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A new fossil species of *Ulmus* (Ulmaceae) in Early Pleistocene deposits of Southern Armenia

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Ulmus ivangabrieljanii Sargsyan sp. nov. is described and illustrated as a new fossil species from Early Pleistocene deposits of the Sisian Diatomaceous Formation in Syunik Province, Southern Armenia. The species is distinguished by a combination of characters: lamina broad elliptical to elliptic, 20.8–38 mm long and 17.2–33.0 mm wide, with a length–to–width ratio of 1.09–1.30; petiole 8–13 mm long; and 10–12 pairs of secondary veins. Photographs and diagnostic tables differentiating this species from *U. minor* and *U. glabra* and detailed morphological characteristics of *U. ivangabrieljanii* sp. nov. are provided. The present fossil species, *U. ivangabrieljanii* sp. nov., is distinguished from all other modern *Ulmus* spp. by its characteristics of leaf shape, leaf size, leaf base, and venation. Key differences between *U. ivangabrieljanii* sp. nov. and fossil *Ulmus* species from Turkey, Iran, and Europe are presented. These morphological features clearly justify recognising *U. ivangabrieljanii* sp. nov. as a distinct fossil species. The discovery of *U. ivangabrieljanii* sp. nov. indicates that the genus *Ulmus* was already widely distributed in South–Western Asia during the Pleistocene, at a time when the regional climate was similar to the present–day conditions.

Keywords: Early Pleistocene; fossils; new species; Southern Armenia; Syunik Province; *Ulmus*.

Introduction

The Ulmaceae Mirb., or elm family, comprises 15 extant genera and approximately 150–200 species distributed across both the Northern and Southern hemispheres (Tutin, 1964; Cronquist & Takhtajyan, 1981; Manchester, 1989; Denk & Dillhoff, 2005a, 2005b; Zhang et al., 2021; Lu et al., 2023). The genus *Ulmus* L. includes at least 45 living species and represents the most diverse genus within the family (Grudzinskaya, 1979; Todzia, 1993; Sherman–Broyles et al., 1997; Fu et al., 2003). Most *Ulmus* species are deciduous and are widespread or dominant in temperate forests of the Northern Hemisphere, with a few extending into subtropical or tropical regions of South-Eastern Asia and Central America (Wiegrefe et al., 1994; Sherman–Broyles et al., 1997; Zhang et al., 2018).

The genus *Ulmus* has an abundant Cenozoic megafossil record throughout North America and Eurasia, preserved mainly as fruits and leaves (Wolfe, 1973; Iljinskaja, 1982; Wolfe & Wehr 1987; Manchester, 1989; Xing et al., 2016; Gabrielyan, 2021). Among the extant genera of the Ulmoideae, *Ulmus* has the earliest known fossil record (MacGinitie, 1941; Ablaev & Iljinskaja, 1982; Burnham, 1986; Tanai & Wolfe, 1977; Kvaček et al., 1994; Basinger et al., 1994; Liu et al., 1996; McIver & Basinger, 1999; Denk & Dillhoff, 2005b). Leaves showing architectural features corresponding to modern Ulmoideae were already widespread in the Northern Hemisphere by the early Cenozoic (Wolfe, 1973).

The oldest confirmed records of the genus, based on fossil fruits, are those described from the late Early to Middle Eocene deposits of the western coastal states and provinces of the United States and Canada (Manchester, 1989; Denk & Dillhoff, 2005b; Wang et al., 2010). Burnham (1986) described a number of leaf morphotypes from the Palaeogene of North America using discriminant analysis. The author's studies indicate that *Ulmus* first appeared during the Middle Eocene. Based on the tree species and their ecological characteristics, the composition of the identified fossil tree communities was reconstructed in Turkey. It is estimated that *Salix* species were present along stream banks, *Liquidambar* species occurred both on and near stream banks, and *Prunus, Myrica,* and *Ulmus* species were present in adjacent areas (Akkemik, 2025).

Since 1937, a total of 8,575 specimens, containing more than 12,300 imprints of various plant organs, animals and fungi, have been collected from the diatomites of the Sisian Formation, exposed at several localities within the Vorotan River Basin (Gabrielyan & Kovar–Eder, 2011; Gabrielyan, 2021). The fossil floras of the Vorotan River Basin rank among the richest worldwide, comprising over 230 taxa of higher plants identified from macro–remains of leaves, fruits, and other organs. Representatives of the Ulmaceae family have been recorded in the Early Pleistocene flora of Armenia. Gabrielyan (2021) listed *Ulmus* cf. *glabra* Huds., *U.* cf. *laevis* Pall., *U.* cf. *minor* Mill., *U.* cf. *pumila* L., and *Zelkova* cf. *carpinifolia* (Pall.) K. Koch among the fossil plants of the Early Pleistocene flora of the Vorotan River Basin.

In the modern flora of Armenia, three species of elm are recorded: *Ulmus glabra* Huds., *U. minor,* and *U. densa* Litv. (the latter in cultivation only). The fossil leaves of *Ulmus* described in this paper as a new species—*Ulmus ivangabrielianii*—were collected from Syunik Region in Southern Armenia. The new species *U. ivangabrielianii,* described here for the first time, has been compared with the modern species *U. minor* and *U. glabra,* which occur naturally in Armenia. *Ulmus densa* was not included in the comparison, as it does not occur in the wild flora of Armenia and is introduced only for ornamental planting in populated areas.

Material and methods

The fossil specimens were collected from the Lesser Caucasus region, along the upper part of the Vorotan River in Syunik Province, Southern Armenia (39°16′–39°52′ N latitude and 45°40′–46°12′ E longitude) (Fig. 1). The samples were obtained from eight stratigraphic layers across five localities within the Early Pleistocene Sisian Diatomaceous Formation. The oldest layer, in terms of absolute age, is the Shm–1/e layer at the Shamb–1 locality, which is 1.31 million years old, while the youngest is the Brn–2/d layer at the Brnakot–2 locality, dated to 1.04 million years ago (Kirscher et al., 2014; Gabrielyan, 2021).

Of the impressions of elm species collected from these localities, 20 samples were identified as belonging to a new species for science, *Ulmus* sp. nova, along with their five counterparts (Tables 1 and 2). This region is characterised by the Vorotan Basins, remnants of the Palaeovorotan River system. These basins are situated between the Zangezur Mountain range (Southern Armenia) and the Syunik uplands.

The fossil material was collected, processed, registered, and prepared using standard palaeobotanical methods (Meyen, 1968). Fossil plant images were mainly obtained using an HP Scanjet 4890 scanner. The plant remains are preserved as imprints, with no cuticle preservation. However, the venation details are well visible, and sometimes even the areolation can be discerned. The descriptions of the foliage follow the methods outlined by Tanai (1978) and Ellis et al. (2009).

Modern species were studied from the herbarium of the A. Takhtajan Institute of Botany, National Academy of Sciences of Armenia (ERE), and from the herbarium of the Komarov Botanical Institute, Russian Academy of Sciences in St. Petersburg (LE).

For the fossil specimens, original schematic drawings were created. The samples were examined using binocular microscopes MBS–2 and Olympus–SZX16. The age of the deposits was determined using the radiometric method (Joannin et al., 2010).

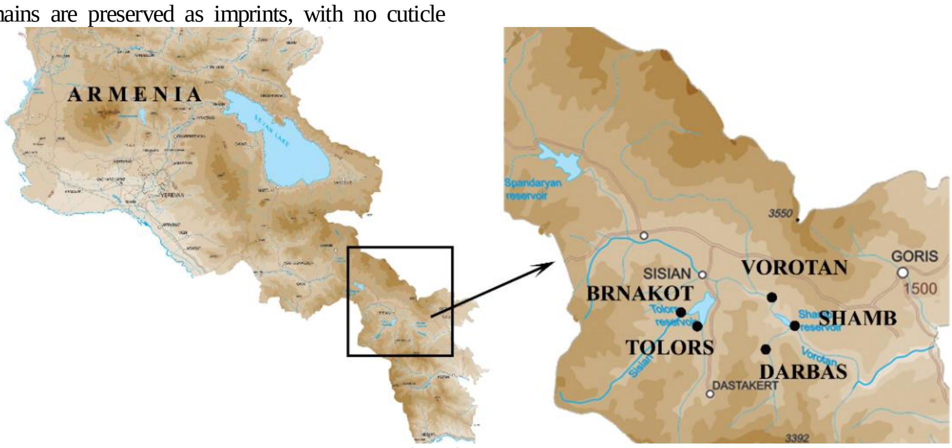

Fig. 1. Map showing the distribution of the fossil *Ulmus ivangabrieljanii* Sargsyan sp. nov.

Table 1
Main characteristics of specimens of *Ulmus ivangabrieljanii* sp. nov. (leaf lamina)

Locality	Specimen	Ieaf lamina length, mm	Leaf lamina width, mm	Ratio	Petiole length, mm	Petiole width (mm) in lower 2/3 of length	Shape of leaf lamina	Leaf apex form	Leaf base form
Shamb–1	Shm–1940/6a	26	22.6	1.15:1	6	1	Broad ovate	Apex obtuse, convex	Base obtuse, truncate, slightly asymmetrical
Shamb–1	624/_30	–	–	–	–	–	–	–	Cordate, asymmetric
Shamb–1	638/_30	40	30.7	1.3:1	–	–	–	Ovate	Cordate, asymmetric
Shamb–1	649a/_30	–	–	–	–	–	Ovate	–	–
Shamb–1	30–Shm/355	25	20	1.25:1	–	–	Ovate	–	Cordate, asymmetric
Shamb–1	30–Shm/454	–	–	–	–	–	Ovate	–	–
Shamb–1	Shm–05/277	25	21	1.19:1	–	–	Broad ovate	–	Base cordate,rounded, asymmetrical
Shamb–1	Shm–05/278	25	23	1.09:1	about 5	about 1.5	Broad ovate	Obtuse, convex	Base obtuse,rounded, asymmetrical
Shamb–1	Shm–12/217	about 32	about 27	1.19:1	13	1.2	Elliptic	Obtuse, convex	Obtuse, rounded, asymmetrical
Shamb–1	Shm–12/217A	–	–	–	–	–	–	–	Obtuse, rounded, asymmetrical
Shamb–1	Shm–13/90	–	–	–	–	–	–	–	–
Darbas–2	30–D/61	36	30.7	1.17:1	8.8	0.8	Broad ovate	Obtuse, convex	Obtuse, rounded, slightly asymmetrical
Darbas–2	30–D/348	38	33	1.15:1	7	1	Broad ovate	Obtuse, convex	Obtuse, rounded, slightly asymmetrical
Darbas–2	30–D/421	29	26	1.11:1	7	0.9	Broad ovate	Obtuse, convex	Obtuse, rounded, slightly asymmetrical
Darbas–2	30–D/422	–	–	–	–	–	–	–	–
Darbas–2	02–D/5a	35	29	1.21:1	10.6	1.5	Broad elliptic	Obtuse, convex	Obtuse, rounded, slightly asymmetrical
Darbas–2	Dr–09/3a	–	–	–	–	–	Broad elliptic	Obtuse, convex	Obtuse, rounded, slightly asymmetrical
Brnakot–2	B–03/3	20.8	17.2	1.21	4.8	0.9	Ovate	–	Acute/obtuse, convex, asymmetrical
Brnakot–2	B–03/3A	–	–	–	–	–	–	–	–
Brnakot–2	B–03/81a	30.3	23.3	1.3:1	–	–	Broad elliptic	Obtuse, convex	Obtuse, rounded, slightly asymmetrical
Brnakot–2	B–03/81A	–	–	–	–	–	–	–	–
Vorotan–1	30–Vr/15	–	–	–	–	–	–	–	–
Vorotan–1	30–Vr/15A	–	–	–	–	–	–	–	–
Tolors–2	Tlr–06/21(22)	26.5		1.3:1	12	1	Elliptic	Obtuse, convex	Cordate, strongly asymmetric
Tolors–2	Tlr–06/22a(21)	26.5	20.5	1.3:1	–	–	Elliptic	Obtuse, convex	Cordate, strongly asymmetric

Table 2
Main characteristics of specimens of *Ulmus ivangabrieljanii* sp. nov. (margin and venation)

Specimen	Leaf margin	Sinus	Secondary veins number (left and right)	Secondary veins average angle	Tertiary veins average angle with main	Fourth order venation	Fifth order venation	Marginal ultimate venation	Interveins
Shm–1940/6a	Serrate, teeth 1 order	Angular/rounded	12/–	57	–	–	–	Irregular, looped to sometimes incompletely looped	–
624/_30	Serrate	–	–	–	–	–	–	–	No
638/_30	Serrate	Angular	12/11	52	143	Regular polygonal reticulate	Polygonal reticulate, probably forming areoles	Irregular, looped to sometimes incompletely looped	–
649a/_30	Serrate	–	–	–	–	Regular polygonal reticulate	–	–	No
30–Shm/355	Serrate	Angular	–	59	128	Regular polygonal reticulate	Polygonal reticulate, probably forming areoles	Irregular, looped to sometimes incompletely looped	–
30–Shm/454	–	–	–	–	–	–	Polygonal reticulate	Irregular, looped	No
Shm–05/277	Serrate, teeth 1, rare 2 order	Angular	–	61	141	–	–	–	–
Shm–05/278	Serrate (in lower half partly crenate), teeth 1 order	Angular	11/10	50	135	Regular polygonal reticulate	Polygonal reticulate, probably forming areoles	Irregular, looped to sometimes incompletely looped	No
Shm–12/217	Serrate, teeth 1 order	Angular	12/11	58	106	Regular polygonal reticulate	Polygonal reticulate, probably forming areoles	Irregular, looped to sometimes incompletely looped	–
Shm–12/217A	Serrate	–	–	–	–	–	–	–	–
Shm–13/90	–	–	–	–	–	Regular polygonal reticulate	–	Irregular, looped	No
30–D/61	Serrate, teeth 1 order	Angular	13/12	50	109	Regular polygonal reticulate	Polygonal reticulate, probably forming areoles	Irregular, looped to sometimes incompletely looped	No
30–D/348	Serrate, teeth 1 order	Angular	11/10	49	131	Regular polygonal reticulate	Polygonal reticulate, probably forming areoles	Irregular, looped to sometimes incompletely looped	rare
30–D/421	Serrate, teeth 1 order	Angular	11/10	51	130	Regular polygonal reticulate	Polygonal reticulate, probably forming areoles	Irregular, looped to sometimes incompletely looped	–
30–D/422	–	–	–	–	–	–	–	Irregular, looped	No
02–D/5a	Serrate, teeth 1 order	Angular	10/?	54	–	–	–	–	Rare
Dr–09/3a	Serrate, teeth 1 order	Angular	10/9	57	–	Regular polygonal reticulate	Polygonal reticulate, probably forming areoles	Irregular, looped to sometimes incompletely looped	No
B–03/3	Serrate, teeth 1 order	Angular	10/9	–	–	Regular polygonal reticulate	–	–	–
B–03/3A	–	–	–	–	–	–	–	Irregular, looped	No
B–03/81a	Serrate, teeth 1 order	Angular	12/13	51	125	Regular polygonal reticulate	Polygonal reticulate, probably forming areoles	Irregular, looped to sometimes incompletely looped	–
B–03/81A	–	–	–	–	–	Regular polygonal reticulate	Polygonal reticulate, probably forming areoles	Irregular, looped to sometimes incompletely looped	–
30–Vr/15	–	–	–	–	–	–	–	Irregular, looped	–
30–Vr/15A	–	–	–	–	–	Regular polygonal reticulate	–	–	Rare
Tlr–06/21(22)	Serrate, teeth 1, rare 2 order	Angular	11/9	59	129	Regular polygonal reticulate	Polygonal reticulate, probably forming areoles	Irregular, looped to sometimes incompletely looped	Rare
Tlr–06/22a(21)	Serrate, teeth 1, rare 2 order	Angular	11/10	51	146	Regular polygonal reticulate	Polygonal reticulate, probably forming areoles	Irregular, looped to sometimes incompletely looped	–

Results

Description of fossils
Order: Rosales Bercht. and J.Presl
Family: Ulmaceae Mirb.
Genus: *Ulmus* Linnaeus, 1753

Ulmus ivangabrieljanii Sargsyan, sp. nov. (Fig. 2)
Holotype: Shm–12/217 (Figs. 2 (1–7)), ERE!
Paratypes: 30D/61, B–03/81a (Figs. 2 (8–14)), ERE!
Repository: The specimens described in this paper are stored at the Department of Paleobotany, A. Takhtajan Institute of Botany of the NAS RA, Yerevan, Armenia.

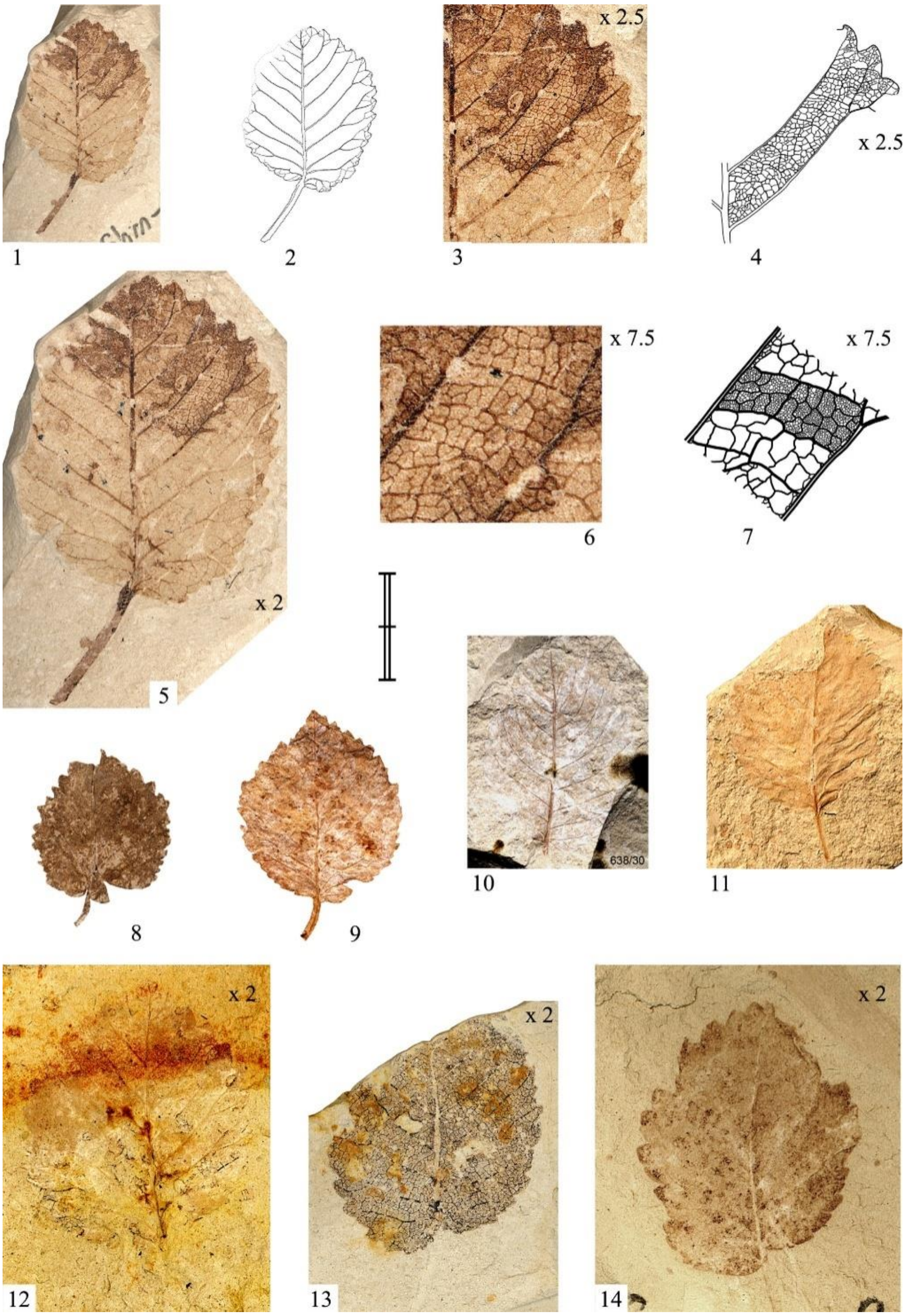

Fig. 2. *Ulmus ivangabrieljanii* Sargsyan sp. nov., Figs. 1–14 – (vertical scale bar = 2 cm)

Type localities: Shamb–1. Darbas–2, Brnakot–2, Syunik marz, Republic of Armenia (Shamb–1 – 39°28′12.11″ N, 46°08′31.61″ E; Darbas–2 – 39°26′46.38″ N, 46°07′46.08″ E; Brnakot–2 – 39°30′34.16″ N, 46°00′04.37″ E).

Localities: Shamb–1. Darbas–2, Brnakot–2, Vorotan–1, Tolors–1, Syunik marz, Republic of Armenia.

Specimens: Shm–1940/6a, 624/30, 638/30, 649a/30, Shm–12/217 + Shm–12/217A (part + counterpart), Shm–13/90, 30–Shm/454, Shm–05/277, Shm–05/278, 30–Shm/355, 30–D/61, 30–D/421, 30–D/422, Dr–09/3a, 02–D/5a, 30–D/348, B–03/3 + B–03/3A (part + counterpart), B–03/81a + B–03/81A (part + counterpart), 30–Vr/15 + 30–Vr/15A (part + counterpart), Tlr–06/21(22) + Tlr–06/22a(21) (part + counterpart).

Stratigraphic horizon: Sisian Formation, Early Pleistocene.

Etymology: The fossil species is named in honour of Dr. Ivan Gabrielyan, who made a significant contribution to the palaeobotanical investigations of the fossil flora of Armenia.

Diagnosis: leaves simple; petiole 8–13 mm in length, 0.9–1.2 mm in width. Lamina broad elliptic to elliptic, microphyllous in size, 20.8–38 mm long, 17.2–33 mm wide, with a length-to-width ratio of 1.09–1.3; secondary veins in 10–12 pairs.

Description: leaves simple, petiolate, with a petiole 8–13 mm long and 0.9–1.2 mm wide. Lamina broad elliptical to elliptic, 20.8–38.0 mm long, 17.2–33.0 mm wide, with a length-to-width ratio of 1.09–1.30; apex obtuse and convex, base obtuse, rounded, and asymmetrical. Leaf margin serrate, with teeth of the first order; teeth short, apically curved towards the apex of the lamina, and the sinuses between the teeth wide and angular.

Venation pinnate, craspedodromous. The midvein is straight to slightly curved, with its thickness gradually decreasing from the petiole to the apex of the leaf. Secondary veins are regularly arranged, straight to slightly curved in the upper part of the lamina, and curved downwards in the lower part (Shm–05/277; Shm–12/217), in 10–12 pairs. These secondary veins are either simple or dichotomously branched one-third to one-half of their length towards the margin, where they end in the tooth tips. The angle of the secondary veins decreases smoothly towards the apex, ranging from 22° to 100° (average 49–61°).

Tertiary veins are thin, well-developed, sinuous, and densely arranged between secondaries, exhibiting a mixed opposite/alternate pattern. The course of the veins is sinuous, convex, or sometimes straight, with the vein angle to the midvein being obtuse, ranging from 100° to 162° (average 106°–146°). Measurements of the third–order veins were taken from the central parts of the leaf blades, where the fine veins were best preserved.

The fourth–order venation is sometimes well preserved (Shm–12/217; 30–D/421; B–03/81a), exhibiting a regular polygonal reticulate pattern. The fifth–order venation is also occasionally well preserved, with a polygonal reticulate pattern (Shm–12/217; 30–D/421), likely forming areoles (Shm–05/277). The ultimate marginal venation is irregular, looped, and sometimes incompletely looped.

1. *Ulmuis* sp. nov.; imprint of leaf, locality Shamb–1, layer Shm–1/f–3, specimen Shm–12/217; 2. *Ulmus* sp. nov.; schematic diagram of leaf, locality Shamb–1, layer Shm–1/f–3, specimen Shm–12/217; 3. *Ulmus* sp. nov.; imprint of leaf fragment, locality Shamb–1, layer Shm–1/f–3, specimen Shm–12/217, x 2.5; 4. *Ulmus* sp. nov.; schematic diagram of leaf venation, locality Shamb–1, layer Shm–1/f–3, specimen Shm–12/217, x 2.5; 5. *Ulmus* sp. nov.; imprint of leaf, locality Shamb–1, layer Shm–1/f–3, specimen Shm–12/217, x 2; 6. *Ulmus* sp. nov.; imprint of leaf fragment, locality Shamb–1, layer Shm–1/f–3, specimen Shm–12/217, x 7.5; 7. *Ulmus* sp. nov.; schematic diagram of leaf venation, locality Shamb–1, layer Shm–1/f–3, specimen Shm–12/217, x 7.5; 8. *Ulmus* sp. nov.; imprint of leaf, locality Darbas–2, layer Drb–2/d–1, specimen 30–D/421; 9. *Ulmus* sp. nov.; imprint of leaf, locality Darbas–2, layer Drb–2/d–2, specimen 30–D/61; 10. *Ulmus* sp. nov.; imprint of leaf, locality Shamb–1, layer Shm–1/f–3, specimen 638/30; 11. *Ulmus* sp. nov.; imprint of leaf, locality Darbas–2, layer Drb–2/d–1, specimen 02–D/5a; 12. *Ulmus* sp. nov.; imprint of leaf, locality Shamb–1, layer Shm–1/f–4, specimen Shm–05/278; 13. *Ulmus* sp. nova; imprint of leaf, locality Shamb–1, layer Shm–1/f–4, specimen Shm–05/277; 14. *Ulmus* sp. nov.; imprint of leaf, locality Tolors–2, layer Tlr–2/b–1, specimen Tlr–06/22a.

Comparison with modern species: The present fossil species is distinguished from all other modern *Ulmus* spp. by its characteristics in leaf shape, leaf size, leaf base, and venation. The key differences between *Ulmus ivangabrieljanii* sp. nov. and its most morphologically related modern species (*U. minor*, *U. glabra*, *U. pumila* and *U. laevis* from Armenia, Turkey, Iran, and Europe) are provided in Table 3.

Comparison with fossil species: The key differences between *Ulmus ivangabrieljanii* sp. nov. and the fossil *Ulmus* species from Turkey and Europe are provided in Table 4.

Table 3

Main differences between *Ulmus ivangabrieljanii* sp. nov.
and its most morphologically similar modern species *U. minor*, *U. glabra*, *U. pumilla*, and *U. laevis*

Feature	*Ulmus ivangabrieljanii* sp. nov.	*Ulmus minor* (Mill.)	*Ulmus glabra* Huds.	*Ulmus pumila* L.	*Ulmus laevis* Pall.
Leaf length, mm	20.8–38	12–25	20–35	≤20	15–28
Leaf width, mm	17.2–33	6–10	15–20	≤12	8–15
Leaf shape	broadly elliptical, oval	narrow, elliptical to ovate	oblong–lanceolate	elongated, pointed	narrowly ovate
Leaf apex	obtuse, convex	acute	sharper	pointed	sharper
Leaf base	rounded, asymmetrical	triangular or slightly cordate	more symmetrical	symmetrical	symmetrical
Petiole length, mm	8–13	5–9	5–9	4–7	5–8
Secondary veins	10–12 pairs, dichotomous branches forming reticulate network	6–9 pairs, simpler	7–10 pairs	5–8 pairs	6–8 pairs
Venation	complex, well–developed tertiary and quaternary veins	simpler, less dense	moderate complexity	simple	moderate complexity
Margin	serrate, teeth 1st order, short, curved towards apex	serrate, less regular	serrate	serrate, small	serrate
Distinguishing feature	large, broad, oval leaves; complex venation; long petiole	narrower leaves, simpler venation	oblong–lanceolate shape, sharper apex	small, elongated, pointed leaves	narrow leaves, simpler venation

Table 4

Main differences between *Ulmus ivangabrieljanii* sp. nov. and fossil *Ulmus* species from Turkey and Europe

Feature	*Ulmus ivangabrieljanii* sp. nov.	Fossil *Ulmus* sp. Turkey (e.g., *Ulmoxylon* / *Ulmus* type woods)	Fossil *Ulmus* cf. spp. Europe (e.g., *U.* cf. *carpinoides*)
Stratigraphic horizon	Early Pleistocene, Sisian Formation, Southern Armenia	Early Miocene, Galatian Volcanic Province, Turkey	Pliocene, Willershausen Formation, Germany (*Ulmus cf. carpinoides*)
Leaf length (mm)	20.8–38	– (not well documented)	– (fragmentary)
Leaf width (mm)	17.2–33	–	–
Leaf shape	Broad elliptical to elliptic	leaves/woods often assigned to Ulmus type but precise shape variable	leaves somewhat narrower, more elongate in many cases
Petiole length (mm)	8–13	–	–
Secondary veins (pairs)	10–12	– (woods often identified only anatomically)	–
Venation detail	Complex with tertiary and quaternary veins forming reticulate pattern	wood anatomy: ring-porous earlywood vessels, *Ulmus* type woods in Turkey	leaves preserved: *Ulmus cf. carpinoides*, Willershausen Germany, show elm-type venation but smaller size
Key distinguishing features	large, broad leaves; long petiole; dense complex venation network	fossil woods assigned to *Ulmus* type in Turkey show general *Ulmus* wood anatomy but few detailed leaf morphometrics	European fossil *Ulmus* cf. often smaller leaves, narrower width, less detailed venation preserved
Geographic region	South-Western Asia (Armenia)	Anatolia (Turkey)	Europe (e.g., Germany)
Implication for palaeo-environment	suggests temperate, moderately humid conditions in Early Pleistocene SW Asia	suggests warm temperate/subtropical in Early Miocene Anatolia	suggests temperate forest elements in European Pliocene environments

The data from Turkey were compared with the studies by Akkemik (2021), Halbritter & Diethart (2005), Diker et al. (2022), and the data from Europe were compared with the studies by Knobloch, E. (1999), Halbritter (2005a; 2005b), Ghavidel et al. (2020), "Ulmus cf. carpinoides Goeppert, 1855. The Fossil Forum (www.thefossilforum.com/collections-database/plants/ulmus-cf-carpinoides-goeppert-1855-r1967).

These morphological features clearly justify the recognition of *Ulmus ivangabrieljanii* sp. nov. as a distinct fossil species.

Discussion

Fossils provide insight into plant systematics, phytogeography, evolution, and climate change in geological periods. The Ulmaceae provide an ideal biological model for investigating the evolutionary dynamics of the northern temperate woody flora, owing to the rich fossil record and the wide extant geographical distribution of the family. It is noteworthy that Eastern Asia was the centre of origin and diversification for temperate species. The Oligocene was a significant epoch for the rapid diversification of broad-winged lineages of *Ulmus*, likely due to the dispersal advantages in the more open forests that emerged as the global climate began to cool (Zhang et al., 2018; Zhang et al., 2021).

Palynological evidence from Early Pleistocene deposits reveals a dynamic pattern of vegetation change, closely corresponding with climatic oscillations. Alternating periods of forest expansion and openness reflect glacial-interglacial transitions, driven by fluctuations in temperature and moisture availability. During warmer and more humid intervals, forest ecosystems became denser and more diverse, while cooler and drier conditions favoured the expansion of steppe and shrubland communities. Within these vegetation complexes, *Ulmus* (elm) emerges as a consistent bioclimatic indicator of moderately humid and temperate conditions. Its presence in pollen spectra is strongly correlated with interglacial or interstadial phases, during which moisture levels were sufficient to support the development of broadleaf deciduous forests. The taxon typically appears alongside other mesophilous woody species, such as *Quercus*, *Fraxinus*, and *Alnus*, forming part of mixed forest and forest-steppe assemblages. These associations suggest that *Ulmus* played an integral role in forest structure during favourable climatic periods.

The geographical distribution of *Ulmus* pollen during the Early Pleistocene is uneven, with the most robust records coming from Western and Southern Europe, including regions such as Spain and Turkey. By contrast, records from Eastern Europe and the Caucasus are comparatively sparse, indicating either more limited regional expansion of elm or insufficient sampling coverage. Interestingly, the palynological data also confirm the presence of *Ulmus* in Arctic and Subarctic areas of North America and Alaska, suggesting that elm populations were able to persist or recolonise these regions during transient warm phases (Pidek, 2015; Fletcher et al., 2021; D'Agostino et al., 2022).

The absence or marked reduction of *Ulmus* in colder or drier stratigraphic layers further supports its use as a palaeoclimatic proxy. Its decline or disappearance from the pollen record often coincides with glacial episodes or climatic deterioration, when forest cover retreated and open, xerophytic vegetation types dominated. In this context, *Ulmus* not only provides insight into vegetation composition but also serves as a sensitive indicator of past moisture regimes and temperature fluctuations. Taken together, the palynological record of *Ulmus* enhances our understanding of the dynamics of Early Pleistocene vegetation and offers valuable contributions to paleoenvironmental reconstructions. Its presence or absence, distribution patterns, and ecological associations provide a reliable framework for interpreting regional climate variability and the nature of interglacial ecosystems across Eurasia and North America.

Bruch & Gabrielyan (2002) presented a preliminary palaeoclimatic evaluation of the Vorotan flora. Palynological data from the Early Pleistocene in the Caucasus region provide critical insights into the interplay between climate and vegetation dynamics during a period marked by significant environmental oscillations. In sum, the presence of *Ulmus* in Early Pleistocene palynological spectra from the Caucasus, though limited, provides important evidence for the occurrence of humid-temperate phases capable of supporting deciduous forest elements. Its ecological associations and spatial distribution enhance our understanding of regional paleoclimate variability and contribute to broader reconstructions of Quaternary vegetation dynamics in the mountainous zones of southwestern Eurasia.

Fossil materials discovered in the Syunik region of Armenia indicate that, during the Early Pleistocene, South-Western Asia had a temperate climate similar to the present day.

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