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Pinguicula (Lentibulariaceae): The Cool Climate Species of the Northern Hemisphere - Morphology, Biology, Cultivation

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A. Introduction

The geographical origin of the genus *Pinguicula* is not known, as fossil witnesses of such tender plants do not exist. But there is some evidence that the genus may have existed already around 50 million years ago, when the the drifting appart of the American from the Eurasian continent was not yet completed, i.e. when - during the miocene - some north-atlantic land bridges and islands still allowed intercontinental plant migrations. Two distribution centers developed in the corresponding areas at that time: one around the Mediterranean Sea, the other one around the Caribbean. In Eurasia some populations remained in the northern regions of the Mediterranean area, others migrated to north (including Iceland) and east as far as Japan and the Himalayas. In America some populations remained in and around the Caribbean, some migrated to north and northwest, others to south along the Andes as far as the Tierra del Fuego. The genus *Pinguicula* is not present in Africa (except for the northernmost region of Marocco), Indonesia, Australia and New Zealand.

During the process of changing environmental conditions three strategies are observed in the evolution of plants: (1) migration, (2) adaptation, (3) extinction. During many millions of years most parts of the earth had subtropical climate. But approximately 1 million years ago a series of ice ages began to force hundreds of plant species to migrate and/or to adapt which resulted in completely new patterns of distribution areas and genetic information. Geographical, morphological and caryological data of *Pinguicula* may provide some evidence concerning the adaptation, migration and differentiation strategies within the genus.

In the thirties Hagerup, Tischler and other authors came up with a hypothesis ('Hagerup-Tischler Rule') saying that periods of hard environmental conditions - particularly unstable, unpredictable conditions - will increase the chromosome number of plants (e.g. ice ages/interglacial periods, heat periods, extreme temperature amplitudes, intensive ultraviolet radiation). This would mean that plants with higher chromosome numbers are likely to have been able to survive one or several ice ages, while lower chromosome numbers may be an evidence for relatively stable environmental conditions (e.g. Hagerup 1932).

	Stable environment	*Unstable environment*
LOW chromosome numbers (haploid gametes)	***Sufficient recombination possibilities***	Insufficient recombination possibilities → long-term survival genetically not guaranteed
HIGH chromosome numbers (e.g. diploid gametes)	No necessity for higher recombination possibilities	***Necessity of higher recombination possibilities***

Fig. 1) Chromosome numbers and environmental conditions

Simply stated this may be explained as follows: Hard and unpredictable environmental conditions are likely to cause an increased rate of mutations. An unfavorable mutation - particularly if it is dominant - in one of the gametes may cause a selection disadvantage to the offspring. Usually the pollen grains and the female gametes are haploid, resulting in a diploid somatic cell when joining. But it is known from other plant groups that in average 1 per thousand plant specimens is tetraploid due to defective processes during meiosis of their parent gametes or during their generative fusion (Briggs & Walters 1973). If a mutation happens in a diploid gamete it is very unlikely that just the very same mutation will affect also the corresponding gene in the second set of - homologus - chromosomes. If two diploid gametes now join to a tetraploid cell the mutation will be present only in one of four homologus chromosomes: Thus the three healthy chromosomes may protect the plant from an eventual selection disadvantage. Polyploid plants will not only be better protected from unfavorable mutations, but the multiple representation of the genetic code for the same feature may result in an increased ecological tolerance due to some heterogeneity of the homologous genes.

Considering the growth type, *Pinguicula* may be divided into four groups: tropical-homophyllus, tropical-heterophyllus, temperate-homophyllus and temperate-heterophyllus. The tropical growth type forms assimilating leaves all the year through. The temperate type hibernates by means of a *hibernaculum*. In the homophyllus growth type only one rosette type is formed, i.e. all leaves of the rosettes have morphologically the same characteristics. The heterophyllus type forms two different rosettes - either a larger rosette in summer and a smaller, morphologically different rosette in winter (tropical-heterophyllus type) or a smaller generative spring rosette followed by a larger vegetative summer rosette with different leaf morphology, which later forms the *hibernaculum* (temperate-heterophyllus type).

	Tropical *Assimilating leaves all the year through*	*Temperate* *Hibernate by means of a hibernaculum*
Homophyllus Only one rosette type	*P. jackii*	*P. vulgaris*
Heterophyllus Two different rosette types	*P. gypsicola*	*P. vallisneriifolia*

Fig. 2) Climate type and growth type with each one representative species

This contribution is focused on the *Pinguicula* species of the temperate-cool, (sub)alpine and (sub)arctic climate regions of Eurasia including three species also distributed in northern North America. The discussed species belong to the subgenera *Pinguicula, Temnoceras* and *Isoloba.*

B. Subgenus *Pinguicula*

It comprises (in alphabetical order) the following species: ***P. balcanica, corsica, dertosensis (submediterranea), fiorii, grandiflora, leptoceras, longifolia, macroceras, mundi, nevadensis, vallisneriifolia, villosa*** and ***vulgaris.***

All species of this group are hibernating by winter buds (s: hibernaculum, pl: hibernacula) which form at their basis little brood buds (s: gemma, pl: gemmae) for vegetative propagation. Their leaves and roots decay in winter. Their chromosomes are multiples of the basic number 8.

1. Pinguicula corsica Bern. & Gren. ex Gren. & Godr. 1850

This well distinct species is an endemism of the Corsica island and was never found elsewhere. Six million years ago the Mediterranean Sea was more or less dry, i.e. the Corsica island was not yet disconnected from the continent by the Atlantic waters entering from the Strait of Gibraltar (Illustr. Wiss. 1998). It is likely that one or more *Pinguicula* predecessors existed in the mountainous areas of southern Europe. When the Mediterranean Sea disconnected the islands of Corsica and Sardinia it also isolated the Corsican Pinguiculas. Corsica remained more or less untouched by several ice ages, the insular climate was probably relatively predictable and there was no necessity for this species to adapt to fundamentally changing conditions and to conquer new territories. Thus there was no reason for it to increase the chromosome number. With 2n=16 *P. corsica* is considered to be one of the old species within this subgenus.

P. corsica is characterized by its rather large and wide leaves (c. up to 40mm long, up to 25mm wide), by the narrow throat of the flower, the slender spur, and by the narrow, well separated calyx tips. The flower may vary from almost white to pale blue. Its overall length is about 25mm. It grows in subalpine and alpine damp meadows and around little springs and lakes, near and above the timberline, sometimes descending into cool ravines, usually from 1000-2400m. The highest sites are covered 4-7 months by snow. The substrate of all sites is granite, but in cultivation *P. corsica* also grows on calcareous substrate. This allows the conclusion that it does not grow on silicate ground due to a preference based on a selection process but just due to the fact that no other substrate is available there.

2. Pinguicula nevadensis (Lindberg) Casper 1962

This again is a well distinct species, an endemism of the alpine zones of the Sierra Nevada in southern Spain. Its leaves are also relatively wide, similarly shaped to those of *P. corsica* but smaller (c. 25mm long, 20mm wide), the flowers are relatively small (overall length c. 13mm), varying between pale violet and whitish, the spur is thicker and more curved than in *P. corsica*. This species reaches far above the timber line and grows at numerous sites near little springs and alpine lakes on granite between 2160m and 3100m. Although *P. nevadensis* is exposed to very intensive sun radiation its leaves show only slight reddish pigmentation. Its highest sites are covered by snow during 5-7 months. The feeding ecology of P. nevadensis was investigated by Zamora (Zamora 1990). During the past ice ages and interglacial periods the mountain ranges in southern Spain were not exposed to such dramatic climate changes as the Alps and most parts of central and northern Europe. So the low chromosome number of *P. nevadensis* (2n=16) is not surprising and may indicate it to be an old species which was not forced to migrate and to conquer new territories.

3. *Pinguicula leptoceras* Reichenbach 1823

P. leptoceras grows on wet subalpine and alpine sites in the Alps of western Austria, northern and northwestern Italy, Switzerland and southeastern France. Its leaves vary considerably in size and sometimes show dark pigmentation at sunny sites. The main characteristic of *P. leptoceras* is the calyx: The central upper tip is usually very wide, the lower ones are deeply split into two slender tips forming an angle of 90 or more degrees. It is also distinguished from most other European *Pinguicula* species by the globular seed capsule. It is not clear why Reichenbach named this species *'leptoceras'* (= slender-spurred) as the spur is often conspicuously wide and thick, even at the holotype site where I have investigated hundreds of flowers. The flowers are around 22mm in length and the corolla lobes are overlapping. At many sites flowers with 6 or 7 corolla lobes and calyx tips are very frequent. In the eastern distribution range the flowers are usually one-colored dark blue-violet or with 1-3 small white spots on the lower corolla lobes, at the holotype site in central Switzerland most specimens have three distinct white spots, and in the Maritime Alps the flowers are pale blue with three large white spots. *P. leptoceras* is usually found between 1800m and 3000m and only rarely descends below 1500m. In the Maritime Alps it grows on limestone, in the northern and eastern distribution area it seems to prefer silicate ground. *P. leptoceras* belongs to the group of tetraploids (2n=32), meaning that it is likely to be a younger species. Occasionally it is associated with *P. alpina* and *P. vulgaris*. At some common sites I recorded natural hybrids of *P. leptoceras* with *P. vulgaris*, but never with *P. alpina.*

P. leptoceras was also recorded from the Apuanian Alps in Italy. I have visited one of the indicated subalpine, almost alpine, sites (above Carrara) and what I found was clearly neither *P. leptoceras* nor *P. longifolia subsp. reichenbachiana*. Probably *P. leptoceras* is restricted to the Alps sensu strictu. The Apuanian Pinguiculas need further investigation.

4. *Pinguicula balcanica* Casper 1962

P. balcanica is so to speak the eastern complement to *P. leptoceras*. It is tetraploid (2n=32) and grows on subalpine and alpine wet places of the Balkan Mountains from Albania, Macedonia and Bulgaria down to the southernmost part of the Pindus Mountains in Greece (in 1995 Jan Schlauer and myself found it in the Vardoussia Range in central Greece, the southernmost site known today). In Bulgaria the northern distribution border still needs to be investigated (Peev 1997). One of its features are the upper corolla lobes which are mostly overlapping and positioned closely together. The corolla color is somewhat similar to *P. leptoceras* but the white spots are less conspicuous. The calyx is distinctly different from *P. leptoceras*: The five tips are similar in shape and length. The seed capsule is conical-pointed. *P. balcanica* grows between 1700m and 2400m, i.e. reaching far above the timber line, both on granite and limestone ground. Casper describes this species as heterophyllus which I hardly can confirm. However the leaves of the specimens I collected in the Vitosha Mountains (south of Sofia) are so different from those of two sites in Greece that is not unlikely that the Balkan Mountains harbor two different subspecies or even species.

Casper also describes a petrophilus ***P. balcanica var. tenuilaciniata*** from Bosnia, Hercegovina and Montenegro with leaves similar to those of *P. longifolia* (Casper 1962*)*. It is likely that this variety is heterophyllus. I have never seen this plant which eventually might be related or identical with a 'new' *Pinguicula* recently found by Poldini in northeastern Italy.

5. *Pinguicula fiorii* Tammaro & Pace`1987

This species was discovered in 1987 as an endemism of the Maiella Mountains in central Italy (Tammaro & Pace 1987). Three sites are recorded up to now, two lower ones in the deciduous tree zone and one in the alpine zone - a remarkable range from 750m-2470m - all with limestone ground. *P. fiorii* is distinct from similar species by the comparatively large, strong calyx and the lack of any white spots on the lower corolla lobes. The corolla color is intensively violet, sometimes almost blue. Unlike another species known from Italy *(P. longifolia subsp. reichenbachiana)* this species is clearly homophyllus. Morphologically there are no particular relationships neither to *P. corsica* and *bàlcanica* nor to the *P. longifolia* group. In spite of the relatively poor description and illustration of this discovery it is certainly a distinct species. The chromosome number is indicated as 2n=32 but based on an unsatisfactory preparation technique.

6a. *Pinguicula grandiflora* Lamarck 1789

P. grandiflora has several disjunct distribution areas reaching from southwestern Ireland to the Plateau Central in France, part of the Jura Mountains of France and Switzerland, the Savoyan Alps around Grenoble, the French and Spanish side of the Pyrenees and some sites at the Atlantic cost of northern Spain. Such distribution patterns, a result of pre-, inter- and postglacial migrations, are quite typical for plants with very specific growing requirements. Webb thinks *P. grandiflora* to have survived the last ice age in southwestern Ireland which has probably been ice free most of the time (Webb 1952). As expected from such distribution *P. grandiflora* is not diploid but tetraploid (2n=32). It is a well distinct species characterized by a relatively vigorous habitus and large flowers (up to 35-45cm) with characteristically tinted veins. The margins of the corolla lobes are mostly somewhat undulated. *P. grandiflora* needs high air humidity and prefers to grow at mossy places underrinsed by cold water all summer. It does not grow in stagnant water or at places where the substrate is warming up to much at noon.

The violet 'normal' form is distributed at all above named sites except the Savoyan Alps. In Ireland it descends almost to sea level, in the Jura and the Pyrenees it reaches up to 1600m. It usually grows in loamy, calcareous substrate or on wet limestone cliffs, exceptionally also on granite at some few sites in the Pyrenees. At sunny places the margin of the leaves, the stalks and calyces may present dark pigmentation.

Concerning the claimed existence of *P. grandiflora* in Marocco, Casper (personal communication 1998) believes this specimen to have been collected elsewhere and erroneously labeled from a Maroccan site (see also Schlauer 1994*)*.

6b. *Pinguicula grandiflora f. pallida* (Gaudin) Casper 1962

The whitish-pale violet *forma pallida* - which also lacks the dark pigmentation of stalk and calyx - grows occasionally amongst dark colored specimens at some sites in the Jura Mountains at 1000-1500m, there amounting to about 20% of the specimens. There is also a site where exclusively *f. pallida* specimens occur. This pale form is likely to be a mutation (but not an albino sensu strictu) which obviously has some positive and consistent selection features as it is recorded regularly since 1828. The pale specimens often have a somewhat thicker spur, giving evidence that the genetic alteration leading to the color mutation might be polyphenotypical.

A pure white form of *P. grandiflora* was found in the Burren Mountains south of the Galway Bay (Co. Clare) in Ireland by Webb in 1956 and later by Nelson in 1991, who described it as ***P. grandiflora f. chionopetra*** (Nelson 1993). I have seen one fresh specimen from there which was not pale blue as *f. pallida* but really white. Whitish or pale blue *P. grandiflora* were also found by other authors in Co. Kerry, but the pure white forms seem to be really rare. If these are to be considered as occasional albinos as they occur in many violet plant species or if they should be ranked as a *forma* is subject of individual viewpoints.

6c. Pinguicula grandiflora subsp. rosea (Mutel) Casper 1962

P. grandiflora subsp. rosea is an endemism of the calcareous mountains around Grenoble (France). In this area the normal form does nor occur. It has all characteristics of *P. grandiflora*, but the flower is somewhat smaller, the spur is shorter and purple and the color of the corolla is pale pink with purple stripes in the throat. The corolla margins are often more undulated than in the normal form.

The Pinguicula longifolia-group

Morphologically this group is characterized by its heterophyllus rosettes. The leaves of the spring rosette are rather short. With and after the flower a second generation of leaves develops which are narrower and longer. *P. longifolia* is petrophilus, i.e. it does not grow in bogs but on wet vertical rock walls, usually below overhanging rocks parts in microclimatic niches not exposed to direct rainfall. I adhere to the nomenclature of Casper (1962a, 1966), knowing that he himself considers the *P. longifolia* group to be revised. As far as known all belong to the tetraploid group with 2n=32.

7a. Pinguicula longifolia subsp. longifolia Ram. ex DC. 1805

P. longifolia is a subalpine endemism of a small area in the central Pyrenees where it grows on both the north and south side of the range on vertical limestone rock walls at 1200-1900m. It is characterized by elegant large flowers with a relatively long and slender spur (c. 35-40mm) and not or only barely overlapping corolla lobes. The flower displays some characteristics of *P. grandiflora* which grows nearby at several sites (together with *P. alpina* which is rather rare in the Pyrenees). The climatic tolerance - the other *P. longifolia* members grow in much milder climate - and the flower morphology may be a hint for some genetic introgression by *P. grandiflora*. The long summer leaves, reaching a length of 130mm, do also present glands on the underside (which is not the case in the other *longifolia* subspecies), but in a much lower density than on the top surface.

7b. Pinguicula longifolia subsp. caussensis Casper 1962

P. longifolia subsp. caussensis is an endemism of the mountains called 'Les Causses' in central. It grows at the damp bottom of high, vertical limestone walls around 400-500m. Compared to the plants of the Pyrenees this subspecies has considerably smaller flowers with less overlapping corolla lobes. Although growing in much milder climate its summer leaves are by far not as long as those of the plants from the Pyrenees and it does not present glands on the underside of the leaves.

7c. Pinguicula longifolia subsp. reichenbachiana (Schindler) Casper 1962

P. longifolia subsp. reichenbachiana grows on wet limestone rocks from 500-600m in the Roya-Valley (Maritime Alps) and its neighboring gorges, but not in the Abruzzi in central Italy as claimed by some authors. It is characterized by relatively large flowers and wide, overlapping corolla lobes. The corolla color may vary from almost white to deep blue with very varying size of the white spots on the lower corolla lobes.

In fact the three mentioned members of the *longifolia* group are so different from each other that I would suggest to consider them as distinct species. I guess future chromatine analysis will support this.

8. Pinguicula dertosensis (Canigueral) G. Mateo Sanz & M.B. Crespo Villalba 1995 (= *P. submediterranea* Blanca, Jamilena, Ruiz-Rejon & Zamora 1996)

This taxon is in fact what Zamora et al. published recently as *P. submediterranea* (Zamora et al. 1996). Their RADP-analysis (Randomly Amplified Polymorphic DNA) revealed a group of butterworts from southern Spain, including the *Pinguicula* population growing near Tortosa, to be distinctly different from other species and they described it as a new species *P. submediterranea.* But Canigueral had already given the Pinguiculas from Tortosa the name *dertosensis* (he considered them as a variety of *P. grandiflora*), and in 1995 Sanz and Villalba gave it the rank of a species. Even if Zamoras' analysis of 1996 was more sophisticated, the international nomenclature rules give the name *dertosensis* priority. *P. dertosensis* is a heterophyllous species and grows in the Sierra de Cazorla (holotype), Sierra Tejeda, Sierra de Segura and Granada and the mountains near Tortosa from 600-1400m. Its flowers are similar to those of *P. longifolia subsp. reichenbachiana*, but somewhat smaller. The chromosome number is 2n=24 (triploid), a new number in the subgenus *Pinguicula*. At one of the sites near Tortosa I was surprised to find not one single plant which was not infested by *Ustilago pinguiculae.*

9. Pinguicula mundi Blanca, Jamilena, Ruiz-Rejòn & Zamora 1996

This is another triploid species (2n=24) recently described from Spain (Zamora et al. 1996). It is known only from the Calar del Mundo: Gorge of the Rio Mundo, c. 1200m, limestone. Zamoras' RAPD-analysis revealed it to be different from all other species. It has a semierect rosette of heterophyllus growth type. The flowers are quite large and the calyx is similar to the calyx of *P. vallisneriifolia*. As it has features of *P. grandiflora, longifolia* and *vallisneriifolia* it might be of hybridogene origin, or introgression of genetic material of one of these species might have been transmitted by viruses. Due to its very restricted distribution and the increasing climate aridity in this region the existence of *P. mundi* is endangered.

10. Pinguicula vallisneriifolia Webb 1853

P. vallisneriifolia is a very distinct species. Zamora found 2n=32 chromosomes (Zamora 1996), I myself counted 2n=16. It grows on wet limestone rocks of the Sierra de Cazorla, Sierra de las Villas, Sierra de Segura and Sierra de Almijara in southern Spain (900-400m). As the individual sites were genetically isolated from each other since thousands of years, the plants of each site show minor but consistent phenotypical differences. The Sierra de Cazorla flowers are pale blue and remarkably large (c. 35mm), those of the Borosa river are whitish-blue and somewhat smaller, and the Sierra de las Villas flowers are white with a yellow spur and a light yellow pubescence in the throat, but at all sites they have relatively large and wide calyx tips. The summer leaves may reach a length of 250mm. Digestive glands are found also on the underside of the leaves as already described in *P. longifolia*. *P. vallisneriifolia* is the only European species which forms gemmae that develop runners (stolons) for vegetative propagation.

11a. Pinguicula macroceras Link 1820

P. macroceras grows along both sides of the Pacific from Japan over Sakhalin and Kamchatka to the Aleutians, along the coast and western mountain ranges of Alaska and British Columbia to Washington and a subspecies even reaches the northernmost part of California. The eastern distribution border in North America is unclear as some authors did not and still do not distinguish *P. macroceras* and *P. vulgaris*. There may be areas of overlappings with hybridizations of the two species which both are octoploid (2n=64; Uchiyama 1990, Rondeau & Steiger 1997). The high chromosome number allowed *P. macroceras* to conquer a wide range of growing conditions. And as both species are rather variable, identification of exsiccata may be difficult. In general *P. macroceras* has larger flowers (18-27mm), longer spurs and shorter stalks than *P. vulgaris* (Casper 1962b). In contrast to *P. vulgaris* the two lower calyx tips are deeply separated, all calyx tips are similar in shape and length, forming a five-pointed star (Casper 1966). The seed capsules of the plants I have seen from Washington, British Columbia, Alaska and Japan were ovate-subglobular, while in *P. vulgaris* they are pear-shaped. In 1831 Chamisso found short spurred specimens in the Aleutians and named those *P. microceras* which later caused much confusion. In fact several species as *P. alpina, vulgaris, leptoceras* and *balcanica* occasionally form stubby spurred flowers, particularly in years with adverse climate conditions. But the same plant may have flowers with both long and short spurs. Therefore, Casper (1962b, 1966) does not assign the *microceras* specimens the rank of a species, subspecies, or variety.

11b. Pinguicula (macroceras subsp.) nortensis Steiger & Rondeau 1996

P. (macroceras subsp.) nortensis grows in a disjuncted, limited area at 100-1660m on serpentine substrate at the border of northwestern California and southwestern Oregon, mainly along the Smith River and the Illinois River and their tributaries, 500km away from the next *Pinguicula macroceras* site in southern Washington. I determined the chromosome number as 2n=64. It is well distinct from *P. macroceras* by its conspicuously long and large central lower corolla lobe and by the globular seed capsule. In fact the striking difference of the seed capsule shape qualifies it to have the rank of a species.

12a. Pinguicula vulgaris Linné 1753

P. vulgaris is (like *P. macroceras*) octoploid and was therefore able to conquer a very large distribution area with a great variety of different growing conditions. It is found from sea level up to alpine sites, on limestone and gypsum as well as in acid *Sphagnum* bogs and coastal sites occasionally overflooded with saltwater, in relatively mild maritime areas as well as in continental climate conditions of Siberia and North America. It is extremely variable in size, shape, pigmentation and number of the leaves, in size and number of flowers, length of the stalks. From most other species *P. vulgaris* is well distinct by the lower calyx tips which are grown together for about two thirds of their length. In North America the corolla lobes are generally longer and narrower than in European specimens.

12b. Pinguicula vulgaris f. bicolor (Nordst. ex Fries) Neumann 1901

In different regions of Europe *P. vulgaris* occasionally appears with totally white corolla lobes while the rest of the flower is violet. Sometimes *f. bicolor* specimens are found amongst the normally colored, in other regions there are sites with exclusively 'normal' and exclusively two-colored specimens. Chromosomes: 2n=64. As far as I know the *f. bicolor* was not recorded in North America.

What about *P. bohemica*? I grow both and cannot identify any pertinent difference between *P. vulgaris f. bicolor* and *P. bohemica. P. bohemica* was published to be tetraploid (2n=32) but considering the difficulty of chromosome counting in *Pinguicula* the technical quality of this count is not convincing.

12c. Pinguicula vulgaris var. transsilvanica Krajina 1933

This variety differs from *P. vulgaris* mainly by the wider, often slightly overlapping corolla lobes, the usually deeper separation of the lower calyx tips and the non-existence in lower altitudes. It is restricted to the southern Carpathians east of the Olt River where it grows on different substrates from 1600-2000m, at some sites associated with *P. alpina.*

13. Pinguicula villosa Linné 1753

In fact *P. villosa* does not really fit well into the pattern of the subgenus *Pinguicula*. It is by far the smallest of all discussed species: The tiny flower has a length of only 6-9mm. It has a disjunct circumpolar distribution in the boreal regions of Eurasia and North America, but it is not recorded from Iceland or Greenland. In east Asia it seems to reach as far south as North Korea. *P. villosa*, a self-pollinator, is restricted to ever wet *Sphagnum* bogs (mainly *Sphagnum fuscum*). In late summer its two to four leaves are often not visible at all as they become completely overgrown by the surrounding *Sphagnum.* The conspicuous involution of the leaves' margins prevents the overlaying *Sphagnum* to irritate the digestive glands. The next hibernaculum is usually formed 1-3cm above the last one. If prepared carefully one can follow several 'floors' of rosettes from the past years. There is never more than one stalk per rosette. The stalks bears innumerable hairs. *P. villosa* has a very limited ecological tolerance and grows exclusively in a very specific environment in hard but relatively constant and predictable climate conditions which is compatible with its low diploid chromosome number of 2n=16. It is likely to have survived the last ice ages in the area of the Gulf of St. Lawrence which was more or less ice-free at that time.

14. A new *Pinguicula* from Italy?

In April of this year Jan Schlauer, Heiko Rischer, Joachim Nerz and myself had the unique opportunity to join Prof. Livio Poldini (Botanical Institute of the University of Trieste) who showed us a *Pinguicula* population detected by him some years ago in the Alps between the city Udine and the Italian border to Austria around 500m a.s.l. It grows at three or four sites in a remote gorge on vertical limestone rocks. It is heterophyllous and at sunny places the leaves are tinted completely purple. The flower is similar to the flower of *P. longifolia subsp. caussensis*, but a little larger and somewhat more reddish. At the site we visited numerous flowers had 7 or 8 corolla lobes and supernumerary calyx tips as well. The chromosome number is yet unknown. We all think I might be a new species related to the *P. longifolia* group. But it also might be related if not identical with Caspers' ***P. balcanica var. tenuilaciniata***. If this should be the case it should be given - in my opinion - the rank of a species and not a variety of *P. balcanica* from which it is rather different. It would be important to find someone who could collect fresh material of the *P. balcanica* variety in Bosnia, Hercegovina or Bosnia in order to compare it with the Italian specimens.

Pinguicula fontiqueriana Romo, Peris & Stübing 1996

The somewhat confusing records and rather poor description with insufficiant drawings of this *Pinguicula* recently described from the Er Rif Mountains in Marocco (1700-2100m, Romo et al. 1996) does not provide stringent evidence that it is really a distinct taxon. It might also to be a population within the variability range of *P. vulgaris.*

It is likely that 1-3 additional new species may be described within the next years from Italy and Spain. It seems that the Mediterranean region is particularly rich in stenochorus endemisms which are found in very restricted areas with peculiar environmental conditions where they diversified from their ancestors due to genetical isolation. For me there is no doubt that e.g. the species growing in the Abruzzi Mountains is *not P. longifolia subsp. reichenbachiana* as claimed by Tammaro (1987). I also think that the different subspecies of *P. longifolia* should be given the rank of species as they are distinctly different from each other.

B. Subgenus *Temnoceras*

The subgenus *Temnoceras* is mainly characterized by relatively small upper and lateral corolla lobes while the central lower corolla lobe is conspicuously large. The pubescence in the entrance of the corolla throat is usually yellow.

14. Pinguicula alpina Linné 1753

P. alpina is distributed in (sub)alpine and (sub)arctic regions of all Eurasia, reaching from sea level in northwestern Siberia up to 2600m in the Alps and 4100m in the Himalayas. It does not exist in North America, i.e. it neither crossed the Atlantic (not recorded from Iceland and Greenland) nor the Bering Sea (alleged records from Alaska were not confirmed). In Eurasia it obviously migrated through the northern areas, thus not reaching the Balkan, Turkey and the Caucasus. Some authors think its origin are the Himalayas from where it migrated through Siberia to Scandinavia, the Alps und finally the Pyrenees (but how did its ancestors get to the Himalayas?). Others assume its origin in the Alps from where it migrated in opposite direction. It is said to prefer calcareous substrate but I also found it on silicate substrate associated with *Soldanella pusilla* and even in *Sphagnum* bogs. Regarding the large distribution range an octoploid chromosome number might be expected, but *P. alpina* is tetraploid (2n=32) which might explain its - compared with *P. vulgaris* - relatively limited ecological tolerance. Morphologically this white flowered species shows only little variability. Only the yellow spot on the central lower corolla lobe may vary in size and color. *P. alpina* is the only winter bud forming species with perennial roots. At some sites it is associated with *P. vulgaris, leptoceras, grandiflora, longifolia subsp. longifolia* or the recently detected butterwort population in northeastern Italy. In boreal sites it sometimes grows in the neighborhood of *P. villosa.* At most common sites it usually flowers earlier than the other species (but not in Siberia). In nonflowering stage one can tell *P. alpina* from all other species by its lack of globules of secretion on the stalked glands along the central axis of the leaf (in the other species the central glands are morphologically identical with the marginal ones). *P. alpina* does not form brood buds but occasionally it develops sort of runners which remain connected with the mother plant. Its cultivation is rather difficult.

15. *Pinguicula algida* Malyshev 1966

I have not seen this little Siberian species in flower. *P. algida* seems to have some similarities with *P. variegata* and *villosa* but the winter buds are wider and look more like those of *P. variegata*. Of the six *Pinguicula* species recorded in Siberia this seems to be the species which grows at the coldest sites. The beginning of its very short flowering period varies considerably - depending on the weather conditions - from year to year, but does not exceed 7-10 days (Molozhnikov 1998). Malyshev, who first described it, was so fascinated by this new finding that he used it as the cover decoration of his book 'Flora Putorana'. It might be of hybridogene origin. Prof. Vladimir Molozhnikov will try to collect *P. al-gida* this summer.

16. *Pinguicula variegata* Turczaninev 1840

In some literature this species is named *P. spathulata* Ledeb. or *P. glandulosa* Trautv. et Mey. *P. variegata* is distributed in central and northeastern Siberia, reaching with its southernmost sites to Sakhalin island. It grows from sea level in the northern and eastern coastal areas up to 2000m in the southern distribution regions. In 1980 I had the opportunity to collect it - under the guidance of V. Molozhnikov and V. Voronin - in *Sphagnum* bogs of alpine tundras above the timber line of the mountain range along the west shore of the Baikal lake. The plant forms brood buds (gemmae) which again form plants with brood buds, finally resulting in clones of up to 50 and more plants. Innumerable densely glandular stalks emerge from such clones but only a small percentage of them bear a flower. I have not seen rosettes forming more than one stalk. The flowers of *P. variegata* are similar in shape to those of *P. alpina*, but a little smaller and beautifully three-colored (white/yellow/blue). The leaves and stalks are more like those of *P. villosa*, but most specimens develop a little 'scaly leaf' with only few digestive glands, marking the end of the rosette growth. In fact this species totally looks like a hybrid of *P. alpina* and *villosa*. While *P. alpina* has 2n=32 and *P villosa* 2n=16 chromosomes, I counted 2n=64 in *P. variegata*. If *P. variegata* is of hybridogene, allopolyploid origin, different chromosomal portions of *P. alpina* and *villosa* may result in a chromosome number of 64. A number of 64 might result e.g. from each 32 chromosomes originating from *P. alpina* and *P. villosa;* or 48 from *P alpina* and 16. from *P. villosa* or other portions (the F2 generation of polyploid hybrids does not split up according to Mendels rule but behaves as a new species). Experimental hybridization of both species will hopefully reveal more insight. A good argument for the hybrid hypothesis is the non-existence of *P. variegata* in northern Scandinavia, where both *P. alpina* and *villosa* are rather common. Here the flowering period of *P. alpina* usually ends before *P. villosa* starts. In the short Siberian summer the flowering periods of both species overlap which of course facilitates hybridization.

P. alpina P. villosa	n = x 8	n = 2x 16	n = 3x 24	n = 4x 32	n = 5x 40	n = 6x 48
n = x 8	16	24	32^{C}	40	48	56
n = 2x 16	24	32^{B}	40	48	56	64^{H}
n = 3x 24	32^{A}	40	48	56	64^{G}	72
n = 4x 32	40	48	56	64^{F}	72	80
n = 5x 40	48	56	64^{E}	72	80	88
n = 6x 48	56	64^{D}	72	80	88	96

Fig. 3) Possible chromosome combinations P. alpina x P. villosa

17. *Pinguicula ramosa* Miyoshi ex Yatabé1890

P. ramosa is an endemism of three mountains in the neighborhood of the town Nikko in central Japan. It grows in moss at the bottom of vertical volcane rock walls in niches not exposed to direct rainfall, within the deciduous tree zone from 1650-2250m. The substrate is only slightly damp, not really wet or even soggy. The plant mainly seems to profit from the high air humidity at these altitudes where the humid sea winds are frequently condensing to fog and clouds. In many specimens the stalk is bifurcated, bearing two flowers, sometimes even three. After the flower the stalk remarkably extends and positions its upper end with the seed capsule upright or even towards the rock what facilitates the seeds to be placed in suitable growing conditions. Morphologically I cannot distinguish the flowers of *P. ramosa* and *P. variegata*. Also the stalks, winter buds and seed capsules are almost identical. The only differences are the stalk bifurcation, the lack of the little 'scaly leaf', the different habitat and the chromosome number of 2n=18 which is unique in the genus. Yoshimura (1973) identified the karyogram to show some unusually large chromosomes probably resulting from the fusion of smaller chromosomes, a phenomenon which is not rarely observed in plants of islands: low necessity of compeditive variability, i.e. low necessity of chromosomal exchange, crossing-overs etc. or in banking language: no reason to avoid 'lump risks'. I guess that at earlier, cooler times the distribution range of *P. variegata* also covered Japan. When the climate was getting milder the plants in Asia as well as in Japan retired to higher altitudes but in Japan they could not go beyond the summits. Due to an adaptive selection process and genetical isolation *P. variegata* might have modified to *P. ramosa*. This would be a classical example where extinction was not avoided by migration but by adaptation.

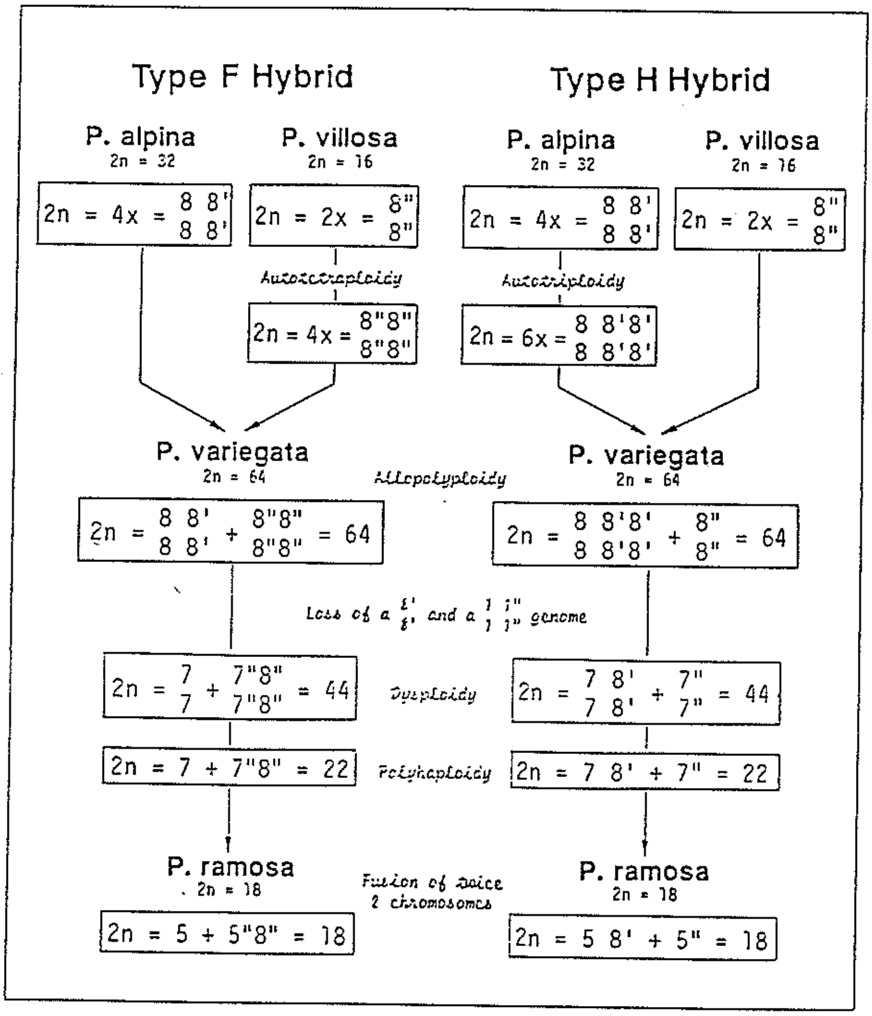

Fig. 4) A possible hypothesis of the chromosome development of P. alpina x P. villosa → P. variegata → P. ramosa

C. Subgenus *Isoloba*

The subgenus *Isoloba* does not form winter buds, its species are of the temperate growth type, some are homophyllus, some heterophyllus.

The Pinguicula crystallina/hirtiflora group

In the seventies Jeanine Contandriopoulos described the *Pinguicula crystallina/hirtiflora* group to consist of morphologically slightly differing populations of four ploidy levels: 2n=16, 24, 32, and 48 (Contandriopoulos 1974). In the last years I collected material of this group in Italy, Turkey, Cyprus and - together both with J. Schlauer and I. Koudela - in Greece. Based on this material J.S. Casper and T. Mikeladse in Jena recently found completely new chromosome numbers for this group which are not compatible with those earlier published by Contandriopoulos. I will therefore not use the nomenclature proposed by Contandriopoulos but I also cannot present Caspers' new suggestions as they are not yet published. In any case *P. crystallina* and *P. hirtiflora* are very closely related with fluent transitions from one to the other species. Both species grow in the northeastern Mediterranean area. Their growth type is tropical-heterophyllus as they are do not hibernate by winter buds but by a small rosette bearing only a reduced number of digestive glands. Due to the construction of water reservoirs and water pipelines even in the remotest gorges many sites have aleady disappeared or will disappear in near future. The *P. crystallina/hirtiflora* group is really endangered and urgently needs governmental protection.

18a. Pinguicula crystallina Sibth. ex Sibth. & Smith 1806

P. crystallina was once considered as an endemism of Cyprus but in the meanwhile very similar specimens were also found in Turkey (Casper 1970, Adamec 1996). In Cyprus (Troodos Mt.) most former sites are destroyed: One remaining site is very small (30 specimens, flowers white), in another *P. crystallina* is still abundant (some thousands), the substrate of both habitats is granite/serpentine. At the larger site the flowers vary in color from almost white to bluish. A feature of *P. crystallina* are the two small upper corolla lobes while the three lower ones are comparingly wide and large. The leaves are larger and wider than the leaves of the *subsp. hirtiflora.* I also have the impression that self-pollination is not as successful as in *P. subsp. hirtiflora.* The smaller site, at 1360m, is regularly exposed to light winter frost, the larger one, in a gorge at 800m, is cool in summer and relatively mild in winter. In Turkey there are several *Pinguicula* populations with morphological transitions to *P. crystallina subsp. hirtiflora.*

18b. Pinguicula crystallina subsp. hirtiflora (Ten.) Strid 1991

= P. hirtiflora Tenore 1811-1836

The holotype of this species was described from the Sorrento peninsula in central Italy, the westernmost point of its distribution. Close to the holotype site it grows on soggy vertical limestone in full sun just at the warm Mediterranean seashore. In Greece we found sites up to 1700m which are certainly exposed to frost and snow each year. *P. crystallina subsp. hirtiflora* grows on limestone as well as on serpentine, it is found on almost naked, vertical rock walls as well as in *Sphagnum* bogs or in wet meadows along calcareous rivulets. Its morphological variability is likewise remarkable from site to site (but in one and the same site there is almost no variability): In some sites the leaves are short and wide, in others they are long and slender. There are sites where all leaves are fresh green in spite of full sun, in others the leaves are tinted deeply purple. The corolla lobes vary from entire-margined to emarginate. In the Calabrian Magna Sila mountains the corolla lobes are narrowly oblong, in the Lithochoron gorge of Mt. Olympus broadly oblong and in the Pelloponnes oblong-spathulate. At one site in the Greek Vardoussia Mts. about 25% of the specimens are albinos (*f. pallida* Casper 1966). If hetero-pollination is prevented this subspecies is spontaneously self-pollinating. Self-pollinated seeds are fertile. Self-pollination may explain the low variability within one site.

19. Pinguicula lusitanica Linné 1753

P. lusitanica is homophyllus and restricted to coastal areas from the Mediterranean coast of north-western Africa along the Atlantic coast of Spain and France to southern England, all coastal regions of Ireland and Scottland, reaching even the Orkney Islands. A former site in the delta of the Rhone River is likely to be destroyed (Contandriopoulos, personal communication 1996). This rather small self-pollinator is bi- or triannual and is characterized by the red tinted veins of the thin, greyish-green leaves, the isolobus pinkish corolla and the tubular-cylindrical throat. It needs soggy, preferably acid substrate, high air humidity and mild winter. P. lusitanica grows mainly in *Sphagnum* bogs, sometimes associated with *Drosera intermedia* and/or *Erica ciliaris.* I have seen sites where - during rain periods - the rosettes are regularly submerged under water for several days. The limited ecological tolerance of *P. lusitanica* fits with the low chromosome number of 2n=12.

D. Cultivation of cool climate *Pinguicula* species

The long-term cultivation of the (sub)alpine and (sub)arctic *Pinguicula* species is rather difficult due to the following reasons:

(1) They are much less resistant to fungus infestations than the tropical species.

(2) While it is easy and cheap to create (sub)tropical climate conditions - dry or wet - the creation of a cool climate with high air humidity is difficult and expensive.

(3) In many species the *hibernaculum* stage lasts considerably longer than the vegetation period. If the summer growing conditions are not optimal the plants form weak *hibernacula* which easily decay. This is particularly the case if the plants are kept to warm and/or if they lack sufficient air humidity and ultraviolet light.

(4) In the temperate growth type the flowering period is usually short and if growing conditions are not adequate from the very beginning no flowers and/or no seeds are produced.

I live in Central Europe, in a suburb of Bern, at 600m, 25km north of the Prealps. Summer maxima reach +30°C, winter minima -15°C.

I grow most Pinguiculas on vertically positioned PVC sheets (20mm thick) equiped with horizontal 'lamellas' put into 45° angle slits. The vertical distance from lamella to lamella is 40mm. The lamellar sheets are fixed within a greenhouse along the north-east wall of my house which is surrounded by some trees on the east side. From mid-December till mid-January the plants do not get any sun at all. In summer they get 1-2 hours of sun in the morning when the sun appears between the trees and the projection of the roof. A timer allows water to trickle from time to time through the substrate which should never be to soggy (to avoid rottenness). The greenhouse is divided into three climate compartments. In all three compartments there are fans to produce wind for 15 minutes each hour and ultrasound fog machines to produce high air humidity.

Compartment A is kept open all spring, summer and automn but closed and slightly heated in winter to avoid frost (winter temperatures +1° to +8°C). In this compartment I grow the *Isoloba* species (*P. cystallina/hirtiflora* group and *P. lusitanica).*

Compartment B is kept open all the year exept in winter days with heavy frost. In light frost it is kept open allowing the substrate to get slightly frozen. In this compartment I grow *P. vallisneriifolia, P. longifolia subsp. caussensis* and *subsp. reichenbachiana*, *P. dertosensis*, *P. mundi* and *P. macroceras ssp.nortensis.*

Compartment C is kept open all winter exept in heavy frost but closed from spring till autumn. It is cooled with a professional cooling system allowing e.g. a night temperature of +5°C and a day temperature of +10°C even if it is 25°C or more outside. Household air conditioners are useless as their compressor is not constructed for temperatures below 18°C. In this compartment I grow *P. alpina, balcanica, corsica, fiorii, grandiflora, leptoceras, longifolia ssp.longifolia, macroceras, nevadensis, ramosa* and *vulgaris*. These species are infested by fungi if not exposed to an ultraviolet source.

From mid-June till end of August *P. variegata* and *villosa* (and hopefully in near future *P. algida*) are grown in a **horizontal refrigerator box** as they are used in food markets. As the air humidity is constantly reduced due to condensation at the surface of the cooling pipes, the entering cooled air must be rehumidified to at least 70% relative humidity. From beginning September till beginning June the named species are kept in a deep freezer at -15°C.

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