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Epidermal characters of *Allium* species autochthonous in Czechoslovakia: their pattern, taxonomic and ecological relationships

Epidermální znaky česneků *(Allium)* autochtonních v Československu: jejich uspořádání a vztahy k taxonomii a ekologii druhů

František Krahulec

Dedicated to Professor Zdeněk Černohorský on his 70th birthday

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Epidermal characters of 15 *Allium* species autochthonous in Czechoslovakia were studied. Particular species have amphistomatous or hypostomatous leaves and vary greatly in the shape of epidermal cells, in sinking of stomata and in cuticular sculpture (presence or absence of ridges around the entrance of stomatal tip and presence of micropapillae or ridges on the cell surface). Variation in particular species is small but is considerable between them. Closely related species have the same type of epidermis, but sections and subgenera do not differ from each other. A great deal of variation appears to be correlated to water stress of the biotopes of particular species. Convergency of characters is seen in different infrageneric taxa. Epidermal characters are very useful in identifying sterile plants.

Botanical Institute, Czechoslovak Academy of Sciences, 252 43 Průhonice.

INTRODUCTION

Seeking new characters for a determination key of the Czechoslovak *Allium* species without flowers I have also paid attention to epidermal characters. These characters proved to be very valuable: they are qualitative and easily ascertainable, which is advantageous particularly for the study of herbarium specimens (the method using nail varnish offprints is non-destructive). By means of epidermal characters some sterile species with determination problems were distinguished. Zahariadi (1975), working on the taxonomically rather homogeneous section of *Codonoprasum*, also successfully used epidermal characters. At present, epidermal characters are frequently used in detailed taxonomic studies. Rapid development of their use has been stimulated by the development of scanning electron microscopy (SEM). The evaluation of these characters from the viewpoint of ecology has not always been in the focus of attention.

Epidermal characters were used only if necessary in the determination key of Czechoslovak species (Krahulec 1977). In this paper, these characters are listed for all autochthonous species. I try to show their relationships to the taxonomy and ecology od the taxa concerned.

METHODS AND MATERIALS

Epidermal characters were studied in two ways: by the indirect offprint method (PAZOUREK 1963), and by direct observation of epidermal slides. Most of the offprints were prepared in the field, a minor part was made from my herbarium specimens and from specimens deposited in herbarium of Charles University, Prague (PRC). Nail varnish was used in making the offprints. For the purpose of the observation, parts of leaves were fixed in FAA directly in the field. Herbarium specimens were also used. Mesophyll was removed by treating the sample with either hot and cold water or lactic acid (CLARKE 1960). In some cases, conclusions based on optic observations were verified by means of SEM. Only material of known origin was used in the study. The localities of specimens studied are given in the following list.

List of species examined

Allium scorodoprason L.

1. Southern Slovakia, Nové Zámky: roadside between villages of Nesvady and Aňala, 120 m
2. Southern Slovakia, Štúrovo: Kamenica nad Hronom village, 120 m.
3. Central Slovakia, Nízke Tatry Mts.: Kyslá Voda near Moštenica village, 700 m.

Allium rotundum L.

4. Southern Slovakia, Štúrovo: Kamenica nad Hronom village, 120 m.
5. Southern Slovakia, Štúrovo: Ďarmotské kopce, near Belá village, 220 m.
6. Central Bohemia, Praha: Velká Chuchle, 250 m.

Allium sphaerocephalon L.

7. Southern Slovakia, Kováčovské kopce: Skala, 300 m.
8. Central Bohemia, Český kras: Koda near Srbsko. Leg. Domin, PRC.
9. Northern Bohemia, Lovosice: Lovoš Mt. Leg. E. Hejný, PRC.
10. Southern Moravia, Hodonín: Velký vrch, 264 m. Leg. F. Weber, PRC.

Allium vineale L.

11. Southern Slovakia, Štúrovo: bank of the Dunaj river, 110 m.
12. Southern Slovakia, Štúrovo: Kamenín village, 115 m.
13. Eastern Bohemia, Česká Skalice: Spyta village, 290 m.
14. Central Bohemia, Unhošť: Podkozí village, 320 m.

Allium oleraceum L.

15. Southern Slovakia, Štúrovo: Ďarmotské kopce, 240 m.
16. Central Slovakia, Slovenská Ľupča, 390 m.
17. Central Slovakia, Nízke Tatry Mts.: Hrby Mt. above Moštenica village, 580 m.
18. Eastern Bohemia, Česká Skalice: Spyta village, 290 m.
19. Central Slovakia, Veľká Fatra Mts.: Ľubochňa, 520 m.
20. Central Slovakia, Veľká Fatra Mts.: Ostredok Mt., 1350 m.
21. Central Slovakia, Veľká Fatra Mts.: Staré Hory, 520 m.
22. Central Slovakia, Veľká Fatra Mts.: Krížna Mt., 1500 m.
23. Central Bohemia. Unhošť: Podkozí village, 330 m.
24. Southern Bohemia, Písek, 370 m.

Allium paniculatum L.

25. Southern Slovakia, Štúrovo: Ďarmotské kopce. Leg. Klokner.

Allium flavum L.

26. Southern Slovakia, Kováčovské kopce: Skala, 300 m.
27. Southern Slovakia, Slovenský kras: Turňa, 350 m.
28. Central Slovakia, Muráňská planina: Cigánka, 930 m.

Allium carinatum L.

29. Central Slovakia, Nízke Tatry Mts.: Kyslá near Moštenica village, 700 m.

30. Central Slovakia, Veľká Fatra Mts.: Krížna Mt., 950 m.
31. Central Slovakia, Kremnické pohorie Mts.: Kordíky village, 790 m.

Allium victorialis L.

32. Central Slovakia, Veľká Fatra Mts.: Rakytov Mt., 1350 m.
33. Western Slovakia, Lúčanská Fatra Mts.: Fačkovský Kľak Mt., 1300 m.

Allium schoenoprasum L.

34. Central Slovakia, Veľká Fatra Mts.: Ploská Mt., 1450 m (subsp. *sibiricum* (L.) HARTMAN).
35. Central Bohemia, Praha: shores of the Vltava near Troja, 180 m (subsp. *schoenoprasum*).

Allium senescens L. subsp. *montanum* (FRIES) HOLUB

36. Central Slovakia, Veľká Fatra Mts.: Kliačik Mt., 1210 m.
37. Central Slovakia, Slovenské rudohorie Mts.: Klenovský Vepor Mt., 1250 m.
38. Central Slovakia, Muráňská planina: Cigánka, 930 m.
39. Central Bohemia, Praha: Podhoří, 240 m.

Allium angulosum L.

40. Southern Slovakia, Štúrovo, 115 m.
41. Eastern Bohemia, Česká Skalice: Rozkoš, 270 m.

Allium strictum SCHRAD.

42. Central Bohemia, Praha: Podhoří, 240 m.
43. Central Bohemia, Praha: Velká Chuchle, 250 m.
44. Northern Slovakia, Poprad: Primovce. Leg. Suza, PRC.

Allium ochroleucum W. et K.

45. Central Slovakia, Veľká Fatra Mts.: Grúň Mt., 980 m.
46. Central Slovakia, Veľká Fatra Mts.: Gäderská dolina, 600 m.
47. Central Slovakia, Muráňská planina: Cigánka, 930 m.
48. Central Slovakia, Veľká Fatra Mts.: Harmanec, 630 m.
49. Central Slovakia, Stratenská hornatina Mts.: Prielom Hornádu. Leg. Domin, PRC (deposited under *Allium strictum*).

Allium ursinum L.

50. Eastern Bohemia, Králický Sněžník Mts.: Velká Morava village, 670 m.

RESULTS

The epidermis of the species studied shows considerable variability in the shape and size of epidermal cells, grade of sinking of stomata and cuticular sculpture.

All narrow-leaved species have their elongated cells arranged in longitudinal files parallel to the long axis of the leaf. Some species have stomata in the level of the leaf surface; others have sunken stomata. Stomata are of the anomocytic type (without subsidiary cells); guard-cells are parallel to the leaf axis. By the sinking of the stoma the front cavity is formed. Its entrance is sometimes surrounded by cuticular ridge (cf. Plate VII.) There are cuticular ridges and micropapillae on the surface of epdermal cells. The term micropapilla is used here in the sense of ATWOOD et WILLIAMS (1979) to define protrusions on the outside wall of epidermal cells. In the following part of this paper, a short description of epidermal characters is given. The infrageneric system follows that by KAMELIN (1973).

Subgen. *Allium*
Sect. *Allium*

Allium scorodoprasum L. (Fig. 1a)

Cells elongated, all of the same type (No. 2) or some rows of short cells in the axis of the adaxial side (No. 1 and 3) and sometimes rare short cells between elongated ones (No. 1).

Stomata a little sunken.

Cuticular sculpture: elongated cells with micropapillae, shorter cells in the axis of adaxial side without them; short cells with one micropapilla.

Allium rotundum L. (Fig. 1b)

Cells elongated, all of the same type.

Stomata a little sunken.

Cuticular sculpture: all cells with micropapillae, these sometimes a little elongated.

Allium vineale L. (Fig. 1c)

Cells elongated, stomata regularly distributed between them. Rows of costal cells without stomata, costal cells a little longer than intercostal.

Stomata slightly sunken.

Cuticular sculpture: each cell with cuticular ridge lowering to the ends of the cell.

Allium sphaerocephalon L. (Fig. 1d)

Cells elongated; sometimes costal cells somewhat broader, with small teeth (No. 7 and 10).

Stomata sunken, front cavity well developed. Entrance to front cavity longitudinally shortened.

Cuticular sculpture: all or intercostal cells only (No. 7 and 10) with rows of micropapillae; entrance to the front cavity with cuticular ridges. No. 7 with oblique connections (ridges) between micropapillae of neighbouring cells.

Sect. *Codonoprasum* Rchb. in Mössl.

Allium oleraceum L. (Fig. 1e, f)

Cells: intercostal cells elongated, parallel to leaf margin; cells at the leaf margin and costal cells so long as the other ones (No. 21 and 23) and broader than the other ones (No. 18), or cells shorter than the other ones (No. 15, 16, 17, 19, 20, 22, 24).

Stomata sunken, front cavity well developed (cf. also Furst 1976: 84, Fig. 3/8).

Cuticular sculpture: entrance to front cavity with cuticular ridges; intercostal cells with micropapillae arranged into rows; cells at the leaf margin with teeth (No. 18 and 23) or with micropapillae (these ones also on costal cells), arranged into rows or dispersed (No. 15 and 16).

Allium paniculatum L. (Fig. Krahulec 1977 : 156)

Cells: intercostal cells elongated; costal cells in rows and shorter than intercostal.

Stomata sunken, front cavity developed.

Cuticular sculpture: all cells with micropapillae; around the entrance to front cavity cuticular ridges. Elongated cells with micropapillae arranged into one row, short cells with dispersed micropapillae.

Allium flavum L. (Plate VII.)

Cells elongated, all of the same type.

Stomata sunken, front cavity well developed. Entrance to front cavity longitudinally shortened.

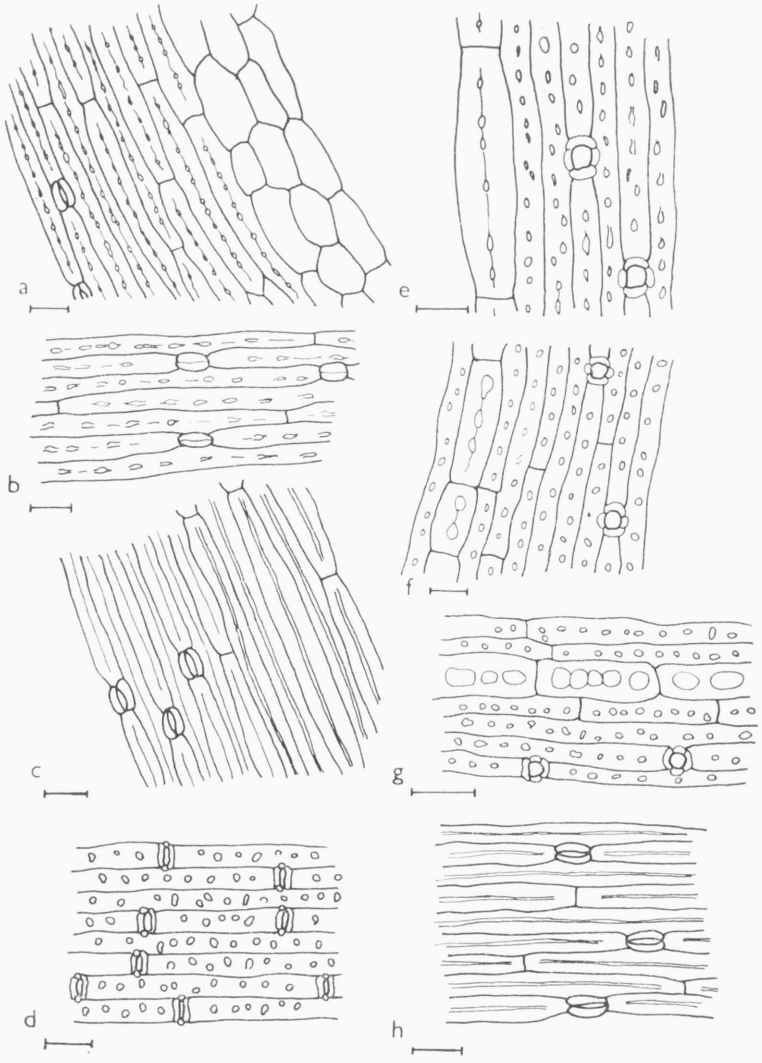

Fig. 1. — Dermograms of *Allium species:* a — *A. scorodoprasum* (No. 1), b — *A. rotundum* (No. 4), c — *A. vineale* (No. 11), d — *A. sphaerocephalon* (No. 7), e — *A. oleraceum* (No. 18), f — *A. oleraceum* (No. 17), g — *A. carinatum* (No. 29), h — *A. schoenoprasum* (No. 34). Scale: 50 μm.

Cuticular sculpture: all cells with rows of micropapillae; entrance to front cavity with cuticular ridges.

Allium carinatum L. (Fig. 1g)

Cells: intercostal cells elongated, costal cells short.

Stomata sunken, with well developed front cavity.

Cuticular sculpture: elongated cells with rows of micropapillae; short cells at the leaf margin with small teeth (No. 29, 30) or with irregularly distributed micropapillae on all short cells. Sometimes (No. 29) micropapillae of short cells connected with micropapillae of neighbouring elongated cells by means of small transverse ridges. Entrance to front cavity with cuticular ridges.

Subgen. *Rhizirideum* (KOCH) WENDELBO
Sect. *Schoenoprasum* KOCH

Allium schoenoprasum L. (Fig. 1h)

Cells elongated, all of the same type.

Stomata not sunken, front cavity virtually absent (cf. FURST 1976: 84, Fig. 3/5).

Cuticular sculpture consists of a ridge on each cell.

Sect. *Rhizirideum*

Allium senescens L. subsp. *montanum* (FRIES) HOLUB (Plate VII a, b)

Cells elongated; at the leaf margin and at the keel 1—3 rows of short cells.

Stomata at the surface of the leaf, front cavity virtually absent.

Cuticular sculpture not uniform: elongated cells with cuticular ridge lowering to the ends of the cell; short cells at the margin and the keel with different number of micropapillae (2—10) arranged into rows; No. 36 and 38 with elongated and amalgamating micropapillae; No. 37 with dispersed micropapillae.

Allium angulosum L. (Fig. 2a)

Cells elongated; at the leaf margin and at the keel 2—5 rows of short cells.

Stomata not sunken, at the surface of the leaf; front cavity absent (cf. FURST 1976: 84, Fig. 3/6).

Cuticular sculpture not uniform: each elongated cell with a cuticular ridge lowering to the ends of the cell; short cells with micropapillae arranged into rows (No. 41) or dispersed (No. 40); micropapillae sometimes elongated and amalgamating (No. 41).

Sect. *Reticulato-bulbosa* R. KAMELIN

Allium strictum SCHRAD. (Plate VII. d, e)

Cells elongated.

Stomata sunken, front cavity well developed.

Cuticular sculpture: each cell with row of micropapillae, sometimes individual cells with dispersed micropapillae (No. 42); around the entrance to the front cavity cuticular ridges.

Sect. *Oreiprason* F. HERMANN

Allium ochroleucum W. et K. (Fig. 2b)

Cells elongated.

Stomata sunken.

Cuticular sculpture: some rows of the cells at the margin of the leaf with clear micropapillae; these amalgamating and creating cuticular ridge toward to the middle of the leaf; most cells with cuticular ridge.

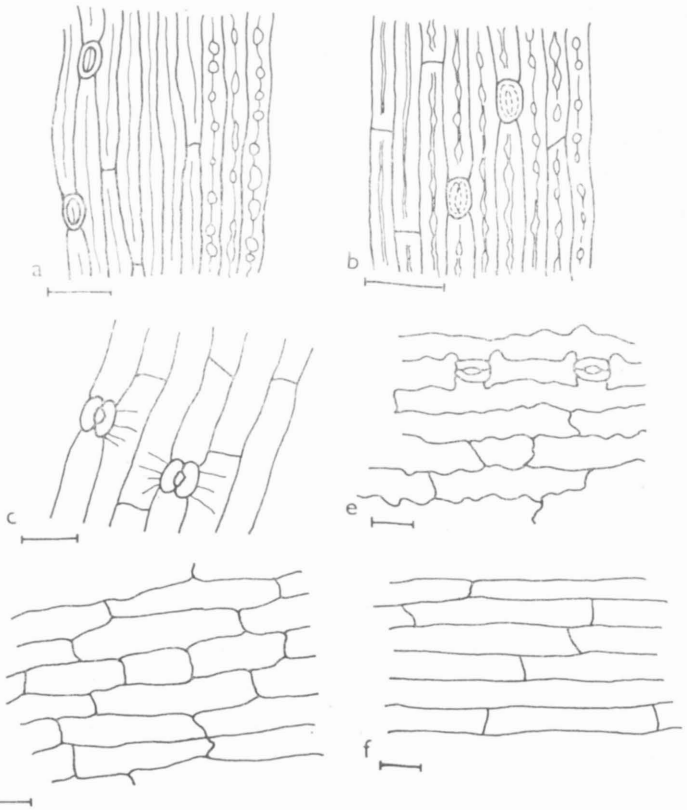

Fig. 2. — Dermograms of *Allium* species: a — *A. angulosum* (No. 41), b — *A. ochroleucum* (No.47), c — *A. victorialis* (No. 32),abaxial epidermal surface, d — *A. victorialis* (No. 32), adaxial epidermal surface, e — *A. ursinum* (No. 50), abaxial epidermal surface, f — *A. ursinum* (No. 50), adaxial epidermal surface. Scale: 50 μm.

Sect. *Anguinum* G. DON

Allium victorialis L. (Fig. 2c, d)

Leaves bifacial, hypostomatous.

Cells relatively short, of the same type on both adaxial and abaxial surfaces.

Stomata at the surface of the leaf, front cavity virtually absent (cf. FURST 1976: 84, Fig. 3/1).

Cuticular sculpture: cuticular ridges radially arranged arround the stomata.

Subgen. *Amerallium* TRAUB

Sect. *Ophioscordon* (WALLR.) VVEDENSKY

Allium ursinum L. (Fig. 2e, f)

Leaves bifacial, hypostomatous.

Cells: on the adaxial side elongated, anticlinal walls straight; on the abaxial side cells short, anticlinal walls undulated.

Stomata slightly sunken.

Cuticular sculpture absent.

DISCUSSION

Epidermal characters of some *Allium* species discussed here had been studied before the present paper was prepared. The following species have been dealt with: *A. montanum, A. angulosum, A. victorialis* (ČEŠMEDŽIEV 1973), *A. flavum, A. carinatum, A. oleraceum, A. paniculatum* (ZAHARIADI 1975), *A. oleraceum, A. victorialis* (FURST 1973), and *A. ursinum* (MÄCKEL 1940). A high degree of agreement with my results may be seen. The only difference is that in *A. oleraceum* ZAHARIADI (1975) found only elongated cells at the margin of the leaf while I found both elongated and short cells.

From the results of the observations, the following taxonomic conclusions can be drawn:

1. The variation between populations is negligible, except for costal cells. The characters are very stable. The material from geographically fairly distant areas — U.S.S.R. (FURST 1973) and Greece (ZAHARIADI 1975) — is also very uniform in the characters under consideration. The same observation was made in *Aloë* by NEWTON (1972). On the other hand, ATWOOD et WILLIAMS (1979) found remarkable intraspecific variation in some species of the genus *Paphiopedilum*.

2. No important difference in the epidermal characters was found between closely related species: *A. angulosum — A. senescens, A. paniculatum — A. oleraceum, A. rotundum — A. scorodoprasum*. The closely related species *A. strictum* and *A. amphibolum* (FURST 1973) are also uniform in their epidermal characters.

3. Higher infrageneric taxa (subgenera, sections) cannot be characterized by the epidermal characters. These conclusions are preliminary, because of the small number of the species studied. However, the constancy of these characters in the various species is advantageous in the compilation of determination keys (ZAHARIADI 1975, KRAHULEC 1977).

For example, specimens collected by Domin in the Stratenská hornatina Mts. (Prielom Hornádu) deposited in PRC under *A. strictum* and mentioned in Flora of Czechoslovakia (HOLUB in DOSTÁL 1948—1950) under *A. strictum* (?) (cf. also MARTINOVSKÝ 1969) are clearly *A. ochroleucum* (agreement in all characters described in the present paper).

The conformity in epidermal characters seems to be due to the ecology of the species rather than to infrageneric taxonomy. Two taxonomically distinct, but similar species (*A. ursinum* and *A. victorialis*) have the same type of bifacial (hypostomatous) leaves. Stomata are present only on the

abaxial side of leaves of both species. This is in agreement with the conclusion of PARKHURST (1978) that hypostomatous leaves are more typical of plants of mesic habitats. The other species vary greatly in sinking of stomata and in shape of the entrance to the front cavity. Based on these characters, we can divide the studied species into four groups.

1. Stomata on the level of the leaf surface: *A. angulosum*, *A. senescens*, *A. schoenoprasum*.

2. Stomata slightly sunken: *A. ochroleucum*, *A. rotundum*, *A. scorodoprasum*, *A. vineale*.

3. Stomata sunken, a cuticular ridge is found around the entrance to the front cavity: *A. strictum*, *A. oleraceum*, *A. paniculatum*, *A. carinatum*.

4. Stomata sunken, the entrance to the front cavity has a cuticular ridge and is longitudinally very shortened: *A. flavum*, *A. sphaerocephalon*.

The stomatal resistance increases with the sinking of the stomata and with the creation of ridges around the entrance to front cavity; the decreasing of transpiration is also connected with this fact. The position of the stomata and the presence of the cuticular ridge can be considered to be an adaptation resulting in decreased transpiration. This confirms our knowledge of the relations of particular species to the water gradient.

The species of the fourth group grow mainly on rocks in rather warm regions of Central Europe. On the other hand, species with stomata not sunken (*A. angulosum*, *A. schoenoprasum*) grow predominantly in wet habitats. An exception in this group is *A. senescens* growing on rocks. However, this species is closely related to *A. angulosum*, and we can trace a trend to succulence — *A. senescens* has thicker leaves.

Based on other cuticular characters, we may distinguish species without distinct sculpture (*A. ursinum*), species with cuticular ridges (*A. angulosum*, *A. senescens*, *A. schoenoprasum*, *A. vineale*, *A. ochroleucum*, and *A. victorialis*) and species with micropapillae (*A. flavum*, *A. carinatum*, *A. oleraceum*, *A. paniculatum*, *A. sphaerocephalon*, *A. rotundum*, *A. scorodoprasum*). Several explanations have been proposed concerning the importance of these structures (cf. ATWOOD et WILLIAMS 1979 : 153). These authors found that the distribution of species with micropapillae was correlated with the darkest habitats of the forest floor environment. In the present paper, however, micropapillae seem to be correlated with sunken stomata. Thus micropapillae may be an adaptation to xeric environment.

Convergent evolution leads to the same epidermal pattern in taxonomically distinct species. This is true especially of the species of the third group; these belong, according to the present knowledge, to two subgenera. Similarly, two species with hypostomatous leaves belong to various subgenera. The selective advantage of particular types of epidermis appears to be due to the above mentioned convergency in different groups. The same type of cuticular sculpture has also evolved in taxonomically distinct groups. For instance, *Aloë schweinfurthii* BAKER has the same cuticular pattern (i.e. micropapillae and ridges around the entrance to the front cavity) as the species of the third group, (e.g. *A. strictum*) — see NEWTON (1972).

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SUMMARY

The pattern of the leaf epidermal characters was studied in all autochthonous Czechoslovak *Allium* species. These species vary greatly in the sinking of the stomata and in the cuticular sculpture (shape of the entrance to the front cavity, presence or absence of micropapillae and ridges). A minor part of the variation seems to be connected with infrageneric taxonomy: only closely related species have the same type of epidermis. A major part of the observed variation appears to be related to water stress in the habitats of the various species. The same type of cuticular sculpture was evolved in different infrageneric groups and indicates strong selective advantage of a certain type of epidermis.

SOUHRN

V práci jsou popsány znaky listové epidermis všech česneků (*Allium* L.) autochtonních v Československu. Mezi jednotlivými druhy jsou značné rozdíly v ponoření průduchů, ve tvaru epidermálních buněk a ve skulptuře kutikuly (utváření ústí vnější dýchací dutiny a presence či absence mikropapilek či kutikulárních hřebenů). Variabilita uvnitř jednotlivých druhů je dosti nízká a projevuje se především ve tvaru epidermálních buněk. Poměrně malá část celkové pozorované variability je ve spojitosti s vnitrorodovou taxonomií: pouze nejblíže příbuzné druhy mají stejný typ epidermis. Největší část pozorovatelné variability je v korelaci s ekologií jednotlivých druhů. Přesněji, s vodními poměry ekotopů jednotlivých druhů je značně korelováno utváření ústí vnější dýchací dutiny a stupeň ponoření průduchů. V práci je ukázáno na skutečnost, že určité typy epidermis jsou zastoupeny v různých vnitrorodových jednotkách a i u odlišných rodů (*Aloë*). Jednotlivé typy epidermis mají zřejmě značné selektivní výhody, i když zatím názory např. na kutikulární skulpturu jsou značně odlišné a protikladné. Epidermální znaky mají také nepopiratelný význam pro určování, zejména rostlin bez květů.

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See also plate VII. in the Appendix.

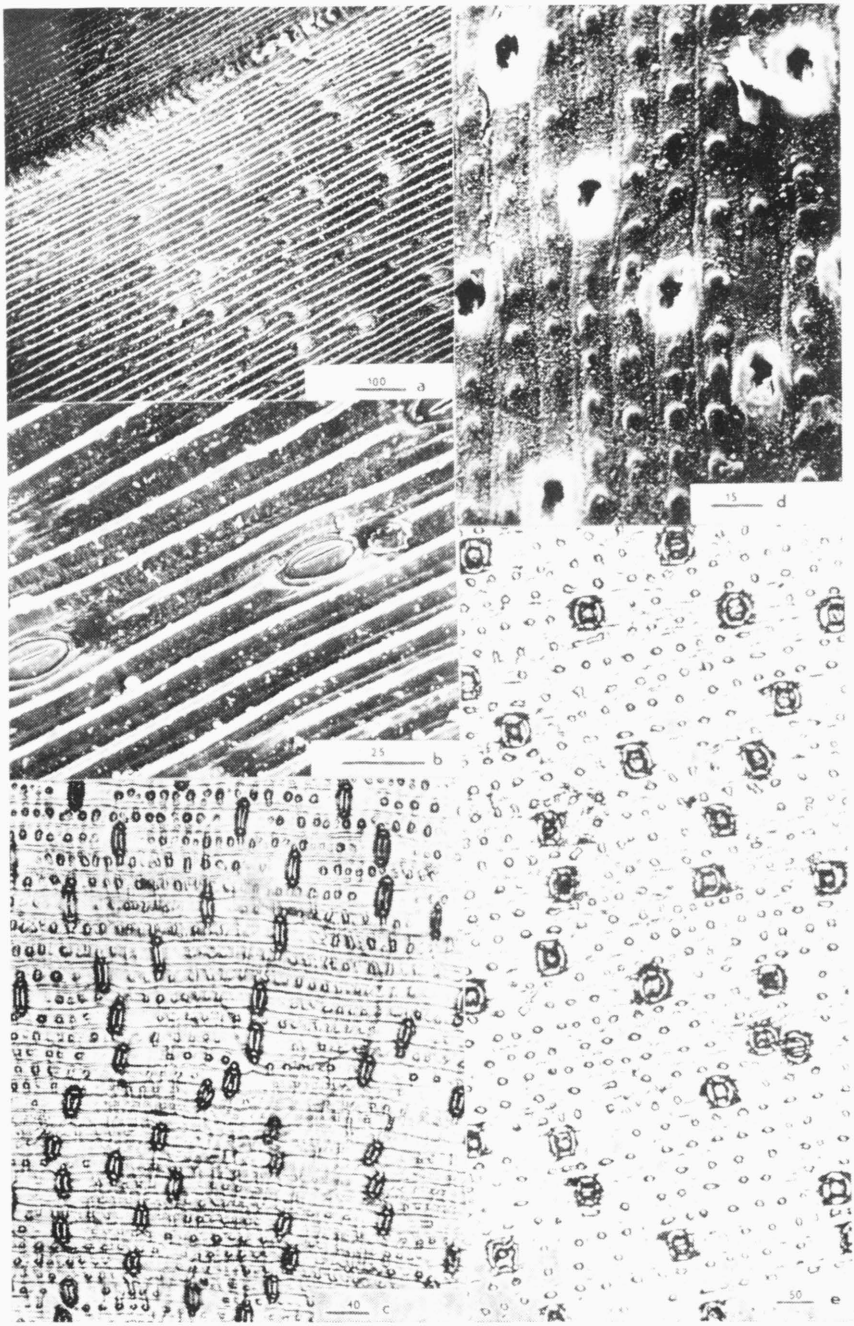

Plate VII. — Dermograms of *Allium* species: a, b — *A. senescens* subsp. *montanum* (No. 38), c — *A. flavum* (No. 26). d, e — *A. strictum* (No. 42). Scale in μm.

F. Krahulec: Epidermal characters of *Allium* species autochthonous in Czechoslovakia: their pattern, taxonomic and ecological relationships