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QUANTITATIVE ANATOMICAL CHARACTERISTICS OF SOME SPECIES OF THE GENUS CRATAEGUS L. (ROSACEAE) OF THE ARMENIAN FLORA

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Abstract

A study of the quantitative anatomical features of the leaf blades' epidermis belonging to six species of the genus *Crataegus* in the flora of Armenia was conducted. The species treated belong to the subsect. *Pentagynae* Series *Pentagynae* (*Crataegus pentagyna* Waldst. et Kit., *C.* × *zangezura* Pojark.) and subsect. *Crataegus* Series *Ambiguae* (*Crataegus meyeri* Pojark., *C. rhipidophylla* Gand., *C. pseudoheterophylla* Pojark., *C.* × *armena* Pojark.). Microscopic samples of leaf blade fragments were prepared according to the Russian State Pharmacopeia XV. The leaf surface samples were observed with the light microscope. For comparative quantitative studies of stomatal apparatus parameters, the site in the middle third of the leaf blade between its margin and the central vein was taken. The quantity and size of CaC_2O_4 idioblasts, simple unicellular hairs, the stalk, and head of the gland were determined. Statistical analysis performed in the IBM SPSS Statistics program. We used Student's criterion for calculations with the critical significance level taken as 0.05. We examined pairwise statistical relationships between the studied quantitative characteristics using the Pearson correlation coefficient. The stomata of both hybrids were significantly smaller in terms of length, width, and area than those of their parental forms. The gland heads in hybrids were significantly smaller in terms of length, width, and area than those of their parental forms. The average sizes of druzes and crystals CaC_2O_4 are almost identical across the species studied. Simple unicellular pointed sinuous thick-walled hairs found only in the epidermis of *Crataegus meyeri*, *C. rhipidophylla,* and *C.* × *armena*. *Crataegus* × *armena* had significantly more of these hairs, and they were significantly longer than those of the parental forms.

Keywords: Armenian flora; Anatomy; *Crataegus*; idioblasts; leaf anatomy; trichomes; stomatal apparatus

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چکیده: صفات کمی آناتومیکی غشای پهنک برگ شش گونه از جنس زالزالک از فلور ارمنستان مطالعه شد. گونه‌های مورد مطالعه به زیر بخش (*Crataegus pentagyna* Waldst. et Kit., *C.* × *zangezura* Pojark.) Series *Pentagynae*، *pentagyna* و زیربخش *Crataegus* Series *Ambiguae* (*Crataegus meyeri* Pojark., *C. rhipidophylla* Gand., *C. pseudoheterophylla* Pojark., *C.* × *armena* Pojark.). تعلق دارند. نمونه‌های میکروسکوپی قطعات پهنک برگ براساس دستورالعمل فارماکوپه شماره ۱۵ کشور روسیه تهیه شد. نمونه‌های سطح برگ به کمک میکروسکوپ نوری مطالعه شدند. برای مطالعات مقایسه‌ای صفات کمی روزنه‌ها، بخش یک سوم میانی پهنک برگ در فاصله بین رگبرگ میانی و حاشیه برگ مورد استفاده قرار گرفت. تعداد و اندازه ایدیوبلاست‌های CaC2O4، کرک‌های ساده تک سلولی و غدد ترشحی پایک دار شناسایی شدند. آنالیز آماری در برنامه IBM- SPSS انجام شد. ما از معیار آموزشی برای محاسبات استفاده کردیم و سطح اهمیت بحرانی را ۰/۰۵ در نظر گرفتیم. روابط آماری دوجانبه بین ویژگی‌های کمی مورد مطالعه را با استفاده از ضریب همبستگی پیرسون بررسی کردیم. روزنه‌های هر دو هیبرید از نظر طول، عرض و سطح به‌طور قابل توجهی کوچکتر از والدین خود بودند. سرغده‌های موجود در هیبریدها از نظر طول، عرض و سطح به‌طور معنی‌داری کوچکتر از سرغده‌های والدین آن‌ها بودند. میانگین اندازه دروزها و بلورهای اگزالات کلسیم (CaC_2O_4) در میان گونه‌های مورد مطالعه تقریباً یکسان است. کرک‌های ساده، تک‌سلولی، نوک‌تیز، مارپیچ و دیواره ضخیم تنها در اپیدرم *Crataegus meyeri*، *C. rhipidophylla* و *C.* × *armena* مشاهده شدند. در *Crataegus* × *armena* تعداد این کرک‌ها به‌طور معنی‌داری بیشتر بود و طول آن‌ها نیز به‌طور معنی‌داری از والدین بیشتر بود.

INTRODUCTION

The genus *Crataegus* comprises approximately 240 species, of which approximately 170 are in the New World and 70 in the Old World (Pojarkova, 1939; Christensen, 1992; Gu & Spongberg, 2003; Dönmez, 2019; Phipps, 2016). Since the 20th century, botanical studies of the South Transcaucasus have been carried out, as well as the collection of rich herbarium material by prominent botanists in Armenia and adjacent territories (Grossheim, 1934; Poyarkova, 1939; Prilipko, 1954; Fedorov, 1958). The region's hawthorns were studied before (Riedl, 1969; Khatamsaz, 1992; Christensen 1992; Dönmez 2004; 2007; Hamzeh’ee & al. 2014; Dönmez & Sevgin Özderin, 2019; Khadivi & al. 2019).

The genus *Crataegus* in Armenia (Fedorov, 1958) is represented by 11 species from three sections: section *Pentagynae* Zabel (*C. pentagyna)*, section *Azaroli* Loud. (*C. orientalis* Pall., *C. szovitsii* Pojark. (possible occurrence on the territory of Armenia), *C. schraderiana* Ledeb.), Section *Oxyacanthae* Zabel. (*C. meyeri*, *C. caucasica* K.Koch, *C. atrosanguinea* Pojark., *C. kyrtostyla* Fingerh, *C.* × *armena*, *C.* × *zangezura, C. pseudoheterophylla*).

In the latest system of flowering plants, Takhtajan (2009) attributed the genus *Crataegus* L. to the subfamily Pyroideae (Maloideae), in the tribe *Crataegeae*, which also includes the genera *Cotoneaster*, *Malacomeles*, *Chamaemeles*, *Pyracantha*, *Mespilus*, *Hesperomeles*, and *Osteomeles*.

Phylogenetic studies, based on DNA sequences from both chloroplast and nuclear markers by Campbell & al. (2007), Lo & al. (2007), Potter & al. (2007), and Li & al. (2012), Lo & Donoghue (2012), Sun & al. (2018) clarified the intergeneric relationships amongst the genera of the tribe Maleae Ufimov & Dickinson, and allocated the genus *Crataegus* L. to subgenus *Crataegus* (Ufimov & Dickinson, 2020).

Phenetic and cladistic approaches allowed taxonomists to establish classifications of the genus at the levels of sections and series, but without revealing clear phylogenetic relationships between these infrageneric groups.

The genus *Crataegus* is represented by 23 species in Armenia and grows in all 12 floristic regions of Armenia (Sargsyan, 2016; Sargsyan, 2022). Hawthorns grow in the low, middle, and high mountain zones in Armenia. They play a significant role in the formation of dendroflora and are an essential component of various forest ecosystems, forming sub-forests alongside other woody species. They thrive in arid, sparse forests, scrublands, and along the coastlines of mountain rivers.

Recent studies suggest that many polyploids originate from hybridization between species belonging to different infrageneric groups. Despite the heterogeneity of individual gene trees, these results support earlier evidence for the importance of hybridization in the *Crataegus* evolution (Liston & al., 2021).

Hawthorn's fruits and flowers are a medicinal raw material used in many drugs.

Research into the anatomical features of plant organs in the *Crataegus* remains limited. In some cases, quantitative data were not provided. The anatomical diagnostic characteristics of the leaf blade (LB) of *C. sanguinea* were investigated by Trofimova (Trofimova, 2014).

Additionally, Rezanova & Baksutov (2009) conducted the morphological and anatomical analysis of leaves from 20 *Crataegus* L. species native to the Belgorod region during the phenological phase of early fruiting. *Crataegus orientalis* subsp. *orientalis* and *C. orientalis* subsp. *szovitsii* (Pojark.) K.I.Chr. from Turkey were investigated about leaf anatomy. For this purpose, transverse sections and superficial sections were taken from samples (Erarslan & Kultur, 2019). Morphological and anatomical study of leaves, shoots, and flowers of *C. flabellata* (Bosc ex Spach) Rydb. and *C. submollis* Sarg. were investigated (Andreeva &al., 2024; Volkova et al., 2023).

The comparative study of several quantitative diagnostic features of the leaf blade (LB) of hawthorn plants from the sect. *Sanguineae* and the sect. *Crataegus*, growing in diverse regions of the Russian Federation, was studied (Sagaradze & al., 2021). The qualitative and quantitative anatomical characteristics of 10 *Crataegus* species from Iran were studied and analyzed (Hamzeh'ee & al., 2025).

Our research aimed to study some quantitative anatomical characteristics of LB (stomatal apparatus, trichomes in leaf epidermis, and idioblasts in mesophyll) of some *Crataegus* species, from the flora of Armenia and evaluate their potential diagnostic significance.

MATERIAL AND METHODS

Type specimens and all herbarium material were from the Caucasus, Turkey, Iran, and neighboring countries (ERE, ERCB, LE, WIR, WHA, MW, TBI, TGM). Field observations in nature and collections from Armenia were carried out from 2020 to 2024 via route and stationary methods.

The leaves were collected from the middle part of the crowns of three model trees. The comparative morphological and anatomical methods were implemented.

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

The six species of hawthorn are presented according to the Ufimov system (2013a; b), two of them were hybridogenic species – *C.* × *zangezura* Pojark. (*Crataegus pentagyna* × *Crataegus pseudoheterophylla*) and *C.* × *armena* Pojark. (*Crataegus meyeri* × *Crataegus rhipidophylla*).

Crataegus* L.** Subgen. 1. *Crataegus* **Sect. 1. *Crataegus. The studied species are presented below:

Subsect. 1. *Pentagvnae* (C. K. Schneid.) Ufimov

Ser. 1. *Pentagynae* (C. K. Schneid.) Russanov

1. *C. pentagyna* Waldst. et Kit. ex Willd.
2. *C.* × *zangezura* Pojark.

Subsect. *Crataegus*

Ser. *Ambiguae* Pojark.

3. *C. meyeri* Pojark.
4. *C. rhipidophylla* Gand.
5. *C. pseudoheterophylla* Pojark.
6. *C* × *armena* Pojark.

1. *Crataegus pentagyna* Waldst. et Kit. ex Willd. 1800, Sp. Pl. 2, 2: 1006.

Tree or shrub, 3 – 8 (12) m. Fl. V – VI, Fr. VIII – IX. At an altitude of 800 – 1200 m above sea level.

Habitat: Forest edges, in thickets of shrubs. Distribution: Armenia (All regions except Dar.). General distribution: Caucasus (all), Crimea, C & E Europe, Anatolia, N Iran.

2. *C.* × *zangezura* Pojark. 1939, Flora of the USSR 9 Addenda 8: 508.

Shrub up to ca. 1.5 – 2 m. Fl. VI, Fr. IX – X. At an altitude of 1200 – 1800 m above sea level.

Habitat: Open forests, in shibliak, rocky slopes. Distribution: Armenia (Zang.) General distribution: Caucasus (S Transcaucasia, Nakhichevan).

3. *C. meyeri* Pojark. Flora of the USSR 9, Addenda 8: 500.

Tree or shrub up to ca. 1.5 – 3 (5) m. Fl. V, Fr. IX – X. At an altitude of 800 – 1200m above sea level.

Habitat: In thickets and rocky slopes. Distribution: Armenia (Lori., Arag., Ijev., Gegh., Sevan, Yerev., Dar., Zang., Meghri). General distribution: Caucasus (C, E, S Transcaucasia, Nakhichevan, Talish), Anatolia, Iran.

4. *C. rhipidophylla* Gand. 1871, Bull. Soc. Bot. France 18: 447.

Small tree or shrub up to 2 – 8 m. Fl. V – VI, Fr. IX. At an altitude of 1200 – 2000 m above sea level.

Habitat: Arid open forest. Distribution: Armenia (all regions except Up. Akhur.) General distribution: Caucasus (all), C & E Europe, Crimea, Anatolia, Iran.

5. *C. pseudoheterophylla* Pojark. Flora of the USSR 9, Addenda 8: 506.

Small tree or shrub up to 3 – 6 m. Fl. V – VI, Fr. IX. At an altitude of 1200 – 2000 m above sea level.

Habitat: On stony slopes of mountains in thickets of bushes. Distribution: Armenia (Lori., Ijev., Gegh., Yerev., Dar., Zang., Meghri.) General distribution: Caucasus (E Ciscaucasia, C Caucasia, W, C, E, S Transcaucasia Nakhichevan), Anatolia, N. Iran, Afghanistan.

6**. *Crataegus* × *armena*** Pojark. 1939, Flora USSR, 9, Addenda 8: 509 (*Crataegus meyeri* × *Crataegus rhipidophylla*); 2n (3x) =51.

Shrub up to ca. 2 – 2.5 m. Fl. VI, Fr. IX – X. At an altitude of 1300 – 2500 m above sea level.
Habitat: Arid and open forest, shibliak, in thickets. Distribution: Armenia (Yerev., Gegh., Dar., Zang., Meghri.) General distribution: Caucasus (S Transcaucasia, Nakhichevan), N Iran.

The leaves of *Crataegus rhipidophylla*, *Crataegus meyeri*, *Crataegus* × *armena* (*Crataegus meyeri* × *Crataegus rhipidophylla*), *Crataegus pentagyna*, *Crataegus pseudoheterophylla*, and *Crataegus* × *zangezura* (*Crataegus pentagyna* × *Crataegus pseudoheterophylla*) have been studied (Table 1).

Table 1. The list of *Crataegus* species examined in the comparative analysis in the Herbarium Takhtajan Institute of Botany of the NAS RA (ERE).

Species	Collection data
Crataegus meyeri Pojark.	Armenia. Marz Vayots Dzor. Between the villages of Yeghegis and Hermon. Xerofile sparse forest. 39º 52' 26, 2" N, 45º 24' 56. 1" E, 1670 m. ERE 202326
Crataegus rhipidophylla Gand.	Armenia, Yerevan, gorge of the river Hrazdan, by the river, in the riverbed forest. 40º 12' 49. 1" N, 44º 29' 49. 4" E, 1030 m. ERE 170558
Crataegus pseudoheterophylla Pojark.	Armenia. Marz Kotayk. Near the village of Arzakan. Sparse forest. 40º 29' 35.8" N, 44º 35' 39.07" E, 1680 m. ERE 202792
Crataegus × *armena* Pojark.	Armenia. Marz Kotayk. Near the village of Arzakan, at the fork to “Park Resort Aghveran”. Xerophytic vegetation 40º 28' 49,1" N, 44º 35' 49. 4" E, 1604 m. ERE 202323
Crataegus × zangezura Pojark.	Armenia, Marz Syuniq, Shikahogh protected area, broadleaf forest. 39º 05', 10, 34" N, 46º 29' 13. 06" ´E, 1085 m. ERE 169656
Crataegus pentagyna Waldst. et Kit.	Armenia. Marz Tavush. Between the villages of Kirants and Acharkut. To the right of the road, a sparse forest. 41º 02' 24. 7" N, 45º 05' 26" E, 756 m. ERE 202316

Microscopic samples of the leaf surface were studied. It is known that different areas of the leaf blade (LB) differ in the quantity of stomata per unit area.

Fragments with the average number of stomata within the LB are located in the middle third of the LB between its margin and the central vein. Therefore, this site was used for comparative quantitative studies of stomata parameters (Miroslavov, 1974). Microscopic samples of LB fragments were prepared according to the General Pharmacopoeial Monograph 1.5.3.0003.15 RSPh XV “Technique of microscopic and microchemical studies of medicinal plant materials and herbal medicines” (https://pharmacopoeia.regmed.ru/pharmacopoeia/izdanie-15/?PAGEN_1=2).

Leaf surface samples were observed with the Altami Bio 2 LED microscope (10x, 20x, and 40x lenses). The length of the stomata was considered as the linear size — the distance between two most distant points (the cell wall of the peristomatic epidermal cells), measured horizontally. By the width of stomata, we mean the distance across the cell walls of the periosteum cells of the epidermis, measured horizontally. The linear dimension, the distance between the two most distant points measured vertically, took the length of the pedicel and head of the gland. The width of the pedicel and head of the gland was taken as the distance between the two most distant points measured horizontally.

Stomata represent a figure close to an elongated ellipse. The ratio of radii by visual analysis was from 4 to 5. The area of the stomata can be represented by the product of their length and width in proportion. We used the conventional specific quantification of stomata area by their number per 1 mm² of LB surface.

The cover glass of the micro specimens was 24x24 mm. Repetition was 50-fold. 10 slides, 5 times each were measured. Statistical analysis performed in the IBM SPSS Statistica program. The Shapiro-Wilk criterion is used to test the normality of the distribution of parameters. It concluded that the distribution of parameters corresponds to a parametric distribution. We use Student's criterion for calculations with the critical significance level taken as 0.05. We examined pairwise statistical relationships between the studied quantitative characteristics using the Pearson correlation coefficient [https://nafi.ru/academy/].

RESULTS AND DISCUSSION

The leaves of the studied species of hawthorn were hypostomatic. The stomatal apparatus was anomocytic type. The stomata are elongated, rarely rounded, and surrounded by 5-7 peristomatic cells.

The striations of the cuticle were folded around the stomata (Fig. 1a) (Trofimova, 2014; Rezanova & Baksutov, 2009). Cuticular folding was observed on the adaxial side in the epidermis of the studied species (Fig. 1b). This is consistent with data from other authors. It has been shown that this element is present in the LB epidermis of many plants in the Pyrinae subtribe (Rosaceae). Based on electron microscopy, there is an opinion that the structural features of the micro-relief in the epidermis of Pyrinae leaves have a high level of stability within the species. This makes it possible to use them as diagnostic features in plant taxonomy (Hamzeh'ee & al., 2016; Babosha & al., 2023).

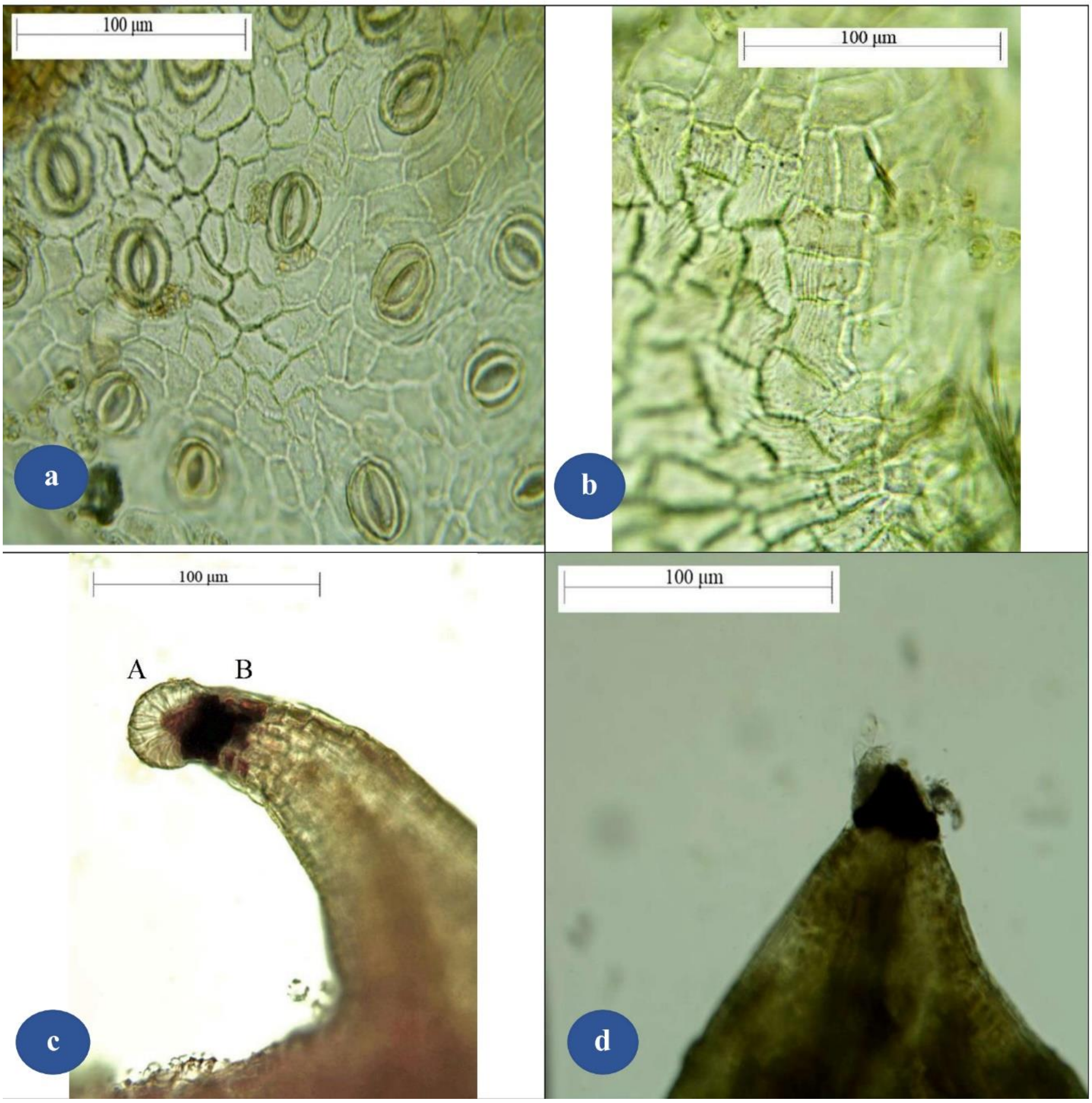

Fig. 1. a, Fragment of *Crataegus pseudoheterophylla* LB, stomatal apparatus; b, fragment of *Crataegus armena* LB, adaxial side of the epidermis, cuticular folding; c, fragment of *Crataegus* × *zangezura* LB, the gland on the prong: A, the head of the gland; B, the pedicel of the gland; d, fragment of *Crataegus rhipidophylla* LB, the gland on the prong: the ruptured head of the gland.

The average length of the stomata and the amplitude of the values were the same (Table 2) in the parental forms *C. pentagyna* and *C. pseudoheterophylla*. Stomatal length averaged 42.0 µm, and the amplitude was 10 µm. The average length of the stomata in the *C. × zangezura* hybrid was significantly shorter (by 33.3%). The amplitude of the values for the hybrid was 20.0 µm. The average width of the stomata in *C. pentagyna* and *C. pseudoheterophylla* was the same. It was 34.38 µm. The average width of the stomata in the *C. × zangezura* hybrid was significantly smaller (by 34.8%). The amplitude of stomatal width in the parent forms and the hybrid was 15 µm. Thus, the stomata of the *C. × zangezura* hybrid were significantly smaller than those of the parental forms. The ratio of length to width was: in *C. pentagyna* 1.13–1.40; in *C. pseudoheterophylla* 1.0–1.17. In the hybrid *C. × zangezura*, this ratio was 1.25–1.26.

The ratio of length to width of the stomata among parental forms differed by 0.17–0.27 according to the minimum and ma×imum data. The hybrid had practically no differences. The minimum quantity of stomata in the parent forms and the hybrid was the same. The amplitude between the minimum and maximum values of the quantity of stomata in *C. pentagyna* and *C. × zangezura* was the same. It amounted to 48.23 pcs/mm^2. The largest amplitude between the minimum and maximum quantities of stomata was observed in *C. pseudoheterophylla*. It amounted to 89.57 pcs/mm^2. The highest average quantity of stomata was also observed in *C. pseudoheterophylla*. In *C. pentagyna* and *C. × zangezura*, the average quantity of stomata was the same. The average value of the largest stomatal area per 1 mm² was found in *C. pseudoheterophylla* and amounted to 103455.98±60.09 µm². The average value of the smallest stomatal area per 1 mm^2 was found for the hybrid *C. × zangezura*, which amounted to 39568.10±38.64 µm^2. As in the previous case, the length of the stomata and the amplitude of these values were practically identical in *C. meyeri* and *C. rhipidophylla* (Table 2). The length of the stomata in their hybrid *C. × armena* was 11.68% shorter. The hybrid's stomatal length values had an amplitude that was 10.0 µm larger than that of the parent forms. The stomatal width of *C. meyeri* and *C. rhipidophylla* was similar. The width of the stomata in the *C. × armena* hybrid was 15.86% smaller. The amplitudes of the width values and the quantity of stomata per 1 mm² were the same for all three species. The stomata quantity's amplitude was the highest in the *C. × armena* hybrid. It was 89.57 pcs/mm^2. The values in the parent forms were 62.01 pcs/mm² and 55.12 pcs/mm² for *C. meyeri* and *C. rhipidophylla*, respectively.

The average stomatal area per 1 mm^2 was similar in the parent forms. The measurements were 88,477.54 ± 5.94 µm² and 87,958.31 ± 5.72 µm² for *C. meyeri* and *C. rhipidophylla*, respectively. The average stomatal area in *C. × armena* was significantly smaller, it was 66288.18 ± 5.80 µm^2. Glands were located on the LB teeth of the studied species. *C. pentagyna*, *C. × zangezura*, *C. rhipidophylla* and *C. × armena* had a pedicel and head of the gland (Fig. 1c). *Crataegus rhipidophylla* had glands with a torn head (Fig. 1d). The gland's head was absent in *C. pseudoheterophylla* and *C. meyeri*. The length of the glandular pedicel on the tooth in *C. pentagyna* and *C. pseudoheterophylla* was the same. The amplitude of values was larger in *C. pentagyna*. The minimum and ma×imum values differed by a factor of five, whereas in C. *pseudoheterophylla*, they differed by a factor of three. The length of the glandular pedicel on the tooth of the hybrid *C. × zangezura* was on average 1.96 times larger than that of the parental forms. The width of the glandular pedicel in *C. pentagyna* and *C. pseudoheterophylla* was the same.

The width of the glandular pedicel on the tooth of the *C. × zangezura* hybrid was, on average, 1.46 times larger than that of the parental forms. The average length of the gland head on the tooth of *C. × zangezura* was 1.24 times larger than that of *C. pentagyna*. The length of the head for this species had an amplitude of 65.0 µm, while that of *C. pentagyna* was only 20.0 µm. The average width of the head for *C. pentagyna* was 2.28 times larger than that of *C. × zangezura.* The minimum and maximum widths of the gland's head of *C. pentagyna* were 3.6 and 2.1 times larger, respectively, than those of *C. × zangezura*. Thus, the gland's head of *C. × zangezura* had an elongated shape. The pedicel length of the *C. × armena* hybrid was significantly longer than that of the parental forms. On average, it was 1.35 times longer. The width of the leg was the same for both parent forms and the hybrid. The largest range of values was observed in the width of gland *C. × armena's* pedicel. It was 160.0 µm. The amplitude was 60.0-65.0 µm in the parental forms. The gland head in *C. rhipidophylla* was 28.92% smaller than in *C. × armena*. The width of the gland head was the same in both species.

A common characteristic of all species was the direct proportionality between the length and width of the gland pedicel (Fig. 2). The pedicle had an elongated shape in cross-section. The median ratio of the mean values for each species from the smallest to the largest was 0.57. The value ranged from 0.54 to 0.70. Hybrids had a more elongated stem cross-section than their parent species (0.70 in *C. × zangezura* and 0.68 in *C. × armena*.

Table 2. Morphometric parameters of stomatal apparatus and leaf teeth glands on the leaf blade of *Crataegus pseudoheterophylla*, *C. pentagyna*, *C.* × *zangezura, C.* meyeri, *C. rhipidophylla*, and *C.* × *armena*.

Morphometric parameters of the stomatal apparatus on the hawthorn leaf blade

Species	***Crataegus pseudoheterophylla***			***Crataegus pentagyna***			***Crataegus × zangezura***		
	Length μm	Width μm	Quantity pcs/mm^2	Length μm	Width μm	Quantity pcs/mm^2	Length μm	Width μm	Quantity pcs/mm^2
min	35.00	30.00	34.45	35.00	25.00	34.45	25.00	20.00	34.45
max	45.00	45.00	124.02	45.00	40.00	82.68	45.00	35.00	82.68
average	41.75±0.75	34.25±1.16	72.35±5.25	42,25±0,77	34.50±1.08	54.78±3.37	31.50±1.03	25.50±0.95	49.26±2.80

Morphometric parameters of hawthorn leaf teeth glands

Species	***Crataegus pseudoheterophylla***				***Crataegus pentagyna***				***Crataegus × zangezura***			
	Stalk		Head		Stalk		Head		Stalk		Head	
	Length μm	Width μm	Length μm	Width μm	Length μm	Width μm	Length μm	Width μm	Length μm	Width μm	Length μm	Width μm
min	25.00	60.00			25.00	50.00	40.00	90.00	45.00	95.00	25.00	25.00
max	75.00	90.00			125.00	110.00	60.00	125.20	100.00	115.00	90.00	60.00
average	35.25±2.42	70.25±2.13			37.25±4.76	69.00±3.41	50.00±1.31	99.75±1.72	71.00±4.38	102.00±1.47	62.00±5.03	43.75±2.88

Morphometric parameters of the stomatal apparatus on the hawthorn leaf blade

Species	***Crataegus meyeri***			***Crataegus rhipidophylla***			***Crataegus × armena***		
	Length μm	Width μm	Quantity pcs/mm^2	Length μm	Width μm	Quantity pcs/mm^2	Length μm	Width μm	Quantity pcs/mm^2
min	35.00	30.00	41.34	35.00	30.00	41.34	25.00	25.00	34.45
max	45.00	40.00	103.35	45.00	40.00	96.46	45.00	35.00	124.02
average	39.75±0.85	35.50±0.72	62.70±3.57	39.50±0.62	34.38±0.63	64.77±3.14	35.00±1.09	29.4±0.88	64.42±^{3}.42

Morphometric parameters of simple unicellular hairs trichomes on the hawthorn leaf blade

	Crataegus meyeri			***Crataegus rhipidophylla***			***Crataegus × armena***		
	Length μm	Width at the attachment point μm	Quantity pcs/mm^2	Length μm	Width at the attachment point μm	Quantity pcs/mm^2	Length μm	Width at the attachment point μm	Quantity pcs/mm^2
	150.00	20.00	6.89	225.00	20.00	13.68	100.00	30.00	34.45
	300.00	30.00	13.78	600.00	40.00	68.90	900.00	45.00	103.35
	215.00±13.62	23.00±0.99	7.23±0.34	382.50±27.99	31.75±1.27	40.98±4.29	590.00±48.61	33.75±1.20	68.90±^{3}.24

Table 2 continued.

Morphometric parameters of hawthorn leaf teeth glands												
Species	***Crataegus meyeri***				***Crataegus rhipidophylla***				***Crataegus × armena***			
	Stalk		Head		Stalk		Head		Stalk		Head	
	Length µm	Width µm	Length µm	Width µm	Length µm	Width µm	Length µm	Width µm	Length µm	Width µm	Length µm	Width µm
min	45.00	70.00	-	-	35.00	50.00	25.00	70.00	45.00	50.00	20.00	70.00
max	55.00	135.00	-	-	60.00	115.00	55.00	100.00	60.00	210.00	165.00	110.00
average	51.25±1.02	85.50±3.05	-	-	40.50±2.26	83.00±4.17	44.25±2.15	86.50±2.35	61.75±5.43	91.25±7.69	62.25±6.33	90.25±3.02

Table 3. Morphometric parameters of *Crataegus pseudoheterophylla*, *Crataegus pentagyna*, *Crataegus* × *zangezura*, *Crataegus meyeri*, *Crataegus rhipidophylla*, and *Crataegus* × *armena* idioblasts CaC_2O_4 in the mesophyll of the leaf blade.

Species	***Crataegus pseudoheterophylla***				***Crataegus pentagyna***				***Crataegus × zangezura***			
	Single prismatic crystals		Druzes		Single prismatic crystals		Druzes		Single prismatic crystals		Druzes	
	Size µm	Quantity pcs/mm^2	Size µm	Quantity pcs/mm^2	Size µm	Quantity pcs/mm^2	Size µm	Quantity pcs/mm^2	Size µm	Quantity pcs/mm^2	Size µm	Quantity pcs/mm^2
min	10.00	13.78	10.00	6.89	10.00	34.45	15.00	13.78	10.00	68.90	15.00	13.80
max	15.00	172.25	25.00	117.13	25.00	137.80	20.00	62.01	20.00	254.93	17.00	34.45
average	13.50±0.49	74.07±9.39	14.75±0.77	32.73±5.83	16.00±1.29	74.76±7.45	16.50±0.53	26.87±3.12	11.75±0.75	180.17±11.02	15.40±0.18	21.01±1.62

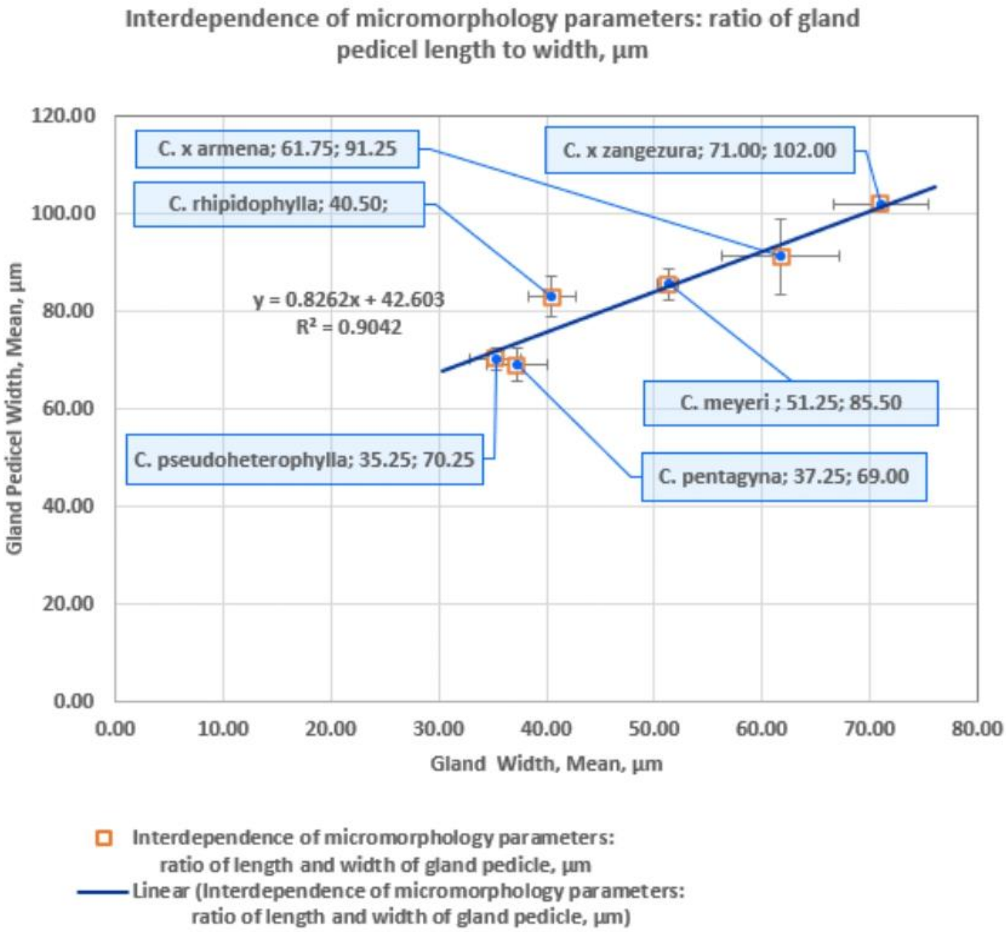

Fig. 2. The ratio between the length and width of the gland pedicel.

The graph analyzing the ratio between the length and width of the glandular pedicel shows that an increase in the size of one side of the cross-sectional shape of the pedicel from species to species corresponds to an increase in the size of the other side. The reverse is also true. The conclusion is based on an analysis of the linear approximation of data on a scatter plot showing the relationship between the length and width of the glandular pedicel by species. The linear approximation equation accurately describes the relationship for all six species studied, with only minor deviations. This allows us to consider the identified ratio as characteristic.

The length of the gland head of both hybrids was significantly larger than that of one of their parental forms (Fig. 3).

Of the parental forms *C. pentagyna*, *C. pseudoheterophylla*, and their hybrid *C.* × *zangezura*, the largest single prismatic crystals of CaC_2O_4 were found in the mesophyll of *C. pentagyna* LB. They were 36.17% larger than those in the mesophyll of *C.* × *zangezura*. The crystals in the mesophyll of *C. pseudoheterophylla* were intermediate in size. Large quantities of small crystals were found in the mesophyll of *C.* × *zangezura*. They were 2.42 times more abundant in the mesophyll LB of the parental forms. *C.* × *zangezura* showed the largest amplitude between the minimum and maximum quantities of crystals per 1 mm^2 compared to the parental forms. It was 186.03 pcs/mm^2. In *C. pentagyna*, it was 103.35 pcs/mm^2, and in *C. pseudoheterophylla*, it was 158.47 pcs/mm^2.

The sizes of the CaC_2O_4 druzes in the three studied species did not differ significantly, averaging 15.55 µm. The amplitude of druze sizes was small. The highest value was observed in *C. pseudoheterophylla* at 15.0 µm. The smallest quantity of druzes was observed in *C.* × *zangezura*, and the largest in *C. pseudoheterophylla* (Table 3).

Pearson's criterion was used to identify paired-correlation dependencies among idioblasts in the LB mesophyll (Table 4).

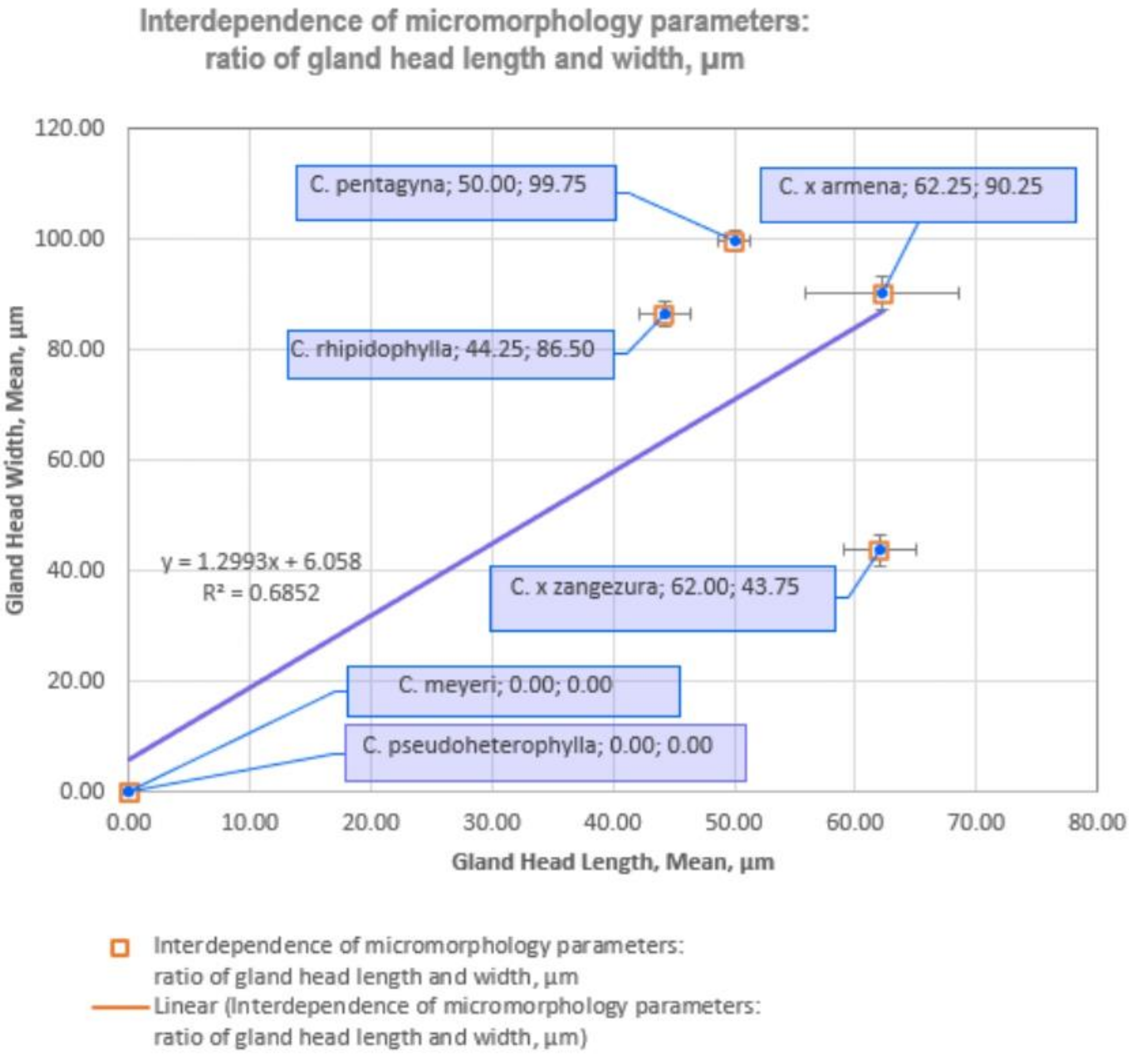

Fig. 3. The ratio between the length and width of the gland head.

There is a weak positive correlation (0.039–0.195) between crystal length and crystal number in the mesophyll of *C. pentagyna* and *C. pseudoheterophylla*. At the same time, in *C.* × *zangezura*, a high negative correlation (-0.648) was observed between the quantity and length of crystals.

It is confirmed by the bilateral significance of the correlation at the level of 0.02. Pairwise dependencies between the size and quantity of druzes for *C. pentagyna*, *C. pseudoheterophylla*, and *C.* × *zangezura* were established. This was a weak negative correlation (-0.243) for *C. pentagyna*, while for *C. pseudoheterophylla*, it was a moderate negative correlation (-0.370). There was a moderate correlation (0.464) between these indicators for the hybrid *C.* × *zangezura*. It is supported by two-sided significance at the level of 0.039. The correlation dependencies between the quantity of crystals and the size of druzes, and the inverse dependencies between the length of crystals and the quantity of druzes of these three species were weak positive and negative.

The size of single prismatic crystals of CaC_2O_4 in *C. rhipidophylla*, *C. meyeri*, and *C.* × *armena* was the same (Table 3). The quantity of these elements in the mesophyll LB varied largely. *C. meyeri* had the highest quantity of these elements (Fig. 4b). CaC_2O_4 idioblasts were represented by single prismatic crystals and druzes (Fig. 4).

We often observed both types of idioblasts present simultaneously in the mesophyll (Fig. 4a).

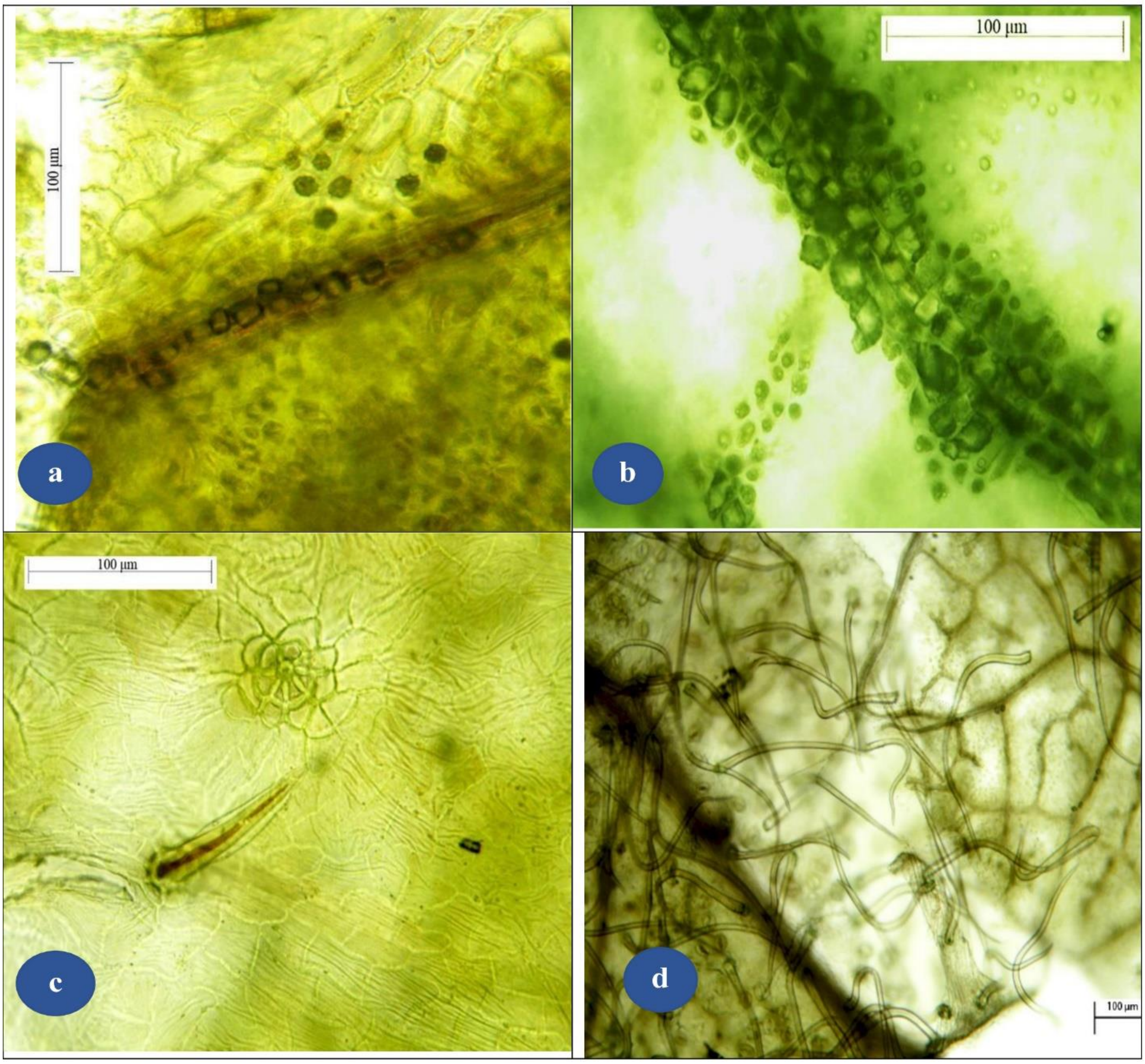

Fig. 4. a, Fragment of *Crataegus rhipidophylla* LB, single prismatic crystals and druzes CaC2O4 in the mesophyll; b, fragment of *C. meyeri* LB, single prismatic CaC2O4 crystals in the mesophyll above the vein; c, fragment of *Crataegus* × *armena* LB, the simple unicellular hair and the rosette of epidermal cells at the site of hair attachment; d, fragment of *Crataegus* × *armena* LB, abundant simple unicellular hairs in the epidermis.

This exceeded the accumulation of single prismatic crystals in the mesophyll of the LB *C. rhipidophylla* by 1.86 times and *C.* × *armena* by 14.06 times. *Crataegus meyeri* also had a very large amplitude of values in terms of crystal quantity, it was 482.3 pcs/mm^2. The amplitude in *Crataegus rhipidophylla* was 192.92 pcs/mm^2, and in *C.* × *armena*, only 13.78 pcs/mm^2. The largest CaC_2O_4 druzes were also found in the *C. meyeri* mesophyll LB. They are 30.77% smaller in *C. rhipidophylla* and 70.0% smaller *in C.* × *armena*. Thus, there was a large quantity of large CaC_2O_4 idioblasts in the *C. meyeri* mesophyll LB. Some paired correlations were established between the size and quantity of idioblasts in the mesophyll of LB *Crataegus meyeri*, *C. rhipidophylla*, and *C.* × *armena*.

Table 4. Pearson correlation coefficients for CaC_2O_4 idioblasts in the LB mesophyll of the examined species of the genus *Crataegus*. Coefficients with a significant two-tailed significance level of 0.05 or less are highlighted in bold.

	C. pentagyna	*C. pseudoheterophylla*	*C. × zangezura*	*C. meyeri*	*C. rhipidophylla*	*C. × armena*
Prismatic crystals length / crystals quantity	0.039	0.195	**-0.648**	-0.328	-0.179	0.085
Druzes size/Druzes quantity	-0.243	-0.370	**0.464**	-0.360	0.028	-0.267
Crystals quantity/ druzes size	0.021	-0.091	-0.136	0.335	**-0.605**	-0.267
Crystals length/druzes quantity	-0.081	-0.016	0.198	-0.208	-0.131	**-0.472**

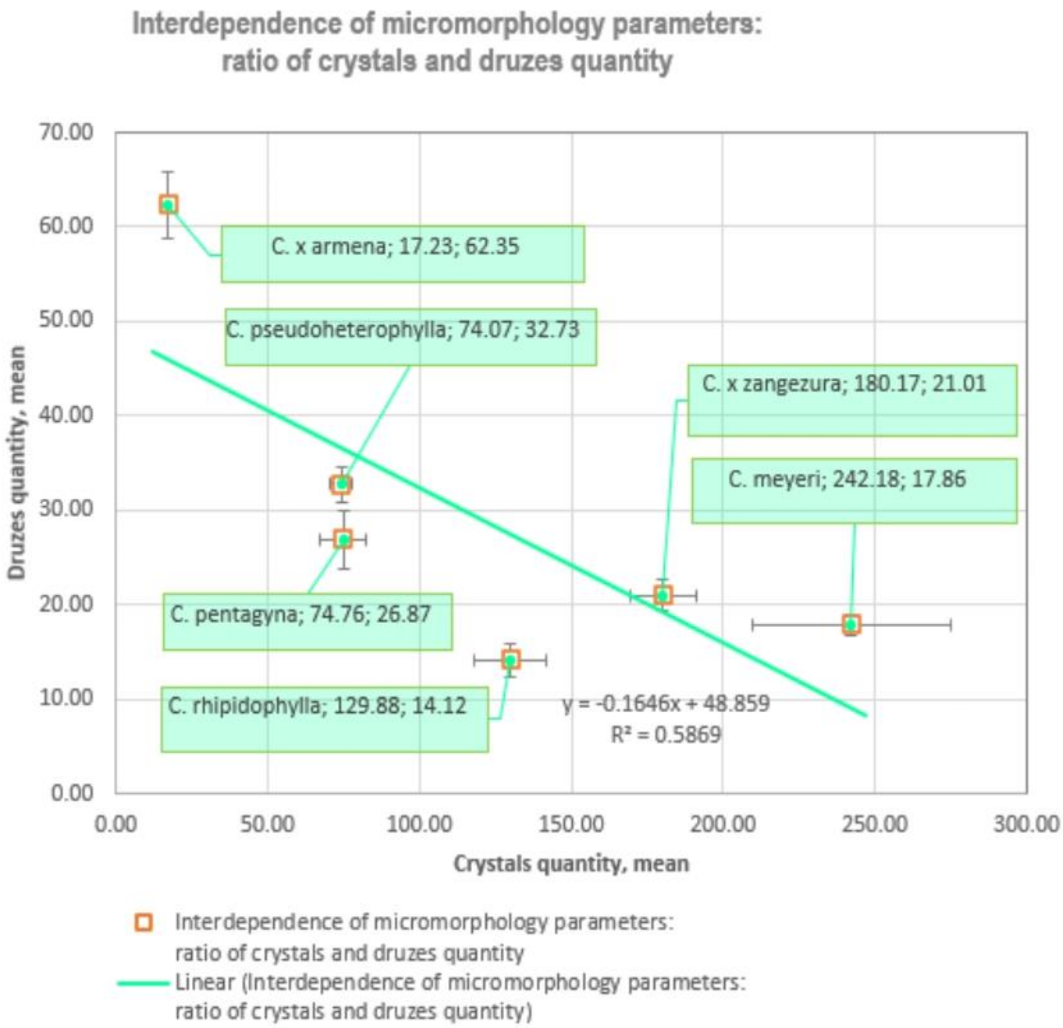

Fig. 5. The ratio between the quantity of CaC_2O_4 crystals and druzes.

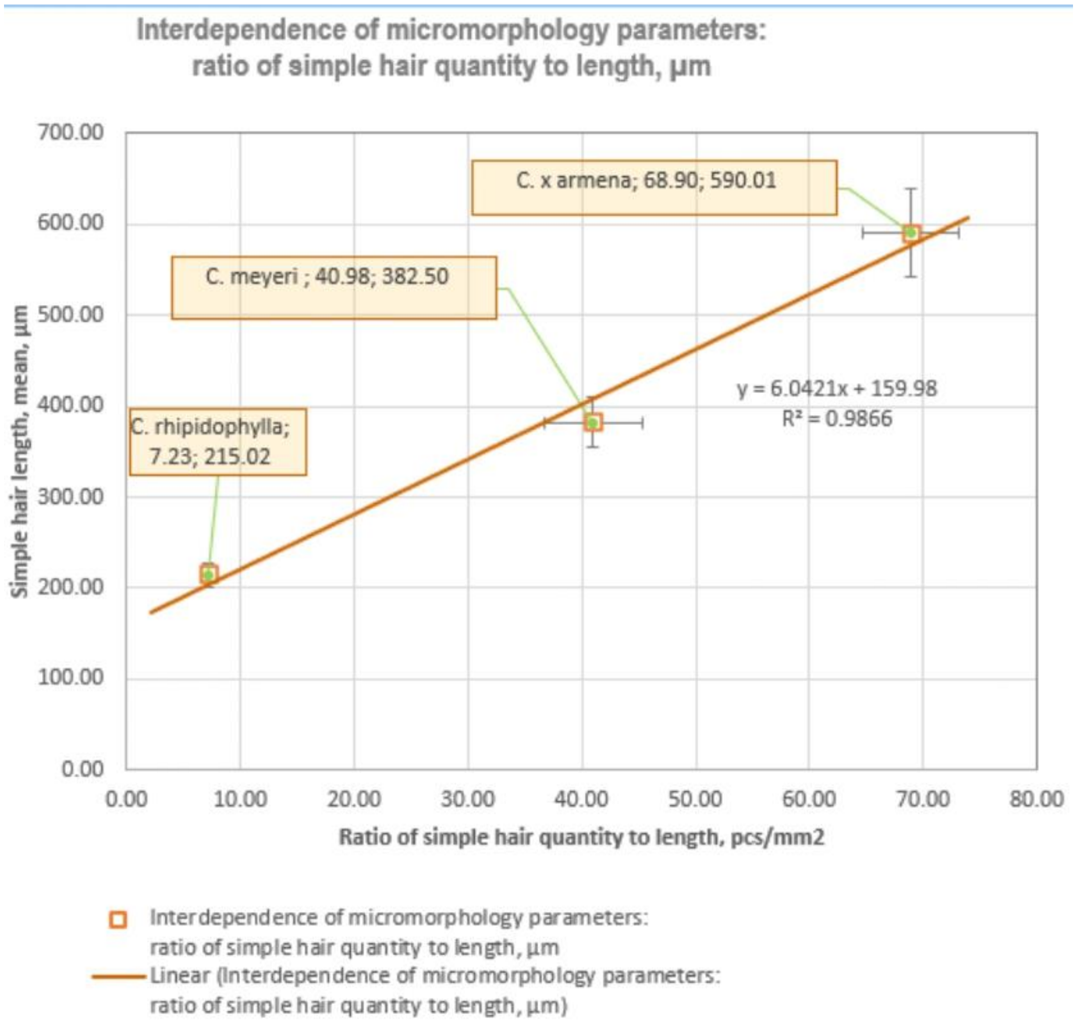

Fig. 6. The ratio of quantity and length of simple unicellular hairs in the epidermis of the *Crataegus* species.

There were moderate negative correlations between the length and quantity of both single prismatic crystals and druzes in *C. meyeri* (-0.328 and -0.360, respectively). Weak correlations were found in *C. rhipidophylla*: between length and quantity of crystals, there was a weak negative correlation (-0.179), and between size and quantity of druzes, there was a weak positive correlation (0.028). The weak positive correlation was found between length and quantity of crystals (0.085), and the moderate negative correlation between size and quantity of druzes (-0.267) in *C.* × *armena*. The following pattern for *C. rhipidophylla* was observed: the larger the quantity of crystals, the smaller the size of the druzes. This is a high negative correlation (-0.605) with a reliable two-tailed significance at the level of 0.005. The moderate negative correlation (-0.472) was established for *C.* × *armena* between crystal length and the quantity of druzes with a reliable two-tailed significance level of 0.036.

A graph analyzing the ratio of the number of druzes to the number of crystals (Fig. 5) shows that an increase in the number of crystals corresponds to a smaller number of druses. The reverse is also true. This conclusion is based on an analysis of the linear approximation data from a scatter plot showing the interdependence of micromorphological parameters expressed as a ratio of crystals and druzes quantity. *C.* × *armena* is a characteristic example. This species has the largest quantity of druzes compared to other species, while the quantity of crystals is the smallest. The opposite in this series in terms of the ratio under study is *C. meyeri*, with the largest quantity of crystals and the smallest quantity of druzes. A large quantity of crystals is characterized by an increase in the spread of values, i.e. an increase in the mean error. Overall, in five out of six cases, the average quantity of crystals exceeded the average quantity of druzes in samples of each species.

C. meyeri, *C. rhipidophylla*, and their hybrid *C.* × *armena* had simple single-celled pointed thick-walled hairs. They were often very long and had a sinuous shape. Epidermal cells (usually 5-6) were arranged in a rosette around the hairs (Fig. 4c).

The maximum length of such hairs and the amplitude of values were observed in the epidermis of the *C.* × *armena* hybrid. The length of the hairs was larger than the corresponding values of the parental forms: *C. meyeri* by 207.5 µm and *C. rhipidophylla* by 375.0 µm.

The amplitude of hair length values in the epidermis of *C.* × *armena* was 800.0 µm, in *C. meyeri* 375.0 µm, and in *C. rhipidophylla* 150.0 µm. The width of the hair at its point of attachment to the epidermal cells was the same in both the hybrid and *C. meyeri*, averaging 32.75 µm. The width of the hair at the point of attachment in *C. rhipidophylla* was significantly smaller (1.42 times). *C.* × *armena* produced significantly more simple unicellular hairs than its parental forms (Fig. 4d).

C. × *armena* had 1.68 times more hairs than *C. meyeri* and 9.53 times more than *C. rhipidophylla*. The amplitude of fluctuations in hair quantity was 68.90 pcs/mm² in *C.* × *armena*, 55.22 pcs/mm² in *C. meyeri*, and 6.89 pcs/mm² in *C. rhipidophylla*. As shown in Fig. 6, the graph of data on the ratio of quantity and length of simple hairs indicates that all three positions on the scatter plot lie close to a single linear approximation.

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