Frontiers of Biogeography 2023, 15.2, e58420

RESEARCH ARTICLE

Frontiers of Biogeography
the scientific journal of
the International Biogeography Society

# Karyo-geographical analysis of Armenian flora

George M. Fayvush[1*] and Anahit G. Ghukasyan[1]

[1] Department of Geobotany and Ecological Physiology, A.L.Takhtajan Institute of Botany, National Academy of Science, Yerevan, Armenia.
*Correspondence: George M. Fayvush, gfayvush@yahoo.com

**Abstract**

Approximately 3,800 species of vascular plant species have been registered in the flora of Armenia, of which chromosome numbers are known for 798. Additionally, many species have several cytoraces in Armenia (a total of 904 cytoraces have been recorded). The main goal of the study was to elucidate some specific features of florogenesis on the basis of karyological data, and the aim is to characterize the distributions of the cytoraces across floristic regions of Armenia, including elevational zones, and habitats. The study is underpinned by results of our long-term study of Armenian flora, which entailed comprehensively characterizing their chromosome numbers and karyotypes. Geographical elements were established based on general distribution. As a result of the analysis, it was found that the Armenian flora was formed over a long period, starting from the Paleocene period, and is composed of nearly equal proportions of migrants from the Boreal and Ancient Mediterranean subkingdoms, and species that evolved in the Armenian Highlands and in the Greater Caucasus. The possession of a significant percentage of endemics (mainly neoendemics) indicates that the territory of Armenia is also an arena of intensive formation and speciation. In addition, we also illuminated a large karyological diversity among species whose distribution is confined to the Ancient Mediterranean subkingdom or its parts, including the Armeno-Iranian province; this is indicative of speciation having occurred in these territories. The "northern root" species, Boreal and Caucasian, became establish in Armenia mainly in the form of karyologically stable cytoraces.

**Highlights**

- The florogenesis Armenian flora is linked to two, equally influential patterns, namely, allochthonous and autochthonous origins.
- The allochthonous side of the florogenesis was initiated in the Paleocene period and was manifested as the migration of species both from the north from the Boreal floristic subkingdom, and from the south from the Ancient Mediterranean subkingdom.
- The largest number of polyploid cytoraces was found in Armenian steppe and meadow ecosystems; this is indicative of both the high diversity of these ecosystems and the corresponding speciation and morphological differentiation of their inhabitants.
- The modern territory of Armenia remains an arena of intensive speciation, as evidenced by the representation of various cytoraces in many morphologically unified species.
- Species that migrated to the territory of modern Armenia from the Ancient Mediterranean are generally distinguished by a great diversity in their karyotypes and ploidy, whereas species that migrated from the north, from the Boreal Subkingdom, primarily exhibit stable cytoraces.

**Keywords:** Armenian flora, chromosome numbers, florogenesis, geographical elements, phyto-geographical patterns, plant evolution, ploidy.

## Introduction

Armenia is a south Caucasian Republic that borders Georgia, Azerbaijan, Turkey, and Iran. It is a landlocked country with a total area of 29,740 km$^2$, located approximately 145 km from the Black Sea and 175 km from the Caspian Sea. It lies between 38°50' and 41°18' northern latitude and between 43°27' and 46°37' eastern longitude and measures 400 km along its main axis (northwest to southeast). Additionally, Armenia is generally a mountainous country, with 44% of Armenia being characterized by high-elevation mountains. The lowest point in Armenia is 375 m above sea level, while its highest point is 4,095 m above sea level, and the average elevation of Armenia is 1,850 m.

e-ISSN: 1948-6596 https://escholarship.org/uc/fb doi:10.21425/F5FBG58420

Modern Armenian flora in its development has a long history. Based on our current models, the modern vegetation of Eurasia and the rest of the world was derived from Cretaceous flora (Krishtofovich 1936). In Cretaceous the Mediterranean Tethys Sea expanded; this expansion resulted in a region where the Caucasus, Armenian Highlands, and Iran are presently located being a set of large and separate islands. During the Paleogene, the Caucasus and the Armenian Highlands took shape as large mountain massifs, within which the most significant processes of florogenesis took place. In the Neogene, the Ancient Mediterranean floristic element was the initial basis from which, due to active speciation, numerous Armeno-Iranian, Armenian, and Atropatenian species emerged. Then, most likely, glacial and postglacial periods provided the best conditions for the mass migration of Boreal and Pannonian-Pontic species to the South Caucasus.

The Armenian flora is the resultant of *in situ* speciation and the migration of species from other (often very distant) areas. According to our calculations, these processes (i.e., *in situ* speciation and migration) have been balanced with regards to the origins of flora in Armenia and the Armenian Highlands were balanced; specifically, speciation and the migration of species had an approximately equal influence on the florogenesis of species in this region (Fayvush 1990). The Armenian flora comprises a wide array of polychorous plant species (*Phragmites australis* (Cav.) Trin. ex Steud., *Lythrum salicaria* L., *Chenopodium album* L.), as well as many species that originated in the Mediterranean, Asia Minor, and Irano-Turanian regions. However, simultaneously, the territory contained powerful foci of speciation of some genera (Gabrielian and Fayvush 1986, 1989, Tamanyan and Fayvush 1987, etc.), resulting in 146 local endemic species (FNC 2014).

Determining the chromosomes numbers across different species is the first step in karyological studies. The importance of such studies lies in their value in clarifying speciation and phylogenetic relationships.

The objectives of this study were to conduct parallel karyological and phytogeographical analyses of the flora of Armenia (i.e., using the 798 species with karyological data) and to assess the presence of diploid and polyploid taxa of vascular plants and their geographical distributions across various ecosystems. Overall, the primary aim of this study is to clarify the evolution of the modern Armenian flora.

## Materials & Methods

The study area lies at the intersection of two phytogeographical regions: the Euro-Siberian and Irano-Turanian (Takhtadjan 1986), and two biodiversity hotspots, namely, the Caucasian and Irano-Anatolian hotspots (Mittermeier et al. 2011), which stand out for their extensive biodiversity and endemism (Fayvush et al. 2013, Fayvush and Aleksanyan 2020). Specifically, within the country's small territory, there are approximately 3,800 species of vascular plants, 428 species of soil and water algae, 399 species of mosses, 4,207 species of fungi, 464 species of lichens, 549 species of vertebrates, and approximately 17,200 species of invertebrates, many of which are considered endemic (FNC, 2014).

This study is underpinned by results of our long-term study of Armenian flora, which entailed comprehensive characterization of their chromosome numbers and karyotypes. Data on the chromosome numbers of the Armenian flora are presented in the book "Number of Chromosomes of Flowering Plants of Armenia" (Nazarova and Ghukasyan 2004). Furthermore, for this study, we also analyzed chromosome data from other, more recent, studies (Nazarova 2009, 2011, Kotseruba et al. 2010, 2012, Ghukasyan 2010, 2011, Oganezova 2013, Ghukasyan and Janjughazyan 2015, Hayrapetyan and Ghukasyan 2015, 2021, Ghukasyan and Akopian 2018, Więcław et al. 2020, Ghukasyan et al. 2022).

To determine the elevational confinement of the studied species, data from the literature were used (primarily Takhtajan 1954–2009), including data from the herbarium of the Institute of Botany after the name A. Takhtajan of the National Academy of Sciences of the Republic of Armenia (ERE), and the results of our own observations in nature for more than 40 years.

To assess the distribution of the studied cytorases in different habitats, we used the EUNIS habitat classification system (Fayvush and Aleksanyan 2016). The latest version of this system can be found at: https://www.eea.europa.eu/data-and-maps/data/eunis-habitat-classification-1.

For the chorological analysis of the studied species and determination of geographical elements, we used the scheme of Portenier (2000), adapted by us for the conditions of the South Caucasus (Fayvush and Adamyan 2015). Adapting Portenier's scheme, we paid more attention to the ecosystems encompassing the Caucasian and Armeno-Iranian provinces, particularly those in the Armenian, Atropatenian, Armeno-Atropatenian, Armeno-Iranian, and Caucaso-Armeno-Iranian areas.

The actual data used in this article for analysis are shown in supplemental Table S1. In this table we list all plant species included in the analysis, their chromosome numbers, ploidy, confinement to mountain belts, types of vegetation and habitats, belonging to a certain geographical element.

## Results & Discussion

Of the 3,800 species of vascular plants that have been recorded in Armenia, 798 (21%) were included in our analysis; and these species allowed us to draw certain, relatively reliable conclusions, especially since among the studied species, all large and medium-sized families known in Armenia were represented (Table 1). The families we are referring to are consistent with those outlined in "Flora of Armenia" (Takhtajan 1954-2009).

Most karyologically investigated samples were diploid (585 races), with fewer tetraploids (178), hexaploids (76), and octaploids (13). There were also races (11) with high ploidy (10 or more), aneuploids (18), triploids (9), and pentaploids (3). Interestingly,

  

**Table 1.** Data on large and medium-sized families of the flora of Armenia

| N/N | Family | # of Genera | # of Species | # of Armenian endemics | # of Karyologically investigated species |
|---|---|---|---|---|---|
| 1. | Asteraceae | 90 | 442 | 27 | 207 |
| 2. | Poaceae | 102 | 336 | 13 | 142 |
| 3. | Fabaceae | 33 | 324 | 15 | 64 |
| 4. | Rosaceae | 29 | 214 | 31 | 29 |
| 5. | Brassicaceae | 68 | 203 | 7 | 18 |
| 6. | Caryophyllaceae | 32 | 183 | 10 | 38 |
| 7. | Lamiaceae | 33 | 153 | 1 | 22 |
| 8. | Scrophulariaceae | 20 | 150 | 8 | 17 |
| 9. | Apiaceae | 61 | 140 | 3 | 25 |
| 10. | Cyperaceae | 16 | 108 | 0 | 13 |
| 11. | Chenopodiaceae | 30 | 87 | 0 | 8 |
| 12. | Boraginaceae | 23 | 78 | 2 | 9 |
| 13. | Ranunculaceae | 17 | 68 | 1 | 19 |
| 14. | Polygonaceae | 7 | 50 | 0 | 6 |
| 15. | Orchidaceae | 17 | 44 | 0 | 3 |
| 16. | Rubiaceae | 9 | 44 | 0 | 2 |
| 17. | Euphorbiaceae | 4 | 43 | 1 | 0 |
| 18. | Alliaceae | 2 | 42 | 3 | 31 |
| 19. | Liliaceae | 5 | 38 | 0 | 17 |
| 20. | Orobanchaceae | 4 | 36 | 6 | 0 |
| 21. | Hyacinthaceae | 6 | 34 | 1 | 27 |
| 22. | Campanulaceae | 4 | 32 | 1 | 6 |
| 23. | Iridaceae | 3 | 29 | 2 | 17 |
| 24. | Geraniaceae | 2 | 28 | 1 | 14 |
| 25. | Papaveraceae | 4 | 28 | 5 | 2 |
| 26. | Plumbaginaceae | 5 | 26 | 1 | 1 |
| 27. | Dipsacaceae | 5 | 25 | 0 | 1 |
| 28. | Primulaceae | 8 | 25 | 0 | 6 |
| 29. | Onagraceae | 5 | 23 | 0 | 2 |
| 30. | Malvaceae | 7 | 22 | 1 | 0 |

49 species are represented by two or more cytoraces: 25 species are represented by di- and tetraploid races; four species have di-, tetra-, and hexaploid races; six species are di- and hexaploid races; three species are di- and octaploid races; six species are represented by tetra- and hexaploid races; and two by tetra- and octaploid races. In addition, diploid and tetraploid species were represented by races with different base numbers. B chromosomes were found in the karyotypes of the 24 species; of particular interest is the Armenian population of *Crepis pannonica*, in which there are five diploid cytoraces with x = 4, 5, 6, 7, and 8, as well as triploid and aneuploid cytoraces. Overall, this diverse karyological spectrum is indicative of the ongoing speciation and morphogenesis in modern Armenian plants.

The distribution of cytoraces across elevational belts revealed that the greatest diversity of this region was confined to the middle mountain belt and was likely associated with the greatest richness of the flora of this belt and not with any extrinsic factors.

When considering the confinement of various cytoraces to certain types of vegetation and habitats, tetraploid, hexaploid, and octaploid species were mostly observed in steppe and meadow vegetation (Table 2; Fig. 1). In addition, species represented by two or more cytoraces, as well as those with B chromosomes were most represented in steppes and meadows.

Of the karyologically studied species, most of them are distributed within the Ancient Mediterranean subkingdom (408), with few occurring in the Boreal subkingdom (173); additionally, 11 of the studied species have an almost global distribution, and 174 of the species were found in both the Boreal and Ancient Mediterranean sub-kingdoms (including 79 with a

  

**Table 2.** Number of cytoraces across the main habitats of Armenia

| | Habitat | *Di- | *Tetra- | *Hexa- | *Octa- | *Tri- | *Penta- | *Aneu- | High ploidy |
|---|---|---|---|---|---|---|---|---|---|
| C3.24 | Medium-tall non-graminoid waterside communities | 2 | 4 | 3 | | | | 1 | |
| D2 | Valley mires, poor fens, and transition mires | 2 | 2 | | 1 | | | | |
| D4.1 | Rich fens, including eutrophic tall-herb fens and calcareous flushes and soaks | 51 | 30 | 12 | | | 1 | 1 | 1 |
| D6.2 | Inland saline or brackish species-poor helophyte beds | 5 | 2 | 2 | | | | | |
| E1.2E | Irano-Anatolian steppes | 287 | 92 | 29 | 8 | 4 | 1 | 4 | 2 |
| E1.33 & E1.45 | East Mediterranean xeric grassland & Sub-Mediterranean wormwood steppes | 154 | 39 | 15 | 4 | 1 | | 1 | 2 |
| E2.32 | Ponto-Caucasian hay meadows | 179 | 57 | 24 | 4 | 2 | 2 | 3 | 2 |
| E4.3A | Western Asian acidophilous alpine grassland | 54 | 16 | 10 | | 1 | | 5 | 2 |
| E4.4 | Ponto-Caucasian alpine grassland | 44 | 17 | 9 | | 1 | | 4 | 2 |
| E5.4 | Moist or wet tall-herb and fern fringes and meadows | 40 | 16 | 2 | 1 | 3 | | | 1 |
| E5.5A | Ponto-Caucasian tall-herb communities | 3 | 5 | | | 1 | | | 1 |
| F2.33 | Subalpine mixed brushes | 46 | 9 | 6 | 1 | 2 | | 1 | |
| F5.13 & G3.93 | Juniper matorral & Grecian juniper - *Juniperus excelsa* - woods | 8 | 5 | | | | | | |
| F5.34 | Western Asian pseudomaquis | 66 | 18 | 9 | 2 | 2 | | 3 | 1 |
| G1.6H | Caucasian beech forests | 43 | 9 | 7 | | 1 | | 1 | 1 |
| G1.A1 | Oak-ash-hornbeam woodland | 78 | 27 | 13 | 2 | 2 | | 1 | 1 |
| H2.3 | Temperate-montane acid siliceous screes | 37 | 10 | 7 | 1 | | | 1 | |
| H2.4 | Temperate-montane calcareous and ultra-basic screes | 17 | 2 | 4 | 1 | | | 1 | |
| H2.5 | Acid siliceous screes of warm exposures | 21 | 13 | 6 | 1 | | | 1 | |
| H2.6 | Calcareous and ultra-basic screes of warm exposures | 34 | 13 | 5 | 1 | | | 2 | |
| H3.1 | Acid siliceous inland cliffs | 31 | 11 | 4 | | | | | 1 |
| H3.2 | Basic and ultra-basic inland cliffs | 27 | 3 | 2 | | | | | |
| H5.32 | Stable sand with very sparse or no vegetation | 9 | 4 | 2 | | | | | |
| I1.3 | Arable land with unmixed crops | 16 | 3 | 1 | | | 1 | | |
| I1.53 | Fallow un-inundated fields with annual and perennial weed communities | 28 | 10 | 6 | | | | | |
| I2.22 | Subsistence garden areas | 6 | | | | | | | |

*Di- Diploid cytoraces, Tetra- Tetraploid, Hexa- Hexaploid, Octa- Octaploid, Tri- Triploid, Penta- Pentaploid, Aneu- Aneuploid

distribution that encompasses the Caucasian and Armeno-Iranian provinces). Another five species belonged to a specific steppe element (Pannono-Pontic-Sarmatian). Overall, the karyotypic patterns of the few species whose karyotypes have been characterized suggest that they provide a fairly accurate representation of the karyotypic dynamics all Armenian flora (Saghatelyan, 2006). The ratios of various geographical elements are similar, and the predominance of species with ranges in the Ancient Mediterranean area can be noted (Table 3). Diploid species predominate in all geographical areas; in particular, only diploids are represented in the steppe area.

Among the species represented only by cytoraces with polyploidy (4n, 6n, 8n, and more), species with a wide Euro-Ancient Mediterranean range prevailed (30), as well as species with Armenian and Caucasian areas (26 each). Species in which only tri-, penta-, and aneuploid cytoraces have been recorded belong to the Armenian (5), Armeno-Iranian (2), Armeno-Atropatenian (1), Ancient Mediterranean (2), and Palearctic (2) geographical elements (Fig. 2).

Most of the species represented by two or more cytoraces with different ploidy (2n–8n and more) have Armenian and Armeno-Iranian (nine each) types of ranges, and another six species each are in Atropatenian and Ancient Mediterranean elements.

Of the 22 species with B chromosomes in their karyotype, five were confined to Armenia, and three species each had Palearctic, East Ancient Mediterranean, Armeno-Atropatenian, Atropatenian, and Euro-Ancient Mediterranean types of ranges.

The most ubiquitous genera within the context of Armenian flora were *Astragalus*, *Centaurea* s.l., *Carex,* and *Allium*. The genus *Astragalus* is widely spread across the entire Irano-Turanian region and is the most abundant plant genus in Armenia (~140 species); however, this genus has relatively few and narrowly distributed endemic species (12), and in terms of geographic distribution, many species of this genus are not restricted to one country or to a floristic region. Additionally, only 14 species of the genus *Astragalus* have been karyologically studied, but among them there is one tetraploid, one hexaploid, one octaploid, and one pentaploid species; furthermore, there is one species (*Astragalus sevangensis* Grossh.) for which tetra- and octaploid cytoraces were registered, respectively.

  

**Table 3.** Geographical elements of the Armenian flora (karyologically investigated species) (Floristic kingdoms are given according to Takhtajan 1986)

| | Geographical element (types of area) | Species |
|---|---|---|
| Special type | Polychorous | 11 |
| Boreal subkingdom (173 species) | Holarctic | 32 |
| | Palearctic | 65 |
| | European | 14 |
| | Caucasian | 62 |
| Ancient Mediterranean subkingdom (408 species) | Ancient Mediterranean | 48 |
| | Mediterranean | 25 |
| | East Ancient Mediterranean | 83 |
| | Armeno-Iranian | 89 |
| | Armeno-Atropatenian | 41 |
| | Armenian | 106 (19 local endemics) |
| | Atropatenian | 16 |
| Transitional type (174 species) | Euro-Ancient Mediterranean | 95 |
| | Caucaso-Armeno-Iranian | 79 |
| Special (Steppe) type | Pannono-Pontic-Sarmatian | 5 |

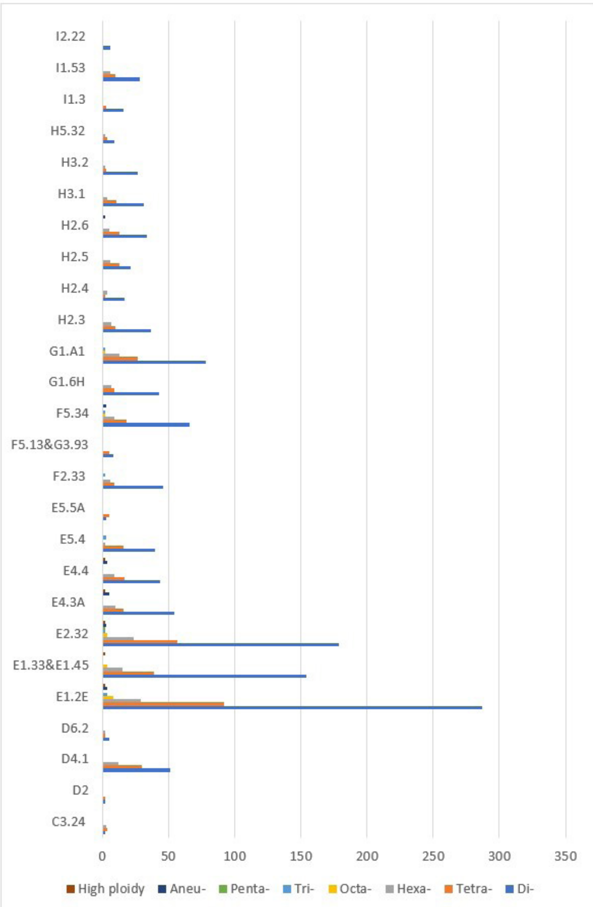


**Figure 1.** Number of plant cytoraces across different Armenian habitats. Habitat definitions are outlined in Table 2.

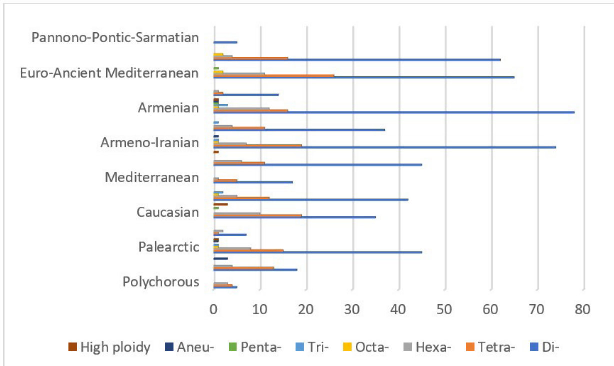


**Figure 2.** Numbers of different cytoraces across the studied geographical elements (following the scheme of floristic regions of the World (Takhtajan 1986)

According to Wagenitz (1975, 1986), a large variety of species and sections of the genus *Centaurea* s.l. (Asteraceae) are concentrated in eastern Anatolia, especially in the region where Iran, Iraq, and Turkey intersect, with a total of 35 species. In parts of eastern Anatolia bordering Armenia, 18–34 species have been found. Wagenitz predicted that a high concentration of species and sections should also exist in the South Caucasus; with regards to this point, the data we obtained greatly exceeded our expectations. For example, in the tiny territory of the Republic of Armenia, there are 70 species of *Centaurea* s.l. Of these, 14 are narrow, local endemics of Armenia (Gabrielian and Fayvush, 1989, Fayvush and Aleksanyan

  

2021). Thirty-two species of the genus *Centaurea* were studied karyologically. Of these, 26 were diploids, six were tetraploids, and four had B-chromosomes.

Many endemic species belong to the genus *Cousinia* (Asteraceae). The distribution of this genus is almost entirely in the Irano-Turanian region. Additionally, most of the species diversity of this genus is confined to Central Iran, where approximately 300 species are concentrated (Rechinger 1972, 1986). Based on the distribution of species in this genus, it may seem that its primary center of speciation is in the Iranian Highlands; however, as the study of the distribution of all *Cousinia* species across the range of the genus has shown, there are several secondary centers of speciation along the periphery of the range (Cherneva 1974). One of these centers is in Armenia (Tamanyan and Fayvush 1987). It should be noted that in the Armenian center, speciation was most intensive in: the mountains in the southern part of the region; the Meghri and South Zangezur floristic regions of Armenia; and in the Nakhichevan Republic. Of the 23 species of the genus in Armenia, five have been karyologically studied; and all of them are diploids with a very narrow distribution.

All 12 species of the genus *Crepis* (Asteraceae) in Armenia have been karyologically studied; 10 of them are diploids, one is octaploid, and four species have B-chromosomes. Of interest is the Pannonian-Pontic-Sarmatian species, *Crepis pannonica*, in which five diploid cytoraces with different basic numbers, triploid and aneuploid cytoraces, and numerous specimens with different numbers of B chromosomes have been recorded. In this case, it is important to note that these patterns were not observed in areas (the steppe region from Pannonia to Sarmatia) where this species is mainly distributed; specifically, only specimens with 2n = 8 were recorded, and none of the species had B-chromosomes (Dimitrova et al. 2003). These patterns could be attributed to this species having formed and spread over the steppe zone of Eurasia as the glaciers retreated, whereas in Armenia, having fallen into new, extreme conditions, it gave rise to a whole spectrum of cytoraces.

Of the 72 *Carex* species (Cyperaceae) in Armenia, only 12 have been karyologically studied; and all are diploids that are widely distributed in the Boreal or Ancient Mediterranean sub-kingdoms. The number of chromosomes (n) in the karyologically investigated species of the genus *Carex* varies from 19 to 42, and these species show different cytotypes. Finally, polyploidy seems to be rare in this genus Carex (Więcław et al. 2020).

Of the 42 wild species of the genus *Allium* (Alliaceae) in Armenia, 30 have been studied karyologically. The vast majority of these are diploids; however, three species have diploid and tetraploid cytoraces, and one has di-, tetra-, and hexaploid cytoraces. In addition, one species was found to be tetraploid, one hexaploid, and five species had B chromosomes. Polyploid species are mainly associated with the Caucasus and Armeno-Iranian province, although there are species that are widespread in Holarctic and Ancient Mediterranean.

The genus *Geranium* (Geraniaceae), represented in Armenia by 20 species, is a typical allochthonous component of Armenian flora (Favush and Adamyan, 2015). Many species of this genus are northern migrants (specifically from the Boreal Subkingdom), because of the southern border of their distribution in Armenia. Of these, 14 were karyologically studied (nine diploids, four tetraploids, and one hexaploid) with different basic chromosome numbers. An aneuploid series of basic chromosome numbers x = 9, 10, 13, and 14 was present in this genus. The species of the section *Rotundifolia* growing in the territory of Armenia (*G. pyrenaicum, G. pussilum, G. molle, G. rotundifolium, G. divaricatum,* all of which have 2n = 26) are characterized by a basic main chromosome number of x = 13. The main basic chromosome number of x = 9 is typical for species in the section *Columbinum* growing in the territory of Armenia (*G. columbinum,* 2n = 18). The main basic chromosome number of x = 10 is typical for the species of the section *Robertiana* (*G. lucidum,* 2n = 40). The main basic chromosome number of x = 14 is typical for species of section *Geranium* (*G. ibericum* and G. *sylvaticum,* both of which have 2n = 28). An asymmetric karyotype was observed in all the karyologically investigated species of the genus *Geranium*.

The second largest family of the Armenian flora is *Poaceae*. Although this family is characterized by a high level of ploidy (38x, 20x, 18x, etc.), only tetra- and hexaploid cytoraces have been registered among the karyologically studied species of cereals in Armenia. Among the polyploids, tetraploid cysts predominated, and the ratios of tetra- and hexaploids were 58% and 42%, respectively. *Colpodium versicolor* and *Zingeria biebersteiniana* had the lowest number of chromosomes (2n = 2x = 4), whereas *Aeluropus littoralis* (2n = 6x = 60) and *Echinochloa crusgalii* (2n = 9x = 54) had the highest number of chromosomes. Among the karyologically studied annuals, species with diploid cytoraces predominate, while among perennials, there are more polyploid species.

With regards to our proposal that the evolutionary trajectories of the Armenian flora have had their origins equally shaped by allo- and autochthonous trends (Fayvush 1990), it should be noted that approximately half of the species migrated to the territory of Armenia from other regions, whereas the second half formed within the territory of the republic. Given that nature does not recognize administrative boundaries, the autochthonous trend should be extended to the Armenian Highlands as a whole, and partially to the Caucasus. Thus, it should be assumed that the Armenian and Caucasian species, which do not have diploid cytoraces in Armenia but have only polyploid cytoraces, formed in this region, while the diploid cytorace was less competitive and was thus excluded. Simultaneously, attention has been drawn to the fact that polyploid cytoraces are best represented in the composition of steppe and semi-desert vegetation and in arid woodlands, which is most likely the result of a morphogenetic "explosion" in large genera in arid ecosystems (Agakhaniants 1981). Caucasian polyploids, on the other hand, are mainly confined to alpine and subalpine vegetation and most likely have a glacial and postglacial age, adapting to and occupying these habitats following glacier retreat. Many polyploid species with the Euro-Mediterranean type range are so widespread that it is possible that diploid cytoraces exist somewhere in this region; but only polyploids have reached the territory of Armenia.

The predominance of representatives of the Ancient Mediterranean geographic element among species with two or more cytoraces with different ploidy, namely, species in the Armeno-Iranian, Armenian, Atropatenian, and Ancient Mediterranean areas, is also most likely evidence of intensive speciation processes in the arid regions of the Armenian Highlands and of the Lesser Caucasus in many genera (e.g., *Centaurea, Astragalus, Cousinia*, etc.) (Fayvush and Aleksanyan 2021). This is also evidenced by the predominance of representatives of the Armenian, Armeno-Iranian, and Armeno-Atropatenian elements among the species in the karyotypes in which B-chromosomes have been recorded.

## Conclusion

Our karyo-geographic analysis of the Armenian flora confirms that this flora has a long evolutionary history, which commenced in the Tertiary period, and consists of nearly equal proportions of migrants from the Boreal and Ancient Mediterranean sub-kingdoms and species formed on the Armenian Highlands and on the Greater Caucasus. The significant percentage of endemics (mainly neoendemics) is indicative of the territory of Armenia being an arena of intensive species and morphogenesis. Simultaneously, a large karyological diversity among species whose distribution is confined to the Ancient Mediterranean or its parts, including the Armeno-Iranian province, indicates that speciation also occurred in these territories. The “northern root” species, Boreal and Caucasian, became established in Armenia mainly in the form of karyologically stable cytoraces.

## Acknowledgements

This work was supported by the Science Committee of RA under the framework of research project №21AG-1F004.

## Author Contributions

Both authors contributed equally to this article. Ghukasyan is a specialist in karyology and provided all the karyological data. Fayvush is a specialist in phytogeography and geobotany. Both authors worked on collecting and analyzing the data and preparing the article.

## Data Accessibility

The actual data used in this article for analysis are shown in supplemental Table S1, as well as in publications reflected in the references.

## Supplemental Material

The following materials are available as part of the online article at https://escholarship.org/uc/fb
**Table S1.** List of plant species of the flora of Armenia, included in karyo-geographical analysis.

## References

Agakhaniants, O. (1981) Arid mountains of the USSR. Moscow.

Cherneva, O. (1974) Short analysis of geographical distribution of the species of *Cousinia* Cass. genus. Botanicheskij Journal (Moscow-Leningrad), 59, 183–191.

Dimitrova, D., Fischer, M.A. & Kaestner A. (2003) *Crepis pannonica* (*Asteraceae-Lactuceae*): karyology, growth form, phytogeography, occurrence and habitats in Austria; including subsp. blavii comb, et stat. nov. Neilreichia, 2-3, 107–130. Available at: https://dokumen.tips/documents/crepis-pannonica-asteraceae-lactuceae-karyology-growth-2-3-107-130-2003.html?page=1

Fayvush, G.M. (1990) On autochthonous and allochthonous tendencies in development of steppes of Armenian SSR. Biological Journal of Armenia, 43, 3, 220–225.

Fayvush, G., Tamanyan, K., Kalashyan, M. & Vitek, E. (2013) “Biodiversity hotspots” in Armenia. Annalen des Naturhistorischen Museums in Wien, B115, 11–20.

Fayvush, G.M. & Adamyan, R.G. (2015) Phyto-geographical analysis of *Geraniaceae* Juss. family in Armenia. Botanical Herald of the North Caucasus, 1, 106–123.

Fayvush, G. & Aleksanyan, A. (2016) Habitats of Armenia. National Academy of Sciences of the Republic of Armenia, Yerevan. Armenia. 360 pp.

Fasyvush, G. & Aleksanyan, A. (2020) The Transcaucasian Highlands. In: Plant biogeography and vegetation of high mountains of Central and South-West Asia (ed. by J. Noroozi), pp 287-313. Springer, Cham. https://doi.org/10.1007/978-3-030-45212-4_8

FNC (2014) The Fifth National Report to convention on biological diversity. Yerevan, Armenia. 106 pp. Available at: https://www.cbd.int/doc/world/am/am-nr-05-en.pdf

Gabrielian, E. & Fayvush, G. (1986) Phyto-geographical analysis of the Armenian species of the genus *Scrophularia*. Biological Journal of Armenia, 39, 170–173.

  

Gabrielian, E. & Fajvush G. (1989) Floristic Links and Endemism in the Armenian Highlands. In: The Davis and Hedge Festschrift (ed. by K. Tan), pp 191-206. Edinburgh.

Ghukasyan, A.G. (2010) Karyological investigations of the family *Poaceae* of the Armenian flora. In: Study of the Flora of the Caucasus (International Conference Abstract) pp. 33-34, Pyatigorsk.

Ghukasyan, A.G. (2011) Speciation in the genus *Zingeria (Poaceae)* of the flora of Armenia. Takhtajania, 1, 142–143.

Ghukasyan, A. & Janjughazyan, K. (2015) Chromosome numbers of some rare flowering plants of Armenian flora. Electronic Journal of Natural Sciences, 24**,** 23–26.

Ghukasyan, A. & Akopian, J. (2018) Karyological study of the endangered species of Armenian flora *Vavilovia formosa* (Fed.) Steven (Fam. *Fabaceae*) from Geghama mountains population. Electronic Journal of Natural Sciences*,* 31**,** 32–34.

Ghukasyan, A., Adamyan, R. & Poghosyan A. (2022) Karyological study of some *Geranium* species (*Geraniaceae*) from Armenia. Botanicheskii Zhurnal*,* 107, 8, 794-799.

Hayrapetyan, A.M. & Ghukasyan, A.G. (2015) Palynological and karyological study of endemic species of the genus *Rhaponticoides* Vaill. (*Asteraceae*), included in the Red Book of plants of Armenia. Reports of National Academy of Sciences RA, 115, 156–162.

Hayrapetyan, A.M. & Ghukasyan, A.G. (2021) Palynological and karyological features of an endemic species *Cousinia fedorovii* Takht. (*Asteraceae*), included in the Red Book of plants of Armenia. Reports of National Academy of Sciences RA, 121, 245–250.

Kotseruba, V., Pistrick, K., Kumke, K., et al., (2010) The evolution of the hexaploid grass *Zingeria kochii* (Mez) Tzvel. (2n=12) was accompanied by complex hybridization and uniparental loss of ribosomal DNA. Molecular Phylogenetics and Evolution Today, 56, 146–155. https://doi.org/10.1016/j.ympev.2010.01.003

Kotseruba, V., Pistrick, K., Gernand, D., Meister, A., Ghukasyan, A. & Houben, A. (2012) Characterisation of the low-chromosome number grass *Colpodium versicolor* (Stev.) Schmalh. (2n = 4) by molecular cytogenetics. Caryologia, Firenze, 58, 241–245. https://doi.org/10.1080/00087114.2005.10589457

Krishtofovich, A.N. (1936) The development of phyto-geographical provinces of the North hemisphere from the end of Cretaceous period. Soviet Botany, 3, 9-24.

Mittermeier, R.A., Turner, W.R., Larsen, F.W., Brooks, T.M. & Gascon, C. (2011) Global biodiversity conservation: the critical role of hotspots. In: Biodiversity hotspots: distribution and protection of conservation priority areas (ed. by F.E. Zachos and J.C. Habel), pp. 3-22. Springer, Heidelberg. https://doi.org/10.1007/978-3-642-20992-5_1

Nazarova, E.A. (2009) Karyosistematic investigation of the Armenian representatives of genus *Vicia* L. II. Sections *Faba, Narbonensis, Peregrinae* (Fabaceae). Flora, vegetation and plant resources of Armenia, 17, 39–42.

Nazarova, E.A. (2011) Lentils (*Lens*, Fabaceae) in Armenia. Takhtajania, 1, 138–141.

Nazarova, E.A. & Gukasyan, A.G. (2004) Chromosome numbers of flowering plants of Armenian flora. Yerevan. Institute of Botany, National Academy of Science, Armenia. 171.

Oganezova, G.H. (2013) Some peculiarities of *Merendera* and *Bulbocodium* species (Colchicaceae): geography, biology, morphology and chromosome number connected with their taxonomic range. Takhtajania*,* 2, 60–68.

Portenier, N.N. (2000) The system of geographical elements of the Caucasian flora. Botanicheskij Zhurnal, 85, 9, 26-33.

Rechinger, K.H. (1972) Compositae-Cynareae I: *Cousinia*. In: Flora Iranica, 90, (ed. by K.H. Rechinger). Akademische Druck- und Verlagsanstalt, Graz.

Rechinger, K.H. (1986) Cousinia: morphology, taxonomy, distribution and phytogeographical implications. Proceedings of the Royal Society of Edinburgh, 89B, 45–58.

Saghatelyan, A. (2006) Flora of Armenia: its composition, analysis and relationships. Turczaninowia, 9, 5–47.

Takhtajan A. (1954-2009) Flora of Armenia, vv. 1-11. Yerevan & Koeltz Scientific books.

Takhtajan, A. (1986) Floristic regions of the world. University of California Press, Berkeley.

Tamanyan, K. & Fayvush, G. (1987) Phyto-geographical analysis of the Armenian species of the genus *Cousinia* (Asteraceae). Biological Journal of Armenia, 40, 464–469.

Wagenitz, G. (1975) Floristic connections between the Balkan Peninsula and the near East as exemplified by the genus *Centaurea*. In: Problems of Balkan flora and vegetation (ed. by D. Jordanov et al.). Bulgarian Academy of Sciences, Sofia.

Wagenitz, G. (1986) *Centaurea* in south-West Asia: patterns of distribution and diversity. Proceedings of the Royal Society of Edinburgh, 89B, 11–21.

Więcław, H., Kalinka, A. & Koopman, J. (2020). Chromosome numbers of *Carex* (Cyperaceae) and their taxonomic implications. PLoS ONE, 15, e0228353. https://doi.org/10.371/journal.pone.0228353

Submitted: 17 August 2022
First decision: 14 September 2022
Accepted: 17 January 2023

Edited by Robert J. Whittaker

  