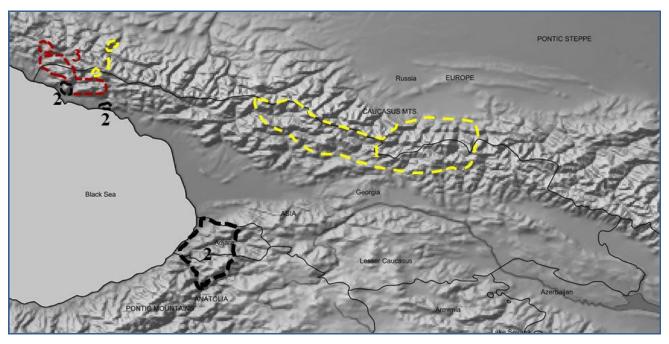


Fig.1. The distribution map of the snowdrop species from the *Platyphyllus* clade within Caucasus (created with SimpleMappr.net):

- 1 yellow G. platyphyllus
- 2 black G. krasnovii
- 3 red *G. panjutinii*

The *Platyphyllus* clade (W and C Transcaucasia, W and C Caucasus) consists of three bright greenleafed snowdrops with supervolute vernation. They possess the most ancient morphological features in the genus: large club-shaped bulbs, supervolute vernation, inner perianth segments without the characteristic sinus, the leaf blade width up to 5.0-6.0 cm, late spring vegetation, the highest in the genus diploid genome size (Cx-value). The known taxa of the clade are more or less clearly separated ecologically and from the microevolutionary point of view can be considered as one biological species with three different ecological races. Possibly they are preglacial relicts of the ancient Colchis flora. It seems this ancient *Platyphyllus* clade gave rise to all other clades in the genus.

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Galanthus platyphyllus was described from a height of 2400 m in the North Ossetia alpine meadows (in general, C and W Caucasus, C and W Transcaucasia – RF), where it is in growth from May to August. The species is generally distributed in the alpine zone of Abkhazia, along the North Ossetia-Alania ridges, RF, and further to the Mtskheta-Mtianeti district ridges in Georgia, sometimes it is found in the inversion dells and river valleys down to 400-600 m [56, 76]. A new find of *G. platyphyllus* was reported in 2017 for W Caucasus (northern macroslope of the Greater Caucasus Range) around Kurdzhinovo vill., Karachay-Cherkessia, RF [18]. A small population is located in the valley of the Bolshaya Laba river (902 m) that is not far from Pyv (Anchkho) Pass (2030 m) in Abkhazia (where the Western Transcaucasian race of *G. platyphyllus* was found) from just opposite southern macroslope of the Greater Caucasus. Looking at the distribution map of this species within Caucasus the disjunctive range can be observed allocating two main areas/geographical races: (1) few scattered populations within Western Caucasus/Western Transcaucasia and (2) the main continuous distribution area within Central Caucasus/Central Transcaucasia.



Fig.5.

Central Caucasus -Galanthus platyphyllus: alpine meadows of Askhi Plateau, Samegrelo-Zemo Svaneti region, Georgia, 2200 m; 22.05.2015; photo credit – R. Mishustin.

Fig.6. Central Caucasus -*Galanthus platyphyllus*: alpine meadows of Askhi Plateau, Samegrelo-Zemo Svaneti region, Georgia, 2200 m; 22.05.2015; photo credit – R. Mishustin.



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Fig.7. Central Caucasus – *Galanthus platyphyllus*: alpine meadows of Askhi Plateau, Samegrelo-Zemo Svaneti region, Georgia, 2200 m; 22.05.2015; photo credit – R. Mishustin.

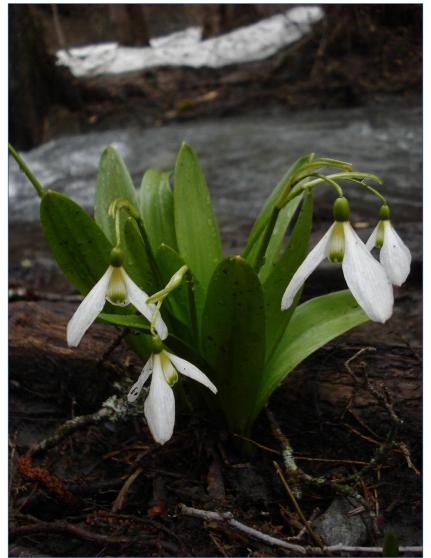


Fig.8. Western Transcaucasia – *Galanthus platyphyllus*: alder-beech forest along Lashipse river, Abkhazia, Georgia, 950 m; the plants were washed out from the higher Pyv (Anchkho) Pass (2030 m); 08.03.2011; photo credit – D. Zubov.

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Fig.9. Central Caucasus – *Galanthus platyphyllus*: clearings within hornbeam forest, valley of Chanchakhi River downward from Mamisoni Pass, Racha-Lechkhumi and Kvemo Svaneti region, Georgia, 1430 m; 10.05.2007; photo credit – J. Ruksans.

From the lower altitudes (600-1200 m) in Adjara (Georgia) Soviet botanist Andrey Khokhryakov described *G. krasnovii*, which has a disjunctive area and it was also found in Abkhazia (Georgia) and Turkey (Artvin province) [38, 72]. The plants of this taxon as well as *G. panjutinii* mainly grow in hard clay (humus-carbonaceous montane forest brown soils) in beech forests (*Fagus orientalis*) of the lower and middle montane zones. Therefore, *G. krasnovii* possesses a disjunctive area of two main sites – (1) Abkhazian race and (2) Artvin-Adjarian race.





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Fig.11. Western Transcaucasia – *Galanthus krasnovii*: near *locus classicus* (Chakvi district, in the river gorge Kintrishi), beech forest, Adjara, Georgia, 900 m; 10.03.2015; photo credit – R. Mishustin.



Fig.12. below: Western Transcaucasia – *Galanthus krasnovii*: beech forest, Mamdzhyshkha Mt., Abkhazia, Georgia, 800 m; 11.03.2015; photo credit – O. Bondareva.



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Fig.13. Western Transcaucasia – *Galanthus krasnovii*: near *locus classicus* (Chakvi district, in the river gorge Kintrishi), beech forest, Adjara, Georgia, 900 m; emerging plants after avalanche shutdown; 08.03.2019; photo credit – D. Zubov.



Fig.14. Western Transcaucasia – *Galanthus panjutinii*: beech forest, Krasnaya Poliana vicinities, Great Sochi, Aibga Ridge, RF, 800 m; this population was completely destroyed; 03.04.2013; photo credit – D. Zubov.

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Fig.15. Western Transcaucasia – *Galanthus panjutinii*: beech forest, Krasnaya Poliana vicinities, Great Sochi, Aibga Ridge, RF, 800 m; a population which was completely destroyed; 07.04.2013; photo credit – D. Zubov.





Fig.16. Western Transcaucasia – *Galanthus panjutinii*: beech forest, Krasnaya Poliana vicinities, Great Sochi, Aibga Ridge, RF, 800 m; this population was completely destroyed; 07.04.2013; photo credit – S. Banketov.

In 2012 Dimitri Zubov and Aaron Davis outlined a new name for an invalidly published species - G. panjutinii, the last one from the Platyphyllus clade [84]. It was collected by G. Sakharov in 1915 in Abkhazia, herbarized by Russian naturalist Platon Panjutin, and its Russian-language description was given by prominent Soviet botanist Alexander Grossheim as G. valentinae nom. herb. The latter taxon was erroneously put in the synonyms of G. krasnovii by Z.T. Artjushenko [4]. However, our phytochorological, morphological and phylogenetic studies have reasserted and finally formalized the species segregation. Galanthus panjutinii is distributed only in the northern Colchis area, on the calcareous ridges of Aïbga (RF), Bzipi and Gagra (Georgia: Abkhazia). Of

note, all three taxa (*G. krasnovii, G. platyphyllus* and *G. panjutinii*) occur within a vertical zonation axis in Abkhazia solely [85]. *Galanthus panjutinii* and *G. krasnovii* are syntopic with *G. woronowii*; it makes them all practically indistinguishable "in the green" after flowering.

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Alpinus clade (Galanthus alpinus agg., G. angustifolius, G. transcaucasicus) [Western and Eastern Ciscaucasia; Western, Central and Eastern Caucasus; North-Western, Western, Central and Eastern Transcaucasia; Talysh – Russian Federation, Georgia, Armenia, Turkey, Azerbaijan, Iran]. Figs. 2, 17-33.

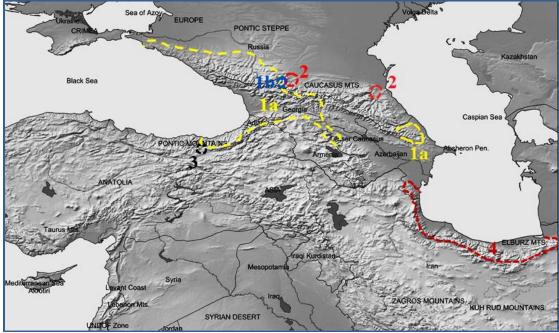


Fig.2. The distribution map of the snowdrop species from the *Alpinus* clade (created with SimpleMappr.net):

- 1a yellow *G. alpinus agg.*
- 1b blue G. alpinus var. bortkewitschianus
- 2 red G. angustifolius
- 3 black G. koenenianus (non Caucasian species)
- 4 wine G. transcaucasicus

From the Caucasian snowdrops with glaucous leaves and supervolute vernation the first one was described by J.G. Baker as a subspecies of *G. nivalis* subsp. *caucasicus* cultivated in Kew. Its type was not preserved [6]. Alexander Grossheim has segregated the Baker's taxon to species rank - *G. caucasicus* (Baker) Grossh., accompanied with Russian-language description [33]. In a paper [17]



Aaron Davis et al. provide a lectotype for Grossheim's taxon (C Transcaucasia: *Tiflis, 1828-1830, Szovits s.n., lectotype K.; isolectotype LE!*).

Further *G. alpinus* was described by D. Sosnowsky from the subalpine zone of Lomis Mta Mt. (W Transcaucasia – Borjomi district, 1800 m, Georgia) [64] and in a narrow sense, it is given also for Armenia (C Transcaucasia) and NE Turkey (Lazistan: Rize and Trabzon provinces) [15-17, 24-26, 73].

Fig.17. Central Caucasus – *Galanthus alpinus* var. *bortkewitschianus*: cultivated plants *ex locus classicus* (Chegem) in the garden of Sergey Banketov, Pyatigorsk, Stavropol Kraj, RF; 01.03.2016; photo credit – S. Banketov.

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Galanthus bortkewitschianus Koss taxon was described as an autotriploid sterile cytorace of glaucous-leafed snowdrops growing in C Caucasus – Chegem area [44]. It is considered by A.P. Davis and E.V. Mordak as a variety *G. alpinus* var. *bortkewitschianus* (Koss) A.P. Davis, on a par with its main variety - *G. alpinus* var. *alpinus* (including syn. *G. caucasicus*). In other words, the authors consider these three taxa conspecific with the priority name *G. alpinus* [17].

The only glaucous-leafed Caucasian snowdrop with clearly applanate vernation is *G. angustifolius* described from Nalchik vicinity (C Caucasus, Belaya Rechka vill. near Nalchik, Kabardino-Balkaria, RF), and recently also found in Dagestan, RF (E Caucasus) [3, 44].



Fig.18. Western Caucasus – *Galanthus alpinus agg.*: Caucasian fir forest, Lagonaki plateau, Adygea, RF, 1200 m; 08.04.2006; photo credit – O. Bondareva.

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However, numerous joint expeditions of Dimitri Zubov, Sergey Banketov, Alexey Kolchenko, Ruslan Mishustin and Olga Bondareva within NW and W Transcaucasia, W Ciscaucasia and C Caucasus revealed a polymorphic picture for glaucous-leafed snowdrops. For example, from Ciscaucasia to W, C and E Transcaucasia there are local populations of the glaucous-leafed snowdrops: (1) solely with applanate vernation and narrowly lanceolate leaves, plants which clump well (as G. angustifolius, C Caucasus - Kabardino-Balkaria, RF: Nalchik vicinity, 600-1200 m); (2) solely with supervolute / enclosed vernation and narrowly lanceolate leaves (W Ciscaucasia, W Caucasus, NW Transcaucasia, W Transcaucasia – Stavropol, Gelendzhik, Maykop, Great Sochi vicinities, 300-700 m, RF); (3) both with applanate and supervolute vernation and narrowly lanceolate leaves in the same population, plants which clump well (W and E Ciscaucasia, W Caucasus - RF: Stavropol, Pyatigorsk and Nalchik vicinities, 500-700 m); (4) diminutive mainly solitary plants solely with narrowly lanceolate to oblanceolate leaves with fully supervolute vernation (C Transcaucasia -Georgia: Borjomi - Bakuriani, 800-1800 m); (5) huge well-clumping plants with long broad strap-like to oblanceolate leaves and supervolute vernation, the earliest to bloom in the wild - late December (W Transcaucasia – Georgia: Adjara, 200-300 m; an outstanding population which was recently found by Ruslan Mishustin); (6) compact clumping plants with broadly lanceolate leaves and fully supervolute vernation (C Caucasus, E Transcaucasia - Georgia: Gombori pass, Shaori reservoir, 1200-1600 m). Such a polymorphism might be reflected as unfinished microevolutionary processes in a plant speciation event and shows the species aggregate, so the components of G. alpinus agg. might be being called segregates or microspecies (up to ~6 microspecies for G. alpinus agg.) distributed within a guite broad range of Western and Eastern Ciscaucasia; Western, Central and Eastern Caucasus; North-Western, Western, Central and Eastern Transcaucasia. Moreover, any distinct microspecies of G. alpinus agg. can eventually receive its own separate taxonomic status based on morphological, ecological or phenological characters, which is very favourable for the conservation of snowdrop biodiversity in the wild.



Fig.19. Central Caucasus – *Galanthus alpinus agg.* (syn. *G. caucasicus*): maple grove, Nalchik vicinities, Kabardino-Balkaria, RF, 600 m; 11.04.2012; photo credit – O. Bondareva.

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Fig.20. Central Caucasus – *Galanthus alpinus agg.* (syn. *G. caucasicus*): hornbeam forest, natural boundary Russian Forest Dacha, Stavropol Upland, Stavropol vicinities, Stavropol Kraj, RF, 620 m; 15.03.2014; photo credit – R. Mishustin.



Fig.21. Eastern Ciscaucasia – *Galanthus alpinus agg.* (syn. *G. caucasicus*): maple-oak mixed forest, Dubrovka Mt. (laccolith-mount), district of the Caucasian Mineral Waters, Pyatigorsk, Stavropol Kraj, RF, 500 m; 08.03.2008; this small population houses the plants with only applanate vernation and intensive vegetative propagation rate; photo credit – S. Banketov.

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For example, interesting plants can be found in the area of the Caucasian Mineral Waters in Stavropol Kraj, RF. They grow in summer-green deciduous forests on the foothills of the laccolith mountains around Pyatigorsk and Mineralnye Vody, such as Yutsa, Dzhutsa, Mashuk and Dubrovka mountains. These plants possess narrow linear leaves with applanate vernation and intensive vegetative propagation rate just as in *G. angustifolius*, but morphologically they differ from the latter, being similar to Stavropol Upland snowdrops *G. alpinus*.

Contrariwise, within the territory of Ciscaucasia and C and E Caucasus (northern macroslope of the Greater Caucasus Range) there is very likely one highly polymorphic continuous geographic race of the same affinity (incl. *G. alpinus var. alpinus, G. alpinus* var. bortkewitschianus and *G. angustifolius*) ranging from the district of the Caucasian Mineral Waters in Stavropol Kraj to Dagestan (Kazbek district), RF, and to the north of Azerbaijan (Quba district). The only quite distinct narrow-leafed and distinctly applanate vernation *G. angustifolius* from the vicinities of Nalchik (Belaya Rechka village) in Kabardino-Balkaria (RF) might be separated as morphologically distinct taxon from this polymorphic Ciscaucasia/Caucasus geographical race. The snowdrops of *G. angustifolius* affinity found in Upper Sulak area in Dagestan have not been seen by me as well as Quba plants of *G. alpinus* affinity. But I suppose they both could be quite similar by their morphology to the E Ciscaucasian plants of *G. alpinus* affinity (syn. *G. caucasicus*) from the laccolith mountains around Pyatigorsk or from the Stavropol vicinities, due to similar more arid biotope conditions in both areas.



Fig.22. North-Western Transcaucasia – *Galanthus alpinus agg.*: oak-beech forest in the upper part of the northern slope of Sakharnaya Golovka Mt., Markotkh Range, Gelendzhik vicinities, Krasnodar Kraj, RF, 500 m; 11.03.2011; photo credit – D. Zubov.

In 1947 Soviet and Georgian botanist Liubov Kemularia-Nathadze described from Georgia (C Caucasus), G. schaoricus Kem.-Nath. [37] distributed in forests around Shaori reservoir, Racha-Lechkhumi and Kvemo Svaneti region, 1200 m. These plants have the broadest glaucous leaf blade with supervolute vernation, but it is conspecific with G. alpinus [4, 37]. To add, the races of *G. alpinus* affinity from southern macroslope of the Greater Caucasus Range and from W Caucasus are also very polymorphic in leaf shape (linear vs oblanceolate) and width (1 cm to 3 cm) as well as in their confinement to different biotopes from coastal forests to alpine zone.

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Fig.23. Eastern Transcaucasia – *Galanthus alpinus agg.*: old apple tree orchard within grass-sedge meadows, Gombori Pass vicinities, Kakheti region, Georgia, 1600 m; 08.03.2015; photo credit – R. Mishustin.



Fig.24. Western Transcaucasia – *Galanthus alpinus agg.*: gorge mixed forest, Batumi vicinities, Adjara, Georgia, 200 m; 21.01.2016; photo credit – R. Mishustin.

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Fig.25. Western Transcaucasia – *Galanthus alpinus agg.*: fruiting phase; gorge mixed forest, Batumi vicinities, Adjara, Georgia, 200 m; 05.03.2019; photo credit – D. Zubov.



Fig.26. Central Transcaucasia – *Galanthus alpinus* var. *alpinus* s.str.: near *locus classicus* (alpine zone of Lomis Mta Mt., Bakuriani, 1800 m), oak-maple-hornbeam gorge mixed forest along Borjomula river, Borjomi Central Park, Samtskhe-Javakheti region, Georgia, 820 m; plants washed out from the heights of Bakuriani; 27.02.2015; photo credit – R. Mishustin.

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Fig.27. Central Transcaucasia – *Galanthus alpinus* var. *alpinus* s.str.: near *locus classicus* (alpine zone of Lomis Mta Mt., Bakuriani, 1800 m), alpine zone, Didveli-Bakuriani, Samtskhe-Javakheti region, Georgia, 1800 m; 25.05.2019; photo credit – T. Galstyan.



Fig.28. Central Caucasus – *Galanthus angustifolius*: hazel-hornbeam forest, Karasu village vicinities, Kabardino-Balkaria, RF, 1200 m; 24.03.2014; photo credit – D. Zubov.

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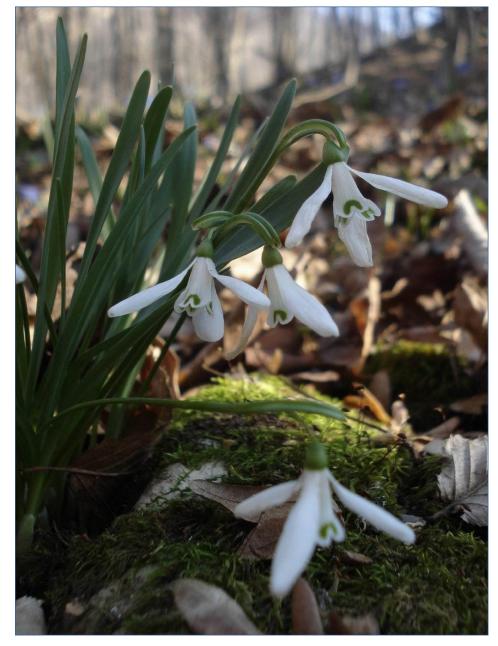


Fig.29. Central Caucasus – *Galanthus angustifolius & Scilla siberica* Haw.: *locus classicus* – hazel-hornbeam forest, Belaya Rechka village vicinities, Nalchik, Kabardino-Balkaria, RF, 700 m; 22.03.2014; photo credit – D. Zubov.

It is necessary to note the morphological peculiarities of G. alpinus plants distributed in Rize Province in NE Turkey. Certain populations from that area, according to Turkish botanist Sirri Yüzbaşioğlu, have the same longitudinal grooves on the abaxial side of a leaf blade, as in G. koenenianus Lobin, C.D. Brickell & A.P. Davis [80]. It is quite possible that, in that Rize area, in addition to common populations of both species, there are also their introgressive populations.

A snowdrop with glaucescent dark green leaves and supervolute vernation was found in the Talysh Mountains forests in 1868 (Lerik village, Azerbaijan). But the main range

of this species lies within Alborz Mountains in north of Iran ended at 1000 m point of Olang Pass (Golestan Province) - the easternmost locality for G. transcaucasicus as well as for whole genus Galanthus. To the end of vegetation, it can be easily confused with broad-leafed races of hexaploid G. lagodechianus agg., but this Fomin's taxon is diploid – G. transcaucasicus [23], initially described long ago by F.J. Ruprecht from Lerik vicinities as a subspecies of G. nivalis y caspius [57]. And it is of the Hyrcan element of preglacial flora (a present-day Hyrcan refugium, or Caspian Hyrcanian Mixed Forests). At one time L.M. Kemularia-Nathadze correctly noted in one of her papers two quite similar snowdrop species distributed in Azerbaijan, and often barely determined in herbaria [38]. Some plants have shiny bright-green leaves and applanate vernation - G. lagodechianus. The other plants have darker green leaves and supervolute vernation - G. transcaucasicus. Also in our recent work it was shown that G. transcaucasicus can be the ancient natural hybrid due to reticulation event revealed in the nuclear (ITS) and plastid topologies [55]. Do these two species occur sympatrically in Talysh, as G. transcaucasicus does (Azerbaijan and Iran): this is a still un-resolved issue. But a more realistic scenario is that in Iran G. lagodechianus may rather be distributed only in the montane forests of northern Iranian province - Eastern Azerbaijan, very close to the Iran-Armenia border, since it directly accepts the southernmost part of Armenian Zangezur Mountains), where this species grows in abundance.

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Fig.30. Talysh – *Galanthus transcaucasicus*: alpine meadows, Asalem Pass, Gilan Province, Iran, 2050 m; 01.05.2017; photo credit – H. Jans.



Fig.31. Talysh – *Galanthus transcaucasicus*: alpine meadows, Asalem Pass, Gilan Province, Iran, 2050 m; 12.04.2017; photo credit – D. Robbins.

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Fig.32. Talysh – *Galanthus transcaucasicus*: alpine meadows, Asalem Pass, Gilan Province, Iran, 2050 m; 12.04.2017; photo credit – D. Robbins.



Fig.33. Talysh – *Galanthus transcaucasicus*: Persian ironwood-hornbeam forest, Hyrcan National Park, Azerbaijan, 600 m; 30.01.2009; photo credit – S. Mayorov.

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Woronowii clade (*Galanthus woronowii*, *G. rizehensis*, *G. lagodechianus agg.*) [Western, Central and Eastern Caucasus; Western, Eastern, Central and Southern Transcaucasia – Russian Federation, Georgia, Armenia, Turkey, Azerbaijan]. Figs. 3, 34-44.

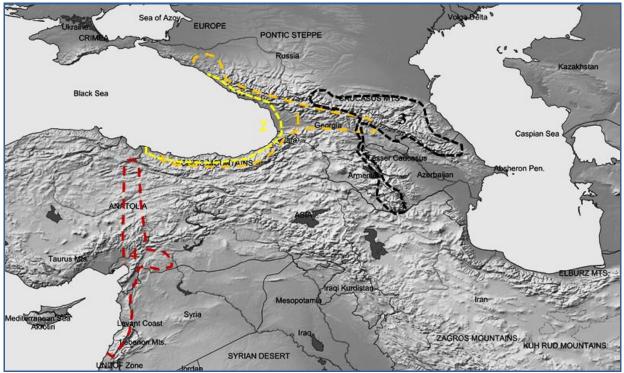


Fig.3. The distribution map of the snowdrop species from the *Woronowii* clade (created with SimpleMappr.net):

- 1 gold G. woronowii
- 2 yellow G. rizehensis
- 3 black G. lagodechianus agg.
- 4 wine G. fosteri (non Caucasian species)

There is longstanding nomenclature confusion caused by a snowdrop with narrow glaucescent dark green leaves and applanate vernation, which grows in the forests of Colchis lowland and Lazistan, from Tuapse-Great Sochi area, RF, to Samsun province, Turkey; it is *G. rizehensis* [73, 75]. From Adjara (Georgia) this species was described by A.P. Khokhryakov as *G. glaucescens* Khokhr. [40], and in the Z.T. Artjushenko textbook work on the genus *Galanthus* she erroneously put the two above-named taxa in synonyms of allopatric *G. cilicicus* Baker from the *Elwesii* clade being narrow local endemic distributed only in southern Turkey. Both are quite similar in herbarium when dried [2, 4]. Under this wrong name (syn. *G. glaucescens*) *G. rizehensis* appeared in the "Local Plant Determinant of Adjara", 1990 [19].

Galanthus rizehensis (W Transcaucasia and Lazistan) populations are represented by diploid (fertile) and triploid (mostly sterile) cytoraces and furthermore there is some ecological disunity for this species. For example, around the Great Sochi the species grows in some populations in the form of numerous narrow-leafed vegetative clones, as well as epilithic (over the rocky ledges); it doesn't flower freely there or set seed. At the same time, there are its populations with still applanate vernation, a small number of clones but broad dark green leaves with morphology similar to *G. woronowii*, like some intermediate morph between *G. rizehensis* and *G. woronowii*. The same pattern previously pointed by A.P. Davis in his monograph [15] and by Turkish botanist Tasci Margoz in a recent paper on the Turkey snowdrops. Nevertheless, phylogenetic analysis performed by Turkish researchers has showed the genetic homogeneity for both analyzed ecomorphic samples of *G. rizehensis* [73].

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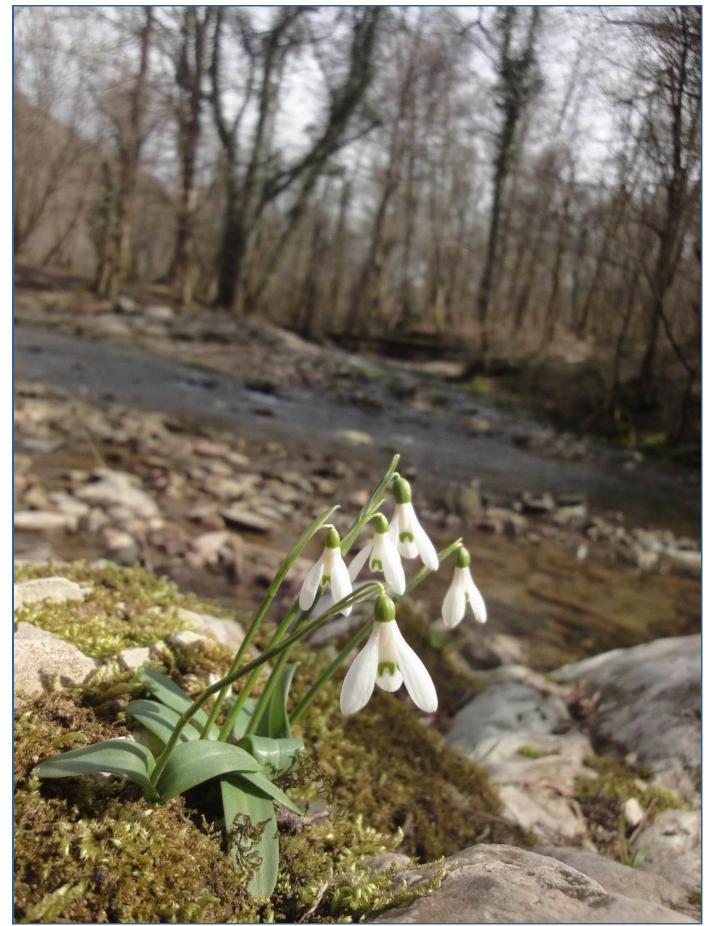


Fig.34. Western Transcaucasia – *Galanthus woronowii*: hornbeam forest along Agura river, Matsesta vicinities, Great Sochi, Krasnodar Kraj, RF, 350 m; 06.03.2011; photo credit – D. Zubov.

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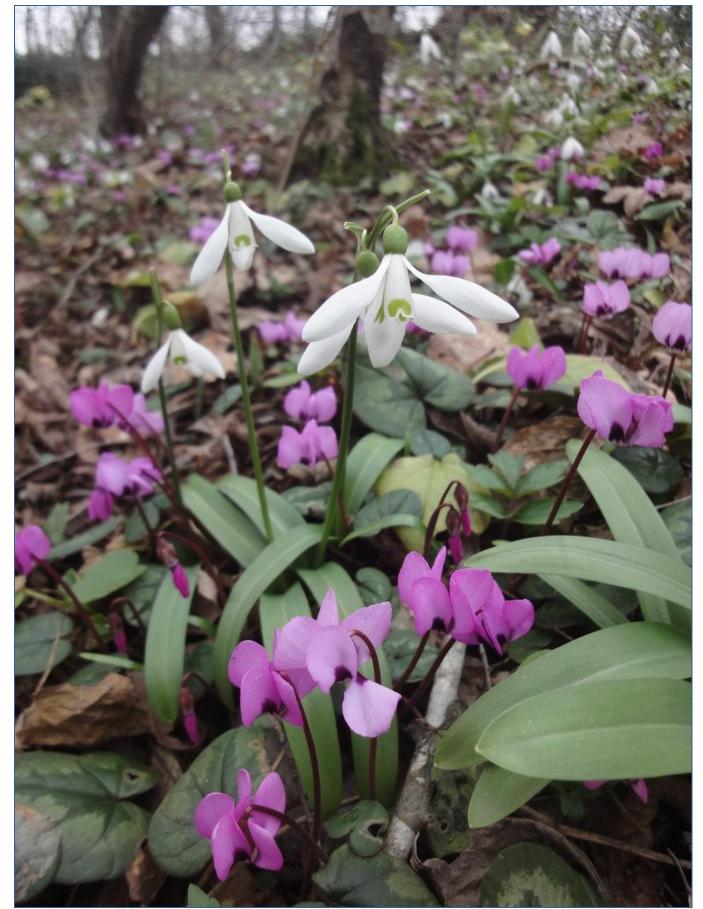


Fig.35. Western Transcaucasia – *Galanthus woronowii* & *Cyclamen coum* Mill.: hornbeam forest, Orlinye Skaly (Eagle Cliffs), Matsesta vicinities, Great Sochi, Krasnodar Kraj, RF, 380 m; 06.03.2011; photo credit – D. Zubov.

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Fig.36. Western Transcaucasia – *Galanthus woronowii*: old tangerine orchards, Kvariati village, Adjara, Georgia, 60 m; 04.03.2019; photo credit – D. Zubov.

The most recognizable bright green-leafed Caucasian snowdrop with supervolute vernation and characteristic sinus at the apex of inner perianth segment is *G. woronowii*, described from the W Transcaucasia, Krasnaya Polyana



vicinities, RF [48]. The total distribution area of the species lies in the range of NW, W Transcaucasia from Maykop (W Caucasus foothills, Adygea Republic, RF) via Tuapse, Sochi, Batumi (Colchis Lowland) to Lazistan (Artvin, Rize, Trabzon, Ordu provinces, Turkey) [15, 73, 75]. The cryptic species (species that contain individuals that are morphologically identical to each other but belong to different species) for *G. woronowii* is allopatric *G. ikariae* Baker (*Ikariae* clade) distributed in Aegean islands, Greece. Therefore Z. Artjushenko mistakenly assigned it to the last species by priority of the name, having thought that the merchants brought in boats these Caucasian snowdrops to the Aegean islands, which seems fantastic. So, it can be summarized that *G. woronowii* consists of two geographical races: (1) Lazistan-Western-Transcaucasian and (2) Western-Caucasian. Further to south (Turkey and the Levant) *G. woronowii* is replaced by vicarious species – *G. fosteri* Baker.

Within *G. woronowii* populations two extreme ecomorphs could be distinguished: a rocky form – quite robust plants, with tall upward broad leaf blades, in numerous vegetative clones often hanging from the rocky ledges through the gorges or grow beneath the rocks; and *a woodland form* – the medium-sized plants with a moderate number of clones growing mostly on clay in the forests or open meadow area [15, 75]. However, it is often difficult to discern in the wild which ecomorph *G. woronowii* plants belong to, being of some intermediate morphology as well.

From the recent interspecific/interclade homoploid hybrids only $G. \times allenii$ Baker is known (between *G. alpinus* and *G. woronowii*). Actually, it is distributed as cultivated clone in European gardens. *Galanthus* × *allenii* had been acquired by accident in 1883 by James Allen in the consignment of *G. latifolius* Rupr. (I suppose it was rather a delivery of *G. woronowii* instead of rarely occurred, difficult and short-lived in cultivation *G. platyphyllus* as commonly believed) from the Austrian nurseryman Gusmus [15, 16]. But such hybrids were never observed in the wild within Caucasus. I have observed other similar hybrids with intermediate morphology and distinctive steely tinge of their leaves growing in the 'Caucasus plot' of M.M. Gryshko National Botanic Garden in Kiev, Ukraine, where different geographical accessions/collections of *G. alpinus* and *G. woronowii* meet each other and some of them could generate viable homoploid crosses with resulted different seed clones of various habit. Most likely such clones of considered hybrid origin can also be found in the wild.

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Fig.37. Western Transcaucasia – *Galanthus rizehensis*: thickets of laurel cherries in the hornbeam forest along Stariki creek, Kudepsta vicinities, Great Sochi, Krasnodar Kraj, RF, 6 m; 13.02.2019; photo credit – O. Bondareva.

Fig.38. Western Transcaucasia – *Galanthus rizehensis*: alder forest, Chaysubani village, Adjara, Georgia, 37 m; 18.02.2015; photo credit – R. Mishustin.

Among the Caucasian polyploid snowdrops with green leaves and applanate vernation there have been several described (distributed within C and E Caucasus, C, E and S Transcaucasia): G. lagodechianus s.str. (E Transcaucasia -Lagodekhi Managed Reserve, 600 m, Georgia), G. ketzkhovelii Kem.-Nath. (C Transcaucasia subalpine zone of Khochaldag Mt. in Lagodekhi Managed Reserve, Georgia), G. kemulariae Kuth. (C Transcaucasia – Zedazeni Monastery, one of the summit of Saguramo Range, Tbilisi vicinities, 1300 m, Georgia), G. cabardensis Koss (C Caucasus, Kabardino-Balkaria, RF), and G. artjuschenkoae Gabrielian (C Transcaucasia -Lori, Tavush area, S Transcaucasia - locus classicus: Zangezur Range, Kapan, Syunik area, Armenia). The first four taxa turned out to be conspecific and were aggregated by Z. Artjushenko under the priority name - G. lagodechianus [2-4, 27, 44, 46].



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Fig.39. Central Caucasus – *Galanthus lagodechianus agg.* (syn. *G. cabardensis*): beech forest, Leskensky District, Kabardino-Balkaria, RF, 900 m; 12.03.2009; photo credit – S. Banketov.



Fig.40. Eastern Transcaucasia – *Galanthus lagodechianus s.str. & Scilla siberica* subsp. *otschiauriae* (Mordak) Mordak: *locus classicus* – oak-beech forest along Lagodekhiskhevi river, Lagodekhi Managed Nature Reserve, Kakheti region, Georgia, 600 m; 17.02.2016; photo credit – R. Mishustin.

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Fig.41. Eastern Transcaucasia -Galanthus lagodechianus s.str. & Scilla siberica subsp. otschiauriae (Mordak) Mordak: locus classicus oak-beech forest along Lagodekhiskhevi River, Lagodekhi Managed Nature Reserve, Kakheti region, Georgia, 600 m; 02.03.2019; photo credit - D. Zubov.





Fig.42. Eastern Transcaucasia – Galanthus lagodechianus s.str. & Anemone caucasica Willd. ex Rupr.: locus classicus – oak-beech forest along Lagodekhiskhevi river, Lagodekhi Managed Nature Reserve, Kakheti region, Georgia, 600 m; 02.03.2019; photo credit – D. Zubov.

During an Armenian trip in May 2013 in the locus classicus of G. artjuschenkoae (Zangezur forests around Vaahnavank monastery, Kapan, Syunik area, Armenia) Dimitri Zubov and Leonid Bondarenko found the only typical *G. lagodechianus* plants. It turned out that it grows within whole area of Zangezur Range forests. Moreover, Armenian botanist Nora Gabrielian also gives its distribution for Talysh [27]. In the folder named "G. artjuschenkoae" housed in LE herbarium (V.L. Komarov Botanical Institute, St. Petersburg, RF) and formed by Helena Mordak, when studying myself I found there were mixed sheets both with

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Azerbaijan plants of *G. transcaucasicus*, and with Armenian plants of *G. lagodechianus* (D. Zubov, *pers. observ.*, January, 2015). In addition, in the 10th volume of Flora of Armenia, in the treatment of the genus *Galanthus* by E. Gabrielian, *G. transcaucasicus* and *G. artjuschenkoae* were listed as separate species, along with *G. alpinus*, and in a later paper E. Gabrielian and Nazarova (2002) give also for Armenia a taxon of *G. kemulariae* [24, 25].



Fig.43. Southern Transcaucasia – *Galanthus lagodechianus agg.* (syn. *G. artjuschenkoae*): beechhornbeam forest, Zangezur Range, Shikahogh State Reserve, Syunik Province, Armenia, 1200 m; 10.03.2018; photo credit – T. Galstyan.



Fig.44. Southern Transcaucasia – *Galanthus lagodechianus agg.* (syn. *G. artjuschenkoae*): beech-hornbeam forest, Zangezur Range, Shikahogh State Reserve, Syunik Province, Armenia, 1200 m; 18.03.2017; photo credit – T. Galstyan.

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Thus, as a result of field studies and phylogenetic analysis both taxa (*G. lagodechianus* and *G. artjuschenkoae*) turned to be conspecific [55], but diploid *G. transcaucasicus* is a separate species from the Azerbaijan's Talysh. That is, in Armenia, instead of the previously recognized three / four taxa (by Davis - *G. lagodechianus, G. transcaucasicus, G. alpinus* [15, 16]; by Gabrielian - *G. artjuschenkoae, G. transcaucasicus, G. alpinus, G. kemulariae* [24, 25]), actually there are two: *G. lagodechianus* (Tavush area - Ijevan, Syunik area - Zangezur) and diploid glaucous-leafed *G. alpinus* (Tavush region - Noyemberyan, Ijevan) are distributed. *Galanthus lagodechianus* also grows in Nagorno-Karabakh area, S Transcaucasia (22.IV.1968, № 862, *Mordak,* LE!).

The typical plants of Eastern Transcaucasian race of G. lagodechianus from locus classicus (Lagodekhi Managed Reserve, 600 m, Georgia and in adjacent Zagatala State Reserve in Azerbaijan) are the huge plants with dark green matt leaf blades, up to 30% of them possess a glaucescent hint. Some of the plant clumps of this Eastern Transcaucasian race resemble indistinguishably G. transcaucasicus plants. From the other hand, noticeably large plants of G. lagodechianus with shiny bright green leaves belong to the representatives of the Central Caucasian (syn. G. cabardensis) and the Transcaucasian (syn. G. artjuschenkoae) geographical races. The latter one has some individuals with supervolute vernation and leaf blade width up to 2.8 cm. In its ecological minimum (E Transcaucasia, subalpine zone) the plants are represented by bright green narrow-leafed seldom flowering clones with an active vegetative propagation (syn. G. ketzkhovelii, and Central Transcaucasian G. kemulariae). However, such narrow-leafed clones are also often found in Central Caucasian and Transcaucasian populations. In other words, we can assume the presence of different microspecies within the whole range of distribution of the hexaploid G. lagodechianus agg. differed by morphological, ecological or phenological characters. To summarize, they are: (1) Central Caucasian geographical race, northern macroslope of GCR (Nalchik, syn. G. cabardensis); (2) Eastern Transcaucasian geographical race (Lagodekhi, Zagatala, G. lagodechianus s.str.) with its subalpine ecological elements (Khochaldag Mt. - syn. G. ketzkhovelii; Saguramo Range – syn. G. kemulariae); (3) Eastern Caucasian geographical race (Khasavyurt, Buynaksk, Quba); (4) Southern Transcaucasian geographical race (Zangezur Range: Kapan, Shusha, Ganja, syn. G. artjuschenkoae).

Nivalis clade (*Galanthus plicatus* subsp. *plicatus*) [North-Western Transcaucasia – Russian Federation]. Figs. 4, 45, 46.



Fig.4. The distribution map of the snowdrop species from the *Nivalis* clade within Caucasus (created by SimpleMappr.net):

1 – yellow - G. plicatus subsp. plicatus

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An unexpected find of *G. plicatus* ssp. *plicatus* was made relatively recently in NW Transcaucasia (Krasnodar Kraj, Novorossiysk district, Glebovka Mt., with hornbeam-oak forest at the top, 19 March 1997, *A. Zernov*, LE!) in 1997 by A.P. Seregin in the forests (four known localities at the moment) around Novorossiysk, RF [59, 81-83]. The nearest core subspecies area lies within the Crimean Mountains. However, its Transcaucasian race plants, of course being a part of whole species disjunctive area, possess diminutive and gracile habit and larger apical mark on the inner perianth segments or it occupies the entire segment, but it has never two basal and apical marks like in northwestern Anatolian subspecies *G. plicatus* subsp. *byzantinus* (Baker) D.A. Webb.



Fig.45. North-Western Transcaucasia – *Galanthus plicatus* subsp. *plicatus*: oak-hornbeam-ash forest, Glebovka Mt., Novorossiysk vicinities, Krasnodar Kraj, RF, 400 m; 11.03.2011; photo credit – D. Zubov.

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Fig.46. North-Western Transcaucasia – *Galanthus plicatus* subsp. *plicatus*: oak-hornbeam forest, Glebovka Mt., Novorossiysk vicinities, Krasnodar Kraj, RF, 470 m; 04.02.2019; photo credit – T. Vinokurova.

The general speciation pattern for the genus Galanthus

In Novorossiysk district *G. plicatus* ssp. *plicatus* (entire range of *G. plicatus* runs by the western side of Black Sea from NW Anatolian plateau via Balkan Peninsula, Crimean Peninsula to NW Transcaucasia) and *G. alpinus* var. *alpinus* (whole range runs by the eastern side of Black Sea from Lazistan to W Caucasus and NW Transcaucasia) co-exist sympatrically with complete reproductive isolation (no hybrids reported). Thereof, at this geographical point of Crimea-Novorossiysk the whole area of the genus *Galanthus* is locked, forming the ring of overlapping geographical intergrading races – "*Galanthus* Euxine ring including Colchis primary speciation centre and Crimea-Novorossiysk locking point with irradiations" within Caucasus, Crimea, Asia Minor and Near East, Balkans, Mediterranean and Europe. It generates a wide circumcoastal snowdrop clades ring around the Black Sea (clockwise from NW Transcaucasia to Crimea: *Alpinus* and *Woronowii* clades, *Platyphyllus* clade, *Elwesii, Trojanus* and *Ikariae* clades and *Nivalis* clade) with overlapping closure of the extreme reproductively isolated elements (species) from the *Nivalis* and *Alpinus* clades in Crimea-Novorossiysk floristic province [86].

Autopolyploid patterns in the Caucasian snowdrops

In the genus *Galanthus* three naturally occurring polyploid taxa are identified for the moment, such as autotriploid *G. rizehensis* (2n=24, 36), *G. alpinus* var. *bortkewitschianus* (2n=36) and autohexaploid *G. lagodechianus* (2n=72) [72, 84]. It is accepted the polyploids are common in habitats affected by significant climatic and edaphic fluctuations, which was undoubtedly the case of Caucasian landscapes, the primary centre of speciation and biodiversity for the genus *Galanthus*, which was subjected to last repetitive glaciation peaks within Quaternary [14, 30, 65, 79]. The diploids are usually conserved in disjunctive glacial refugia (e.g. *G. woronowii, G. rizehensis, G. transcaucasicus*) but polyploids are mostly distributed across post-glaciation territories [20]. Such a pattern is observed in almost all autopolyploid plant complexes and suggests that genome doubling is significantly associated with environment extreme changes during periglacial periods [52].

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Following Stebbins, [66], a secondary contact of pre-glaciation sympatric (parapatric) populations under extreme environmental conditions (Stebbins' hypothesis on the allopolyploids origin: climatic fluctuations contribute to the establishment of secondary contact and admixing between previously allopatric taxa with the resulted hybrids via chromosome doubling with their fertility restoration) could also favour likewise the autopolyploid lineage's genesis in order to restore fertility in interbreeding individuals between distinct populations. A similar mechanism may explain why polyploid lineages appear as discrete bursts during periods of intense climate changes [22]. For example, autotetraploid race emergence occurs mainly via union of unreduced gametes, both through the fusion of two unreduced gametes (bilateral polyploidy), or by mean of fusion of the reduced and unreduced gametes resulted in unbalanced triploids, which in turn can generate balanced tetra- or hexaploid offspring by selfing or backcrossing (unilateral polyploidy) [11]. It is known, the production of unreduced gametes is genetically inherited been under control of several genes. It increases with stress environmental conditions enhancing (e.g., chionization, frost, drought, nutrients deprivation, etc.) that may further force the rate of autopolyploid races' genesis in a changing environment [52]. It is noteworthy that the formation of autopolyploids allows a significant part of the genetic diversity of diploid progenitors to be integrated into the autopolyploid gene pool [35].

There are many indications on *multiple origins of autopolyploid taxa* (e.g., *Heuchera micrantha* Dougl. ex Lindl. [61] and *Biscutella laevigata* L. [51]), which also increases the genetic diversity of autopolyploid populations through involvement in a process the different maternal lineages. That is called *polytopic autopolyploidy* [62]. Briefly, natural autopolyploid lineages potentially include differentially adapted genotypes. For example, in a complex of *B. laevigata* (*Brassicaceae*) the diploid populations are genetically depauperate and relictual to a glacial refugium, while its autotetraploid populations colonized large areas across the European Alps since the last Quaternary glacial peak and exhibit a substantial genetic diversity [49, 77]. Multiple origins of autotetraploid lineages within different diploid populations of *B. laevigata* is the most acceptable explanation of high genetic diversity in their recently mass colonized post-glacial distribution areas. C. Parisod and G. Besnard showed [51] that the independent autotetraploid lineages are distributed through entire not-habitat-specific altitudinal gradient. So, they make an assumption that such ample ecological amplitude for autotetraploids was a result of spatial juxtaposition of lineages with distinct ecotope requirements [8, 63].

In other words, a similar autopolyploid races' formation pattern can be extrapolated to the snowdrop taxa/races from the *Woronowii* clade. It is one of the two clades in genus *Galanthus* possessing the highest number of autopolyploid lineages (taxa) within. As Ronsted et al. analysis [55] didn't show the incongruence and any reticular nodes for the *Woronowii* clade, it could be very likely assumed that its considered triploid and hexaploid recent cytoraces are rather of the autopolyploid origin based on genome doubling due to environment extreme changes during late Pleistocene periglacial periods. Thus, the populations of diploid and thermophile ancestor of *G. woronowii* were preserved in Colchis refugium within Pleistocene W Transcaucasia territory. Presumably, diploid thermophile ancient progenitor races of *G. woronowii* were distributed before the Quaternary Last Glacial Maximum (LGM, 26,5-19 thousand y. a.) across the ancient subtropical and more pluvial Pliocene W Transcaucasia (current Colchis refugium) and they successfully captured the territories of current Transcaucasia and Lazistan, Anatolia, Caucasus, Ciscaucasia and Talysh (current Hyrcan refugium).

Galanthus rizehensis is syntopic and closely sympatric with *G. woronowii* and could be very likely considered as its derivative in the past unbalanced triploid cytorace now been spread to a larger territory up to the north-eastern Turkey and it is polymorphic possessing both diploid and triploid cytoraces in the same mixed population. For example, its Western Transcaucasian representatives have smaller plant habit, but Turkish plants are larger in all plant parts [15]. In this case the phenomenon of polytopic autopolyploidy formation within diploid progenitor lineages of *G. rizehensis* after LGM could be observed. Turkish botanists reported about findings in north-eastern Turkey the

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plants bearing the intermediate morphology between G. woronowii and G. rizehensis [74]. Moreover, there are some new reports of Russian botanists on findings of G. woronowii [1, 45] in a cooler territory of Northern Caucasus (Adygea republic, RF). Both species are currently restricted to narrow physiological limits of relictual ecotopes such as subtropical forests and limestone outcrops in the foothills, the lower and middle montane forest belts. But to restore the fertility for unbalanced polyploid lineages by G. rizehensis ancestor races and for their further Caucasian expansion, recent balanced post-glaciation autohexaploid races of G. lagodechianus agg. were successfully generated after LGM by mean of polytopic autopolyploidy mechanisms. It occurred probably via secondary contact under extreme environmental conditions during repeated periglacial periods of intense climate changes between diploid progenitor lineages of G. woronowii (reduced and unreduced possible euploid gametes 1x or 2x) and triploid G. rizehensis progenitor lineages (reduced and unreduced possible euploid gametes 1x, 2x or 3x) across the periglaciated Caucasus. In a paper of Ronsted et al. the phylogenetic network analysis and hybridization analysis showed that G. lagodechianus might be a putative hybrid between G. woronowii and G. rizehensis. But G. lagodechianus is topologically congruent between plastid and nuclear (ITS) analyses, it is probable that these non-tree-like phylogenetic patterns are caused by a lack of resolution in the plastid analyses, rather than by hybridization, or other processes [fig. 3 in 55]. Of note, in contrast to hybrids in homoploid species, triploids may actually facilitate rather than diminish the fixation of tetraploids by enhancing the rate of formation, like in Chamerion angustifolium (L.) Holub. (Onagraceae) [35]. Formation of more plastic and fertile balanced autohexaploid lineages of G. lagodechianus were likely caused in non-habitat specific manner via polytopic autopolyploidy mechanisms and secondary contact between diploid and triploid populations of ancestors of the Woronowii clade, which led to successful recent post-glaciation expansion of this hexaploid lineages and gradual increase of populations/races effective size throughout the Caucasus, invading all sorts of ecological niches of the deciduous forests of the lower montane forest belt up to the subalpine belt, expressing whole spectre of ecomorphological variability.

The second clade which includes apparently recently emerged autotriploid *G. alpinus* var. *bortkewitschianus* (Koss) A.P. Davis, is the *Alpinus* clade. This unbalanced fully sterile autotriploid lineage of *G. alpinus* occupies beech forest (*Fagus orientalis*) of 5-6 hectares only in its *locus classicus* in Central Caucasus (the upper reaches of Kamenka River, 1200 m, Kabardino-Balkaria, RF) and multiples only by vegetative manner. However, it is reported about new finds of this variety in the same geographic area [60], although the *locus classicus* was never found later. But all living material of this morphologically uniform sterile taxon sustained in private and public collections was originated from the authentic gathering made in March 1947 by Soviet botanist Yuri Koss from type locality and further introduced to the Kabardino-Balkarian Republican Botanical Garden of the State Farm "Decorative Cultures" in Nalchik, RF.

Due to polysomic inheritance the autopolyploid populations show higher degree of heterozygosity and almost doubled effective population size value in comparison with populations detecting disomic inheritance pattern [53, 54]. In response to inbreeding, the degree of heterozygosity, respectively, decreases slower in autopolyploid than in diploid populations. Genome doubling could protect the autopolyploids from inbreeding depression in contrast to diploids, and thus could provide an immediate advantage favouring the establishment of autopolyploid populations. Such plants can contain more than two alleles per locus, which allows them to produce a variety of allozymes (multiple forms of enzymes characteristic to the heterozygotic state), which, in principle, allows them to adapt to different ecotopes and landscapes.

Only strict sympatric speciation requires immediate niche differentiation between cytotypes or competitive superiority of autopolyploid over diploid progenitors. Balanced autopolyploid lineages, e.g. *G. lagodechianus agg.*, distributed on both sides of the Greater Caucasus Range, spread as a rule from the periphery of the diploid taxa area, for example, thermophile *G. woronowii*, which is

restricted by the narrow coastal strip of the Euxine relictual subtropical forests, jammed between the sea and the mountain range, and to be fixed in places where their progenitors are absent. It forms a source for further lineage expansion, as we could observe the case of the massive distribution of *G. lagodechianus agg.* in the current geological epoch of Holocene from Ciscaucasia up to the Transcaucasia and possibly Talysh Mountains [47]. In other words, these new postglacial polyploidy snowdrop races have occupied such a vast territory after the last Pleistocene glaciation, which ended 10-12 thousand years ago, giving rise to the more pluvial Holocene climate in Caucasus.

Thus, in repeated extreme periglacial conditions, the polyploidization process can serve as an escape from genetic and ecological niche depauperation leading to the gene drift and selfing in diploids [13]. In other words, polysomic inheritance in autopolyploids may have a short-term evolutionary advantage compared to diploids, in extreme climatic and edaphic shifts. In addition, autopolyploid populations should have considerable genomic plasticity, which allows them to adapt and be secured in distinct ecological niches for a long time [52].



Fig.47. Dr. Zinaida Artjushenko (1916-2003) – prominent Soviet and Russian botanist-morphologist, doctor of biological sciences, professor; from 1949 till 1995 she was a researcher in the Komarov Botanical Institute of the Russian Academy of Sciences, Saint-Petersburg, RF; she is the author of the first full critical taxonomic revision of the genus *Galanthus* published in 1970: *"Amaryllidaceae Jaume St.-Hilaire of USSR. Morphology, systematics and uses"*, where she paid a special attention to the Caucasian snowdrop species [2, 4]; photo credit – Botanical Information Databases, <u>http://info.botdb.ru/</u>.

Fig.48. Dr. Aaron Davis, an author of the latest academic **RBG Kew botanical** magazine monograph about snowdrops in the wild "The Genus Galanthus", 1999; he is actually Senior Research Leader in **Royal Botanic** Gardens, Kew, Richmond, Surrey, UK; Dr. Davis pictured

with Kew colleague Dr. Anna Trias Blasi during our joint Ukrainian-British field expedition to study snowdrops in



Ukraine; locality of *Galanthus nivalis* L. in oak forest, Stavyshche district, Kiev area, Ukraine; 18.03.2011; photo credit – D. Zubov.

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Dimitri Zubov with Sergey Banketov and Olga Bondareva in Dombai, North Caucasus, RF; August 2016.

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---South American Update---

Sarah meets her namesake. Zephyranthes sarae is still alive and kicking at Tambillo

John and Anita (Ana Rosa Flores) Watson

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The malingerer

Towards the end of last year John contracted a quite serious septicaemia infection resulting from a simple routine internal check. It required hospitalization at Los Andes with prolonged daily intravenous antibiotic treatment [Fig.1]. At the time public protests against various perceived economic inequities and injustices, including low minimum salaries, hefty road tolls and inadequate pensions, as well as deficiencies in the health service, were in full swing throughout Chile. They included massive peaceful marches, but also a large, widespread and uncontrolled element of anarchic destruction, shop theft, arson, street blockades and attacks against the police, mainly by young adult males and late adolescents. One day the whole area of Los Andes was paralyzed by this

ravaging and pillaging, and Anita had to walk the six kilometres from our home to the hospital and back to visit John. Meanwhile he was being driven mad by enforced inactivity and the interminable, inescapable and depressing reports of nationwide violence on the ward TV from morning to lights-out at night.

Fig.1: John at the start of hospitalization for septicaemia. (Oct 2019. ARF)

Daughters Sarah and Nicola back in England were deeply concerned by this situation, and Sarah began to plan to fly out to Chile as soon as she could to be with us in 'our hour of need'. But John's antibiotic remedy



was changed after a week for another requiring only a short period of intravenous connection. Anita's mother lives quite close to the hospital, well clear of that 'mob rule', and we discovered a medical team could visit us there daily. So, albeit against the recommendation of his specialist, John opted for the mobile treatment and discharged himself. Able to resume his work schedule, and with morale boosted back to normal levels, he made his customary speedy recovery, which as usual took the medics (and family) by surprise! We returned home and that was that.



Fig.2: The serious drought in Chile. Lagunillas above Santiago at 2200 m in high summer. It should be green and flowery everywhere. (15 Dec 2019. JMW)

To fly or not to fly?

So where did John's unexpected recuperation leave Sarah? Although acceptably comfortable economically, she's by no stretch of the imagination well off, and air fares between the UK and Chile aren't cheap at best.

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Not only was the flowering season nearly at an end by then, but it had also been - and remains - a serious drought-stricken year in much of Chile, including the mountains [Fig.2], not least in the parts we might be able to reach during her possible short stay. These were unattractively dry and sere almost without exception. We tried gently to dissuade her, but she'd been bitten by the urge to come down to be with us, and couldn't be deterred. By serendipity we also realised the new species we had named for her in the December IRG (Watson & Flores 2019), *Zephyranthes sarae*, flowers late, meaning we could at least take her to it on spec and enjoy other sectors of that attractive part of Chile at the same time. So Sarah found a reasonably priced flight and we met her in the café of Santiago airport on the 14th of February 2020. Fortunately the coronavirus pandemic caused no problems for her in transit.

We're off!

The first four days were spent with us at home, and the poor wee thing found herself helping to lug furniture around as we emptied out our computer workroom ready to plaster the walls and lay a new floor (still in the early stages as we write). But ample compensation lay shortly ahead. The seven-day trip northwards to the Pacific coast had already been planned, including overnight stops with relatives and friends here and there. We set out in the jeep on Tuesday the 18th. With some 400 kilometres by road to cover to our first destination, La Serena, most of the day was spent on the move. But we did stop off to enjoy a lunch of their renowned fried and creamy cheese-filled 'Cornish pasties' (Chilean empanadas) at our favourite Huentelauquén drive-in. A few showy wayside plants also caught the eye in passing, and of course we couldn't resist pulling up on the hard shoulder to take photos. Prime among them was the Mexican yellow poppy, *Argemone mexicana* [Figs.3, 4]. No less compelling were the several wind farms along the mid-coastal stretch with their up to 50 aerogenerators each [Fig.5]. We feel someone ought to commission a modern sculptor to produce a don Quixote in the same style to tilt at them in situ! By the side of the road at one site a propeller blade is laid out as a display. It's impressively huge close to.



Fig.3: En route and well 'up north'. Sarah photographing *Argemone mexicana*, the Mexican poppy, a welcome encounter by the roadside. (18 Feb 2020. JMW)



Fig.4: And here is that *Argemone mexicana* in close-up. (18 Feb 2020. JMW)

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Fig.5: Sarah's general and professional interest in things environmental was stimulated by the several wind farms we passed near the coast. (18 Feb 2020. JMW)

Heading for the heights

That night we stayed in La Serena with the ex-wife of Anita's elder brother. She's always remained a very good friend. Our first intended objective was to get as far as we could during the next day along the Elqui Valley due east of Serena, heading up towards the Agua Negra Pass across to Argentina at 4780 m, one of the highest in the world. The route contains such tasty morsels as *Erythranthe (Mimulus) depressa*, *Cruckshanksia macrantha*, *C. palmae*, *Malesherbia lanceolata* and the dwarf *Alstroemeria andina*. Being at such an elevation, we felt there was a fair chance of finding the Andean flora in flower so late, although the

drought did cast serious doubts on that likelihood. In the event we reached the border police and customs post at just over 3100 m, still 40-50 km short of the actual pass. There we were regretfully informed we couldn't go further as Sarah didn't have her passport. But as we'd feared, everywhere was parched, with little hope even if we'd been able to continue. Despite this set-back, the happy



Fig.7: Natural-based cocktails are a speciality of Sarah's 'Wildfeast' enterprise, and we took her to the famous pisco vineyards of the Elqui Valley. (19 Feb 2020. JMW)

holiday mood was sustained by the choice of a delightful tree-shaded lunch spot and paddle in the Elqui River alongside [Fig.6].

Fig.6: Our first sortie. A stop for lunch and a paddle in the Elqui River as we head for the heights of the Cordillera de Coquimbo. (19 Feb 2020. JMW)



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Fig.8: Pisco is to Chile what whisky is to Scotland! (19 Feb 2020. ARF)

We rounded off by taking Sarah on a tour of the famous Elqui Valley pisco vineyards and local distilleries [Figs.7, 8]. Pisco is a highproof spirit of historic origin reduced from the fermented juice of local grapes. It's the basis of a well-known cocktail, pisco sour, but in the course of her professional foraging enterprise, Wildfeast, Sarah invents a multitude of her own. We were treated to a different one most days during her stay [Fig.9]. As far as botanising went, that day we had to be content with adding the rarish regional endemic *Argylia potentillifolia* [Fig.10] to the cameras,

nothing else. It had first been seen in this sector by Beckett, Cheese and Watson in 1971, then more recently much lower down the valley by us both in 2008.



Fig.10: Bad luck and drought dogged our attempts to see the Elqui Andean flora. *Argylia potentillifolia* from fairly high up was the consolation. (19 Feb 2020. JMW)

Fig.9: One of the numerous memorable pisco-based cocktails Sarah invented for us during her two-week stay. (21 Feb 2020. ARF)



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On Thursday, we met up again with Juan Alegria, another Chilean amateur natural history enthusiast, at Vallenar in the next region to the north, Atacama. We'd got to know him, as a number of others, when he contacted us to ask for the identity of a viola. It turned out to be a new one we were already investigating. Two and a half years ago he took us to see it at what would become its type site. We named it Viola marcelorosasii in the IRG, and also mentioned in another issue Juan's time with us in the flowering desert (Watson & Flores 2017, 2018). We spent the day on a local sortie with him before he took us up behind Vallenar on Friday for our second attempt to reach the main Andean chain. History repeated itself. Very recent storms generated by systems driving across the Andes from Argentina had caused devastating mud avalanches which had not only blocked our road ahead, but swept through a village in the valley, destroying property, laying a thick bed of silt [Fig.11], and, worst of all, killing two inhabitants. Not a single wildflower fell to our cameras, although Sarah took advantage of a prime foraging opportunity beside the road [Fig.12] when Juan pointed out the fallen fruit pods [Fig.13] of the graceful Geofroea decorticans tree, a xerophytic species of the Fabaceae. The yellow pea flowers are typical of the family, but the round, nut-looking pods with their large, solitary, Prunus-like stones could fool the most expert taxonomist. The quite thin layer of fruit is very tasty. Sadly for her, Sarah accidentally left them behind when she packed to leave.

Fig.11: Blocked roads stymied a second attempt at the Andes, in Atacama Region, witness a mud avalanche from recent devastating floods. (21 Feb 2020. ARF)

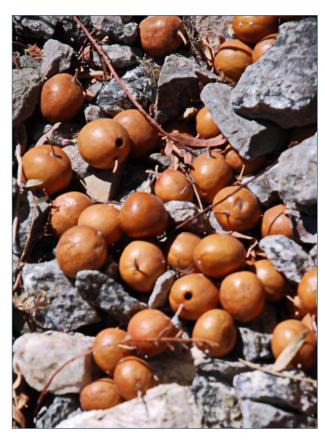




Fig.12: With the help of Anita and our friend and guide Juan, Sarah at least managed some exotic foraging - fruits of the *Geofroea decorticans* tree. (21 Feb 2020. JMW)

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Huasco Vallenar Pallenar CHILE La Serena Tambilo Combarbala 13) These unlikely *Geofroea* fruits don't seem to belong to the pea family! The thin skin is brittle, but the delicious soft flesh tastes of fruity toffee! (21 Feb 2020. JMW)

We enjoyed a tasty meal with Juan, his wife Karen and their parents that evening, drinks by courtesy of Sarah [Fig.14]. The younger couple had been given surprise tickets for the famous international Viña del Mar Festival of popular singers, humour and folk music, so had to rush off to catch the bus afterwards, and we left to lodge with Juan's parents nearer the coast.

Fig.14: A royal feast at Juan and his wife Karen's house with - from L to R - Juan, Sarah, Anita, John, Juan's parents and Karen's mother. (21 Feb 2020. Photo Karen)



Fig.15: *Zephyranthes sarae* global distribution. First known small Coquimbo colony - yellow circle. Atacama type site plus main third population - green circle.

When she came there, the cupboard was bare

With just three days left, now came our serious objective: to seek Sarah's plant at or near its Huasco type site in the hope of showing it to her: see map, green circle [Fig.15]. Being significantly closer to the sector as we were with

Juan's parents was usefully convenient. The *Zephyranthes* ought to be in full floral display in February: but would it be in this drought year? Or had the seasonal timing changed, and were we too late or too early? We were soon to find out.

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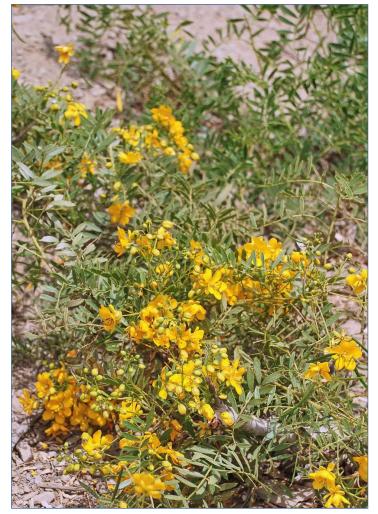
In fact we'd already done a brief survey with Juan two days earlier, but had got no further than the actual type site immediately adjacent to Huasco. Nothing doing then, which didn't dismay us unduly as we only knew it from there the once, in December 2001, and hadn't seen it when we'd visited in February and March subsequently. The best possibility lay in the main large populations some way along the coast to the south.



Fig.16: The main aim and hope of the seven day sortie was to show Sarah her namesake *Zephyranthes* in flower. Here's the stretch of coast it inhabits. (16 Mar 2010. JMW)

We were soon underway along the familiar littoral route [Fig.16] in the midst of a surprising flow of traffic on the very narrow, track-like road where we'd hardly encountered a vehicle on other occasions. The reason? We learned an annual festival was taking place further along, where local fisherman cook

the previous day's catch and provide a free feast for all-comers! No time for such indulgencies for us though - we'd have our work cut out seeking our quarry as it was.



Initial signs were guite encouraging, with a few, albeit very few, flowering plants on view. Senna (Fabaceae) species keep on producing their yellow corollas freely and almost indefinitely throughout the year, so it was no great surprise to come upon S. urmenetae [Fig.17], even though a first record ever of it for us. Our specimen was deceptively prostrate, as it should actually be a small shrub, but had been cut down to the ground. The sea heath Frankenia chilensis [Fig.18] is the commoner of two species endemic to Chile, and one of 70 worldwide - including F. laevis the British native. The genus is halophytic (salt tolerant), and able to excrete white saline crystals out of its system and onto the leaves. Here, although much of the foliage had been cooked brittle-brown and it was well past the typical flowering period, several plants were still putting on a brave show for us.

Fig.17: Despite the drought year, early signs were promising, as this heavily cut-back *Senna urmenetae* shrub indicates. (22 Feb 2020. JMW)

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Fig.18: Another seen during our search and not recorded in flower by us from the sector before, *Frankenia chilensis*. (22 Feb 2020. JMW)

We* searched high (on the dunes) and low (in the slacks) in vain, straining our poor jeep to the limit in 4WD low and second gear up and down deep, loose sand 'roads'. That caused a problem for the vehicle our mechanic had to sort out when we got back home! An audience of Dominican or kelp gulls, *Larus dominicana*, laughed to see such fun [Fig.19].



Fig.19: A resting flock of Dominican gulls mock our long and fruitless hunt for Sarah's plant. Well, it was more in hope than expectation. (22 Feb 2020. JMW)

* 'We' in the context of driving actually means Anita, as the requirements for John at his age to get either a British or International driving licence are out of the question for us. So he can only take the wheel on remote 'policefree' mountain tracks. At least Sarah was able to take turns on the long drives to and from home.

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Fig.20: The day's highlight - a lone, dead tree festooned with cormorant nests, now a national monument in a former mineral exporting cove. (22 Feb 2020. JMW)

When we reached the crowded fish festival we were obliged to take an improvised diversion to continue. After stopping for our own quick snack we finally gave up and made our way back rather disconsolately. Still, despite the failure we did notch up a few more positive memories, among them an elegantly skeletal dead tree [Fig.20] at the abandoned former site of a small bay and jetty where minerals had been exported from Chile long since. Originally planted there when the place was populated, it's now a preserved monument. There are no other trees - dead or alive - anywhere else along that coastline! Another treat for the eyes was the impressive stretches of Pleocarphus revolutus [Fig.21] in full cry. We introduced it in close-up to IRG readers in December (Watson & Flores 2019, Fig. 24), but this season has been an annus mirabilis for it, including here and there alongside much of the main motorway.





Fig.21: *Pleocarphus revolutus*, introduced to readers recently in the account describing Sarah's new species, was exceptional and widespread this year. (22 Feb 2020. JMW)

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One irresolute last throw of the dice

On the day before our drive back we took it easy and relaxed, doing little more than driving to Huasco for a look around town, where we met an enthusiastic photographer who manned a local tourist information cubicle. He showed us large numbers of his fine prints of the local flora which he'd got identified (mostly correctly!) and had made some into a calendar for sale. We queried him about Sarah's bulb, which he didn't know, but asked us to send photos. We've got in touch since, and he says he actually has seen it, but never taken pictures.

That night we returned to La Serena and packed early the following morning ready for the long slog home. We needed time in hand as we'd decided to call in at the location where Anita and her father first saw *Zephyranthes sarae* way back in 1973, which John had also visited with her once in the late 1990s: see map, yellow circle [Fig.15]. Full details of that are given in Watson and Flores (2019, page 31). We believe this must have been the population found by Ravenna even earlier still, as mentioned, but which he failed to publish (his loss, our gain!). The site lies just 30 km south of La Serena, so we soon arrived, in fact too early for the dense morning Pacific mist (camanchaca) to have cleared, which meant poor light for photography if we were to happen upon our quarry. Well, we had scant expectation of that. Considering the very small number of plants seen there previously and the close proximity to rural centres of population as well as the extensive and quite intensive agricultural activity all around, we presumed the population was most likely to be extinct by now anyway.

A fast double-lane highway to Ovalle has been constructed fairly recently. We had to branch off that to join the former 'main' road passing through Tambillo, then double back and take a minor road heading east across the open flats in the direction of the Andean foothills. It was shortly along this that the *Zephyranthes* had been recorded all those years ago. Luckily Anita had this complex manoeuvre and the exact spot well stamped on her memory. John was completely lost!

We started out along the unpromising-looking little branch road, with everything dry and desert-like on all sides, wondering how far it would be worth searching, when Anita at the wheel suddenly gave an excited cry. "There it is!" John in the back seat had limited vision, but by craning saw the first small but very evident starry, pink flower and another budded scape or two with it a metre or so from the road. After parking the jeep safely at the edge, we searched diligently and gradually added to the tally. Only a couple of rather unimpressive plants were found on the open northern side bordering agricultural land. But the rubbish-strewn south side of waste ground behind a mine processing plant offered much more desirable subjects for our attention and in greater numbers - if only just [Figs.22a, 22b, 23, 24]! Some, such as an individual flowering through the dense twiggery of a seasonally leafless shrub, took some spotting as well, and many were either just coming into bud or already forming fruits, even from the same bulb-clump. This was a valuable new observation, as it told us the species is capable of flowering over a very prolonged period.

The practical problem we faced was a stout barbed wire fence around the habitat. Photography of one or two not too far inside was possible, and luckily the worst of the mist had dispersed by then too, but we needed a specimen for the relevant botanical expert Nicolas García (Watson 2019). The two which were easily accessible on the other side of the road looked obviously to be solitary bulbs, and we didn't want to completely eliminate a plant from any situation. So it had to be one of the 'corralled' multiple clumps. John began to look for some way through or over the forbidding barrier, but law-abiding Anita wagged a finger and went off to try to get permission from the mine office. No go, they wouldn't permit it, and having alerted them we could hardly try to get in sneakily. In the end we managed to locate a beefy plant [Fig.24] just close enough to the fence to allow our operation - albeit with no mean difficulty and discomfort. Apart from the unavoidably awkward position, the compacted ground was stony and baked hard. The bulbs, which must not be damaged, seemed to go down to

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whichever part of the Northern Hemisphere is opposite Coquimbo [Figs.25, 26]! But by taking turns at excavating we got there in the end, extracting just one bulb and a small offshoot to be grown ex situ, with the flower scape cut off for pressing. The remaining majority of bulbs forming the clump were covered up with replaced soil and stones to be left in peace, we hope. Perhaps this insalubrious, unattractive habitat may in fact turn out to be a blessing in disguise for the population. Provided it remains untouched and fenced-off, the plants inside should remain in a state of 'accidental conservation'.



Fig.22a: As a last folorn possibility, on our way home we visited the site where we first knew *Z. sarae* and presumed it to be extinct. Not a bit of it! (24 Feb 2020. JMW)

Fig.22b: below - The same shot of Sarah's species among rubbish on a waste patch behind barbed wire. Arrows show more plants than meet the eye. (24 Feb 2020. JMW)



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Fig.23: One of the very best *Zephyranthes sarae* individuals of the small, scattered local population. What a glorious climax to our short trip. (24 Feb 2020. JMW)

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Fig.24: This clump by the barbed wire was chosen for the specimen the expert on the group, Nico García, requested from us ... if we managed to find it. (24 Feb 2020. JMW)



Fig.25: Sarah and Anita (in front) digging down carefully into the concrete-like compacted, baked soil. (24 Feb 2020. JMW)



Fig.26: Down and down she goes! Our excavation finally revealed bulbs. One was taken for the specimen, the rest left and the soil replaced. Note barbed wire. (24 Feb 2020. JMW)

It hardly takes much to imagine our state of euphoria during the drive back, and how elated we were to have added this final 'icing on the cake'. Even that was brightened further still by adding a fine roadside specimen of *Cristaria glaucophylla* (*Malvaceae*) [Fig.27], as seen against the light, to our photographic records. A golden sunset a good few hours later when we reached the end of the coast and were nearing home was a singularly appropriate finale [Fig.28].

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Fig.27: Another photographed by the roadside, this time on our way back. *Cristaria glaucophylla* of the *Malvaceae*. (Feb 24 2020. JMW)

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Fig.28: A magical pool of late sunlight on the Pacific as we return home. (24 Feb 2020. JMW)

Taxonomy

Zephyranthes sarae J.M. Watson & A.R. Flores. [Figs.23, 24]

CHILE. Coquimbo Region, Elqui Province, slightly north of Tambillo and shortly to east of main Coquimbo to Ovalle route, ca. 30°11'42"S 71°14'24"W, ca. 207 m, leg. J.M. Watson, A.R. Flores & S.G. Watson, 24 Feb 2020, F.& W. 13204.

Forming a small, scattered population of fewer than 30 individuals over one or two hundred metres on flat, open ground near a mine processing plant. Distributed along the unadopted wayside strip of an intensely cultivated sector, and also in a rubbish-strewn waste field behind barbed wire fencing. The latter is part of the private property of the mining corporation. In deep, compacted, stony soil, seasonally baked dry during anthesis.

Acknowledgements

The hospitable kindness and friendship of Anita's sister-in-law, Carmen-Luz, also of Juan Alegria, his wife Karen and parents, is stamped indelibly on any account or memories of these unforgettable few days.

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---Walking in Nature---

Wildflowers of the Appalachian Trail by Will Hembree

I have always enjoyed the outdoors, and ever since I was just learning to walk, I have gone backpacking with my family in the mountains of southern Appalachia near our home outside of Atlanta. By the time I was finished with the Boy Scouts, I had probably been on enough camping trips for most people's lifetimes. When I got to college, I fell in love with plants through my horticulture classes at the University of Georgia and started to fully appreciate the botanical beauty that stitched together the world around us. When I was finally taken botanizing for the first time in college, my two loves were finally formally introduced. From that point on, as much as my schedule would allow it, I was out in the woods simply for the sake of seeing what plants I could find growing there. So, when my dad and I first had the idea of thru-hiking the Appalachian Trail at the intersection of my graduation from graduate school and his retirement from a career in horticulture, I knew it was an opportunity that I could not waste.

The opportunity to spend months in my favourite place, doing my favourite thing, with one of my favourite people was a very gratifying experience. We covered over two thousand miles of Appalachian flora, encountering over five hundred identifiable species, with many thousands more surely evading our attention entirely. In my mind, we were paralleling the legendary father-son plantsmen duo of John and William Bartram, separated by two hundred- and fifty-years' worth of land development and exotic plant introduction. On many days, it seemed as if the flora around us was entirely alien, and occasionally it seemed as if we had stumbled off the trail for the lack of apparent "wilderness" in sight. But whenever we would come across a plant new to us, which became more and more frequent the further we walked from our home, everything around us stopped as we tried to classify our new floral friend.



The beginning of our hike saw much more ice than wildflowers. Here is a view near Wayah Bald, NC, taken on March 5th, the morning after a fifteen degree cold front froze most of the rain from the day before.

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Our hike did not start off with a whirlwind of botanical treasures. Hiking out of Amicalola Falls State Park on February 18th, we realized that we were decidedly still in the midst of winter as we summited Springer Mountain. While we kept our eyes open for signs of colour on the forest floor, we kept ourselves entertained by taking note of the dormant shrubs and trees around us, learning to appreciate the buds that would soon give way to flowers and foliage. Except for the odd *Houstonia* or *Cardamine*, it took twenty days and a hundred and sixty miles to see our first significant wild-flowers, patches of toad trillium at Lake Fontana just before entering the Smoky Mountains. And after that trillium patch, save for the odd *Claytonia* popping out at high elevation in the Smokies, another two weeks would pass before what we could comfortably call spring was upon us. But when it came, it came with a fury. As we passed through Davenport Gap at the northern end of the Great Smoky Mountains National Park, we were greeted with trout lilies, toothworts, mitreworts, cohosh, bloodroot, bellworts, (*Erythronium, Dentaria, Mitella, Actaea, Sanguinaria, Uvularia*) and everything that we had been scanning the ground for over the first two hundred miles. From this point on, it didn't really slow down!

Will's Dad stopped to admire the carpet of *Claytonia virginica* we walked through for over a week in Tennessee during the beginning of spring.

To be enveloped by spring each day as you wake up and walk along a mountain trail was electrifying. Every day, I knew we would be finding new treasures potentially at every turn, all the while being treated to some of the most miraculous landscape views in North America.

From the Smokies, we quickly crossed over Max Patch, the Roan Highlands,

Grayson Highlands, and into the Washington and Jefferson National Forests. By the time we got to the James River in early May, we had seen everything from skunk cabbages to Catawba rhododendrons flowering on the trail. The first seven hundred miles had delivered more to us in terms of plant diversity than I was hoping to find on the entire trail, and with the remaining two thirds farther and farther out of my botanical comfort zone I knew I would be equally gratified with the rest.

One of the most illuminating days of the entire hike happened in the Jefferson National Forest as we criss-crossed the Blue Ridge Parkway between giant colonies of *Trillium grandiflorum*.







The James River

After a small off-trail break, we resumed our hike four hundred miles north of the James River in Lickdale, Pennsylvania, so that we could keep some previous appointments made with family who would be joining our hike. The difference three weeks and four hundred miles made was stark. Gone were the soaring peaks of the southern Appalachians. It seemed that we had landed on a trail that was much closer to civilisation and much less untouched by all that that

brings. Road crossings were busier and more frequent, and fields of grain replaced the unbroken forests that we had grown accustomed to hiking through. But it was summer, and there were still plenty of flowers to be appreciated. There were many days where most of the new plants we encountered were Eurasian field weeds, but to us, they were enjoyable all the same. And of course, native plants still abounded all around us. Over the rocks of Pennsylvania, through the wetlands of New Jersey, and in the rocky woodlands of New York and Connecticut, we were seldom out of eyesight of the blooms of the mountain laurel, *Kalmia latifolia* as well as *K. angustifolia*, a new species to us. The pink and white clouds surrounded us as we were introduced to new wildflowers including rockcresses, moonseeds, meadow-rues, indian hemp, spiraeas and starflowers (*Arabis, Cocculus, Thalictrum, Apocynum, Spiraeas* and *Trientalis*). When we arrived in Massachusetts, we immediately found our second species of *Cornus, C. canadensis,* which indicated to us that we were



arriving in an altogether unfamiliar climate than what we were accustomed to back home.

One of the most exciting discoveries of the trail, this was one of two patches of Twinleaf (*Jeffersonia diphylla*) that we came across in Virginia.

While the diversity of the flora in the northern section of the trail was perhaps slightly less than what we had

encountered in the south, the variety of habitats that were new to us kept us on our toes all the same. We came across our first bogs, filled with sundews and pitcher plants on sphagnum laden shores. Beaver ponds that were ringed with spiraea, *Viburnum*, and ericaceous species held large mats of floating spatterdock and water lilies. The forests, especially when we began to regain elevation as we headed into Vermont, became much more coniferous in nature. Shrubs and wildflowers suddenly were appearing around us that I was unable to key out in my out in my Weakley's Flora, which had faithfully served us for as long as we were within its jurisdiction of the southern and mid-atlantic states. Orchids, which had been sparse on the journey thus far, were becoming more and more common to see. Ericaceous herbs beyond pipsissewa, including moneses and pyrola were dotting

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the forest floor. Summiting moosilauke, the first of New Hampshire's infamous White Mountains, we encountered our first true alpine plants.

The imposing view back over Franconia Ridge, home to *Geum peckii* and *Potentilla robbinsiana.* This was, without a doubt, one of the most scenic days of our thru-hike.

Vast cushions of diapensia covered the rocky, treeless summits throughout the Whites, along with many other diminutive taxa including *Empetrum nigrum, Minuartia* groenlandica, and Geum peckii. At the summit of Mount Washington, the climate proved too extreme for



everything but lichens to thrive, and I recall being amazed at the huge gap between this landscape at the top of New England and the lush forest that had greeted us as we exited the Smoky Mountains all those miles ago.

The last few hundred miles of Maine were similar to what we had seen since Vermont. Vast coniferous forests between treeless summits dotted with mats of alpine plants, interspersed with occasional mountain top bogs colonized with *Eriophorum, Platanthera, Rubus, Drosera, Carex*, and more. I marvelled at them as I had been doing along the whole trail, but for the first time for me, the views were actually taking the place of the most beautiful sights of the hike. The wilderness that we experienced in Maine was un-matched anywhere else on the entire trail. I remember thinking about how John and William Bartram would have seen all the landscapes that we had seen as we were now seeing Maine - pristinely. The unspoilt nature of the terminal state of the AT, punctuated by the final "hundred miles of wilderness", gave me time to reflect on how much Appalachia had changed since westerners arrived and settled here.



Will Hembree in Maine.

Summiting Katahdin was rather anticlimactic, as I had heard it would be from the many previous thru-hikers I had met along the trail. It was the end of the trail, and as the northernmost high elevation summit of the trail, the flora was relatively depauperate. A few grasses and sedges, some conifers, lots of what we had seen in the Whites dominated the rocky landscape, which was already beginning to feel the first grips of winter. Luckily, our break in May meant we had a last four hundred miles remaining in

Virginia, with a victory walk through the Shenandoahs in autumn in our final miles.

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Platanthera dilitata

As our hike northward out of Pennsylvania had started in a rather cultivated area, so did our final south-bound stretch begin. I was not bothered by this now, as the fields were full of milkweeds, ironweeds, and asters and the woods were filled with lobelias and smartweeds. The chance to see the final season was here, and the trail did not disappoint. Through ever deepening reds and burgundies, autumn cloaked the woods around the trail, first in the pokeweeds (Phytolacca), then the Sassafras and tupelos (Nyssa). Pawpaws (Asimina triloba) made for plentiful snacks around Harper's Ferry, and the fall herbs gave us reason to reconsider the seasonality of a single piece of earth. What else would we have found here had the hike carried on in a more linear fashion? Would it have been better than all that we were seeing now that otherwise would have escaped our attention for the sole reason of being in the right

place in the wrong season? Being able to round out the season of botanizing with the fall flowering herbs such as *Symphyotrichum, Aconitum*, and *Gentiana*, as well as the fruits of the forest like the berries of the mountain ash (*Sorbus*) or odd capsules of burning bush (*Euonymous*), which greeted me on the final day of the hike, was an unexpectedly perfect end to the journey.

Carex magellanica

The opportunity to botanise the entire range of what I call my home mountains, beginning before the first buds of spring opened and finishing as the fruits of autumn were falling to the ground, was something I never knew that I needed to do. To become intimately familiar with the Appalachian flora through first hand observations over the course of a whole growing season and across almost the entire range of the mountains was simply an indescribable experience. The plants that we saw were only a small part of the trip as a whole, but they played such a central role in the journey, stitching together our experiences as we walked each day from one campsite to the next. I truly felt their vitality seep into me more and more as we walked further I hope those who share my passion for the flora of the world can experience for themselves one day.



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