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Studies in the Caucasian Species of *Cardamine* L. *(Cruciferae)*

By

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With 5 Figures

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Summary

KHATRI K. S. 1988. Studies in the Caucasian species of *Cardamine* L. *(Cruciferae).* – Phyton (Austria) 28 (1): 55–80, 5 figures. – English with German summary.

A critical taxonomic review is provided in the Caucasian species of *Cardamine* L. *(Cruciferae),* based on the study of herbarium material. Different morphological characters were examined but special attention was paid to morphology of flowers, pollen, nectaries, fruits and seeds, complemented with anatomical studies of fruits and seeds. Along with morphological data, taxonomic importance of nectaries and anatomy of fruit valves, replum and seed-coat are emphasized at the level of species or supraspecies. 8 species have been recognised that are arranged in 4 subsections under *Cardamine* sect. *Cardamine* viz., 1. *Tenerae (C. acris, C. uliginosa* and *C. tenera),* 2. *Amarae (C. wiedemanniana),* 3. *Brachypetalae (C. hirsuta* and *C. parviflora)* and 4. *Sagittatae (C. impatiens* and *C. pectinata).*

Zusammenfassung

KHATRI K. S. 1988. Studie über die kaukasischen Arten von *Cardamine* L. *(Cruciferae).* – Phyton (Austria) 28 (1): 55–80, 5 Abbildungen. – Englisch mit deutscher Zusammenfassung.

Eine auf Herbarmaterial basierende, kritische, taxonomische Studie der kaukasischen Arten der Gattung *Cardamine* L. *(Cruciferae)* wird vorgelegt. Die verschiedenen morphologischen Merkmale wurden untersucht, wobei besonderes Augenmerk auf Blütenmorphologie, Pollen, Nektarien, Früchte und Samen gelegt wurde. Weiters

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wurde die Anatomie der Fruchtwand, sowie von Replum und Samenschale berücksichtigt. All diese Merkmale wurden zur Charakterisierung der Arten ebenso wie der supraspezifischen Einheiten herangezogen. 8 Arten werden anerkannt, die in 4 Subsektionen von *Cardamine* sect. *Cardamine* gestellt werden: 1. *Tenerae (C. acris, C. uliginosa* und *C. tenera),* 2. *Amarae (C. wiedemanniana),* 3. *Brachypetalae (C. hirsuta* und *C. parviflora)* und 4. *Sagittatae (C. impatiens* und *C. pectinata).*

Introduction

Cardamine is one of the largest (160 species) and taxonomically complex genera of *Cruciferae.* In most of the important systems of the family, it has consistently been placed under the tribe *Arabideae* DC. (HAYEK 1911, SCHULZ 1936, JANCHEN 1942). Most of the authors have followed LINNAEUS 1753, 1754 accepting *Cardamine* and *Dentaria* as separate genera, however some have included *Dentaria* in *Cardamine* following CRANTZ 1769.

The last critical work on the genus (containing 116 species) for the whole World was provided by SCHULZ 1903. Since then, many new species have been described from various parts of the World and some conspecies have been splitted in more taxa according to recent findings. But, taxonomically it has been revised only for some parts of Europe (JANCHEN 1958, SPASSKAYA 1978) while there is no such revisional work for adjoining parts.

The genus is divided into 13–15 sections, two of which, viz. *Dentaria* and *Eutreptophyllum,* are usually treated as separate genus *Dentaria* L. by many authors. Seven sections are monotypic while most of the remainings are merely of regional importance and only *C.* sect. *Cardamine,* the largest one containing about two third of the total species, is occurring all over the World but is concentrated in temperate regions and high mountains of the tropics. In Caucasia the genus is represented by eight species of *C.* sect. *Cardamine.* Out of these, *C. acris, C. uliginosa* and *C. hirsuta* are polymorphic while the others are more or less uniform.

The Caucasian taxa have been explored since the early 19th Century, but the first complete account was provided by LEDEBOUR 1841 which refers all the previous works. Later on, more extensive explorations were made bringing out some new additions which were further compiled by LIPSKÝ 1899. Since then the taxonomic composition remains the same, but reports on *C. pratensis* L. and *C. amara* L. were found as erroneous.

Ultimately, Caucasian plants were included in SCHULZ 1903 and then, were worked out more comprehensively by BUSCH 1909 retaining *C. acris* (sub nomine *C. seidlitziana* ALBOV), *C. wiedemanniana* (s. n. *C. lazica* BOISS. & BAL,) and *C. pectinata* as separate species which were reduced to intraspecific status by SCHULZ. The same treatment prevails in later works (BUSCH 1939, GROSSHEIM 1950, AKHUNDOV 1953, DAVLIANIDZE 1979, GALUSHKO 1980, KOLAKOVSKÝ 1982 etc.), however a confusing name *C. iliciana* (FRITSCH) N. BUSCH also has been retained by GROSSHEIM 1950: 183. This name was recognised by BUSCH 1909: 354 but he was doubtful about its

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distribution in Caucasia, hence, later on it was avoided by him (cf. BUSCH 1939). Indeed, this name is applicable to a certain form of *C. pratensis* s. lat., but none of the recent works confirm its presence in Caucasia. Furthermore, there is no herbarium record from Caucasia. The legitimate name for this plant is *C. matthioli* MORETTI which does not extend eastwards beyond the Carpathians, thus undoubtedly its report from Caucasia seems erroneous.

Recently, more extensive botanical explorations have been carried out in Caucasia providing voluminous botanical literature, mainly in the form of local floras and keys. This lead to the description of many infraspecific taxa, based on single morphological characters not correlated with others and without regard to the variability of populations.

For the present work a synthetic approach has been made to clarify taxonomic delimitations of these taxa and on the basis of these studies supraspecific grouping has been attempted tracing out phylogenetic trends within the whole group.

Material and Methods

The present study is based on herbarium material available at LE, LECB, MHA, MW and MOSM (abbreviations according to STAFLEU 1981). Furthermore, authentical specimens and additional material from adjoining parts were examined at LINN, BM, K and B for comparison of population variation within the taxa treated herewith.

Different morphological characters were examined. Although indumentum has been widely used in taxonomy of *Cruciferae,* however in *Cardamine* it does not seem of taxonomic importance, hence special attention was paid to morphology of flowers, pollen, nectaries, fruits and seeds. Furthermore, the anatomy of fruits and seeds was also covered. Pollen were studied with the LM in fuchsine-glycerine and after acetolysis. Average pollen diameter is based on c. 100 counts for each species. For greater detail of surface features non acetolysed pollen grains were studied with SEM (JSM-35 C Model).

For anatomical studies fruits and seeds were sectioned by hand with a razor blade and then mounted in water-glycerine for LM observations. In case of fruit valves sections were treated with metal-blue or safranin before mounting. Prepared material is preserved in the Department of Botany, Leningrad State University. Referred chromosome numbers are based on literature.

Life Forms

All these species are hygrophilous, however exhibit some variations in habitat preference. On the basis of life form they fall in two groups:

1. Annuals or biennials with a more or less prominent tap root – *C. hirsuta, C. parviflora, C. impatiens* and *C. pectinata.*

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2. Perennials with a shortened or ± elongated, stoloniferous rhizome – *C. acris, C. uliginosa, C. tenera* and *C. wiedemanniana.*

In the first group *C. hirsuta* and *C. parviflora* are annuals having cylindrical stems and comparatively smaller leaves but *C. parviflora* is glabrous and multifoliate having upto 8 pairs of narrower leaflets with a subequal terminal one. *C. hirsuta* is pubescent with scattered hairs and few leaves with 1–5 pairs of leaflets with a distinctly larger terminal one. *C. impatiens* and *C. pectinata* are annuals or biennials having a glabrous, ridged stem, larger leaves with auriculate petiole bases. *C. pectinata* has only 1–5 pairs of leaflets while *C. impatiens* has 5–9 pairs.

In the second group *C. wiedemanniana* is somewhat isolated in having a multifoliate stem, leaves with 1–3 pairs of smaller lateral leaflets and an exceedingly larger terminal one. *C. tenera* remains apart by a shortened rhizome, slender stem and long leafy stolons often having simple leaves. *C. acris* and *C. uliginosa* are very similar in habit, however *C. acris* differs by robust, usually glabrous stem, 1–5 paired leaves with an exceedingly larger terminal leaflet. *C. uliginosa* has usually a glaucous stem, 5–9 pairs of leaflets, often with a subequal terminal one (at least in the upper cauline leaves).

Distribution

C. uliginosa, C. hirsuta and *C. impatiens* are widespread while the others are rather restricted in some localities only. *C. uliginosa* is more abundant in high elevations except steppes. *C. hirsuta* is common in lowlands but does not enter steppes and beyond medium heights while *C. impatiens* covers a wide range from lowlands to the subalpine zone, but in upper limits (from 1800–2500 m) the typical form is replaced by its var. *eriocarpa* DC. (= *C. dasycarpa* BIEB.).

C. tenera is restricted in lowland broadleaved woods becoming rather sporadic upwards. It is frequent in the West but scattered eastwards, however reappears again in Talysh. *C. pectinata* has the same range but is rather frequent while *C. parviflora* is highly scattered, being, restricted in a few localities of Western Transcaucasia from Kuban to Adzharia and Talysh. *C. acris* is common in alpine-subalpine belts of Western Transcaucasia from Kuban to Adzharia while *C. wiedemanniana* occurs sporadically in coastal Western Transcaucasia from Abkhazia to Adzharia. Thus, only *C. impatiens* is a plant of wide range, occurring from the lowlands to the subalpine zone. *C. acris* and *C. uliginosa* are characteristically high altitude plants rarely descending down into the forest zone along hill streams while the remaining species have their ranges in lowlands and subhills hardly extending to subalpine elevations.

Regarding the general distribution, *C. hirsuta, C. parviflora* and *C. impatiens* are widespread Eurasian elements. *C. acris, C. uliginosa, C.*

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tenera and *C. pectinata* also extend their ranges far away from Caucasia but *C. wiedemanniana* is restricted to the immediately adjacent eastern coast of the Black Sea in N. Lazistan.

Morphological Characters

A. Flowers

Inflorescence usually a many flowered raceme. Pedicels straight or ascending; sepals flat or saccate, oblong-ovate, greenish with hyaline margins, sometimes purple-tinted; petals unguiculate in larger flowers and spathulate in smallers, rarely absent, white-cream, lilac, rarely yellowish, rounded or emarginate; stamens 6 (4), filaments linear and free, anthers oblong-elliptic, yellow, sometimes greenish; ovary glabrous, rarely hairy, narrowed in a very short to distinct style, with stigma subequal or wider than style.

Floral characters are of great significance for distinguishing species or group of species. *C. acris, C. uliginosa, C. tenera* and *C. wiedemanniana* show some similarities in floral characters having saccate, ovate, often purple-tinted sepals, unguiculate petals, larger, oblong-elliptic, yellow anthers and a glabrous ovary with distinct style. *C. wiedemanniana* differs by smaller (5–8 mm long), white, rounded petals, 0.8–1.2 mm long anthers, 16–20 ovulate ovary having a 1–1.5 mm long, subulate style and a small, disc-shaped stigma. *C. acris, C. uliginosa* and *C. tenera* are characterised by larger (8–15 mm long), white-yellowish to dark lilac, emarginate petals, 1.2–1.8 mm long anthers, 20–40 ovulate ovary with a 0.5–1 mm long, thickened style and a wider, capitate-bifid stigma.

The remaining species are distinguished by having smaller flowers, straight, oblong, blunt sepals, spathulate, white, rounded petals, integrate stigma which is subequal to the style. Out of these, *C. hirsuta* and *C. parviflora* have smaller (0.3–0.6 mm long), broadelliptic, yellow anthers, glabrous and an 18–36 ovulate ovary with a very short (0.1–0.3 mm long) style. *C. hirsuta* differs by ciliate sepals, often lacking lateral stamens etc. *C. impatiens* and *C. pectinata* are distinguished by having 0.6–1 mm long, oblong, greenish anthers and a 10–24 ovulate, often pubescent ovary with a distinct style. Sometimes petals are lacking in *C. impatiens,* however *C. pectinata* is distiguished by consistent and larger (3.5–5.5 mm long) petals and a longer (0.8–1.2 mm long), slender style.

B. Pollen Grains

The dry pollen grains are ellipsoidal, however when treated with fuchsine-glycerine or acetolysed they appear spheroidal or occasionally oblate-spheroidal. But in some populations the latter form predominates. This type of behaviour may be attributed to allelic segregation (cf. LÖVKVIST 1956: 30). Size 16.5–27.4 μm, tricolpate, colpae 3.4–8.5 μm wide, fairly long running

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along th e polar axis, with cuneate ends and a smooth membrane. Exine 0.5–2.8 μm thick, more thicker at the centre of mesocolpium, decreasing in thickness towards apertures and polar regions. Sexine thicker than nexine, consisting of a columellae layer of cylindrical rods which are united on the surface forming a reticulate texture which breaks down in the region of endoapertures. Nexine thin and smooth (Fig. 1).

As demonstrated by some authors (LÖVKVIST 1956, ELLIS & JONES 1970, CHIGURYAEVA 1975, SPASSKAYA 1979) the pollen grains showed some variations in diameter, exine thickness, size of lumina (reticulation pattern) and breadth of colpae as shown in Table 1. But pollen characters are not correlated with floral ones and do not seem very useful in distinguishing species or groups of species. But on the basis of size (cf. ERDTMAN 1952) and reticulation pattern (cf. CHIGURYAEVA 1975) they can be grouped as follows:

A. Pollen small sized (diameter less than 25 μm) and finely reticulate (lumina 0.4–2.5 μm) – *C. wiedemanniana* (Fig. 1 c, d), *C. parviflora, C. impatiens* (Fig. 1 e, f) and *C. pectinata.*

B. Pollen medium sized (diameter exceeding 25 μm) and coarsely reticulate (lumina 1.5–4 μm) – *C. acris, C. uliginosa* (Fig. 1 a, b), *C. tenera* and *C. hirsuta.*

Thus among closely related species *C. acris, C. uliginosa* and *C. tenera* have almost similar grains except *C. tenera* which has pollen with larger brochi and wider colpae. *C. impatiens* and *C. pectinata* are characterised by finely reticulate grains having the thinnest exine, however *C. hirsuta* and *C. parviflora* have different pollen. *C. wiedemanniana* comes nearer to *C. parviflora* in pollen characters but differs by comparatively larger size and broader colpi.

Table 1. Measurements of pollen grains of *Cardamine* (in μm)

Species	Diameter Min.	Aver.	Max.	Exine thickness	Breadth of colpi	Size of exine lumina
1. *C. acris*	22.3	24.6	26.5	2.0–2.7	4.9–6.0	1.8–3.0
2. *C. uliginosa*	22.3	24.7	26.7	2.0–2.7	5.4–6.7	1.8–3.2
3. *C. tenera*	22.5	25.0	27.4	2.0–2.8	6.7–8.5	2.5–4.0
4. *C. hirsuta*	23.0	25.4	27.8	2.0–2.5	4.3–6.5	1.8–3.3
5. *C. parviflora*	16.5	18.5	20.7	1.7–2.4	3.4–4.4	1.5–2.3
6. *C. wiedemanniana*	17.2	19.5	22.0	1.4–2.0	4.5–5.6	1.3–2.4
7. *C. impatiens*	16.2	17.6	19.2	0.6–1.0	3.5–4.7	0.5–1.0
8. *C. pectinata*	17.4	19.5	22.3	0.5–0.9	4.0–5.4	0.4–0.8

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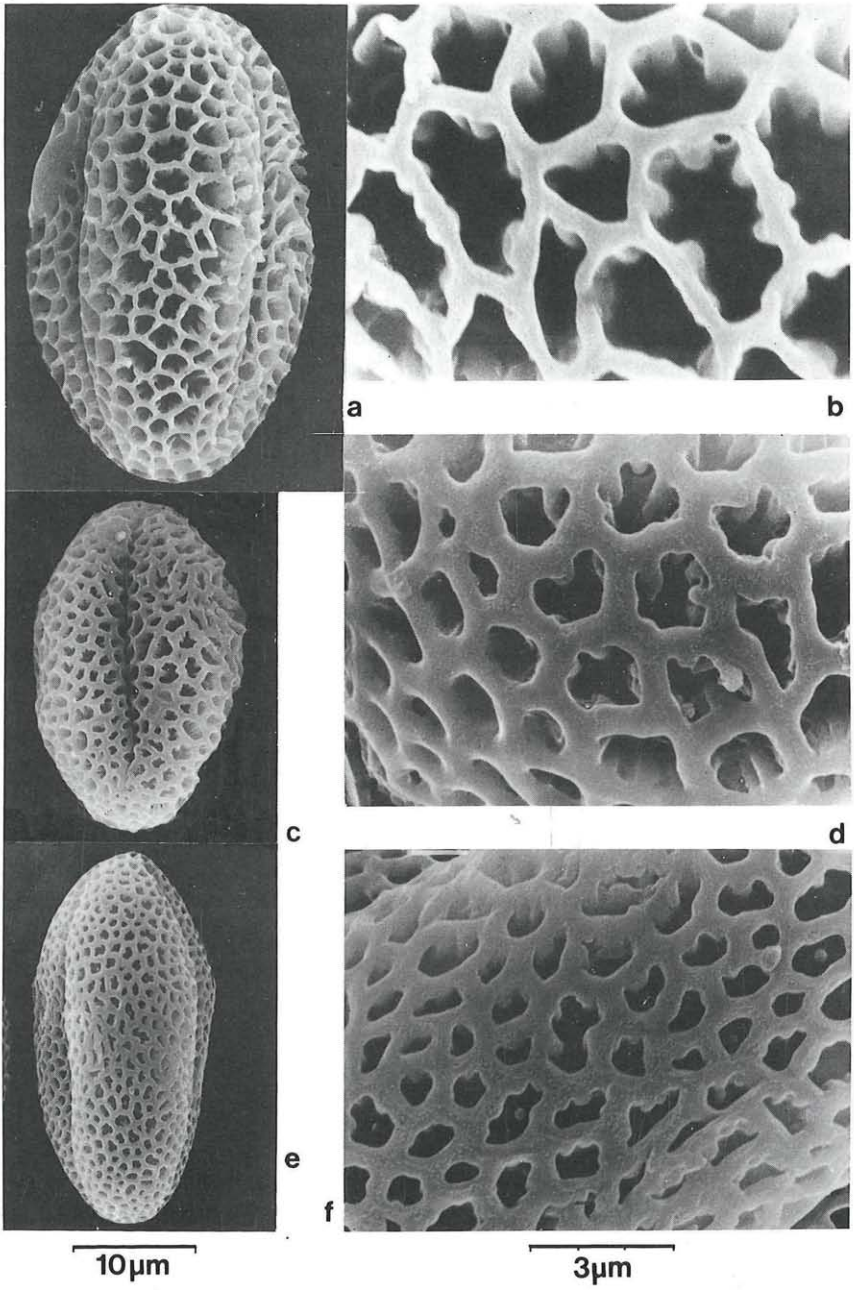

Fig. 1. Pollen grains of *Cardamine* species. – a, b *C. uliginosa*.– c, d *C. wiedemanniana*. – e, f *C. impatiens*.

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C. Nectar Glands

Nectaries have been widely used in the taxonomy of *Cruciferae* following the initial work of CRANTZ 1769 and DE CANDOLLE 1821. In the case of *Cardamine,* the first illustrated account on nectaries was provided by VELENOVSKÝ 1883 and later on these characters have been used in the taxonomy of the genus (PRANTL 1891, SCHULZ 1903, 1936, HAYEK 1911). However until recently, the nectaries have been regarded as not confluent following VELENOVSKÝ (BUSCH 1939, KOTOV 1979). But the present study confirms the recent investigations (NORRIS 1941, SPASSKAYA 1979) showing that lateral and median glands are confluent forming a complete annular ring of nectarial tissue just outside the stamens.

Nectaries are always well developed, however the size seems to correlate positively with the petal size in general. The continuous nectarial tissue around the torus is differentiated by prominent lateral glands surrounding the bases of lateral filaments and median glands between the bases of paired stamens. The nature of lateral and median glands is of some taxonomic value as their form and configuration of nectarial tissue is characteristic of species or groups of species.

Thus *C. acris* and *C. uliginosa* are characterised by ring-shaped lateral glands which are uniformly thickened or sometimes thinner on the inside and conical and patent median glands. The remaining species have horseshoe-shaped lateral glands with an opening on the inside, however they vary in detailed structure. In *C. tenera* these glands are uniformly thickened with a small opening inside while the median glands are similar to those of the above mentioned species. In *C. wiedemanniana* they often have a heavier swelling on the lateral sides only forming a narrower furrow at the centre and the inner ends project towards the ovary but are not coalesced, the median glands are horizontally placed cones. *C. hirsuta* and *C. parviflora* are characterised by comparatively smaller glands having lateral glands which are slightly thickened on lateral sides and thinner outside and small, knobby median glands. Although *C. hirsuta* often lacks lateral stamens, the lateral glands are consistent. *C. impatiens* and *C. pectinata* also have the same pattern, but in *C. impatiens* the lateral glands are very thin on the outside having a bulging on lateral sides forming two closely placed islets and the median glands usually consists of two tightly fused knobs. *C. pectinata* differs by having uniformly thickened lateral glands and single knobbed median glands.

D. Fruit

Fruit ± compressed, 10–40 × 0.6–1.8 mm, a linear, bilocular siliqua; apex a persistent, 0.3–3.5 mm long style with 0.2–0.6 mm wide capitate-bifid stigma; valves glabrous rarely hairy, smooth, straw-greenish to light-brown, sometimes dotted lilac, midrib almost indistinct, usually opening

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suddenly and coiling spirally upwards flinging the seeds to some distance; pedicels 5–20 mm long, erecto-patent or horizontal; seeds uniseriate, on thin funicules.

Fruit variations are characteristic of species or groups of species. Thus *C. acris, C. uliginosa* and *C. tenera* have 20–40 mm long siliques with 1–2.5 mm long, stout, terete style and wider or rarely subequal, capitate-bifid stigma. *C. tenera* differs by slightly narrower (1.0–1.4 mm wide), somewhat convex siliques and strongly patent pedicels. The remaining species have smaller but variable siliques. *C. wiedemanniana* differs distinctly by subulate-filiform, 2–3,5 mm long style with a small, punctate stigma which is narrower than the style. *C. hirsuta* and *C. parviflora* have a very short (0.3–1 mm long) conical style with subequal stigma while *C. impatiens* and *C. pectinata* differ by having often pubescent siliques with 0.8–3.5 mm long and slender style.

E. Seeds

Seeds 0.6–2 × 0.5–1.2 × 0.3–0.8 mm, oval-oblong to orbiculate-quadrate, apex sometimes eccentric; margin with a notch between the tip of radicle and that of cotyledons, sometimes almost indistinct; flattened, planoconvex or slightly biconvex; cotyledonary part 2–3 times wider than the radicular one; radicular furrow distinct on one or either sides; margin edged, surrounded with a dark line; base and apex sometimes with a light border; hilum elliptic, callous, Testa semitranslucent, glabrous, lustreless or barely lustrous, smooth to areolate-reticulate, ground colour brown, orange-yellow, often with red-brown to dark-brown patches. Embryo accumbent or obliquely accumbent, cotyledons sessile to subsessile, smooth, tip blunt or slightly truncate.

C. acris, C. uliginosa, C. tenera and *C. wiedemanniana* have oval, areolate-reticulate, brown seeds with darker patches, *C. acris* and *C. uliginosa* have 1.2–1.7 × 0.8–1.2 mm seeds while *C. tenera* and *C. wiedemanniana* differ by having 1–1.4 × 0.7–1 mm seeds. *C. hirsuta* and *C. parviflora* are characterised by smaller (0.7–1.2 × 0.5–0.9 mm), orange seeds which are orbiculate-quadrate in *C. hirsuta* but oval-oblong in *C. parviflora. C. impatiens* and *C. pectinata* have slightly rugulose, light-brown, 1.2–2 × 0.6–1 mm, oblong seeds.

Anatomical Characters

A. Fruit Valves

The fruit valve (Fig. 2 a, b) represents a dry pericarp consisting of an outer epidermis of tangentially elongated cells, often with thickened outer wall. It is followed by a 4–11 layered parenchyma having chloroplasts and intercellular spaces; the 2–3 outer layers consist of tangentially elongated

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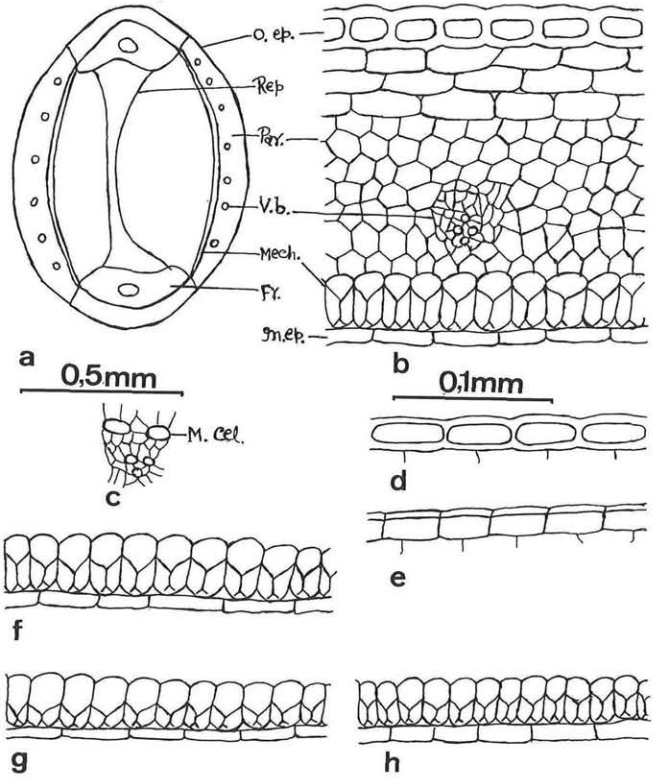

Fig. 2. – *Cardamine tenera;* a diagrammatic transversal section of the fruit, b detailed structure of the fruit valve, c vascular bundle with myrosin cells. – d, e outer epidermis of the fruit valve; d *C. acris,* e *C. wiedemanniana.* – f–h mechanical layer; f *C. wiedemanniana,* g *C. hirsuta,* h *C. impatiens.* – O. ep. outer epidermis, Rep. replum, Par. parenchyma, V. b. vascular bundle, Mech. mechanical layer, Fr. frame of the replum. In. ep. inner epidermis.

cells forming a outer hypodermis and the inner cells are polygonal. The parenchyma is followed by a sclerenchymatous layer of inner hypodermis having larger, radially elongated and heavily lignified cells. It is also known as "mechanical layer" because it is responsible for the sudden opening of fruit valves. It is followed by an inner epidermis having tangentially elongated, rather compressed cells, often with diffused radial walls. There are 4–10 vascular bundles arranged within the inner layers of parenchyma; they lack sclerenchymatous sheaths, but sometimes they are provided with myrosin cells just outside the phloem.Valves are attached to the frame of replum by thick walled cells that detach easily after maturation, helping dehiscence.

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As demonstrated by some authors in *Cruci ferae* and by SPASSKAYA 1979 in *Cardamine,* fruit anatomy provides some variations in the quantity of parenchyma and vascular bundles, presence or absence of myrosin cells, nature of mechanical and epidermal layers. *C. acris, C. uliginosa* and *C. tenera* are characterised by an 8–11 layered parenchyma, 4–10 vascular bundles, absence of myrosin cells and heavily thickened mechanical layer (Fig. 2 b, d). *C. tenera* differs by stronger thickening of outer epidermis.

The remaining species have thinner valves with weakly thickened outer epidermis and myrosin cells. *C. wiedemanniana* has 5–7 layers of parenchyma, 3–6 vascular bundles and comparatively stronger thickening of the mechanical layer (Fig. 2 e, f). *C. hirsuta* and *C. parviflora* have a 4–6 layered parenchyma, 4–6 vascular bundles and a weakly thickened mechanical layer (Fig. 2 g). *C. impatiens* and *C. pectinata* also have a 4–6 layered parenchyma but they differ by having 5–9 vascular bundles, a narrower but strongly thickened mechanical layer and comparatively wider inner epidermis (Fig. 2 h).

B. Replum

Following PRANTL 1891, to the replum has been given ± importance in taxonomy of *Cruciferae* (HAYEK 1911, SCHULZ 1936, JANCHEN 1942) and recently its phylogenetic importance has been treated by DVOŘÁK 1971. In *Cardamine* it has been referred at sectional (SCHULZ 1903, HAYEK 1911, BUSCH 1939) as well as infrasectional (SPASSKAYA 1979) levels.

All these species are characterised by a well developed, smooth replum, sometimes having fibres (Fig. 3 b) along the centre. It is thicker at the periphery along the attachment with the frame, decreasing in thickness towards the centre. Sometimes the central portion is sloughed away at maturity. Epidermal cells are ± elongated towards the perpendicular axis of fruit, with or without calcium oxalate crystals.

The replum provides variations in thickness, nature of epidermal cells, presence or absence of crystale and fibres. *C. acris, C. uliginosa* and *C. tenera* are characterised by somewhat thicker replum having fibres, perpendicularly elongated epidermal cells with crystals and sometimes with irregular walls (Fig. 3 a, b). *C. wiedemanniana* differs by more elongated epidermal cells lacking crystals (Fig. 3 e).

The remaining species have thinner replum lacking fibres. *C. hirsuta* and *C. parviflora* have strongly elongated epidermal cells without crystals while *C. impatiens* and *C. pectinata* differ by having crystals and smaller cells (Fig. 3 c, d, f).

C. Seed-Coat

The seed-coat anatomy is uniform. The outer integument consists of an epidermis of tangentially elongated cells, filled with starch and slime. It is

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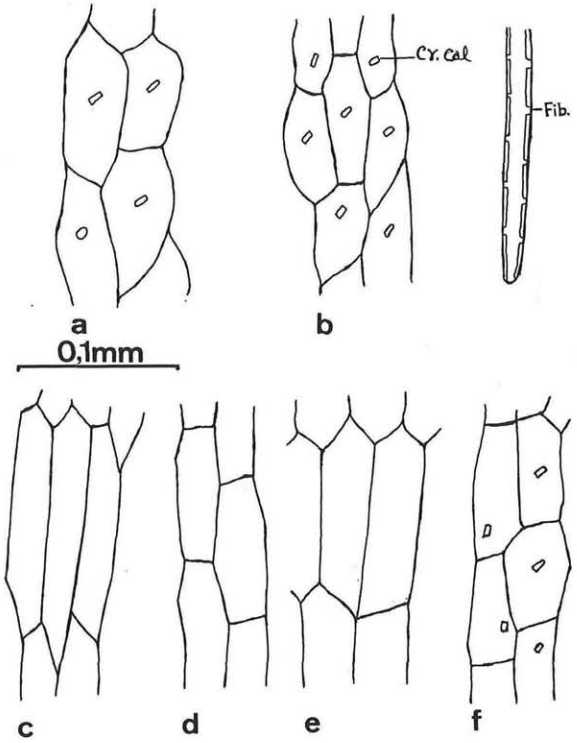

Fig. 3. Epidermal cells of the replum in *Cardamine* species. a *C. acris,* b *C. tenera,* c *C. hirsuta,* d *C. parviflora,* e *C. wiedemanniana,* f *C. impatiens.* – Cr. cal. crystals of calcium oxalate, Fib. fibre.

followed by a palisade layer having variously thickened and often pigmented cell walls. The inner integument is represented by a pigmented, cellular membrane tightly appressed to the palisade layer. The innermost layer consists of aleurone cells; it is a remnant of endosperm and is often followed by a hyaline layer.

As demonstrated by many authors in *Cruciferae,* the taxonomic importance of seed-coat anatomy also has been emphasized in *Cardamine* (ČERNOHORSKY 1974, VAUGHAN & WHITEHOUSE 1971, SPASSKAYA 1979). Recently the pigmented and aleurone layers also have been given taxonomic importance (cf. PORTELA and MORINO 1985). Here only epidermis and palisades seem to be of taxonomic value as in most of the Cruciferous taxa. The epidermal cells are mucilaginous and when soaked in water a column develops at the centre and after absorbing sufficient water often the outer periclinal wall ruptures. Usually the column develops easily and quickly but in some cases with difficulty *(C. wiedemanniana).* The form of this column

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has been studied in different Crucifers by many authors and 15 basic types have been distinguished by VAUGHAN & WHITEHOUSE 1971, out of which two have been observed here:

1. Mucilaginous cells with large columns on the inner tangential wall protruding into the lumen – *C. acris, C. tenera, C. uliginosa* and *C. wiedemanniana.*

2. Mucilaginous cells with minute protuberance from the inner wall – *C. hirsuta, C. parviflora, C. impatiens* and *C. pectinata.*

The palisade layer also shows variations in cell shape and thickening pattern of cell walls. Out of 8 main types discerned by VAUGHAN & WHITEHOUSE 1971 the following two types have been observed here:

1. Inner tangential walls thickened and the thickening flat or concave, cells almost isodiametric – *C. parviflora, C. impatiens* and *C. pectinata.*

2. Inner tangential and lower half of radial walls thickened, radial thickening almost conical, cells radially elongated or isodiametric – *C. acris, C. tenera, C. uliginosa, C. hirsuta* and *C. wiedemanniana.*

Thus as a whole, all these species are characterized by mucilaginous seed-coats. Anatomically *C. acris, C. tenera, C. uliginosa* and *C. wiedemanniana* show similarities, however the outer periclinal walls of the epidermis are convex in *C. acris, C. tenerea* and *C. uliginosa* (Fig. 4 a) but almost flat in *C. wiedemanniana* (Fig. 4 b). Furthermore, palisade cells are tangentially elongated with somewhat curved radial walls in the former species but broader and almost isodiametric in the latter. *C. hirsuta* and *C. parviflora*

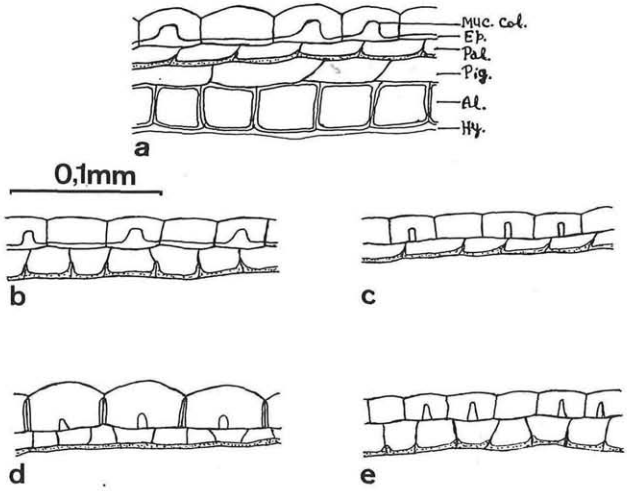

Fig. 4. Seed-coat structures in *Cardamine* species. a *C. tenera,* b *C. wiedemanniana,* c *C. hirsuta,* d *C. parviflora,* e *C. impatiens.* – Muc. col. mucilage column, Ep. epidermis, Pal. palisade layer, Pig. pigmented layer, Al. aleurone layer, Hy. hyaline layer.

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have similar mucilaginous columns but the epidermal cells are larger in *C. parviflora* with convex outer walls and thickened radial walls due to the accumulation of mucilage. Also they differ in palisade characters (Fig. 4 c, d). *C. impatiens* and *C. pectinata* are distinguished by having conical columns and broader palisade cells (Fig. 4 e).

Chromosome Numbers

Recently much attention has been paid to cytological investigations for understanding of the relationship of Cruciferous taxa. But within Caucasian taxa, chromosome data seem to be of little taxonomic or phylogenetic value. For most of these, chromosome numbers are known from Caucasia (SOKOLOVSKAYA & STRELKOVA 1948, DAVLIANIDZE 1980, GVENIANIDZE & AVAZNELI 1982, GAGNIDZE & al. 1985) or from adjoining parts which show that these are diploids. *C. tenera, C. uliginosa, C. impatiens, C. hirsuta* and *C. parviflora* have consistently the same number, 2n = 16, but *C. acris* seems an exception having 2n = 12 (DAVLIANIDZE 1980). Although its closer relative *C. raphanifolia* POURR. also has an exceptional number, 2n = 44–46 (LÖVKVIST 1956) which distinctly deviates from the normal x = 8. In the case of *C. acris* further confirmation is highly desirable. No karyological report exists for *C. pectinata* and *C. wiedemanniana,* but the size of the pollen grains indicates that these also are diploids.

Conspectus of Taxa

The conspectus is intended to summarize in a monographic way facts given in the previous accounts, however morphological data are provided in short. For easier identification a key is also included. The synonymy is carried only for names applied to material from the concerned and adjoining areas. Names below the rank of species are mentioned only when they are of special interest. General distribution is based on herbarium material and literature, however unverified reports have not been considered.

Cardamine Sect. *Cardamine*

Annuals, biennials or perennials with rhizome. Leaves pinnate and highly variable. Raceme many flowered. Flowers variable in colour and size. Sepals flat or seccate at base. Petals unguiculate or spathulate, rounded or emarginate. Nectaries annular with ring- or horseshoe-shaped lateral glands. Fruit valves with or without myrosin cells; septum smooth, with or without fibres, epidermal cells ± elongated towards the perpendicular axis of fruit, with or without calcium oxalate crystals. Funicules thin, rarely somewhat flattened at base. Seed-coad 3-layered, usually mucilaginous, embryo accumbent to obliquely accumbent, cotyledons plane, subsessile to short petiolate.

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Key to the Species

1. Annuals or biennials; flowers upto 5 mm; sepals flat; petals spathulate . . 2
– perennials with rhizome; flowers 5–15 mm; sepals saccate; petals unguiculate 5
2. Petioles with small, semiamplexicaul auricles 3
– Petioles without auricles 4
3. Leaves with 2–5 pairs of leaflets; siliques 0.8–1 mm wide, horizontally patent and secund, with 1.5–3.5 mm style . . . . . *C. pectinata*
– Leaves with 5–9 pairs of leaflets; siliques 1–1.4 mm wide, erecto-patent, with 0.8–1.5 mm style . . . . . *C. impatiens*
4. Glabrous; leaves with 3–8 pairs of leaflets with a subequal terminal one . . . . . *C. parviflora*
– Pubescent; leaves with 1–5 pairs of leaflets with a distinctly larger terminal one . . . . . *C. hirsuta*
5. Petals 5–8 mm, white, rounded; style filiform, stigma narrower than style, disc-shaped . . . . . *C. wiedemanniana*
– Petals 8–15 mm, white-lilac, emarginate; style thickened, stigma wider that style, capitate-bifid 6
6. Terminal leaflet in upper cauline leaves subequal or slightly larger than laterals; stem somewhat glaucous; petals cream-yellowish . . . *C. uliginosa*
– Terminal leaflet always strongly larger than laterals; plants green; petals pink-lilac or purple 7
7. Plants slender; petals 10–15 mm, pink-lilac rarely white . . . . . *C. tenera*
– Plants robust; petals 8–10 mm, light to deep-purple . . . . . *C. acris*

Subsect. *Tenerae* SPASSK.

Perennials with stoloniferous rhizome. Flowers 8–15 mm, white-lilac; sepals saccate; Petals emarginate; lateral nectaries ring- or horseshoe-shaped; anthers 1.2–1.8 mm, yellow. Siliques 20–40 × 1.0–1.8 mm, style 1–3 mm, stout and terete with capitate-bifid stigma; valves without myrosin cells; replum with fibres and calcium oxalate crystals.

Type Species: *C. tenera* S. G. GMEL. ex C. A. MEY.

C. acris GRISEBACH
Spicil. Fl. Rumel. 1: 253, 1843

Type: Hab. in regione alpina Macedoniae et Serbiae australis: Socialis in herbosis humidis et ad rivulos m. Nidze alt. 4400–5000′, 1839, GRISEBACH (K syntype, examined).

C. seidlitziana ALBOV, Bull. Herb. Boiss. 2: 448, 1894. – *C. raphanifolia* POURR. subsp. *acris* (GRISEB.) O. E. SCHULZ, Bot. Jahrb. 32: 512, 1903.

Perennial with ± elongated rhizome. Stem 15–65 cm, straight, robust, glabrous or with scattered hairs. Leaves upto 20 cm, petiolate, glabrous or sparsely hairy, with 1–5 (6) pairs of crenate leaflets and an exceedingly

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larger terminal one; lower cauline leaves similar to rosette leaves but smaller, uppermost ones sometimes simple; sometimes cauline leaves with short, leafy axillary buds. Raceme 15–40 flowered, dense at anthesis; pedicels 5–12 mm, stout; sepals 3.5–4.5 mm; petals 8–10 × 4–7 mm, pinkish to dark purple; lateral stamens 4.5–5.5 mm and medians 5.5–6.5 mm, anthers 1.2–1.8 mm, oblong-elliptic, yellow; ovary glabrous, with 20–28 ovules, narrowed in 0.5–1 mm style. Siliques 20–40 × 1.2–1.8 mm, erect, smooth, straw-colored to brownish; pedicels 10–20 mm, erecto-patent; style 1–2.5 mm, thickened, cylindrical, with almost subequal stigma. Seeds. 1.2–1.7 × 0.8–1.2 mm, oval, brown, narrowly winged. Flowering from late May to early September. 2n = 12.

Wet places, bogs, streamsides etc. in alpine-subalpine zones up to 2800 m, sometimes descending to 1350 m along hill streams. Western Transcaucasia from Kuban to Adzharia; Balkan and Asia Minor.

The systematic position of *C. acris* has remained unclear until now owing to different taxonomic understanding as some authors have placed it under the Pyrenean *C. raphanifolia* as its subspecies (SCHULZ 1903, JONES 1964, CULLEN 1965) while Soviet authors have recognised *C. seidlitziana* as a separate species merely for Causasian plants (BUSCH 1909, 1939, GROSSHEIM 1950, DAVLIANIDZE 1979, KOLAKOVSKÝ 1982 etc.). After a comparative study of large series of specimens from its range (including type specimens of *C. acris* and *C. seidlitziana*) the present author agrees fully with CULLEN 1965 regarding the Caucasian plants, Turkish and Balkanian ones, as identical but *C. acris* has been accepted as a separate species following previous authors (BOISSER 1867, 1888, FRITSCH 1895, HAYEK 1925).

C. acris is a perfectly good species, closely related to the Pyrenean *C. raphanifolia* from which it is sharply distinguished by pubescent leaves having upto 6 pairs of leaflets, a long and lax infructescence, patent siliques which are almost two times longer than pedicels, smaller stigma that is hardly wider than style and other morphological characters. These morphological differences are further complemented by geographical distribution and karyology as *C. rephanifolia* has a range from N. Italy to Spain and is hexaploid, with 2n = 44–46 (cf. LÖVKVIST 1956) while *C. acris* is distributed from the Balkan to Western Transcaucasia and is a diploid, with 2n = 12 (cf. DAVLIANIDZE 1980).

It is fairly polymorphic showing variations in several respects throughout its range depending on growth conditions. Consequently some infraspecific taxa have been recognised on the basis of pubescence, size of leaflets, axillary buds on stem leaves etc. (SCHULZ 1903, BUSCH 1909, 1939, GROSSHEIM 1950, KOLAKOVSKÝ 1982). Such variations are not correlated, hence these taxa do not seem worthy of recognition.

Specimens studied: All available at LE, LECB, MHA, MW and MOSM.

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C. uliginosa BIEBERSTEIN
Fl. Taur.-Cauac. 3: 438, 1819

Type: Circa Tatartup Promonterii Cauc. septentr. etiam repertur, in Ucrania c. Charkovian pariter occurrens, BIEBERSTEIN (LE holotype, examined).

C. caucasica WILLD. ex LEDEB., Fl. Ross. I: 126, 1841. – *C. olympica* BOISS., Diagn. Pl. Orient. Nov. ser. 1, 8: 19, 1849. – *C. ochroleuca* STAPF, Denkschr. Akad. Wiss., Math.-Naturw. Kl. (Wien) 51: 297, 1886. – *C. tenera* auct. non S. G. GMEL. ex C. A. MEY.: BOISS. Ann. Sci. Nat. (Paris), ser. 2, 17: 56, 1842.

A perennial with ± elongated rhizome. Stem 10–70 cm, straight, usually glaucous. Leaves upto 22 cm, petiolate, with 4–9 pairs of leaflets which are orbiculate-ovate, entire to wavy in basal leaves with distinctly larger terminal one, congested, narrower and entire in cauline leaves with slightly larger to subequal terminal one. All leaves hairy. Raceme dense with 15–40 flowers; pedicels 5–12 cm, stout; sepals 3.5–4.8 mm; petals 7–12 × 3.5–7 mm, white-cream to yellowish, occasionally with purple-tinted claws; lateral stamens 4.5–5.5 mm and medians 5.5–7 mm, anthers 1.2–1.8 mm, oblong-elliptic; yellow; ovary glabrous, with 20–34 ovules, narrowed in 0.5–1 mm style. Siliques erect, 20–40 × 1.2–1.7 mm, smooth, straw-colored to brownish; pedicels 15–20 mm, erecto-patent; style 1–2.5 mm, stout and terete. Seeds 1–1.6 × 0.8–1.2 mm, oval, brown, narrowly winged. Flowering from late April to early August. 2n = 16.

Damp meadows, bogs, streamsides etc. in alpine-subalpine belts upto 3000 m, sometimes descending to 1000 m along hill streams. Throughout Causasia; N. and W. Iran, N. Iraq, W. Syria and Asia Minor to Istambul.

It is a highly polymorphic species showing variations in the degree of pubescence, shape, size and number of leaflets, colour and size of petals etc. Hence infraspecific taxa have been recognised (SCHULZ 1903, BUSCH 1909, 1939, GROSSHEIM 1950, AKHUNDOV 1953), but such variations are not correlated and are rather caused by growth conditions as plants in drier and open habitats show diminution in floral and vegetative parts while pubescence becomes stronger. Therefore these taxa are not to be recognised taxonomically.

Specimens studied: All available at LE, LECB, MHA, MW and MOSM.

C. tenera S. G. GMEL. ex C. A. MEY.
Verz. Pflanz. Cauc.: 179, 1831

Type: Hab. in sylvis montium Talüsch, locis humidis, sylvaticis montium prope Lenkoran, 1830, GMELIN, no. 1592 (LE holo and isotypes, examined).

C. uliginosa BIEB. subsp. *tenera* (S. G. GMEL. ex C. A. MEY.) SCHMALH., Fl. Sred. – Yuzhn. Ross. 1: 50, 1895 (sine auct. comb.). – *C. uliginosa* auct

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non BIEB.: STEVEN, Bull. Soc. Nt. Moscou, 29 (2): 301, 1856, p.p. – *C. latifolia* auct. non VAHL: KUNTZE, Acta Horti Petropol. 10 (1): 165, 1887.

A perennial with shortened rhizome. Stem 20–50 (60) cm, slender, from axils of basal leaves develop long, leafy stolons often bearing simple leaves. Leaves up to 15 cm, petiolate, with 1–4 pairs of small, sessile, entire leaflets, with strongly larger terminal ones. Raceme rather lax, with 10–25 flowers; pedicels 8–15 mm slender and somewhat declining; sepals 3.5–4.5 mm; petals 8–15 × 4–8 mm, pink-lilac rarely white; lateral stamens 5.5–6.5 mm and medians 6.5–8 mm, anthers 1.4–1.8 mm, oblong-elliptic, yellow; ovary glabrous, with 20–40 ovules, slightly narrowed in 0.5–0.8 mm style. Siliques 25–40 × 1–1.4 mm, somewhat convex, spreading, straw-colored; pedicels 15–25 mm, strongly patent; style 1–2.3 mm, thickened and terete. Seeds 1–1.2 × 0.7–0.9 mm, oval, brown, narrowly winged, Flowering in April to July. 2n = 16.

Bogs, damp meadows, along watercourses from lowland woods to subhills. W. and E. Transcaucasia, Talysh; Crimea, Kursk and Kharkov Provinces, N. Anatolia and N. Iran.

Specimens studied: All available at LE, LECB, MHA, MW and MOSM.

Subsect. *Amarae* SPASSK.

Perennials with repent, stoloniferous rhizome. Stems multifoliate. Flowers 5–10 mm; sepals saccate, ovate; petals white rarely pink-lilac, unguiculate, rounded or slightly emarginate; lateral nectaries horseshoe-shaped; anthers 0.8–1.4 mm, oblong, elliptic, yellow or violet. Siliques 15–30 × 1–1.5 mm, style 1.5–3.5 mm, tapering to a minute disc-shaped stigma which is narrower than the style or rarely subequal. valves with myrosin cells, replum with fibres and without oxalate crystals.

Type species: *C. amara* L.

C. wiedemanniana BOISS.
Fl. Orient. 1: 162, 1867

Type: Hab. in Aladagh, Anatoliae, WIEDEMANN (G-BOIS holo- and isotypes, K isotype, examined).

C. lazica BOISS & BAL. in BUSER, Fl. Orient. Suppl. 1: 31, 1888. – *C. amara* L. prol. *lazica* (BOISS. & BAL.) O. E. SCHULZ, Bot. Jahrb. 32: 500, 1903.

Perennial with repent, stoloniferous rhizome. Stem 15–40 cm, straight, multifoliate, glabrous rarely pubescent. Leaves upto 9 cm, all similar, petiolate, with 1–3 pairs of sessile, small, oblong-ovate, entire laterals and a strongly larger terminal one which is orbiculate-ovate, emarginate in the lower leaves and oblongelliptic, lobate-crenate in the upper ones. Raceme lax, with 12–30 flowers; pedicels 5–10 mm, slender and ascending; sepals 2.5–3.2 mm; petals 5–8 × 2.5–3.5 mm, white, rounded; lateral stamens

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3–4 mm and medians 4–5 mm, anthers 0.8–1.2 mm, oblong-elliptic, yellow; ovary glabrous, with 16–20 ovules, style 1–1.5 mm, filiform with a minute, disc-shaped stigma. Siliques 20–25 × 1–1.5 mm, distant, smooth, straw-colored; pedicels 8–15 mm, patent; style subulate, 2–3.5 mm, stigma punctate, narrower than the style. Seeds 1–1.4 × 0.8–1 mm, oval, darkbrown, narrowly winged. Flowering in April to July.

Moist places in subcoastal lowlands to medium altitudes. Western Transcaucasia from Abkhazia to Adzharia; Asia Minor (N. Anatolia).

This species has long been referred to as *C. lazica* BOISS. & BAL. which is a latter substitute name for the same plant. Firstly, it was described as *C. wiedemanniana* (BOISSIER 1867), however later on it was passed under a new name *C. lazica* (BOISSER 1888) from the same locality (Anatolia near Rize and between Anden and Djimil, 1866, BALANSA). Previously it was said to have a "non stoloniferous" rhizome and to be closely related to *C. amara* and *C. uliginosa* while under the second name as having "stolonoferous" rhizome and to be closer to *C. tenera*. Despite the fact that either names were based on the same plant, the binome *C. lazica* was retained by some authors (ALBOV 1895; LIPSKÝ 1899) neglecting the first legitimate binome *C. wiedemanniana*.

Later on, SCHULZ 1903 passed the Lazistanian plant under *C. amara* as its infraspecific taxon, prol. *lazica*, however the first name *C. wiedemanniana* was cited in synonymy of *C. amara*. Apparently, SCHULZ also got as confused as BOISSIER, hence thought that these names were applicable to two different plants. Immediately after SCHULZ, again it was recognised as a separate species by BUSCH 1909, but he also retained the name *C. lazica* following his predecessors and this remains accepted until now (BUSCH 1939, GROSSHEIM 1950, DMITRIEVA 1960, CULLEN 1965, DAVLIANIDZE 1979, KOLAKOVSKÝ 1982).

After examining authentical specimens of *C.lazica* and *C. wiedemanniana* (isotypes at K and photocopies of holo- and isotypes from G-BOIS) it has been confirmed that either names are based on the same plant. Thus the epithet *wiedemanniana* being the first valid one can not be discarded.

Literature shows that *C. wiedemanniana* is glabrous throughout its range, but during this investigation some specimens from Adzharia Province were found having pubescent stems with short hairs. Possibly, such variations are related to growth conditions.

Specimens studied: Abkhazia: 1902, WORONOW no. 333 (LE); 1925, STEUP (LE); Belaya-Laba Rivers, 1930, LESKOV (LE); Kavk. Gos. Reserve, 1929, LESKOV & PUSALEEV no. 396 (LE); Batumi Pr.: pr. Budiet, 1902, ALEXEENKO & WORONOW no. 5390 (LE); fontes fl. Murgul-Su, 1902, ALEXEENKO & WORONOW no. 5392 (LE); Gadarsk Pass, 1913, LITVINOV (LE); 1957, SHRETER no. 52/57 (LE); Kindrizhskoe ravine, 1967, KRYLOVA & al. (MW); Adzharia: Nonus-oglje, 1300 m, 1913, LITVINOV (LE); near Khino, 1914,

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KIKODSE (LE); Chokhatauri, 1952, SCHLOTH. (MOSM); Korolis-Tskhali, 1958, MAZURENKO (MHA); Khulaisk, 1961, DMITRIEVA (LE); SE. territory, 1965, SHRETER & PUMEROV (MOSM); Tsebeljdo, 1903, MARCOWICZ (LE); Trape Sondenses, near Karshut Bazar, 1916, TURKEVICZ no. 132 (LE).

Subsect. *Brachypetalae* JANCHEN ex SPASSK.

Annuals; flowers 1.5–4 mm; sepals flat, oblong, blunt; petals, spathulate, rounded, white; lateral nectaries horseshoe-shaped; anthers 0.3–0.6 mm, elliptic, yellow; ovary glabrous with very short style. Siliques 10–30 × 0.7–1.3 mm, style short, conical, valves with myrosin cells, replum without fibres and oxalate crystals.

Lectotype species: *C. hirsuta* L.

C. parviflora L.
Syst. Nat. ed. 10,2: 1131, 1759

Type: "Hab. in Europae" (LINN, fot. 835–10 lectotype, examined).

Annual, 7–40 cm, straight or flexuous, simple or branched, glabrous with nonpersistent basal leaves. Cauline leaves petiolate, up to 7 cm, lower ones with 3–5 pairs of lanceolate-obovate, lobate leaflets; upper ones with 3–8 pairs of pectinate, linear-oblong, entire leaflets; terminal leaflets subequal. Raceme 20–30 flowered, compact; pedicels 2–4 mm; sepals 1–1.5 mm; petals 1.5–2.5 × 1–1.2 mm; lateral stamens 1.4–1.8 mm and medians 1.8–2.2 mm, anthers 0.3–0.4 mm; ovary glabrous, with 20–36 ovules, style hardly distinct to very short (0.1–0.3 mm) with subequal, entire stigma. Siliques 10–20 × 0.7–1 mm, erect, smooth, straw-colored, sometimes purple tinted; pedicels 5–8 mm, strongly patent; style 0.3–1 mm, conical and slender. Seeds 0.6–0.9 × 0.5–0.7 mm, oblong-oval, orange, narrowly winged. Flowering in May and July. 2n = 16.

Moist places in forests ascending to medium altitudes. Scattered in Western Transcaucasia and Talysh; Eurasia, N. America, N. and E. Africa.

Specimens studied: Lenkoran: 1829, C. A. MEYER no. 159 (LE); FISCHER (LE); 1838, HOHENACKER no. 2795 (LE); Azerbaij. SSR, Pr. Astarinsk: BOBROV & TSVELOV nos. 231, 753 (LE); Pr. Pagum, Gamishavan: 1838, C. A. MEYER no. 1594 (LE); Batumi Pr.: 1913, LESHVISOV (LE).

C. hirsuta L.
Sp. Pl.: 655, 1753

Type: "Hab. in Europae areis, hortis, arvis" (LINN, fot. 835–13 lectotype, examined).

C. tetrandra HEGETSCHW., Fl. Schweiz: 64, 1840. – *C. hirsuta* L. subsp. *multicaulis* (HOPPE ex KOCH) ČELAK., Prodr. Fl. Böhm. 3: 451, 1874 (cum auct. comb. HOPPE).

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Annual, 5–35 cm, simple or branched, glabrous or pubescent with scattered hairs and 2–6 leaves. Leaves up to 9 cm, petiolate, with straight cilia at the base and 1–5 pairs of hairy leaflets. Basal leaves in rosettes having orbicular-obovate, entire to trilobed lateral leaflets and a larger orbicular-reniform, 3–5 lobate terminal one. Cauline leaves smaller with angular, linear-lanceolate leaflets. Raceme dense at anthesis, with 12–25 flowers; pedicels 1–2 mm; sepals 1.5–2 mm, hirsute on dorsal side; petals 2.5–3.5 (4) × 1–1.5 mm, white; stamens 6 (4), laterals absent or 1.8–2.2 mm and medians 2.2–2.6 mm, anthers 0.3–0.6 mm; ovary glabrous, with 24–36 ovules, hardly narrowed in a 0.1–0.3 mm style with subequal, entire stigma. Siliques 15–25 × 1–1.3 mm, erect, overtopping the flowers, smooth, straw-colored, sometimes lilac dotted; pedicels 5–10 mm, ascending; style 0.5–1 mm, conical. Seeds 0.9–1.3 × 0.6–0.9 mm, oval-orbiculate, orange, narrowly winged. Flowering from late March to July. 2n = 16.

Widespread in plains and subhills of Caucasia, often adventive in fields, lawns etc.; Europe, Asia Minor, Iran, Himalayas, N. and E. Africa; introduced in N. America, Australia and New Zealand.

It is a highly polymorphic species showing variations in habit, flower size, degree of pubescence etc. throughout its range, hence infraspecific taxa have been recognised by some authors (SCHULZ 1903, BUSCH 1909, GROSSHEIM 1950). But such variations rather are caused by growth conditions.

Specimens studied: All available et LE, LECB, MHA, MW and MOSM.

Subsect. *Sagittatae* JANCHEN ex SPASSK.

Annuals or biennials with auriculate petioles. Flowers 2.5–5.5 mm; sepals straight, oblong, blunt; petals white, spathulate, tip rounded; lateral nectaries horseshoe-shaped; anthers 0.5–1 mm, oblong, greenish. Siliques 15–30 × 0.8–1.4 mm, sometimes hairy, patent, style distinct and slender, valves with myrosin cells, replum with oxalate crystals and without fibres.

Type species: *C. impatiens* L.

C. impatiens L.
Sp. Pl.: 655, 1753

Type: "Hab. in Europae in nemoribus ad radives montium" (LINN, fot. 835–9 lectotype, examined).

C. apetala GILIB., Fl. Lith. 4: 42, 1785. – *C. dasycarpa* BIEB., Fl. Taur.-Cauc. Suppl. 3: 437, 1819. – *C. impatiens* L. var. *impatiens* CULLEN in DAVIS, Fl. Turk. 1: 443, 1965.

Annual or biennial, 20–75 cm, straight, simple or branched upwards, glabrous, ridged. Rosette leaves non persistent at anthesis. Cauline leaves upto 15 cm, petiole auriculate at base, with 4–9 pairs of glabrous or ciliate,

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crenate-lobate, ovate-lanceolate leaflets; terminal one slightly larger. Raceme dense, with 10–40 flowers; pedicels 2–5 mm; sepals 1.5–2 mm; petals 2.5–3.5 × 1–1.5 mm; outer stamens 2.3–2.6 mm and inners 2.6–3 mm, anthers 0.5–1 mm, oblong, greenish; ovary glabrous or hairy, with 10–24 ovules, style 0.3–0.5 mm with subequal, entire stigma. Siliques 15–30 × 1–1.4 mm, suberect, smooth or with scattered hairs, straw-colored; pedicels 5–10 mm, strongly patent; style 0.8–1.5 mm, conical. Seeds 1.2–1.7 × 0.7–1 mm, oval-oblong, light brown, sometimes narrowly winged. Flowering from May to early August. 2n = 16.

Widespread throughout Caucasia in waste lands and forests ascending to 2500 m in subalpine zone; Eurasia, introduced in N. America.

Throughout its range it exhibits some variations, consequently some infraspecific taxa have been recognised (DE CANDOLLE 1821, SCHULZ 1903, BUSCH 1909, 1939, GROSSHEIM 1950), however in Caucasia only var. *eriocarpa* DC. (= *C. dasycarpa* BIEB.) seems distinct which replaces the typical form in higher elevations from 1800 to 2500 m.

Specimens studied: All available at LE, LECB, MHA, MW and MOSM.

C. pectinata PALL. ex DC.
Syst. Nat. 2: 264, 1821

Type: "Hab. in Persia, PALLAS" (B-W syntype, examined).

C. oxycarpa BOISS., Ann. Sci. Nat. (Paris), ser. 2, 17: 56, 1852. – *C. impatiens* L. var. *pectinata* (PALL ex. DC.) TRAUTV., Acta Horti petropol. 4 (1): 105, 1876. – *C. impatiens* L. prol. *pectinate* (PALL. ex DC.) O. E. SCHULZ, Bot. Jahrb. 32: 458, 1903 (cum auct. comb. TRAUTV.).

Annual or biennial, 15–45 cm, glabrous, profusely branched from the base. Rosette leaves non persistent at anthesis. Stem leaves up to 14 cm, petiole auriculate at base, with 2–5 pairs of crenate-lobate, ovate-oblong-lanceolate, ciliate leaflets; terminal one larger. Raceme with 8–30 flowers; pedicels 2–5 mm, slender; sepals 2–2.5 mm; petals 3.5–5.5 × 1.5–2.5 mm; outer stamens 2.7–3.1 mm and inners 3.1–3.5 mm, anthers 0.6–1 mm, oblong, greenish; ovary glabrous or hairy, with 10–78 ovules, narrowed in 0.7–1.2 mm style with subequal stigma. Siliques 15–30 × 0.8–1 mm, horizontally patent and often secund, smooth or with scattered hairs, straw-colored; pedicels 5–8 mm, horizontaly patent; style 1.5–3.5 mm, slender. Sleeds 1.4–2 × 0.6–0.8 mm, oblong-oval, light brown, often narrowly winged. Flowering in April to July.

Damp and shady forests ascending in subalpine zone along hill streams. W. and E. Transcaucasia, Talysh; Balkan, Asia Minor, N. Iran.

C. pectinata has been widely accepted as a separate species, but some authors have passed it under *C. impatiens* as a infraspecific taxon (TRAUTVETTER 1876; SCHULZ 1903; CULLEN 1965; HEDGE 1968). The morphological and anatomical similarities and the occurrence of transgressing forms

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indicate that they are of common origin, but in its typical form *C. pectinata* differs sharply by a stem profusely branched at base, 2–5 paired leaves with larger leaflets, larger and consistent petals, pollen and nectary characters; narrower, horizontally patent, often secund siliques with longer and slender style etc. Usually, both have the same range but *C. pectinata* prefers damper, shady habitats while *C. impatiens* thrives on exposed, comparatively less mesic localities.

Infraspecific taxa have been recognized on the basis of indumentum of siliques and leaf size (ALBOV 1895, BUSCH 1909, GROSSHEIM 1950), however such variations do not seem taxonomically relevant.

Specimens studied: All available at LE, LECB, MHA, MW and MOSM.

Conclusion

Present distribution and karyology support that these species are tertiary relicts as assumed by BUSCH 1909 and may be regarded as derivatives of ancient Mediterranean flora, but owing to the fact that they do not constitute a single homogenous group, the problem of their origin and relationships is somewhat complicated. *C. hirsuta, C. parviflora* and *C. impatiens* are widespread Eurasian elements and must have entered from the West. *C. hirsuta* and *C. parviflora* are so closely related that they must be regarded as parallel divergents of a common ancestry. *C. parviflora* is rather sparse in Caucasia, however the far extending range shows that it is a relic of former wide distribution.

C. pectinata represents a direct offshoot from *C. impatiens* and the place of divergency seems within the present distribution which took place immediately after the entering of *C. impatiens* from the West. This divergence is of old age, consequently *C. pectinata* has undergone parallel development beside habitat preferences, thus it sufficiently differs as a separate species.

C. wiedemanniana is somewhat more isolated from the ancestral Eurasian *C. amara* L. and Balkanian *C. barbaraeoides* HAL. But it is rather clear that it moved eastward from the Balkan; it is a direct divergent from *C. barbaraeoides* or a form from which the latter was developed and its closeness to *C. amara* seems definitely through *C. barbaraeoides*.

C. acris is so close to the Pyrenean *C. raphanifolia* POURR. that they must have a common origin; *C. acris* moved eastwards up to West Caucasia while *C. raphanifolia* extended westwards up to Spain. *C. uliginosa* is sufficiently similar to *C. acris* in its general morphology, anatomy, habit and ecology to give an impression of common origin or possibly *C. acris* itself was the parental type. *C. uliginosa* is so common in Caucasia that it forces one to assume that the place of divergency was in Caucasia or in immediately adjacent parts of Asia Minor from where *C. uliginosa* became widespread

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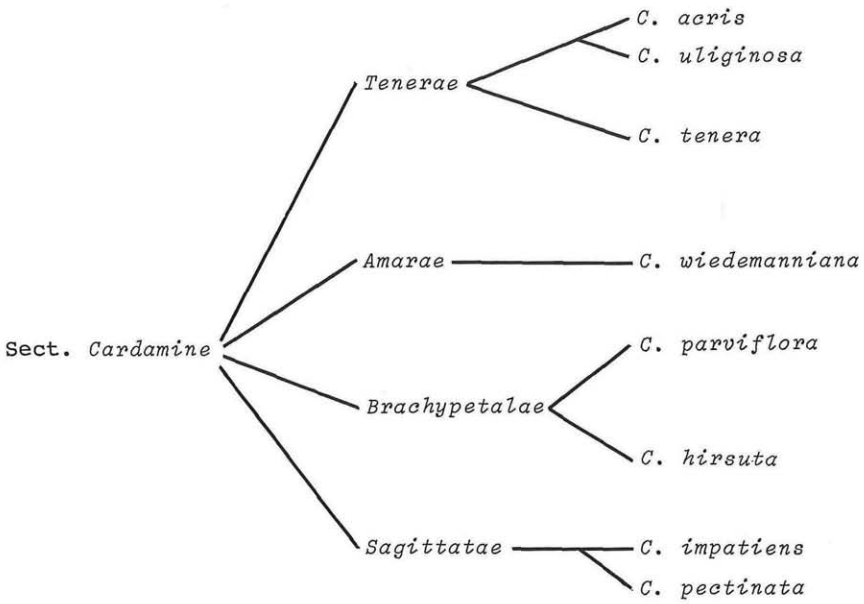

Fig. 5. Scheme of the supposed relationships in *Cardamine* sect. *Cardamine*.

even beyond the access of *C. acris,* and also extended westwards into Asia Minor. It is regarded as an introduced one in European Turkey (cf. CULLEN 1965: 422) which also supports the thought of its eastern origin.

In the case of *C. tenera,* the extended range in the North, specialization to habitat preference and the absence of any such closer species from its range indicate direct ancestral relationships with *C. acris* and *C. uliginosa.* It is quite close to these in general morphology and anatomy, but differs in ecological requirements, rhizome and nectary characters. So it seems difficult to predict whether *C. tenera* is an offshoot from *C. uliginosa* or sprang more directly from *C. acris.* The present distribution pattern shows that it is a relic of formerly more widespread distribution.

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