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Seed morphology in the genus Pinguicula (Lentibulariaceae) and its relation to taxonomy and phylogeny

By

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With 34 figures and 2 tables

Abstract

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Seed morphology, anatomy and spermoderm ultrasculpture are studied using SEM and light microscopy in 19 of about 80 species of the genus *Pinguicula* (Lentibulariaceae). All subgenera recognised by CASPER are covered by the study. Seeds of *Pinguicula* are small and have ellipsoidal or spindly form. Seeds of all examined species are characterised by the same groundplan. On the other hand, we found differences in some characters between studied samples. Some characters of seed coat structure are probably significant at the sectional level. Some other characters are probably significant on specific or infraspecific level. The data on seed coat structure generally confirms that section *Pinguicula* represents a natural taxon. Embryo structure of *Pinguicula* is of special interest due to variation in the cotyledon number. We found two cotyledons in *P. crystallina*, *P. lusitanica*, *P. moranensis*, *P. variegata*, and *P. villosa*, which represent all three subgenera. The rest of the examined species possess a single cotyledon. We suggest that cotyledon number was quite unstable in the evolution of *Pinguicula*. Some features of seed coat morphology are much more congruent to flower morphology than embryo structure. This is in contrast to many other families of Lamiales, where an embryo with two cotyledons is a very conservative character. However, it is difficult to demonstrate that cotyledons of *Pinguicula* are homologous to cotyledons of other dicots.

1. Introduction

Pinguicula is the second-largest genus of the family Lentibulariaceae. It comprises about 80 species distributed in arctic, temperate, and tropical areas

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of Eurasia, Africa and America. Like other members of the family, species of *Pinguicula* are carnivorous plants growing usually in nutrient-poor habitats. The genus can be distinguished from other genera of Lentibulariaceae by a combination of plesiomorphic character states, such as presence of more or less typical roots and leaves and passive flypaper type of trapping mechanism. Nevertheless, molecular phylogenetic analyses confirm monophyly of *Pinguicula* (MUELLER et al. 2001, JOBSON et al. 2001).

In the worldwide monographic study of the genus *Pinguicula* by CASPER (1966) three subgenera, 13 sections, and 47 species are accepted. After publication of CASPER's monograph, many new species of *Pinguicula* were described, mainly from mountain regions of Mexico (SPETA & FUCHS 1982, ZAMUDIO 1988, 1997, 1999, 2001, ZAMUDIO & ORTEGA 1994, ZAMUDIO & SALINAS 1996), but also from Europe (TAMMARO & PACE 1987, ZAMORA et al. 1996, CASPER & STEIGER 2001) and Morocco (ROMO et al. 1996). CASPER's sectional delimitation in *Pinguicula* has been questioned by BLANCA et al. (1999). According to the classification by LEGENDRE (2000), the genus *Pinguicula* includes 15 sections and 75 species. Therefore, new studies should be conducted to clarify disputable problems of *Pinguicula* taxonomy. Recent molecular phylogenetic analyses (ALBERT et al. 1992, ALBACH et al. 2001, BREMER et al. 2001, JOBSON et al. 2001, MUELLER et al. 2001) add much to our knowledge of Lentibulariaceae and *Pinguicula* phylogeny. However, many important morphological features still require more careful investigation. This paper aims at studying the seed morphology in selected species of *Pinguicula* and its relation to taxonomy and phylogeny of the genus.

Seeds of *Pinguicula* are unusual among seeds of dicotyledons being variable in cotyledon number. Some species of *Pinguicula* possess embryo with two cotyledons, while others have only one cotyledon (TREVIRANUS 1839, 1848, BUCHENAU 1865, DICKSON 1869, KAMIENSKI 1891, VELENOVSKY 1907, NETOLITZKY 1926, CRÉTÉ 1956, HACCIUS & HARTLE-BAUDE 1957, CASPER 1966, STUDNIČKA 1986). As far as known, monocotyly is found in several other unrelated groups of dicots, such as some Umbelliferae, Ranunculaceae, Primulaceae etc. (e.g., GOEBEL 1932, EAMES 1961). The majority of published data on seeds of *Pinguicula* is focused in the phenomenon of monocotyly. According to traditional viewpoint (VELENOVSKY 1907, HACCIUS & HARTLE-BAUDE 1957), monocotyly in *Pinguicula* is a result of full loss of the second cotyledon. According to CRÉTÉ (1956), who studied embryo development in *P. leptoceras*, primordia of two cotyledons are initiated in this species, but only one cotyledon is present in the mature seed. GOEBEL (1932) suggested that syncotyly has taken place in the evolution of *Pinguicula*. TREVIRANUS (1848) considered that so-called cotyledon of "monocotyledonous" embryos is in fact the first eophyll and suggested that cotyledons are wanting. Although so different interpretations of monocotyly in *Pinguicula* have been proposed, only limited set of species has been studied in respect of embryo structure, and much more information is still needed to analyse embryo evolution within the genus.

External seed morphology in *Pinguicula* has been discussed in several taxonomic publications (NETOLITZKY 1926, CASPER 1962, 1975). DWYER (1983) studied seeds of carnivorous plants and suggested that seeds of *Pinguicula* look similar and have the same basis shape. ZAMORA et al. (1996) studied seed coat ultrasculpture with SEM in six European species (*P. grandiflora, P. submediterranea, P. mundi, P. vallisneriifolia, P. longifolia*, and *P. nevadensis*). MIKELADSE (1996) made SEM micrographs of seeds in nine European and Central American species (*P. hirtiflora, P. crystallina, P. alpina, P. ehlersae, P. pumila, P. lutea, P. caerulea, P. lusitanica, P. vulgaris*).

Seed coat and endosperm anatomy has been studied and illustrated in a limited set of *Pinguicula* species (*P. vulgaris, P. alpina* – HACCIUS & HARTLE-BAUDE 1957, CASPER 1962, 1966). NETOLITZKY (1926) suggested that seed anatomy should be used as a character distinguishing infrageneric groups in *Pinguicula*. However, NETOLITZKY (1926) neither listed studied species of *Pinguicula* nor published any illustration. No data have been published on internal structure of seeds of American species of *Pinguicula*.

2. Material and methods

Seed material was obtained from the seed collection of the Institut für Spezielle Botanik der Friedrich-Schiller Universität Jena[1] (JE), from herbarium specimens of Gray Herbarium of Harvard University (GH) and the Herbarium of the Main Botanical Garden of the Russian Academy of Sciences (MHA), and from plants cultivated in the Main Botanical Garden of the Russian Academy of Sciences, Moscow (Table 1).

Seed morphology was studied with binocular lens in 10–20 seeds from each sample. Besides, 5–10 seeds from each sample were studied with SEM. For SEM studies, a Hitachi S-405A microscope at Moscow University was used. The material was coated by a thin layer of platinum-palladium.

Seed anatomy was studied for 5–10 seeds from each sample using a light microscope. Cross, longitudinal and paradermal sections were made by hand razor and mounted in glycerine. Before sectioning, seeds were maintained for three days in a mixture of equal

Table 1. Location and collection dates of specimens.

Species	Location	Date	Collector
P. alpina L.	Rumänien, Transs. Alpen (Südkarpaten)		Steiger S 41 (JE)
P. balcanica Casper	Bulgarien, S of Sofia		Steiger S 30 (JE)
P. caerulea Walter	USA, Florida, E of Newport	02.V.1956	Kral & Godfrey 2338 (GH)

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[1] Prof. J. STEIGER kindly sent the majority of this material to Jena for this study.

Table 1. (cont.)

Species	Location	Date	Collector
P. corsica M.Bernard et Gren. ex Gren. et Godr.	France, Central		Steiger S 17 (JE)
P. crystallina Sibth. ex Sibth. et Smith	Zypern	1996	Steiger (JE)
P. fiorii Tammaro et Pace	Italien, Maiella		Steiger S 27 (JE)
P. grandiflora Lam. subsp. *grandiflora* f. *grandiflora*	France, Dep. Hautes Pyrenées		Steiger S 10 (JE)
P. grandiflora subsp. *grandiflora* f. *pallida* (Gaudin) Casper	France, Dep. Ain		Steiger S 9 (JE)
P. grandiflora subsp. *rosea* (Mutel) Casper	France, Dep. Isère		Steiger S 11 (JE)
P. hirtiflora Ten.	Italy, near Salerno	V.1996	Steiger S 34 (JE)
P. leptoceras Rchb.	France, Col di Tende		Steiger S 14 (JE)
P. longifolia Ramond ex DC. subsp. *longifolia*	France, Dep. Hautes Pyrenées		Steiger S 20 (JE)
P. longifolia subsp. *caussensis* Casper	France, Dep. Lozère		Steiger S 21 (JE)
P. longifolia subsp. *reichenbachiana* (Schindler) Casper	France, Alp. Maritimes		Steiger S 22 (JE)
P. lusitanica L.	Ireland, Co. Galway	13.VIII.1964	Ferguson 7898 (MHA)
P. lutea Walter	USA, North Carolina	09.V.1954	Channel 2808 (GH)
P. macroceras Link subsp. *nortensis* J.Steiger ex J.Steiger et H.Rondeau	USA, northernmost California del Norte County		Steiger S 28 (JE)
P. moranensis Kunth	cultivated in the Main Botanical Garden of the Russian Academy of Sciences, Moscow		
P. primuliflora C.E.Wood et Godfrey	USA, Mississipi, Harrison County	IV.1957	Gooley & Ray 3225 (GH)
P. vallisneriifolia Webb	Spain, Vall Cazorla		Steiger S 25 (JE)
P. variegata Turcz.	Russia, Khabarovskiy kray, near Okhotsk		Steiger S 29 (JE)
P. villosa L.	Russia, Karelia, Loukhi distr.	21.VI.2001	Schlauer S 44 (JE)
P. vulgaris L.	Russia, Karelia, Loukhi distr.	21.VI.2001	Schlauer S 30 (JE)

parts of glycerine, ethyl alcohol and water at a temperature of 56 °C. Sections were treated partly by phloroglycine and hydrochloric acid, partly by Ch/Zn/J, partly by Sudan-IV, and partly by Ruthenium red.

For some taxa (*P. vulgaris, P. grandiflora* subsp. *grandiflora*) abundant seed material was available, and it was possible to study the variability of seed structure within a sample with SEM and LM.

3. Results

General morphology

Seeds of *Pinguicula* are developing from anatropous ovules (HACCIUS & HARTLE-BAUDE 1957). Seeds are small, 0.4–1.0 mm lg. (Table 2) and have ellipsoidal (most species) or spindly (*P. alpina, P. fiorii, P. moranensis, P. vallisneriifolia*) forms (Figs. 1, 2).

In all examined species, seeds have a more or less pronounced appendage at the micropylar end. The appendage is formed exclusively by the seed coat; it lacks parts of embryo or endosperm (see also HACCIUS & HARTLE-BAUDE 1957). Micropylar appendage length varies among studied species (Figs. 1–5, Table 2). The longest appendage (1/4 of total seed length) has *P. vallisneriifolia* (Fig 3).

Some species (Table 2) have a second, chalazal appendage, which is also formed exclusively by the seed coat. Usually, presence/absence of the chalazal appendage appears to be constant within a species. However, in two subspecies of *P. longifolia* (subsp. *longifolia*, subsp. *caussensis*) the appendage is absent, while in subsp. *reichenbachiana* (Figs. 4, 5) there is a short appendage.

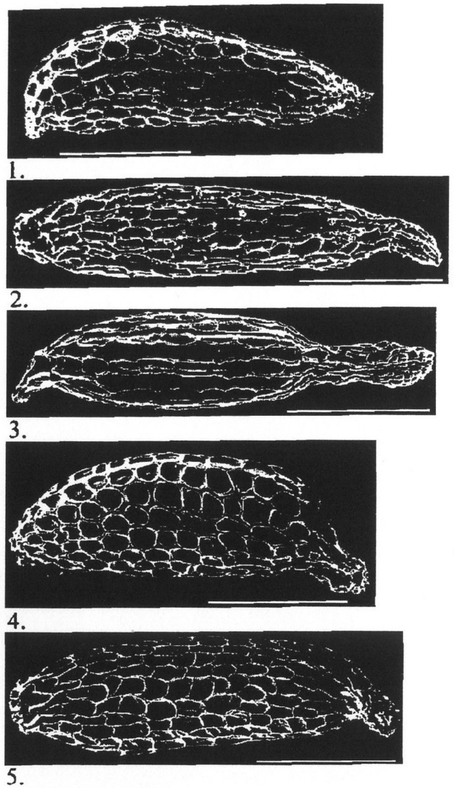
The hilum is situated on the micropylar appendage. It is always very small and possesses no specialised structures. Raphe and micropyle are not visible in mature seeds.

Structure of exotesta cells as revealed on surface view (SEM)

Cellular structure of exotesta is always well visible when the seed coat surface is studied with SEM. Cell outline in surface view varies from rectangular to rounded-polygonal (Table 2). Rectangular cells are usually quite long (e.g., in *P. villosa, P. vallisneriifolia*), but may be almost square (some cells of *P. alpina*). In the vast majority of species, exotesta cells of dry seeds have concave outer walls. Seed surface is thus foveate, with each fovea corresponding to an exotesta cell. In *P. villosa, P. alpina,* and *P. variegata*, outer walls of exotesta cells are almost flat (Figs. 6, 7, 8). In *P. villosa*, seed surface may be described as reticulate; the reticulum consists of narrow and low crests situated along contacts of adjacent cells. In *P. alpina*, exotesta cells are arranged into longitudinal rows; the crests are moderately developed along longitudinal cell margins, while between

Table 2. Seed structure characters variation in studied species of *Pinguicula*.

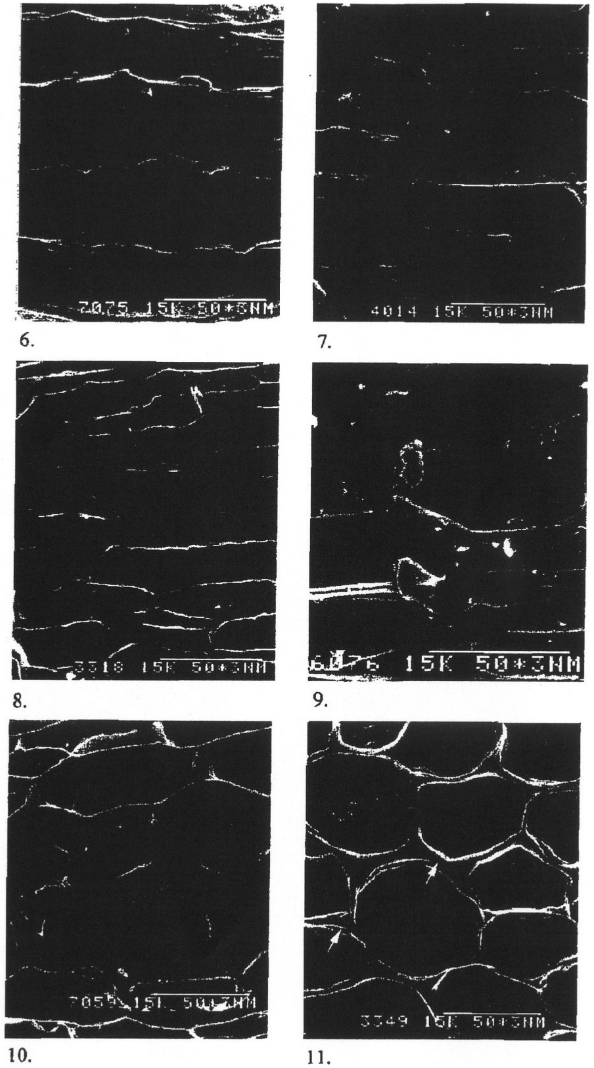
	P. alpina	**P. balcanica**	**P. caerulea**	**P. corsica**	**P. crystallina**	**P. florii**	**P. grand. subsp. grand. f. grand.**	**P. grand. subsp. grand. f. pallida**	**P. grand. subsp. rosea**	**P. hirtiflora**	**P. leptoceras**	**P. long. subsp. longifolia**	**P. long. subsp. caussensis**	**P. long. subsp. reichenbachiana**	**P. lusitanica**	**P. lutea**	**P. macr. subsp. nortensis**	**P. moranensis**	**P. primuliflora**	**P. vallisneriifolia**	**P. variegata**	**P. villosa**	**P. vulgaris**
Seed shape:																							
- Elliptic		+	+	+	+		+	+	+	+	+	+	+	+	+	+	+		+		+	+	+
- Spindly	+					+												+		+			
Mean seed length, mm:																							
- < 0,6			+												+	+			+				
- 0,6-1	+	+		+	+	+	+	+	+	+	+	+	+	+			+	+		+		+	+
- > 1																					+		
Chalazal seed appendage:																							
- present	+				+					+				+				+	+	+	+		
- absent		+	+	+		+	+	+	+		+	+	+		+	+	+					+	+
Micropylar seed appendage:																							
- > 1/6 of total seed length	+	+		+		+	+	+			+	+	+	+					+			+	+
- ≤1/6 of total seed length			+		+				+	+					+	+	+	+		+	+		
Structure of exotesta cells as revealed on surface view of dry seeds (SEM)																							
Cell shape:																							
- rectangular	+																	+		+	+	+	
- polygonal or rounded-polygonal		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+				+
Outer cell surface:																							
- uniformly concave; each cell forms a separate depression.		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+			+
- almost flat:	+																				+	+	
Outer parts of anticlinal walls of adjacent cells:																							
- ± free, i.e. divided by a furrow		+		+		+	+	+	+		+	+	+	+	+		+			+			+
- almost completely united	+		+		+					+						+		+	+		+	+	
Seed structure as revealed on cross sections of seeds treated by water, alcogol, and glycerol (LM)																							
Thickening of anticlinal walls of exotesta cells:																							
- absent	+	+				+															+	+	
- in the outer part of the wall			+	+	+/–				+	+	+	+	+	+	+	+	+	+	+	+			+
- in the middle part of the wall					+/–						+		+		+/–		+			+			
- in the interior part of the wall				+	+/–		+	+	+			+	+		+/–		+	+	+	+			+
Layers of non obliterated cells in mesotesta:																							
- always absent	+		+		+				+	+	+		+	+		+		+	+		+		
- absent or 1		+		+		+						+			+		+			+			+
- up to 3							+	+														+	
Cotyledon number:																							
- 2					+										+			+			+	+	
- 1	+	+	+	+		+	+	+	+	+	+	+	+	+		+	+		+	+			+
Cotyledon symmetry:																							
- symmetric	+		+	+	+	+			+	+	+				+		+	+	+	+	+	+	
- asymmetric		+					+	+				+	+	+		+							+
Cotyledon aestivation:																							
- flat					+										+			+			+	+	
- convolute							+	+	+														
- plicate	+	+	+	+		+		+	+	+	+			+		+	+		+	+			+
- intermediate													+										



Figs. 1–5. General view of seed. Chalazal side left, micropylar side right. Scale unit = 300 µm. — 1, *P. leptoceras*, ellipsoidal seed; — 2, *P. moranensis*, spindly seed; — 3, *P. vallisneriifolia*, spindly seed, the longest appendage at micropylar end; — 4, *P. longifolia* subsp. *longifolia*, ellipsoidal seed, without chalazal appendage; — 5, *P. longifolia* subsp. *reichenbachiana*, ellipsoidal seed, short chalazal appendage.

adjacent cells of the same row the crests are scarcely visible. In *P. variegata* the crests are scarcely visible along all cell margins. The crests in *P. alpina* and *P. villosa* are probably formed due to slight depression of outer cell wall and thus these species are not fundamentally different from the rest of the examined species, which possesses pronouncedly concave outer walls.

P. moranensis differs from the rest of examined species in presence of papillae



Figs. 6–11. Seed surface. SEM micrographs in the middle part of the seeds. Scale unit = 50 µm. — 6, *P. alpina*, seed surface is almost flat, outer parts of anticlinal walls are completely united; — 7, *P. variegata*, seed surface is almost flat, outer parts of anticlinal walls are completely united; — 8, *P. villosa*, seed surface is almost flat, outer parts of anticlinal walls are completely united; — 9, *P. moranensis*, seed surface is foveate, outer parts of anticlinal walls are completely united, exotesta cells with papillae; — 10, *P. caerulea*, outer walls of exotesta cells form cracks; — 11, *P. corsica*, seed surface is uniformly concave, outer parts of anticlinal walls are divided by a furrow.

on exotesta cells (Fig. 9). The papilla represents a hollow outgrowth of outer cell wall.

In *P. caerulea* and *P. lutea*, in contrast to other species, the outer periclinal walls form cracks (Fig. 10).

Outer parts of anticlinal walls of adjacent exotesta cells may be almost completely united (*P. alpina, P. caerulea, P. crystallina, P. hirtiflora, P. lutea, P. moranensis, P. primuliflora, P. variegata, P. villosa*) (Figs. 6–10). In the rest of examined species, outer parts of anticlinal walls are divided by a furrow (Fig. 11).

Seed structure as revealed on cross sections (LM)

According to published data, *Pinguicula* has unitegmic and tenuinucellar ovules, nucellus is destroying during early stages of embryo sac development (PODDUBNAYA-ARNOLDI 1982). HACCIUS & HARTLE-BAUDE (1957) report that at anthesis integument of *P. vulgaris* and *P. alpina* consists of 3–4 layers. Mature seeds consist of seed coat, endosperm, and embryo (Fig. 12).

a) Seed coat

The seed coat of studied species is thin (0.02-0.05 mm). The seed coat apparently always consists exclusively of died cells in mature seeds.

Exotesta has always large, not obliterated cells. The outer periclinal walls are always thin. When material treated by water, alcohol, and glycerol is used, periclinal walls are almost flat or convex. In dry material, the outer walls are

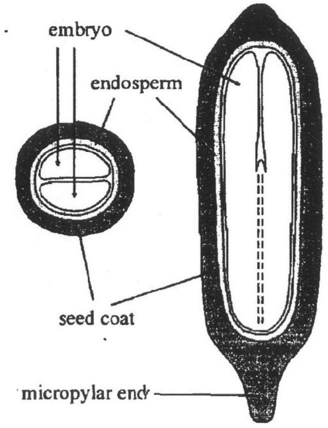
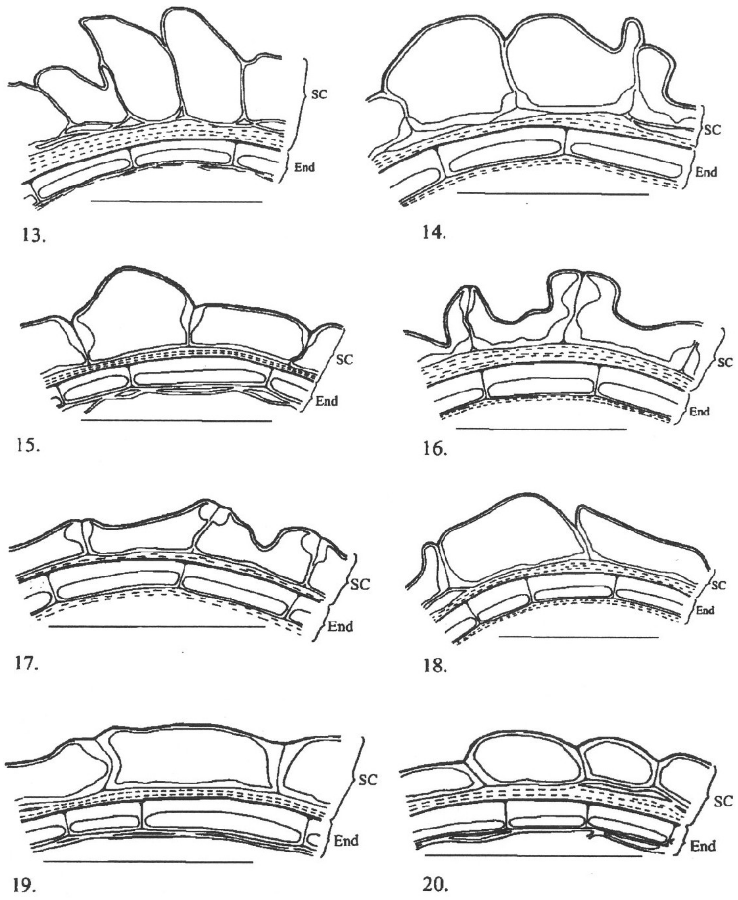


Fig. 12. Schemes of seed of *P. villosa* on cross and longitudinal sections.



Figs. 13–20. Cross sections of seed coat (SC) and endosperm (END). Pattern of anticlinal walls thickening. Scale unit = 0.1 mm. — 13, *P. balcanica*, anticlinal walls are thin throughout their height; — 14, *P. grandiflora* subsp. *grandiflora*, anticlinal walls are thickened in the inner part only; — 15, *P. leptoceras*, anticlinal walls are thickened in the outer and middle parts; — 16, *P. grandiflora* subsp. *rosea*, anticlinal walls are thickened in the outer and inner parts; — 17, *P. lutea*, anticlinal walls are thickened in the outer part only; — 18, *P. macroceras* subsp. *nortensis*, anticlinal walls are thickened throughout their height, but thicker in the inner part; — 19, *P. longifolia* subsp. *caussensis*, anticlinal walls are thickened throughout their height, but thicker in the outer part; — 20, *P. vallisneriifolia*, anticlinal walls are thickened throughout their height.

usually concave (see above). In *P. moranensis*, outer periclinal walls form papillae (Fig. 9).

This study revealed a great variation in pattern of anticlinal walls thickening among examined species (Figs. 13–20). In *P. alpina*, *P. balcanica*, *P. fiorii*, *P. variegata*, and *P. villosa* the anticlinal walls are thin throughout their height (Fig. 13). In *P. grandiflora* subsp. *grandiflora* the anticlinal walls are thickened in the inner part, but thin in the middle and outer parts (Fig. 14). In *P. leptoceras*, they are thickened in the outer and middle parts, but thin in the inner part (Fig. 15). In *P. corsica*, *P. grandiflora* subsp. *rosea*, *P. longifolia* subsp. *longifolia*, *P. moranensis*, *P. primuliflora*, and *P. vulgaris* the anticlinal walls are thickened in the outer and inner parts, but thin in the middle part (Fig. 16). In *P. caerulea*, *P. hirtiflora*, *P. longifolia* subsp. *reichenbachiana* and *P. lutea* the anticlinal walls are thickened in the outer part only (Fig. 17). In *P. macroceras* subsp. *nortensis*, *P. longifolia* subsp. *caussensis*, and *P. vallisneriifolia*, the anticlinal walls are thickened throughout their height. Among these taxa, in *P. macroceras* subsp. *nortensis* the walls are thicker in the inner part of the wall (Fig. 18); in *P. longifolia* subsp. *caussensis* the walls are thicker in the outer part of the wall (Fig. 19); in *P. vallisneriifolia* the thickening is almost constant throughout the wall height (Fig. 20). In *P. crystallina* thickenings of the anticlinal walls form vertical bolsters (Figs. 21, 22). Therefore, in some cross sections anticlinal walls appear to be thick throughout their height, while in others they appear to be totally thin. A peculiar type of thickening is characteristic to *P. lusitanica* (see below).

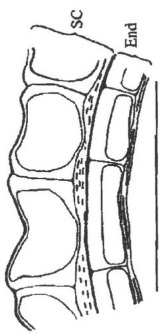
The inner periclinal walls are usually uniformly thin or slightly thickened. However, in three species (*P. caerulea*, *P. lusitanica*, *P. lutea*) the inner periclinal wall forms cross outgrowths. In *P. caerulea* and *P. lutea* the outgrowths are flat and very regular in arrangement (Figs. 10, 23, 24). They occupy a considerable part of cell cavity. In *P. lusitanica* thickenings of the inner periclinal wall form a sparse reticulum consisting of low bolsters. The bolsters are continuing into adjacent anticlinal walls, where they are running obliquely up to joining with a continuous bolster of thickening in the outer part of the anticlinal walls (Figs. 25, 26). As a consequence, the thickening pattern of exotesta cell walls revealed on cross sections is highly variable in *P. lusitanica*.

In *P. variegata* and *P. hirtiflora* exotesta cells possess a dark content (Figs. 27, 28). In the rest of the species, cells appear to be empty when studied with light microscope.

Mesotesta consists as rule of obliterated cells only. However, in *P. villosa* and *P. grandiflora* subsp. *grandiflora*, there are up to three layers of non obliterated cells. In *P. balcanica*, *P. corsica*, *P. fiorii*, *P. longifolia* subsp. *longifolia*, *P. lusitanica*, *P. macroceras* subsp. *nortensis*, and *P. vallisneriifolia* sometimes there is a single layer of non obliterated cells.

In all studied species except *P. moranensis* endotesta in mature seeds has obliterated cells (Fig. 29).

Vascular bundles and their derivates are always absent in seed coat of all examined species.



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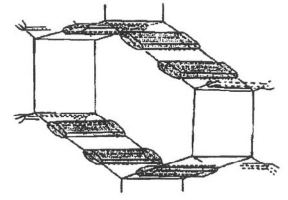

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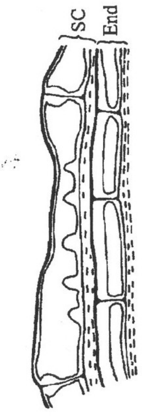

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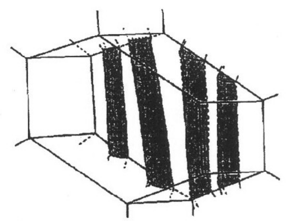

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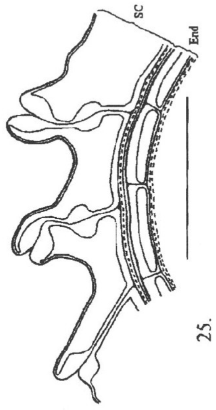

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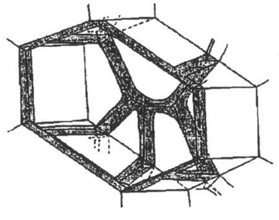

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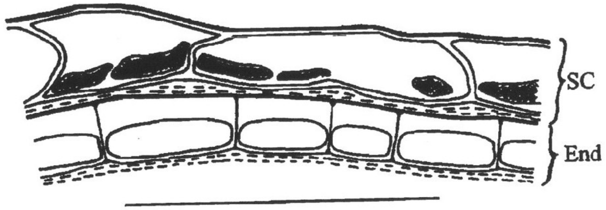
Figs. 21–22. Cross section of seed coat (SC) and endosperm (End) (Fig. 21) and three-dimensional schema of exotesta cells (Fig. 22) of *P. crystallina*. Thickening of the anticlinal walls in the form of a vertical bolster. Scale unit = 0.1 mm. – Figs. 23–24. Longitudinal section of seed coat (SC) and endosperm (End) (Fig. 23) and three-dimensional schema of exotesta cells of *P. caerulea* (Fig. 24). The outgrowths of inner periclinal wall are flat and regular in arrangement. Scale = 0.1 mm. – Figs. 25–26. Cross section of seed coat (SC) and endosperm (End) (Fig. 25) and three-dimensional schema of exotesta cells (Fig. 26) of *P. lusitanica*. The thickening of the inner periclinal wall form sparse reticulum. Scale unit = 0.1 mm.



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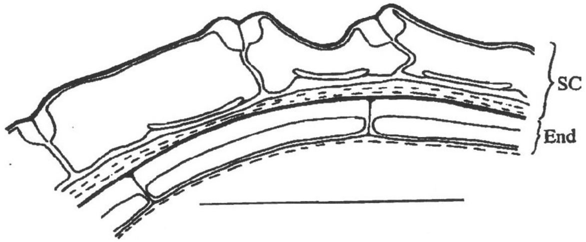

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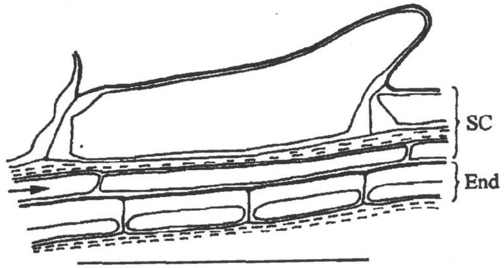


29.

Figs. 27–28. Outer exotesta cells with dark content. Cross section of seed coat (SC) and endosperm (End). Scale unit = 0.1 mm. — 27, *P. variegata*; — 28, *P. hirtiflora*. — Fig. 29. Endotesta with not obliterated cells in mature seeds. Longitudional section of seed coat (SC) and endosperm (End). Scale = 0.1 mm. *P. moranensis*.

b) **Endosperm** (Figs. 13–20)

The endosperm consists of 2–3 cell layers in the mature seeds. The external endosperm cell layer contains numerous starch grains (not shown in the figures). The external periclinal walls of external cells are strongly thickened. The cells of the rest endosperm layers do not contain starch grains and are often obliterated.

c) **Embryo** (Fig. 12)

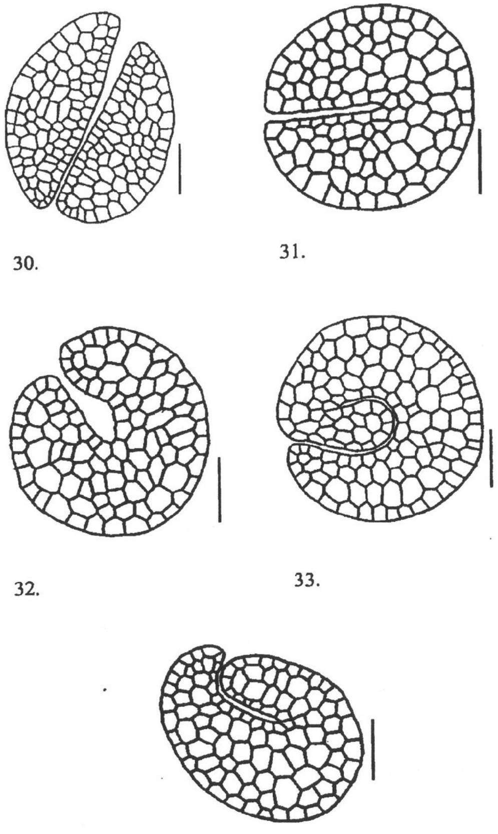
The embryo is straight, well developed and possesses radicula, hypocotyl, one or two cotyledons, and a very small shoot apex. We found two cotyledons in *P. crystallina*, *P. lusitanica*, *P. moranensis*, *P. variegata*, and *P. villosa*. The rest of the examined species possess a single cotyledon. In our material, cotyledon number was stable at the specific level. If the embryo has two cotyledons, they are similar to each other in shape and size in our material. Besides, each cotyledon is symmetric in dicotyledoneous embryos. In embryos with a single cotyledon, the cotyledon is symmetric (*P. alpina*, *P. caerulea*, *P. corsica*, *P. fiorii*, *P. grandiflora* subsp. *rosea*, *P. hirtiflora*, *P. leptoceras*, *P. macroceras* subsp. *nortensis*, *P. primuliflora*, *P. vallisneriifolia*) or asymmetric (*P. balcanica*, *P. grandiflora* subsp. *grandiflora*, *P. longifolia*, *P. lutea*, *P. vulgaris*). Cotyledon aestivation is of four types: flat, convolute, plicate, and intermediate between convolute and plicate (Table 2). *P. crystallina*, *P. lusitanica*, *P. moranensis*, *P. variegata*, *P. villosa* (i.e., species with dicotyledoneous embryos) have flat cotyledons (Fig. 30). The rest of the examined species have a plicate type of cotyledon aestivation (Figs. 31, 32). *P. grandiflora* typically has a convolute cotyledon (Fig. 33). In *P. grandiflora* subsp. *grandiflora* f. *pallida* and *P. grandiflora* subsp. *rosea* we found some embryos with a plicate cotyledon. *P. longifolia* subsp. *caussensis* is characterised by a cotyledon of intermediate type of aestivation (Fig. 34).

The radicula and the hypocotyl possess a procambial strand. Cotyledons have no procambial tissue.

Plumule of a mature seed is very small, undifferentiated, without leaf primordia.

4. Discussion

The results of the present study are largely in agreement with published data on seeds of *Pinguicula*. However, our study covered more species of the genus and provided more information on internal seed structure. Using light microscopy of cross sections, we were able to make a correction to SEM data by MIKELADSE (1996). According to MIKELADZE (1996), cross cell wall outgrowths in exotesta cells of *P. lutea* and *P. caerulea* belong to the outer periclinal wall. We have revealed that they belong to the inner periclinal wall. NETOLITZKY (1926) stated that cells of the outer endosperm layer possess thick cuticle and thin cell walls. We have revealed, in contrast, a very thick outer cell wall of the outer endosperm cells in all examined species. This is in agreement with data of HACCIUS & HARTL-BAUDE (1957). Similar thickenings of endosperm cells are found also in *Utricularia* and some other Lamiales (e.g., Globulariaceae, Gesneriaceae, NETOLITZKY 1926, G.V. DEGTJAREVA, pers. obs.). The thick walls of endosperm cells in *Pinguicula* and related taxa should have a protective function to the embryo, which is especially evident since the seed coat contains usually



30. 31. 32. 33. 34.

Figs. 30–34. Types of cotyledon aestivation. Cross sections of cotyledons of an embryo. Scale unit = 0.1 mm. — 30, *P. crystallina*, two cotyledons, flat type of cotyledon aestivation; — 31, *P. fiorii*, one symmetric cotyledon, plicate type of cotyledon aestivation; — 32, *P. vulgaris*, one asymmetric cotyledon, plicate type of cotyledon aestivation; — 33, *P. grandiflora* subsp. *grandiflora* f. *pallida*, one asymmetric cotyledon, convolute type of cotyledon aestivation; — 34, *P. longifolia* subsp. *caussensis*, one asymmetric cotyledon, intermediate type of cotyledon aestivation.

a single layer of non-obliterated cells. A similar situation is found in some other groups, e.g. in Asparagaceae (OGANEZOVA 1981).

The data of the present study allow to analyse seed character evolution in *Pinguicula* and to discuss taxonomic significance of seed characters.

Seed shape: Spindly seeds are found in four taxonomically unrelated species.

Chalazal seed appendage: Presence/absence of the appendage may be used to distinguish taxa of *P. longifolia* complex.

Exotesta cell shape: The majority of examined *Pinguicula* species possesses rounded-polygonal cells. These species belong to several different sections of two subgenera. In such species as *P. alpina, P. moranensis*, and *P. vallisneriifolia* this character is correlated to a spindly seed shape. However, in other species there is no such correlation. It seems that this character does not have a great taxonomic importance. Probably, it can be used to distinguish some species, but further studies are needed to demonstrate this precisely.

Exotesta cell surface: *P. alpina, P. variegata* and *P. villosa* differ from each other in prominence degree of crests along margins of adjacent cells. Interestingly, *P. variegata* seem to be intermediate between *P. alpina* and *P. villosa*. This is in agreement with observations of gross morphology, which lead to a conclusion that *P. variegata* may represent a hybrid between *P. alpina* and *P. villosa* (Steiger 1998).

Outer parts of anticlinal walls of adjacent exotesta cells: united/divided by a furrow. The furrows are present in all studied taxa of section *Pinguicula* and may thus represent a synapomorphy of the section. We may postulate that this is a character of great taxonomic importance. It is interesting in this respect that the furrow is found also in *P. lusitanica* of section *Isoloba* (MIKELADSE 1996). Since the furrows are absent in other studied species of section *Isoloba* (*P. primuliflora, P. lutea, P. caerulea*), this may indicate that sect. *Isoloba* is a heterogenous group.

The present and the previous character may have certain adaptive significance. Seeds of *Pinguicula* are dispersed by wind and water (FLEISCHER 1929). The reticular sculpture of the seed coat surface allows seed floating on water surface (CASPER 1962). Air bubbles are retaining in depressions of seed coat (note that exotesta cells are covered by hydrophobic cuticle). Ability of the bubbles to retain in the depressions as well as the bubble size should be higher in species with presence of furrows between adjacent cells. If the furrow is present, outer margins of cell depression are much more incurved; this leads to better bubble adhesion. It is necessary to stress that the furrows are found in species with concave exotesta cells only.

Presence of large papillae on outer exotesta cells is characterised only in *P. moranensis*. Similar papillae are present in some other *Pinguicula* species, which share with *P. moranensis* geographical distribution in Mexico (MIKELADSE 1996, SPETA & FUCHS 1982, ZAMUDIO 1997, 1999). The character seems to have a taxonomic significance, but more material from Mexico should be studied yet. Interestingly, similar papillae are found also in some *Utricularia* (TAYLOR 1989); they possibly represent a result of parallel evolution.

Cracks of the outer periclinal cell walls of exotesta cells are found in *P. lutea* and *P. caerulea*. These two species share distribution in SE North America and were allied on the base of morphological characters (CASPER 1996). The character seems to be taxonomically important. MIKELADSE (1996) described similar cracks of outer cell walls in *P. pumila* (not included in this study). According to CASPER (1996) *P. primuliflora* is closer to *P. lutea* and *P. caerulea* than *P. pumila*. In *P. primuliflora*, according to our data, there are no cracks. Therefore it is possible that this character state appeared independently in different sections.

Pattern of thickenings of exotesta cell walls: The pattern of thickening was constant within each sample studied. However, in some closely related taxa we found different patterns of thickening. The character (more precisely, a set of characters) is seemingly characterised by fast evolutionary changes and may be used to distinguish species and/or infraspecific taxa. For example, *P. grandiflora* subsp. *grandiflora* differs from *P. grandiflora* subsp. *rosea* in the absence of peculiar thickenings in the upper part of anticlinal walls. In *P. hirtiflora*, the thickenings form a continuous ring in the upper part of anticlinal walls; the remaining part of anticlinal walls is thin. In *P. crystallina*, the thickenings form several vertical bolsters while the continuous ring in the upper part of the walls is absent. These data contrasting to the opinion that *P. hirtiflora* should be treated as a subspecies of *P. crystallina* (e.g., MIKELADSE 1996). In the *P. longifolia* complex, various subspecies differ from each other in the pattern of thickening. This is in accordance with the opinion based on molecular data, that *P. longifolia* s.l. may be a heterogeneous taxon.

Four examined species of *Pinguicula* have peculiar bolster-shaped thickenings of exotesta cell walls. In *P. lusitanica* the bolsters are irregularly positioned, sometimes anastomosing and occurring both on anticlinal and inner periclinal walls. In *P. crystallina* the bolsters are restricted to anticlinal walls, while in *P. lutea*, *P. caerulea* (this study) they were found exclusively on inner periclinal walls. Comparing our data with SEM-micrographs by MIKELADSE (1996), we should postulate presence of bolsters on inner periclinal cells also in *P. pumila*. These data indicate close relationships between *P. pumila*, *P. caerulea* and *P. lutea*. It is uncertain, whether bolsters of *P. crystallina* and *P. lusitanica* are homologous to bolsters of the three above-mentioned species. They have a different position (in *P. crystallina*) and structure (forming a reticulum: *P. lusitanica*). However, we should note that all five species belong to the same subgenus, *Isoloba*, according to CASPER's (1966) classification.

Endosperm structure is largely uniform among the examined species. This character seems to play on a higher taxonomic level (see above).

Cotyledon number: Species with different cotyledon number are found in each of the three subgenera recognised by CASPER (1966). It should be stressed that *P. crystallina* with two cotyledons and *P. hirtiflora*, which has a single cotyledon, form the separate section *Cardiophyllum*. Grouping of these two species is in good agreement with data of general morphology (CASPER 1966). Members of plant families related to Lentibulariaceae possess embryos with two cotyledons. Therefore, we may postulate that the presence of two cotyledons represents a plesiomorphic condition in *Pinguicula*. It is possible that embryos with a single cotyledon appeared independently in all subgenera of *Pinguicula*. We think that parallelisms rather than reversals took place in embryo evolution of *Pinguicula*, because changes from monocotyly to dicotyly seem to be extremely rare (if at all well documented) in angiosperms (see, however, EAMES 1961). It is interesting, that according to SCHULTZ (1965), seedlings of *P. lusitanica* are variable in presence of a single or two cotyledons; he even reported "all transitions" between seedlings with one and two cotyledons. In *P. alpina*, some seeds with two cotyledons were found along with numerous monocotyledoneous seeds in a sample (HACCIUS & HÄRTLE-BAUDE 1957). This leads us to the conclusion that the cotyledon number should not be treated as a character of greatest importance in *Pinguicula* taxonomy.

Cotyledon symmetry and aestivation: All species with a dicotylenoneous embryo have flat and symmetric cotyledons. Single cotyledon may be pilcate (symmetric or asymmetric) or convolute (always asymmetric). Since in each of the two subspecies of *P. grandiflora* we found various types of cotyledon symmetry and aestivation, the characters seemingly are of low taxonomic importance.

5. Conclusions

Our study revealed that seeds of all examined species are characterised by the same groundplan (thin seed coat, thick outer walls of outer endosperm cells, embryo with non-vascularised cotyledons, etc.). On the other hand, there is a great variation in such characters as presence of the chalazal appendage, pattern of thickening of exotesta cells, cotyledon number. It is important that seed coat anatomy characters are almost constant within each seed sample studied.

Some of the revealed characters are probably significant at the sectional level, e.g. presence/absence of furrows between outer parts of anticlinal walls of adjacent exotesta cells. Some other characters are probably significant on specific or infraspecific level, e.g. pattern of thickenings of exotesta cell walls, presence of chalasal seed appendage.

The seed data generally confirms that section *Pinguicula* represents a natural taxon, which is also in accordance with molecular data. All studied species of section *Pinguicula* share presence of furrows between outer parts of anticlinal walls of adjacent exotesta cells as well as always monocotyledonous embryo.

Our data show great differences between subspecies of *P. longifolia* in seed structure. It may be possible that subspecies of *P. longifolia* should be treated as separate species. The seed data set does not confirm the proposal by BLANCA et al. (1996) to segregate species with narrow leaves and undulate leaf margins (i.e., *P. longifolia* s.l., *P. vallisneriifolia*) into a separate section.

We suggest that cotyledon number was quite unstable in the evolution of *Pinguicula*. Homoplasy in embryo evolution is of special interest, because it seems that members of all related families of the order Lamiales possess embryos with two cotyledons.

Since CASPER (1966) based subgeneric delimitation mainly of flower morphology, our results imply data incongruence between embryo morphology and flower morphology. It is interesting that some features of seed coat morphology are much more congruent to flower morphology then embryo structure. We believe our data does not indicate unnaturalness of CASPER's subgenera. CASPER's system is in general agreement with our molecular phylogenetic study, which is in progress.

A difficult question, which is important in the light of these data, is whether cotyledons of *Pinguicula* are homologous to cotyledons of other dicots. Besides, it is not clear, which kind of homology can be established between cotyledons of dicotyledonous *Pinguicula* species and the cotyledon of monocotyledonous species of the genus. It should be stressed that cotyledons of *Pinguicula* are very simple structures in their morphology, which makes difficult their homologisation. Although the vast majority of authors reject TREVIRANUS' (1848) viewpoint that so-called single cotyledon of *P. vulgaris* is in fact the first eophyll, it seems that no strong arguments against his theory were found. Morphologically, the single cotyledon differs from true leaves mainly in its smaller size (TREVIRANUS 1848, STEIGER 1973). A comparison with the closely related genus, *Utricularia*, shows that the question of organ identity may be very difficult (e.g., RUTISHAUSER & ISLER 2001). Several species of *Utricularia* have seeds without cotyledons (DICKSON 1869, KAMIENSKI 1891, CASPER 1975, NIKITICHEVA 1987), while others may possess two very small or many relatively large outgrowths (GOEBEL 1932), which are currently weakly homologised to true cotyledons *Utricularia* (TAYLOR 1989).

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The orophilous cushion-like vegetation of the Sila Massif (S Italy)

By

S. Brullo, C. Gangale and D. Uzunov

With 10 figures and 6 tables

Abstract

BRULLO, S., GANGALE, C. & UZUNOV, D.: The orophilous cushion-like vegetation of the Sila Massif (S Italy). — Bot. Jahrb. Syst. 125: 453–488. 2004. — ISSN 0006-8152.

The orophilous dwarf shrub vegetation dominated by pulvinate (often thorny) chamaephytes occurring in the Sila Massif (S Italy) is investigated. This vegetation is localized in the mountain belt between 1100 and 1900 m of altitude, and is characterized by numerous endemics exclusive of this territory or circumscribed to S Italy and Sicily. Basing on multivariate analysis, four groups of relevés can be distinguished, corresponding to four plant communities well differentiated from the floristic, ecological and structural point of view. They are proposed as new associations (Astragaletum calabrici, Plantagini serpentinae-Chamaecytisetum spinescentis, Festuco microphyllae-Genistetum silanae, Armerio-Potentilletum calabrae potentilletosum and seselietosum peucedanoidis), included in a new alliance Koelerio-Astragalion calabrici. These communities show close floristic relations with the orophilous shrubby vegetation of Sicily belonging to the class Rumici-Astragaletea siculi (= Cerastio-Carlinetea nebrodensis), while the hypothesis claimed by other authors to refer them to the basiphilous class Festuco-Brometea is not acceptable, since there are neither floristic nor ecological similarities. In particular, the Sila communities are closer to those ones of the Aspromonte Massif and have been grouped in the order Anthemidetalia calabricae, endemic of the Calabrian Apennine.

Introduction

The Sila Massif is localized in Northern Calabria (S Italy), and thanks to its geographical position, geology and bioclimatic peculiarities represents a territory of remarkable geobotanical interest (Fig. 1). A great part of the landscape of Sila, between 1100 and 1900 m a.s.l., is characterized by a cushion-like vegetation,

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