Acta Palaeobotanica 64(2), 351–359, 2024
https://doi.org/10.35535/acpa-2024-0012

e-ISSN 2082-0259
ISSN 0001-6594

Fossil remains of the genus *Crataegus* (Rosaceae, Amygdaloideae) from south-eastern Armenia

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Received 20 July 2024; accepted for publication 19 September 2024

ABSTRACT. As a result of the research, we determined the sectional affiliation of fossil remains of the genus *Crataegus* from the Early Pleistocene of the south-eastern part of Armenia, in the middle reaches of the Vorotan River.

Plant fossils and imprints help to establish the distribution of species over the Earth's surface during different geological periods. Of particular interest are the findings of species of the genus *Crataegus*, which is considered to be systematically very complex due to its inherent hybridization, apomixis, and polyploidy.

In the modern flora of Armenia, the genus *Crataegus* is represented by three sections with 23 species.

Comparative macromorphological analysis of fossil and modern hawthorns showed that the studied fossil remains belong to the section *Crataegus*. Among the species found in the territory, in terms of macromorphological characteristics, they are close to *Crataegus rhipidophylla*, *C. caucasica* and *C. monogyna*.

KEYWORDS: *Crataegus*, palaeobotany, fossil leaves, fossil thorns

INTRODUCTION

Armenia has a unique and diverse flora, due to its geographical location.

The South Caucasus is a mountainous region comprising modern Armenia, Georgia, Azerbaijan, and the easternmost part of Turkey. Together with eastern Turkey to the west and Iran to the east, the region serves as a biogeographical corridor connecting Asia, Europe, and Africa. The South Caucasus has become a refuge for diverse ecosystems and endemic life forms due to its unique geographic location, variety of natural landscapes, and mild climate (Tarkhnishvili, 2014; Nakhutsrishvili et al., 2015; Lazarev et al., 2023). It is located at the junction of two floristic provinces: the Armeno-Iranian and the Caucasian (Takhtayan, 1978).

The genus *Crataegus* L., commonly known as hawthorn, is one of the largest in the Rosaceae family. It belongs to the subfamily *Amygdaloideae*, tribe *Maleae*, and comprises about 200 species worldwide (Campbell et al., 2007; Benli et al., 2008; Phipps, 2015; Sun et al., 2024). This genus includes small shrubs and trees distributed throughout the temperate zones of the Northern Hemisphere, encompassing Eurasia and North America (Phipps et al., 1990; Lo et al., 2009).

Crataegus is a difficult genus to classify due to its inherent hybridization, apomixis, and polyploidy.

Palmer (1932) stated that the genus *Crataegus* originated in the high latitudes of Eurasia

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Publisher: W. Szafer Institute of Botany, Polish Academy of Sciences

during a period of favourable climatic conditions. The species of this genus were dispersed from a circumpolar centre southward into both hemispheres before the end of the Neogene. Closely related genera, such as *Osteomeles* Lindl., *Cotoneaster* Medik., *Pyracantha* M. Roem., and *Mespilus* L. are found only in the Old World, whereas *Crataegus* occurs in both the Old and New Worlds, indicating a relatively early separation of this genus from the Maloideae. This is also supported by fossil leaves and fruits of hawthorn found in both hemispheres (Rusanov, 1965).

According to Shaparenko and Baikovskaya (1956), from the Late Oligocene onwards, Rosaceae are quite common in all Neogene deposits of Europe, Asia, and North America. The most common leaf imprints are *Crataegus* L., *Sorbus* L., *Amelanchier* Medik., and *Spiraea* L. Sometimes, mainly in Quaternary deposits, seed remains are also found.

According to palaeobotanical data (Tsinovskis, 1971), hawthorn species with deeply dissected leaves grew in Eurasia and North America during the Neogene period.

Rusanov (1965) agrees with Krishtofovich (1957) that it is possible that in the Neogene period, the predecessors of modern European hawthorns formed in the broad-leaved oak forests of prior to the Pleistocene, which gave rise to *C. oxyacantha* L., *C. pentagyna* Waldst. et Kit., *C. nigra* Waldst. et Kit. and others. According to Rusanov (1965), American large-thorned hawthorns with undissected or shallowly dissected leaves separated from the Neogene deeply dissected hawthorns at a later time and formed groups of species that differed ecologically and morphologically. Their appearance and development were facilitated by numerous migrations of the genus from north to south and backward, as well as in other directions. This probably occurred during the transition from the Neogene to the Quaternary periods, primarily due to alternating cold and warm phases.

During the Quaternary, Eurasian hawthorns migrated southwards to the area of the Ancient Mediterranean and settled mostly in mountainous regions. The xerophytic conditions of the south had a strong influence on their development, resulting in the emergence of hawthorns of the sections *Azaroli* and *Monogynae*. The majority of European species have retained the appearance of ancient hawthorns, characterized by dissected leaves. Rusanov (1970) states that hawthorns are well-suited to new living conditions due to their xerophytic nature and are better adapted than many other associated plant species. In the south and south-west of the Mediterranean, the section *Azaroli* diversified under xerothermic interglacial conditions.

The Catalogue of fossil plants of Caucasus (Kolakovsky, 1973) provides information on the discovery of hawthorn fruit imprints from the North Caucasus (upper Miocene), as well as leaves from South Georgia (Upper Miocene-Lower Pliocene) and Abkhazia (Upper Pliocene).

Based on cladistic analyses of morphological data, Phipps (1990) proposed that the genus originated in south-western China and Mexico and that there was trans-Beringian migration of Asian and American *Crataegus*. It was suggested that *Crataegus* migrated westward.

However, some authors have taken a contrary view. For instance, Evans and Campbell (2002) included *Crataegus* within subtribe *Pyrinae*. They suggested, based on both molecular and non-molecular characters, that *Crataegus* originated in North America. Lo et al. (2009) reconstructed phylogeographic relationships for 72 Old and New World *Crataegus* species using combinations of four chloroplasts and up to five nuclear regions. According to their results, Europe and eastern North America are proposed as the most recent common areas for *Crataegus*.

Phylogenetic analyses using specific locus amplified fragment sequencing (SLAF-seq) indicated two independent speciation events in Chinese hawthorn taxa (Zhang et al., 2022). Phylogenetic and structure analysis indicated that the species in south-west China shared the gene pool with European species, while species in north-eastern China may have originated from North American species (Du et al., 2019).

The Rosaceae became increasingly important components of fossil floras during the-Neogene, with taxa adapted to many habitats (DeVore and Pigg, 2007). For example, the Miocene–Pliocene Saugbagger flora of Alsace, eastern France contains fruits of *Rubus*, *Crataegus*, *Mespilus*, *Sorbus*, and *Prunus* (Geissert et al., 1990).

The purpose of this work was to identify (to genus, section or species level) two leaf imprints and one thorn of Early Pleistocene plants discovered in the southern part of Armenia in the Sisian diatomaceous formation in the Shamb-1

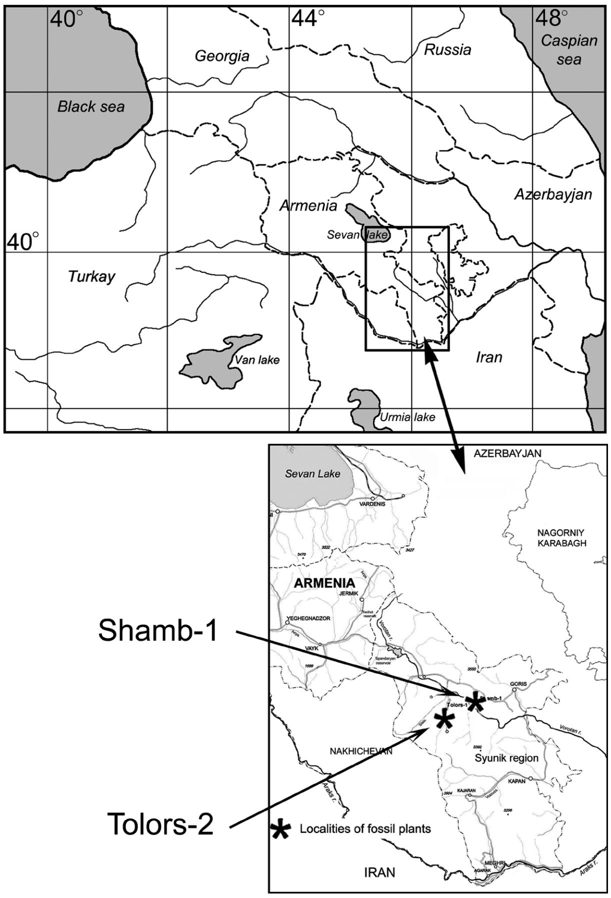

Figure 1. Location of the study area: localities of Shamb-1 and Tolors-2

and Tolors-2 localities as far as possible due to their preservation. This would complement our knowledge of fossil representatives of the Rosaceae from the territory of the Republic of Armenia, and also trace how hawthorn taxa are distributed today among the floristic regions of Armenia.

Currently, in the modern flora of Armenia, the genus *Crataegus* is represented by 23 species belonging to 3 sections – *Crataegus*, *Pentagynae*, *Azaroli* (Sargsyan, 2016, 2022).

MATERIAL AND METHODS

During the present study, type specimens and herbarium material of modern hawthorns from the Caucasus, Turkey, Iran, and Nakhichevan (ERE, ERCB, LE, WIR, WHA, MW, TBI, TGM) were studied. Field observations were carried out between 2005 and 2022 in Armenia to collect herbarium material from the same plant at both the flowering and fruiting stages.

According to Christensen (1992), species can be inherently variable. Hybridization, introgression and subsequent polyploidy or apomixis can blur the boundaries between species. Obtaining all taxonomically important structures at once can be challenging, and it may be necessary to revisit the same populations or individuals during both flowering and fruiting. We visited all floristry regions of Armenia and 456 specimens of 12 *Crataegus* species were collected. During fieldwork, we numbered the hawthorn trees during the flowering period and visited them again in autumn when the fruits were ripe.

Leaf descriptions are based on the subterminal leaves of flowering and short shoots, and on the leaves from the central part of elongated shoots. Accounted for quantitative characteristics of leaves of flowering and elongated shoots – length and width of leaf blade, length and width of basal lobe, number of teeth on basal lobe.

Parameters were measured from 25–38 specimens of each species in nature and in the ERE herbarium. The measurements of leaves from 11 hawthorn species, belonging to different sections, are reported in Table 1.

Fossil remains of hawthorn leaves and thorns were discovered at the Shamb-1 and Tolors-2 localities of the Sisian Formation (Fig. 1).

The Shamb-1 locality in the Sisian Suite has the thickest sediment layer. It is located north-west of the village of Shamb, on the left bank of the Vorotan River. The locality is 1.25 km long and sedimentary rocks are almost 150 m thick. At the locality, horizontally, local

Table 1. Quantitative characters of leaves from flowering shoots and elongate shoots of some *Crataegus* species

No	Species *Crataegus*	Sections	Blades of flowering shoots		Blades of elongate shoots		Basal lobe of flowering shoots		Basal lobe of elongate shoots		No. of teeth on basal lobe
			Length cm	Width cm	Length cm	Width cm	Length cm	Width cm	Length cm	Width cm	
1	*C. atrosanguinea* Pojark.	*Crataegus*	2.8–5.8	3.9–6	4.2–8.3	3.8–6.2	1.8–3.4	1.2–2.4	2.4–4.4	1.4–3.2	4–8
2	*C. caucasica* K. Koch	*Crataegus*	2.8–4.5	2.2–4.4	3.2–5.8	3.5–5.2	1.2–2.2	0.8–2.2	2.8–3.4	1.2–2.6	3–12
3	*C. meyeri* Pojark.	*Crataegus*	1.8–4.5	1.2–4.6	2.7–5.2	2.5–2.8	1.8–2.2	0.6–1.4	2.2–2.8	0.8–1.8	3–8
4	*C. rhipidophylla* Gand.	*Crataegus*	2.2–6.5	1.4–5.8	1.4–6.2	2.2–6.4	1.2–2.4	0.6–1.4	1–2.2	0.8–1.6	2–12
5	*C. pseudoheterophylla* Pojark.	*Crataegus*	1.8–4.6	1.4–4.4	2.8–5.4	3–5.2	1.4–2.2	0.8–1.4	1.6–2.8	1–1.6	4–6
6	*C. microphylla* K. Koch	*Crataegus*	1.2–3.2	1.2–2.2	1.6–3.2	1.2–2.8	0.6–1.8	0.5–1.2	0.8–2.1	0.8–1.4	3–8
7	*C. pallasii* Griseb.	*Crataegus*	1.8–3.3	1.6–3.2	1.8–4.1	1.8–3.8	0.6–1.6	0.6–1.8	0.8–2.2	0.6–1.8	6–12
8	*C. monogyna* Jacq.	*Crataegus*	1.1–5.7	0.8–6.0	2.2–6.2	2.2–6.4	1.0–2.2	0.6–1.2	0.8–2.2	0.8–1.4	1–8
9	*C. pentagyna* Waldst. et Kit.	*Pentagynae*	2.2–5.8	2.2–5.8	2.4–6.2	2.4–6	1.6–3	1–2.2	1.8–4.4	2.2–4	3–8
10	*C. orientalis* Pall. ex M. Bieb.	*Azaroli*	2–4.4	1.6–3.2	2.2–4.2	1.8–3.8	1.8–2.6	0.6–1.6	2–3.2	0.8–1.8	1–6
11	*C. szovitsii* Pojark.	*Azaroli*	2.6–4.8	2.4–4	2.8–5.2	2.6–4.5	1.8–3	0.8–2.2	2–2.4	0.8–2.4	1–8
12	*C. pontica* K. Koch	*Azaroli*	3.2–6.2	3.2–5.2	3.8–6.8	3.8–6.2	1.8–2.8	0.8–1.4	2.2–3.2	1.2–1.8	2–6

points are most widely located along the Shm-1/f horizon line, at a distance of 800 m (Fig. 1). Among them, the imprints and their counterparts of leaves of hawthorn (Sample 609/30 (Fig. 2A), 30-Shm/342 (Fig. 2F) and 30-Shm/342A (Fig. 2I) were found.

The Tolors-2 locality is situated to the south-west of Tolors village, on the opposite bank of the Tolors reservoir. Here, 452 samples were collected from different horizons (Fig. 1).

Among them, the imprint and counterpart of a thorn, Tlr-06/31 (Fig. 2N) and Tlr-06/31A (Fig. 2P), were found.

The fossil material was collected, processed, registered and prepared using accepted methods in palaeobotany (Meyen, 1968, 1970, 1987). Fossil taxa were identified using the comparative morphological method (Krumbigel and Walter, 1980). To depict both fossil and modern species, we used photographic and schematic drawings (Raup and Stanley, 1974) along with the scanning method. Plant images were mostly obtained with a scanner (HP Scanjet 4890).

For fossil specimens, original schematic drawings were made. The two fossil leaves and the thorn were identified using conventional methods (Tanai, 1978; Ellis et al., 2009).

The samples were examined using binocular microscopes MBS-2 and OLYMPUS-SZX16.

The age of the deposits was determined using radiometric dating (Joannin et al., 2010).

A comparative macro-morphological study of the thorns and leaves of modern hawthorns and fossil specimens was carried out. For this purpose, an OLYMPUS-SZX16 binocular microscope was used.

RESULTS

CRATAEGUS IN THE MODERN FLORA OF ARMENIA

In the modern flora of Armenia, species of the genus *Crataegus* are represented by three sections:

– Section 1. *Crataegus* – sect. *Oxyacanthae* Loud. 1838, Arbor Fruit. Brit. 2:829; Poyarkova 1939, Fl. USSR 9: 436. – sect. *Oxyacanthae* Zabel ex C.K. Schneider 1906, Ill. Handb. Laubholzk 1:768.

– Section 2. *Pentagynae* C.K. Schneid. 1906, Ill. Handb. Laubholzk 1: 768. – *Pentagynae* Zabel Poyarkov 1939, Fl. USSR 9:430; – *Melanocarpae* Zabel 1903, Beissn., Schelle and Zabel Handb. Laubholzk-Bennenn.: 178, nom. nud.

– Section 3. *Azaroli* Loud. 1838 Arbor. frutic. Brit. 2:826. – Sect. *Orientales* Zabel 1903 in Beissn., Schelle and Zabel, Hand. Laubholzk-Bennenn.: 179, nom. nude; Schneid. 1906, Ill. Handbuch der Laubholzk 1:781, in clavem.

The shape and size of leaves and thorns differ at the sectional level among representatives of these three sections of the genus *Crataegus*. The thorns, which are modified shortened shoots, are a continuation of the wood of the branch that carries them, therefore the thorn is torn off along with the wood. Like many European, Caucasian, and Mediterranean hawthorn species, Armenian hawthorns have two types of thorns: leafy and long, or leafless and short. The leafy thorns are 5–10 cm long, thick, and sometimes bear inflorescences that end in a short dot. The short thorns are thin, straight and up to 0.8–1.2 (2) cm in length.

Among the representatives of the section *Crataegus*, *C. armena* and *C. meyeri* have leafy and short thorns, while *C. microphylla*, *C. pallasii*, *C. stevenii*, *C. pseudoheterophylla* and *C. rhipidophylla* have only short thorns.

Representatives of the section *Pentagynae* do not have leafy thorns, they bear a few, sometimes even single, axillary thorns. Representatives of the section *Azaroli* have well-developed leafy thorns, that are thick and strong. They often bear inflorescences and fruits (*C. orientalis*), although in some species the thorns are rare (such as *C. pontica*). *C. szovitsii* and *C. tournefortii* have numerous short and thick thorns with lengths ranging from 0.8 to 1.5 cm.

The shape of the leaves retains the diagnostic value. In representatives of the section *Crataegus*, the leaves of the lower part of the shoot are oblong-oval or obovate, with a narrow cuneate base, while the leaves of the upper part are obovate, rhombic or oblong-rhombic with a broader wedge-shaped, rarely almost truncate base. Representatives of the section *Pentagynae* have leaves, that are broadly obovate to rhombic in outline. The base of the leaves is broadly wedge-shaped or truncate (*C. pentagyna*). The representatives of the section *Azaroli* have oblong-ovate or obovate leaves with a wedge-shaped base (*C. orientalis*, *C. szovitsii*, *C. pojarkoviae*). The base of the leaf of *C. pontica* can be wedge-shaped, as well as wide wedge-shaped. The leaf blade in different species is dissected into 1/2, 1/3, 2/3, and 3/4, sometimes extending to the main vein. The number of lobes of the leaf blade and the depth of the cut are constant features. In representatives of the section *Crataegus*, the leaf blade is 3-5-7-lobed. The lobes vary from narrow (*C.* × *armena*, *C. meyeri*, *C. pallasii*, *C. stevenii*) to wide (*C. atrosanguinea*, *C. caucasica*, *C. rhipidophylla*). In the species *C. stevenii* and *C. pallasii*, the blade is sometimes dissected almost to the main vein. The lobes are sharp, narrow and have uneven serrations along the edge, with a pointed apex. *C. stevenii* has 5-7-9-11 lobes, while *C. pallasii* has 3-5 (7) lobes.

C. rhipidophylla, *C. microphylla* and *C. pseudoheterophylla* have wide lobes. The leaf blade of those species is dissected into 1/3–2/3. In the representatives of the section *Pentagynae*, the lower leaves of sterile shoots are usually 3-lobed, and the upper ones are 5-7-lobed. The lobes are wide, blunt (*C. pentagyna*, *C. atrofusca*) or pointed at the top (*C. susanykleinae*). The upper leaves of sterile shoots are 3-5-7-lobed. On the flowering shoots, the lower leaves are usually 3-lobed, while the rest are 5-7-lobed, the lobes are blunt (*C. pentagyna*), sharp-toothed near the top. The members of the section *Azaroli* have 3-5-lobed lower leaves on their fertile shoots. The upper leaves are 3-5-7-lobed. The lower leaves of sterile shoots are 3-5-7-lobed, the upper leaves are 5-7-9-11-lobed. The leaf blade is dissected into 1/3, 3/4, or almost to the base of the main vein (*C. orientalis*, *C. pontica* and *C. pojarkoviae*). The lobes of the leaves can be narrow (*C. orientalis*, *C. pojarkoviae*) or wider (*C. pontica*, *C. szovitsii*). In some cases, the lobes are entire, with only 2–3 large teeth at the tip (*C. pojarkoviae*, *C. pontica*). Alternatively, they may be unevenly serrated from the middle of the lobes to the tip (*C. orientalis*, *C. szovitsii*).

The leaves in all three South Caucasian sections have entire, finely serrated, coarsely serrated, serrated or doubly serrated edges. In some species, the teeth start from the base of the leaf blade to the top (*C. rhipidophylla*, *C. caucasica*), while in others, they start from the middle of the leaf blade to the top (*C. zangezura*, *C. meyeri*, *C. pentagyna* and *C. tournefortii*). There are also species with entire lobes and with only 1–3 large teeth at the top (*C. atrosanguinea*, *C. pseudoheterophylla* and *C. pontica*).

SYSTEMATIC PALAEOBOTANY

Specimen 1

Samples studied. 30/609

Locality. Shamb-1.

Description. The collection contains one imprint of a hawthorn leaf fragment. The leaf is simple, the lamina is rounded, the lower half of the leaf is preserved 1.6 cm long and 2.0 cm wide, the base is rounded, the main vein is thick, two lateral main veins depart from the base of the leaf lamina at an angle of 31–40°, ending, most likely, in the lower large lobes of the lamina; leaf margin coarsely bluntly serrated; the right lobe is most likely broken off and moved down closer to the petiole. The petiole is short, thick, 5 mm long (Fig. 2A–C).

Comparison. According to morphological characteristics, the leaf imprint corresponds to the leaves of modern species *Crataegus caucasica* K. Koch (Fig. 2D, E, M, L).

Specimen 2

Samples studied. 30-Shm/342, 30-Shm/342A.

Locality. Shamb-1.

Description. The collection contains an impression and counterpart of a hawthorn leaf. The leaf is simple, the lamina is ovate; on sample 30-Shm/342 a fragment of the lower lobe, 1.6 cm long and 0.7 cm wide, is preserved. The fragment is well preserved, the shape of the leaf lamina is elongated-ovate, the apex is pointed and oblique, the edge is sharply curved, serrated, the teeth are blunt or sharp, often hooked towards the lamina. The venation is pinnately marginal-loop-shaped, the main vein of the blade is passing, thick, two secondary alternate veins are well defined, rising above half the length of the plate, extending from the main vein at an acute angle. Veins of the following orders are also clearly visible, the last of which form large, polygonal cells (Fig. 2F–H). Imprint on specimen 30-Shm/342A, poorly preserved, 2.8 cm long, 1.2 cm wide; however, almost half of the leaf blade is preserved, with an incomplete apex and three lobes extending from the presumed midrib at angles of 65°, 43° and 35°. The petiole has not been preserved (Fig. 2I–K).

Comparison. The leaf imprint corresponds in morphological characteristics to the leaves of modern species *Crataegus caucasica* K. Koch (Fig. 2D, E, M, L).

Specimen 3

Samples studied. Tlr-06/31, Tlr-06/31A.

Locality. Tolors-2.

Description. The collection contains an impression fossil and its counterpart of a twig

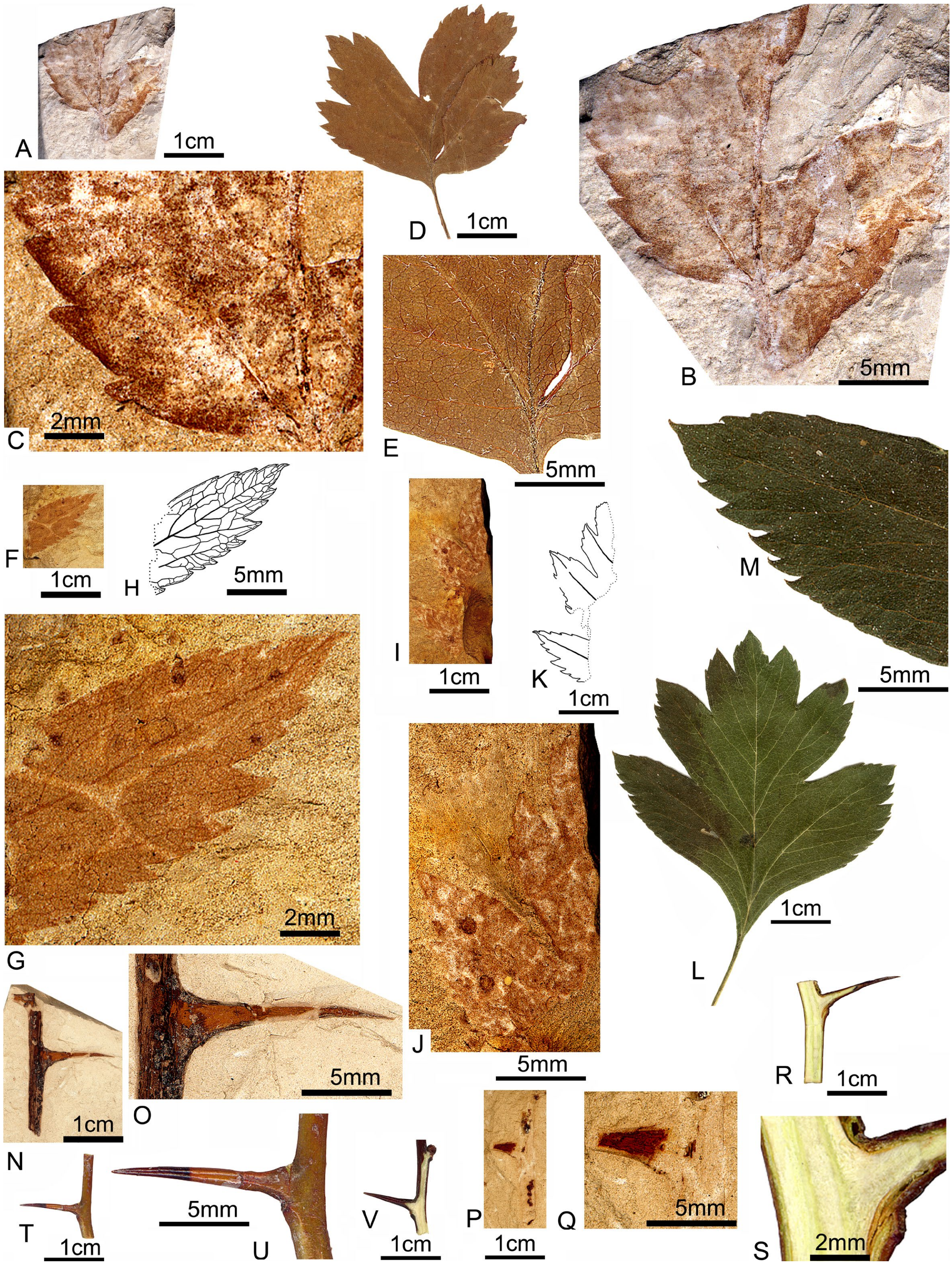

Figure 2. Fossil and modern leaves and thorns of the *Crataegus* from Armenia. **A**. *Crataegus* sp.; imprint of leaf, locality Shamb-1, layer Shm1/f, specimen 30/609; ERE, palaeobotany; **B**. Same specimen, leaf; × 3; **C**. Same specimen, fragment of leaf lamina; × 5; **D**. *Crataegus caucasica* K. Koch.; modern plant, leaf, Armenia, Vayots Dzor province; ERE, palaeobotany; **E**. Same specimen, fragment of leaf lamina; × 3; **F**. *Crataegus* sp.; imprint of leaf fragment, locality Shamb-1, layer Shm-1/e, specimen 30-Shm/342; ERE, palaeobotany; **G**. Same specimen, fragment of leaf lamina; × 5; **H**. Same specimen, schematic picture of leaf lamina fragment; × 2; **I**. *Crataegus* sp.; imprint of leaf fragments, locality Shamb-1, layer Shm-1/e, specimen 30-Shm/342A; ERE, palaeobotany; **J**. Same specimen, a fragment of leaf lamina; × 3; **K**. Same specimen, schematic picture of leaf lamina fragment; × 2; **L**. *Crataegus caucasica* K. Koch.; modern plant, leaf, Armenia, Kotayk province; ERE, 202325; **M**. Same specimen, a fragment of leaf lamina; × 3; **N**. *Crataegus* sp.; imprint of thorn with branch, locality Tolors-2, layer Tlr-2/b-1, specimen Tlr06/31; ERE, palaeobotany; **O**. Same specimen; × 3; **P**. *Crataegus* sp.; imprint of thorn fragment with branch, locality Tolors-2, layer Tlr-2/b-1, specimen Tlr-06/31A; ERE, palaeobotany; **Q**. Same specimen; × 3; **R**. *Crataegus rhipidophylla* Gand.; anatomical incision of thorn with branch, Armenia, Tavush province; ERE, 198963; **S**. Part of same specimen; × 5; **T**. *C. monogyna* Jacq.; fragment of thorn with branch, Armenia, Yerevan botanical garden; **U**. Same specimen; × 3; **V**. *C. monogyna* Jacq.; anatomical incision of thorn with branch, Armenia, Yerevan botanical garden

with two hawthorn thorns. Fragment of a branch on specimen Tlr-06/31, 2.4 cm long, 2.8 mm wide. One complete thorn, 12.4 mm long, has been preserved on the branch and the widened part of the base is 5 mm wide, as well as one incomplete thorn imprint 3.5 mm long, and the widened part of the base is 3.8 mm wide (Fig. 2N, O).

On the counterpart, specimen Tlr-06/31A, the preservation of the morphology is less complete. A fragment of a branch, 5 mm long, 5 mm wide, and 3.5 mm long, 3.8 mm wide has been preserved (Fig. 2P, Q). On the branch there are two incomplete imprints of thorns, as well as one incomplete imprint of a thorn, 3.5 mm long and, at the expanded part of the base, 3.8 mm wide. The thorns are widened at the base, extending from the branch almost at a right angle, slightly arched in the middle part, with a pointed apex (specimen Tlr-06/31). At the base of the thorn (sample Tlr-06/31) there is a widened part, most likely a place of attachment to the tree trunk.

Comparison. The imprint of the thorn, according to its morphological characteristics, corresponds to the thorns of modern species *Crataegus rhipidophylla* Gand. (Fig. 2R, S) and *Crataegus monogyna* Jacq. (Fig. 2T–V).

DISCUSSION

A detailed examination of the fossil thorn (Tlr-06/31, Tlr-06/31A) reveals a layer of bark, confirming its woody origin. The combination of morphological characters, thorns up to ~4 cm long, stout or fine leaf blades (30/609, 30-Shm/342, 30-Shm/342A) more or less deeply lobed, lobes serrate or crenate, intercalary veins running to sinuses present. Subterminal leaf laminas of flowering shoots with 1-3(-4) pairs of lobes. Macromorphological study of fossil and modern hawthorns showed that the plants found belong to the section *Crataegus*.

According to morphological characteristics, the specimen 1 and the specimen 2 imprints correspond to the leaves of modern species *Crataegus caucasica* K. Koch. The imprint of the thorn according to its morphological characteristics corresponds to the thorns of modern species *Crataegus rhipidophylla* Gand. and *Crataegus monogyna* Jacq.

In Armenia, species of section *Crataegus* are flowering in May, and fruiting in July to October. They occur in the lower and middle mountain belts, at an altitude of 800–1800 m a.s.l. and grow alone or in groups in arid woodlands, on dry stony slopes of gorges of mountain rivers and in thickets of bushes at the lower edge of the forest.

Representatives of the section *Crataegus* are found in Armenia in all floristic regions, except Upper Akhuryan which is in Northwest Armenia. Members of the section *Crataegus* are distributed in northern Africa, Europe and western Asia.

The present study suggests that representatives of the section *Crataegus* have been widespread in Armenia since the Early Pleistocene.

CONCLUSION

This study provides valuable insights into the fossil record of the genus Crataegus from the Early Pleistocene in south-eastern Armenia, specifically from the Shamb-1 and Tolors-2 localities within the Sisian diatomaceous formation. Through comparative macromorphological analyses of fossil leaves and thorns with their modern counterparts, we have identified the fossil specimens as belonging to the section *Crataegus*. The leaf and thorn imprints exhibit significant morphological similarities to leaf and thorns of contemporary species, such as *Crataegus caucasica*, *C. rhipidophylla*, and *C. monogyna*.

These findings contribute to the understanding of the historical distribution and evolution of *Crataegus* in the South Caucasus. They confirm that the genus, with its complex characteristics of hybridization, apomixis and polyploidy, has a long-standing presence in the region, tracing back to the Early Pleistocene. The identification of these fossil taxa aligns to suggest that the sectional classification of *Crataegus* has been relatively stable through geological time.

By correlating the fossil evidence with contemporary species, this research not only enriches the palaeobotanical record of Armenia but also provides a framework for future investigations into the evolutionary history of *Crataegus* and other Rosaceae species in the region.

ACKNOWLEDGMENTS

Thanks are due to both reviewers whose comments have improved this manuscript and we are thankful to the curators of the following herbaria: ERE and ERCB.

ADDITIONAL INFORMATION

CONFLICT OF INTEREST. The authors declare that they have no conflict of interest.

ETHICAL STATEMENT. No ethical statement was reported.

FUNDING.The work was carried out with basic funding from the A. Takhtajian Institute of Botany of the NAS RA.

SAMPLING AND FIELD STUDIES. All necessary permits for field studies and sampling have been obtained by the authors from the competent authorities.

DATA AVAILABILITY STATEMENT. All data generated or analyzed during this study are included in this published article.

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