

TYPES OF MESOPHYLL IN ASSIMILATING ORGANS IN CONNECTION C₃ AND C₄ PHOTOSYNTHESIS TYPES IN THE SPECIES OF GENUS *CLIMACOPTERA* BOTSCH. (*CHENOPODIACEAE* VENT.) CENTRAL ASIA

Guljan M. Duschanova

Academy of Sciences, Republic of Uzbekistan, Institute of Gene Pool of Plants and Animals. 232
Bagishamol Str., Tashkent, 100053

Corresponding author: Guljan M. Duschanova

ABSTRACT: The structure of assimilating organs in five species of *Climacoptera* is described: mesophylls of cotyledon, leaf, bract and perianth. The change type mesophylls assimilating organs from the cotyledons (and leaf bracts, bracteoles) to perianth in species *Climacoptera* on saline soil and Mirzachul (Uzbekistan, Province Sirdarya) and Kyzylkums (Uzbekistan, Province Buhora, Navoiy, Karakalpakstan, Province Miskin) related C₃ and C₄ types of photosynthesis. Identified quantitative parameters Kranz-cells and their variability in the ontogeny of plants and species specificity. The level of their specialization, xeromorphy and halomorphy is determined. Regularities of adaptation of succulent species with the Kranz anatomy to xero- and halo factors, which enable insights into the nature of their halophytism, are revealed. A high coefficient of the similarity of species from one section in different habitation conditions was shown using the cluster analysis.

Keywords: adaptation, assimilating organs, *Climacoptera*, halophyte, xerophyte, Mirzachul, Kyzylkum, Kranz-anatomy.

INTRODUCTION

In some *Chenopodiaceae* species the combination of C₃ and C₄ types of photosynthesis is observed during ontogeny. This is connected with the structure of different assimilating organs.

The structure of leaves in some species of the order and ecological groups of *Chenopodiaceae* has been studied for a long time due to the processes of their adaptation and in the last few years due to the type of metabolism (Carolin et al. 1975; Butnik et al., 1991; Fisher et al. 1997; P'yankov et al. 1997). Butnik et al. (1991) indicated the necessity of the study and comparison of the cotyledon structure with that of the leaf, i.e. changes in the mesophyll type in ontogeny.

Further studies by V. P'yankov et al. (1998), E. Voznesenskaya et al. (1999), H. Freitag, W. Stichler (2000) and Butnik (1999) indicated the promising feature of comparison of assimilating organs for the understanding of the evolutionary level of a taxon and changes in the type of metabolism. In this connection it is important to identify in which organs and at what stages of ontogeny Kranz cells are present.

The goal of the work is to reveal types of mesophyll in vegetative organs, which perform the assimilating function at different levels of plant ontogeny.

MATERIALS AND METHODS

Assimilating organs in five species of the genus *Climacoptera* species from three sections were examined: 1. Section *Ulotricha* Pratov. – *Climacoptera ferganica* (Drob.) Botsch. is an annual plant, euhalophyte, grows in solonchaks (saline soils), takyrs (dry-type playa) and saline sands. Geographical range: Iran, Afghanistan, Central Asia, and Dzungaria. 2. Section *Amblyostegia* Pratov. – *Climacoptera intricata* (Iljin) Botsch. is an annual plant, euhalophyte, grows in solonchaks (saline soils). Endemic to Central Asia. – *Climacoptera aralensis* (Iljin) Botsch. is an annual plant, euhalophyte, grows in solonchaks, saline sands. Endemic to Central Asia. 3. Section *Climacoptera* Pratov. – *Climacoptera lanata* (Pall.) Botsch. is annual plant, euhalophyte. The species with a wider area: Turkey, Iran, Afghanistan, Pakistan, northeastern area of Russia, Central Asia, Dzungaria and therefore more diverse ecology, solonchaks (saline soils), pit-run fines-gravelly soils, saline sands. – *Climacoptera longistylosa* (Iljin) Botsch. is an annual plant, grows on saline soils. Natural habitat: Afghanistan, Central Asia and Kazakhstan (Pratov, 1986).

C. intricata and *C. longistylosa* grow in Mirzachul (Uzbekistan, Province Sirdarya) in compacted less saline soils, *C. ferganica*, *C. lanata* and *C. aralensis* grow in southwestern Kyzylkum (Uzbekistan, Province Buhora, Navoiy and Karakalpakstan, Province Miskin) on less compacted sandy loam, but more saline soils.

The mesophylls of cotyledons and leaf (from the mid-layer of annual shoots), bract, bracteole and perianth in the beginning of flowering were studied. The material collected for the study was fixed in 70° ethyl alcohol. The type of mesophyll was identified on cross-sections. The sections were made using the straight razor, dyed in the methylene blue, glued in glycerol- gelatin. The form and shape of major epidermal cells were described using the methods described by Zakharevich (1954). Measurements were made using the routine methods (Barykina, Chubatova, 2005). The preparations were drawn by using the drawing apparatus RA-6 under the microscopy MBI-3.

The measurements were replicated 30 times and the average value was calculated; errors of the measurement and significance were identified using Zaitsev formula (1991). The cluster analysis was conducted using the software Past on the basis of Jaccard index of similarity (Shmidt, 1984).

RESULTS AND DISCUSSION

Cotyledons in the species of the genus *Climacoptera* are lamellate, oval. The longest and widest are recorded in *C. intricata* and *C. longistylosa*; the small ones in *C. ferganica* and *C. lanata*, *C. aralensis*.

The mesophyll in cotyledons is dorsoventral, of the non-Kranz type, with one row of palisade cells (*C. ferganica*, *C. longistylosa* and *C. aralensis*), two rows (*C. intricata*) or 2-3 rows (*C. lanata*). The tallest palisade cells were recorded in *C. Ferganica* and *C. aralensis*; the lowest in *C. lanata* (Table 1, Fig. 1).

The cells of the lacunose parenchyma were largest in *C. intricata*, while smallest in *C. lanata* and *C. aralensis*. Conducting bundles in *C. ferganica* and *C. aralensis* are not scleral; in other species are weakly scleral and surrounded by one row of parenchymal liner.

Mesomorph traits prevail in the structure of cotyledons: the absence of indumentums and a low palisade index.

Table 1. Quantitative values of the cotyledons of the *Climacoptera* species (n=30)

Value	<i>C. ferganica</i>	<i>C. lanata</i>	<i>C. intricata</i>	<i>C. ongistylosa</i>	<i>C. aralensis</i>
Cotyledons:					
length, mm	5,8±0,2	8,8±0,2	11,2±0,2	10,8±0,2	5,2±0,2
width, mm	1,5±0,02	3,4±0,02	4,8±0,2	4,8±0,2	1,3±0,02
thickness, µm	338,2±2,3	297,3±2,8	321,7±8,1	284,0±4,4	264,1±2,4
Epidermis:					
height, µm	31,0±0,4	26,9±0,3	28,9±0,8	28,3±0,6	27,4±0,2
Thickness of outer wall, µm	5,4±0,1	5,1±0,1	4,4±0,1	4,5±0,1	4,6±0,1
Palisade cells:					
number of rows	1	3	2	1	1
layer thickness	40,0±0,7	72,1±0,8	68,2±1,3	32,3±0,5	40,5±0,4
height, µm	40,0±0,7	29,0±0,5	30,1±0,9	32,3±0,5	40,5±0,4
width, µm	18,5±0,4	17,1±0,2	22,9±0,5	14,3±0,2	17,7±0,2
palisade index	2,1	1,7	1,3	2,2	2,3
Lacunose parenchyma:					
number of rows					
thickness, µm	8-10	6-7	7-8	8-9	8-10
d – cells, µm	236,2±0,9	171,4±1,3	186,2±2,4	195,1±2,7	204,0±1,9
	34,2±0,3	25,5±0,3	34,5±0,5	28,4±0,5	25,3±0,2
Number of conducting bundles	11,1±0,2	17,4±0,2	22,2±0,2	21,6±0,2	8,9±0,1

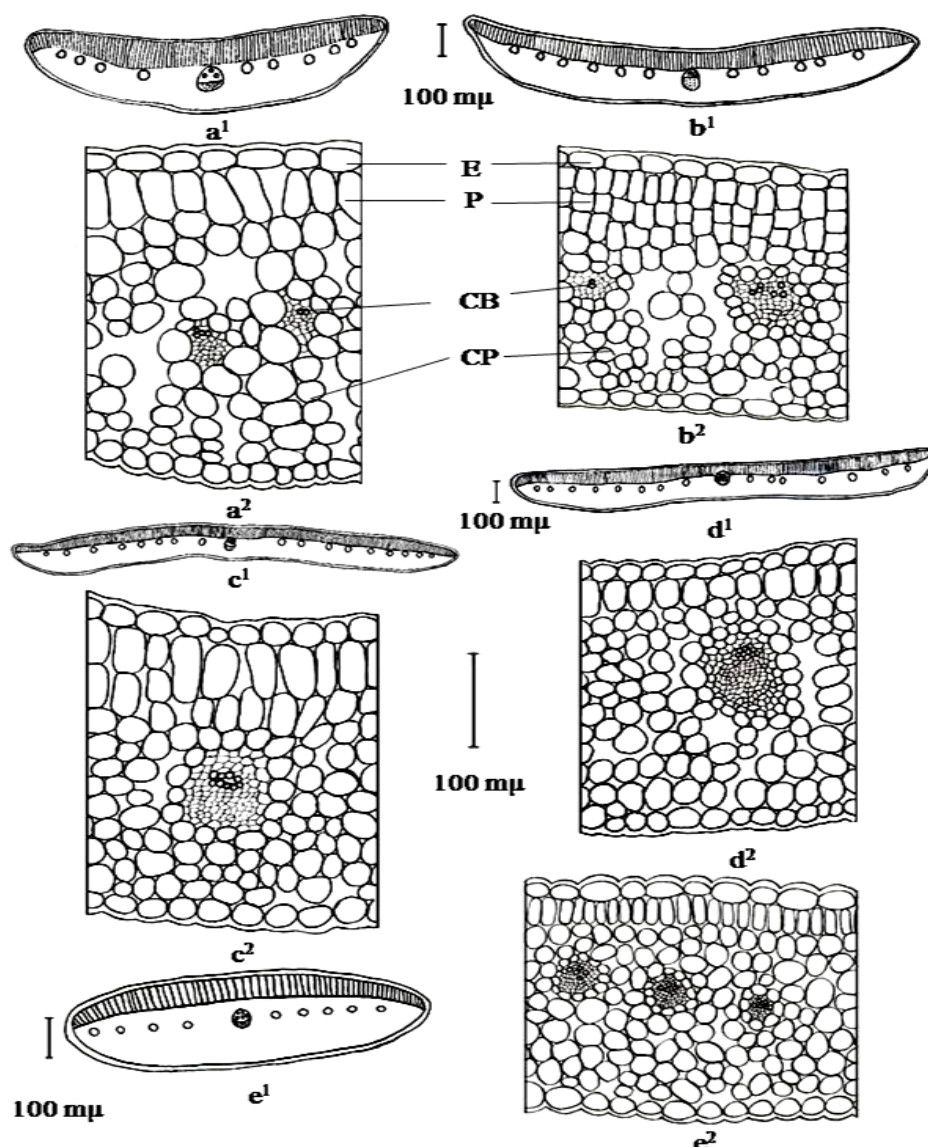


Fig. 1. Structure of the cotyledons in the species *Climacoptera* on the cross-section: a¹ – a² – *C. ferganica*; b¹ – b² – *C. lanata*; c¹ – c² – *C. intricata*; d¹ – d² – *C. longistylosa*; e¹ – e² – *C. aralensis*. a¹ – e¹ – scheme, a² – e² – detail. Key: P – palisade parenchyma, spongy parenchyma, CB – conducting bundle, E – epidermis.

The species of the genus *Climacoptera* are typical leaf succulents. Adaptive traits of the succulent group are the presence of a specialized water bearing tissue, performance of water- and salt-retaining function by other leaf tissues, including the epidermis.

The analysis of quantitative indexes of the leaf revealed characteristic traits of species of the genus *Climacoptera* Botsch. The largest leaves are in *C. longistylosa* and *C. intricata*, the small, *C. ferganica*, *C. lanata* and *C. aralensis*. The leaf is covered with three types of trichomes: long 3-8 cellular monostichous trichomes with a broad basis, falling; short 1-2 cellular with narrow basis (3 species); thin numerous long filiform of a single type (*C. intricata*). Least covered were the leaves of *C. ferganica* (Table 2).

Two Kranz types of mesophyll were found in the leaf: Kranz-ventro-dorsal mesophyll at the basis; close to Kranz-centric (Salsoloid - type) but differing from it by the openness of chlorenchyma on the adaxial side and separation of conducting bundles from the Kranz lining by water-bearing cells. As G. Kadereit, T. Borsch, K. Weising et al. (2003), we believe that this type of mesophyll as an independent *Climacoptera*-type (Fig. 2).

Table 2. Quantitative measures of leaves of *Climacoptera* species (n=30)

Indicator	Species				
	<i>C. ferganica</i>	<i>C. lanata</i>	<i>C. intricata</i>	<i>C. longistylosa</i>	<i>C. aralensis</i>
Leaf:					
length, cm	19,8±0,6	21,8±0,8	30,0±0,8	31,6±0,5	17,4±0,3
width, mm	1,8±0,04	2,2±0,07	1,9±0,04	2,4±0,7	1,6±0,04
thickness, mm	1,28±0,01	1,46±0,02	1,43±0,01	1,33±0,01	1,1±0,01
Epidermis:					
height, µm	37,0±0,3	32,1±0,3	45,1±0,4	31,4±0,3	40,0±0,5
thickness of outer wall, µm	4,3±0,1	3,7±0,1	7,5±0,1	4,5±0,1	5,8±0,1
area of cell, µm ²	2908±38,5	2155±19,1	3610±52,4	3621±39,7	2890,6±50,3
Palisade parenchyma:					
height, µm					
width, µm	49,2±0,4	56,3±0,6	50,0±0,3	65,4±0,4	49,4±0,3
index of palisade layer	14,0±0,2	12,0±0,2	13,3±0,2	15,1±0,1	13,6±0,2
	3,5±0,06	4,7±0,08	3,8±0,06	4,3±0,04	3,7±0,1
Waterbearing cells, µm:					
layer thickness					
% of d – leaf	1197,4±4,1	1180,9±7,8	1316,2±8,2	1087,7±7,3	1245,2±7,3
d-cell	95	91	89	88	91
number of rows	189,8±4,3	138,5±3,9	200,3±5,3	218,8±3,2	332,2±2,7
	6-7	7-8	6-7	5-6	4
Kranz-lining, height, µm	18,3±0,2	16,0±0,1	28,0±0,3	19,3±0,4	19,1±0,1
Number of vascular bundles	25	23	23	24	21
Number of vessels in the main vascular bundle	14	16	18	24	23
Diameter of vessels, µm	9,0±0,2	9,1±0,2	15,8±0,3	9,9±0,2	11,3±0,3

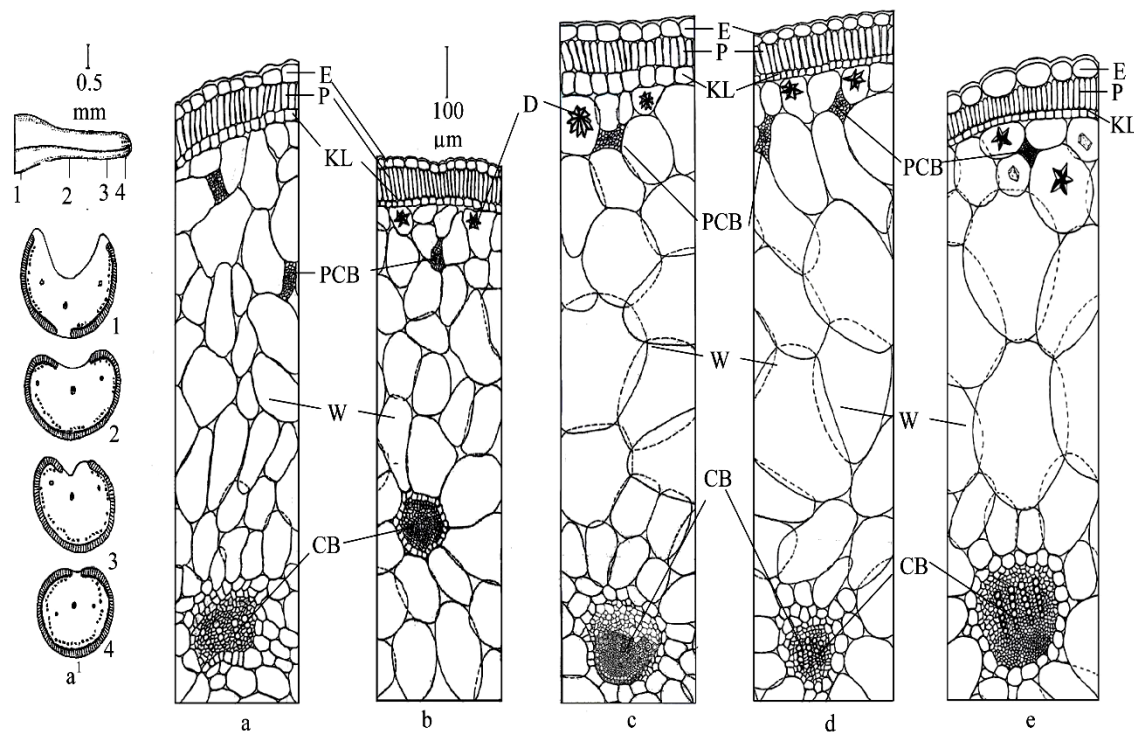


Fig. 2. Structure of the leaves in the species *Climacoptera* on the cross-section: a, a¹ – *C. ferganica*; b – *C. lanata*; c – *C. intricata*; d – *C. longistylosa*; e – *C. aralensis*. a – e – detail, a¹ – schemes of different parts of leaves. Key: W – water-bearing parenchyma, D – druse, KL – Kranz-lining, P – palisade parenchyma, CB – conducting bundle, PCB – peripheral conductive bundle, E – epidermis.

The combination of xeromorphic and halomorphic signs is observed in all types of leaves, which are manifested in different combinations. Xeromorphic signs in *C. Ferganica* are small vessels in the conducting bundle; a high palisade index, smaller water-bearing cells and Kranz-lining, small vessels in conducting bundle in *C. lanata*; in *C. longistylosa*, high palisade cells, high palisade index, dense indumentum from numerous thin trichomes, significant height of epidermal cells with a thickened external wall (*C. intricata* and *C. aralensis*).

Halomorphic signs of leaf are present in all species in different combinations: a scarce indumentums, thick water-bearing layer; in *C. intricata* large water-bearing leaves, high Kranz lining and large vessels; in *C. longistylosa* and *C. aralensis* water-bearing cells, numerous vessels in conducting bundles (Fig.4, Table 4).

In general the leaves of *C. intricata*, *C. longistylosa* and *C. aralensis* are characterized with a high succulent feature, while *ferganica* and *C. lanata*, with a xeromorphic feature. We considered quantitative traits of the leaf in relation to the ecology of the habitat and sectional belonging. The quantitative indices of the leaf length, thickness of water-bearing layer, height of Kranz lining, vessel diameter in the main conducting bundle are close in the species from different sections, however growing in similar conditions.

As a generative organ, the bract protects the flower from the environmental effects. The bract, bracteole and leaves of perianth in some species (*C. intricata*, *C. lanata* and *C. longistylosa*) were studied by D.T. Khamraev (2006) and their diagnostic traits were revealed.

We for the first time studied the structure of the bract, bracteole and leaves of perianth only in *C. aralensis*. The bract in *C. aralensis* is very succulent, a little blunt-pointed, egg-like. Contrary to the leaf, the bract and bracteole are pubescent with short prominent hair.

Epidermal cells are rounded and oval. The mesophyll is Kranz ventrodorsal in the bract and bracteole; in cross-section it has the shape of a crescent as in the leaf base. On the adaxial side, the water-bearing parenchyma borders on the epidermis; the palisade parenchyma and Kranz lining are situated on the abaxial side.

The palisade parenchyma is smaller than in the leaf in the mid-part of the bract and bracteole. The Kranz lining consists of cubic cells. The number of rows of water-bearing cells in bract and bracteole is 3-4; in the leaf, 5-8. Three conducting bundles lie in the center of the leaf, while in bract and bracteole only one. The main vein is situated in the center of the cross section. In the leaf, the central conducting bundle contains more vessels than in the bract and bracteole (24 and 17-18, respectively). The peripheral conducting bundles are numerous (20); similarly to the leaf they are separated from the Kranz-lining by 3-4 rows of water-bearing cells, which contain with druses of calcium oxalate (Fig. 3; Table 3).

The structure of the lower part of leaves of perianth in *Climacoptera brachiata* and *C. lanata* was described by A.A. Butnik (1972), *C. ferganica*, by S.A. Paizieva (1983). Their significant parenchyma growth was noted.

The leaves of the perianth in *C. aralensis* are lancet-shaped and pubescent with short unicellular hair. The cells in the inner (adaxial) is smaller than the exterior (abaxial) epiderm of the perianth; their outer walls are thickened to $4,9 \pm 0,1 \mu\text{m}$. The height of the epidermis is $19,7 \pm 0,3 \mu\text{m}$.

The mid-part of the mesophyll leaves of the perianth consists of five rows of parenchyma, of which three are large and two are small. The thickness of the parenchyma layer in the cross section reaches $78,4 \pm 0,3 \mu\text{m}$; the diameter, $34,1 \pm 0,3 \mu\text{m}$.

The number of conducting bundles varies from 6 to 10. The central conducting bundle is large; it contains 8-10 small vessels. In mid- and lower part of ЛОЦ some cells in all tissues are filled with druses of calcium oxalate. The bract and bractioles protecting the flower have a specialized structure similar to that of the leaf. The perianth is deprived of chlorenchyma.

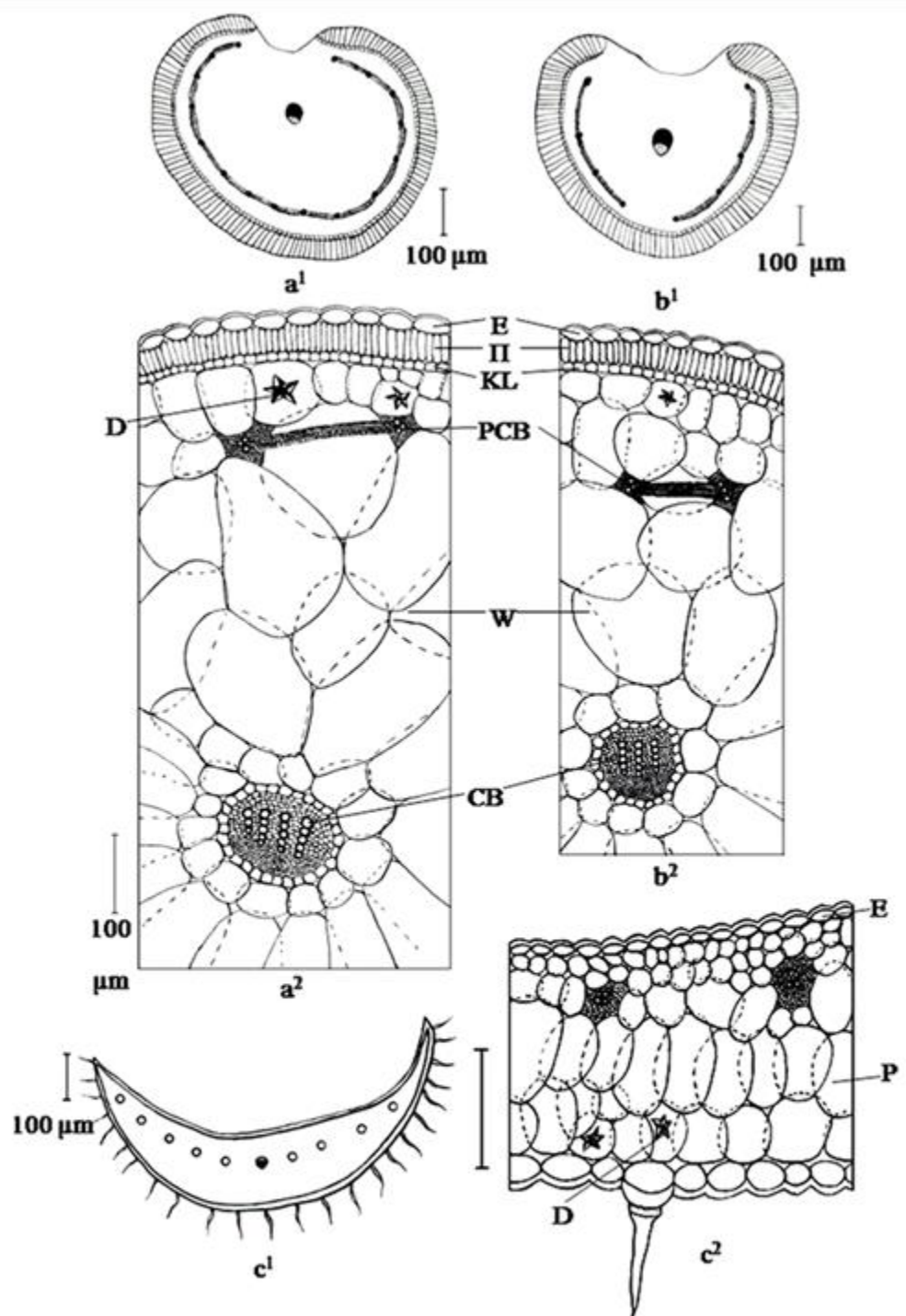


Fig. 3. Structure of the bract (a¹- a²), bracteole (b¹- b²), perianth leaf (c¹- c²) *Climaoptera araliensis* on the cross-section: a², b², c¹, c² - mesophyll details, a¹ - a¹ - schemes. Key: W - water-bearing parenchyma, D - druse, KL - Kranz-lining, P - palisade parenchyma, CB - conducting bundle, PCB - peripheral conductive bundle, E - epidermis.

Table 3. Quantitative indices of *Climacoptera aralensis* structure (n=30)

Organ / tissues	Indices	
Bract		
Epidermis, µm:	height	33,1±0,3
	thickness of outer wall	3,5±0,08
Palisade parenchyma:	height, µm	35,4±0,3
	width, µm	10,5±0,2
	palisade index	3,4±0,05
Water-bearing cells:	thickness of water level, µm	11239±3,7
	d-cells, µm	138,5±3,9
	number of cell rows	3-4
Kranz-lining:	height, µm	12,4±0,1
The number of conducting bundle		20(1)
Number of vessels in the conducting bundle		17-18
Vessel diameter, µm		6,5±0,1
Bracteole		
Epidermis, µm:	height	26,7±0,2
	thickness of outer wall	4,9±0,1
Palisade parenchyma:	height, µm	42,7±0,4
	width, µm	13,3±0,2
	palisade index	3,2±0,1
Water-bearing cells:	thickness of water level, µm	814,9±2,3
	d-cells, µm	177,4±1,4
	number of cell rows	3
Kranz-lining	height, µm	19,3±0,2
The number of conducting bundle		17(1)
Number of vessels in the main conducting bundle		16-17
Vessel diameter, µm		6,0±0,1
Leaf of perianth		
Epidermis, µm:	height	19,7±0,3
	thickness of outer wall	4,9±0,1
Parenchyma:	thickness, µm	78,4±0,3
	d – cells, µm	34,1±0,3
	number of cell rows	5
The number of conducting bundle		6-10 (1)
Number of vessels in the main conducting bundle		8-12

The cluster analysis of the quantitative indices of the cotyledon of species from different sections *C. ferganica* (section *Ulotricha*) and *C. lanata* (section *Climacoptera*) from the Kyzylkum revealed a smaller coefficient of trait similarity (0,15) than in *C. intricata* (section *Amblyostegia*) and *C. longistylosa* (section *Climacoptera*) from Mirzachul (0,28). The species *C. lanata* и *C. longistylosa* belonging to one section, but growing in different conditions showed a lower coefficient of similarity (0,11) than the species *C. intricata* and *C. longistylosa* from different sections. This suggests a significant impact of habitats on the formation of shoots and the relation to the endemism of species in Mirzachul (Table 4, Fig. 4).

Table 4. Jaccard coefficient (Kj) of species *Climacoptera* By the quantitative indices of cotyledons

Indicators and number of species	Kj			
	<i>C. ferganica</i>	<i>C. lanata</i>	<i>C. intricata</i>	<i>C. longistylosa</i>
1- <i>C. ferganica</i>	-	0,15	0,21	0,17
2 - <i>C. lanata</i>	0,15	-	0,11	0,11
3 - <i>C. intricata</i>	0,21	0,11	-	0,28
4 - <i>C. longistylosa</i>	0,17	0,11	0,28	-

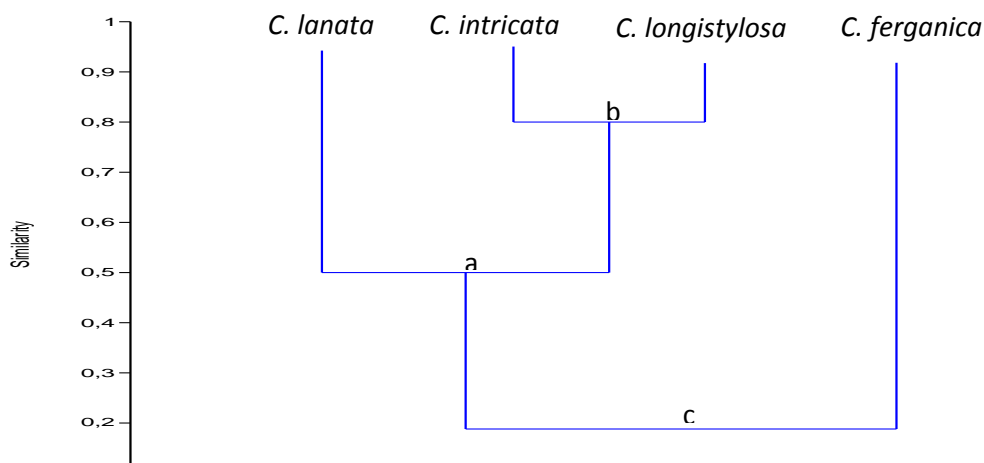


Fig. 4. Cluster analysis by Jaccard similarity coefficient (Kj) in *Climacoptera* species by quantitative measurements of cotyledons. Abbreviations: a = Section *Amblyostegia* Pratov.; b = Section *Climacoptera* Pratov.; c = Section *Ulotricha* Pratov.

The cluster analysis established the coefficient of similarity of leaf traits was 0,17 in *C. intricata* - *C. longistylosa* from different sections in similar conditons (Mirzachul). This value in plants from different sections but in similar conditions (Kyzylkum) showed the following: in *C. ferganica*-*C. lanata* – 0,19, in *C. ferganica* - *C. aralensis* – 0,17. In *C. lanata* - *C. longistylosa*, from one section in different ecological conditions, this value reached 0,24; in *C. intricata*-*C. aralensis* from one section in different ecological conditions – 0,23 (Table 5, Fig. 5).

Table 5. Jaccard coefficient of similarity (Kj) in *Climacoptera* species by quantitative measurements of leaves

Indicators and number of species	Kj				
	<i>C.ferganica</i>	<i>C.lanata</i>	<i>C. intricata</i>	<i>C.longistylosa</i>	<i>C.aralensis</i>
1- <i>C. ferganica</i>	-	0,19	0,12	0,14	0,17
2- <i>C. lanata</i>	0,19	-	0,14	0,24	0,10
3- <i>C. intricata</i>	0,12	0,14	-	0,17	0,23
4- <i>C. longistylosa</i>	0,14	0,24	0,17	-	0,10
5- <i>C. aralensis</i>	0,17	0,10	0,23	0,10	-

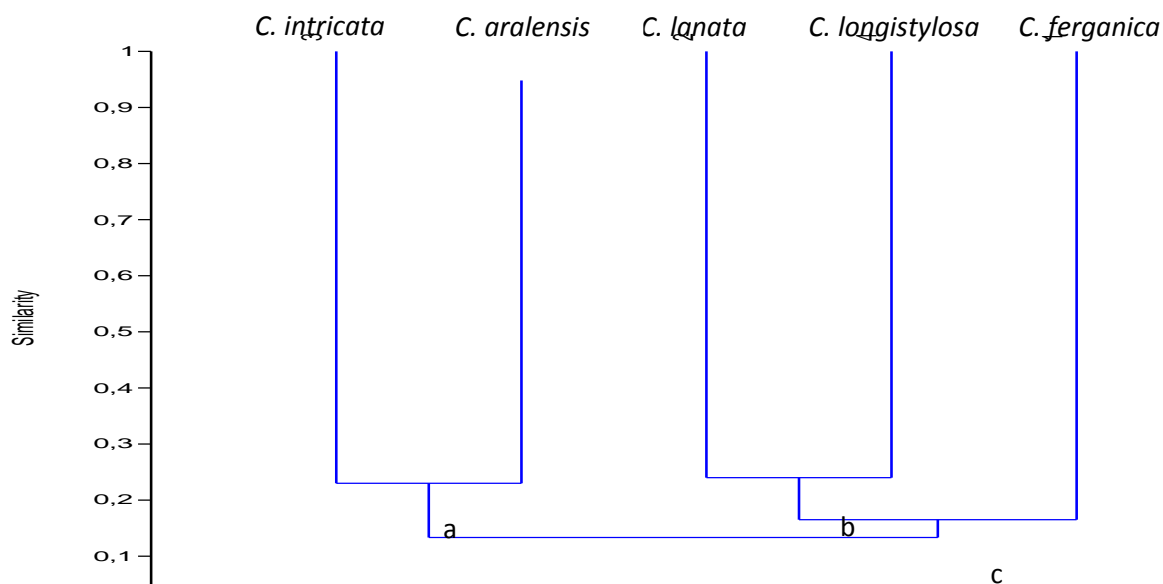


Fig. 5. Cluster analysis by Jaccard similarity coefficient (Kj) in *Climacoptera* species by quantitative measurements of leaves. Abbreviations: a = Section *Amblyostegia* Pratov.; b = Section *Climacoptera* Pratov.; c = Section *Ulotricha* Pratov.

CONCLUSION

Thus, the study of assimilating organs in five species of the genus *Climacoptera* revealed Kranz (the leaf, bract and bracteole) and non-Kranz (cotyledon and perianth) structure types, as well as the level of their xeromorphic and halomorphic traits connected with ecological conditions of habitation. A similarity of many indices of assimilating organs; the genotypic component is manifested more significantly. A considerable level of similarity of *C. lanata* – *C. longistylosa* (section *Climacoptera*) and *C. intricata* – *C. aralensis* (section *Amblyostegia*), in comparison with *C. intricata* and *C. longistylosa* is perhaps attributable to their plasticity under conditions of a larger habitat. The species *C. intricata*, *C. aralensis* (endemic to Central Asia) and *C. longistylosa* (Central Asia-Afghanistan) were perhaps formed later under the conditions of arid climate in a narrower ecological range.

REFERENCES

1. Barykina, R. P. and Chubatova, N. V. 2005. Big practicum of botany. Ecological anatomy of floral plants. – Tov-vo nauch. izd., Moscow, 77 pp.
2. Butnik A.A., Paizieva S.A. 1991. Morphogenesis of *Climacoptera lanata* (Pall.) Botsch. and *Climacoptera ferganica* (Drob.) Botsch. In south-western Kyzylkum. Uzbek biol. Jour. Tashkent, N5. p. 40-43.
3. Butnik A.A. 1972. The structure of the fruit covers in chenopodiaceous plants. Morpho-biological and structural peculiarities of fodder plants of Uzbekistan. Tashkent. p. 17–28.
4. Zaytsev G.N. 1991. Mathematics in experimental botany. – Moscow: Nauka Publishers, 296 p.
5. Zakharevich, S. F. (1954): Methodical of the description of epidermis of a leaf. – Vestnik LGU, Leningrad. 4: P. 65–75.
6. Paizieva S.A. 1983. The structure of fruit and seed cover in the species of genera *Halimocnemis* C.A. Mey and *Climacoptera* Botsch. The anatomical structure and cytoembryology of wild plants in Uzbekistan. – Tashkent. p. 9-19.
7. Prator U.P. 1986. The genus *Climacoptera* Botsch. – Tashkent. 68 p.
8. Khamraeva D.T. 2006. Morpho-biological traits of reproductive organs in species of genus *Climacoptera* Botsch.: Summary of dissertation for the degree of Candidate of Sciences, Tashkent. 21 p.
9. Shmidt V.M. 1984. Mathematical methods in botany. Leningrad: Leningrad State Univ. p. 231-237.
10. Butnik A.A. 1999. Comparative studies in cotyledons and leaves in C4 species of Chenopodiaceae Vent. and their evolutionary implication. XIV. Symposium: Biodiversitat and Evolutionsbiologie. Yena. P. 233.
11. Carolin R.C., Jacobs S.W.L., Vesik M. 1975. Leaf structure in Chenopodiaceae // Journal Botany Jahrb. Syst. Stuttgart, V. 95. P. 226-255.
12. Fisher D., Jochen Schenk H., Jennifer A. Thorsch., Wayne R. Ferren. 1997. Leaf anatomy and subgeneric affiliations of C3 and C4 species of *Suaeda* (Chenopodiaceae) in North America. America Journal of Botany. V. 84. N 9. P. 1198-1210.
13. Freitag H., Stichler W. 2000. A Remarkable New Leaf With Unusual Photosynthetic Tissue in a Central Asiatic Genus of Chenopodiaceae. Plant Biology. Stuttgart. New York. № 2. P. 154-160.
14. Kadereit G., Borsch T., Weising K., Freitag H. 2003. Phylogeny of Amaranthaceae and Chenopodiaceae and the evolution of C4 photosynthesis // Journal Plant Sciences. USA, N 6 (164). – P. 959-986.
15. P'yankov V.J., Kuzmin A., Ku M., Black C., Artyusheva E., Eduvard Y. 1998. Diversity of Kranz-anatomy and biochemical types of CO2 fixation in leaves and cotyledons among Chenopodiaceae // Photosynthesis: Mechanisnis and effect. Netherlands, V. 5. P. 4097-4100.
16. P'yankov V.J., Vosnesenskaya E.V., Alexander N. 2000. Occurrence of C3 and C4 photosynthesis in cotyledons and leaves of *Salsola* species (Chenopodiaceae) // Photosynthesis Research. Netherlands, V. 63. P. 69-84.
17. Voznesenskaya E.V., Franceschi V.R., Pyankov V.I., Edwards G.E. 1999. Anatomy, chloroplast structure and compartmentation of enzymes relative to photosynthetic mechanisms in leaves and cotyledons of species in the tribe Salsoleae (Chenopodiaceae) // Journal of experimental Botany. Oxford, N 341 (50). P. 1779-1795.