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The genus *Pinguicula* L. (*Lentibulariaceae*): an overview

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Abstract.- The carnivorous genus *Pinguicula*, which currently consists of about 74 species, is part of the *Lentibulariaceae* family. All members are active animal and plant organ trappers. The leaves are sticky and constitute flypaper-type traps capable of slow motions. The present review focusses on several aspects of the research activities conducted on this genus. These include the study of its evolution, carnivory, trapping and digestion mechanisms, with a special emphasis on the key role played by the mucilage, its ecology and its pharmacological and culinary utilization. This review also stresses the need for a global taxonomic revision of the genus. Finally, it aims to generate greater interest on these very fascinating plants which are in urgent need of protection.

Key-words : carnivorous plant - *Lentibulariaceae* - mucilage - *Pinguicula*.

Résumé.- Le genre *Pinguicula*, qui est actuellement constitué d'environ 74 espèces, fait partie de la famille des *Lentibulariaceae*. Tous ses membres attrappent et digèrent des animaux et des organes végétaux. Les feuilles collantes constituent des pièges actifs en forme de papier tue-mouche et sont douées de mouvement. Cette revue se penche sur plusieurs aspects des recherches conduites sur ce genre. Ils incluent l'étude i/ de son évolution, ii/ de ses mécanismes d'attraction et de digestion des proies, avec un point plus particulier sur le rôle du mucilage, iii/ de son écologie et iv/ de ses usages pharmacologiques et culinaires. Cette revue insiste également sur la nécessité d'une révision taxonomique globale du genre. Finalement, elle a pour but de stimuler un intérêt pour ces plantes fascinantes qui ont un besoin urgent de protection.

Mots-clés : plant carnivore - *Lentibulariaceae* - mucilage - *Pinguicula*.

I. INTRODUCTION

With their delicate colors, fragile rosettes and bristle leaves *Pinguicula* species do not stick to the common image of carnivorous plants capable of killing muscle-powered insects with vividly colored leaves differentiated into unique and sophisticated traps. A closer look, however, reveals that *Pinguicula* leaves are among the most efficient insect traps and that they exhibit movements, a rare property, even among carnivorous plants. Many scientists

have thus worked at unveiling their carnivorous habit and are still very active at describing many new species which had surprisingly remained undiscovered in many places including Europe. All of these studies have to be concluded quickly as all *Pinguicula* species are rapidly becoming extinct worldwide through habitat destruction.

The term *Pinguicula* was first used by Conrad Gesner in 1555, as he was describing a new nerveless, blue-flowering herb in his alpine flora. This name derives from the latin word *Pinguis*, which means greasy, due to the sticky, greasy touch of the leaves. This feature is actually linked to the carnivorous character of these plants as explained below. Even though this same author termed this plant under the very different name *Liparis* in 1561 in his *Horti Germaniae*, Clusius reused the word *Pinguicula* in 1583, a name which was to be kept by all other authors until now.

II. DESCRIPTION

All species of *Pinguicula* consist of a short vertical stem giving rise to a basal rosette of compact leaves which are more or less broadly ovate and either lie flat on the ground or stand obliquely upward (Fig. 1). Leaf rosettes vary in size from a couple centimeters up to 30 cm in diameter. Even though a few species have to be resawn annually, most of them are perenial. All harbour fibrous advantitious roots. According to Casper (1966) and Steiger (1975) *Pinguicula* species can be grouped into two main categories according to their annual growth cycles, the tropical and the temperate growth types, which only differ by the presence or absence of a winter bud called hibernaculum (Fig. 2). For both growth types, the leaves of the generative and vegetative rosettes may either be similar (homophyllous type) or different (heterophyllous type) thus defining four distinct groups of species (Table 1).

The winter buds formed by the temperate *Pinguicula* species are not carnivorous. They are very tight and may, in some cases, dig themselves slightly under the ground to survive frost periods. The vegetative rosette formed by the tropical growth type species usally resembles *Sempervivum* plants in the winter (*P. moranensis* for example) but may end up as tight bud under the ground (*P. acuminata* for example). These are rarely carnivorous either but keep on carrying active photosynthesis unlike the temperate species. The leaves of the vegetative rosettes of many Mexican species harbor succulent features to survive the dry winters of their habitat (Studnicka, 1991, 1994). This is in contrast with all other *Pinguicula* species which thrive under moist or wet conditions through the entire year.

All species produce very attractive flowers which occur singly on straight leafless scapes (Fig. 1), with the exception of *P. ramosa* which may produce two to three flowers per scape under optimum growing conditions (Casper, 1966). They only appear with the first rosette of leaves of the year in the case of temperate growth type species and may also be brought by the second set of leaves of tropical growth type species (Fig. 2). They are not preformed within the hibernaculum of temperate species except for *P. alpina*. The two-lipped corolla is composed of five petal-like lobes which may vary in size and shape. They fuse into a more or less long spur close to the attachment point of the corolla to the flower stem. Corolla can be either white, pink, purple, lavender, violet, yellow or a combination of these with more or less pronounced veins. The calyx is made of five sepals which are often green or purple and smaller than the petals. In many cases, the floor of the throat develops a hairy palate. Round, elliptoid or pointed seed pods are produced. They rarely exceed twice the size of the sepals and house 20 to 100 seeds.

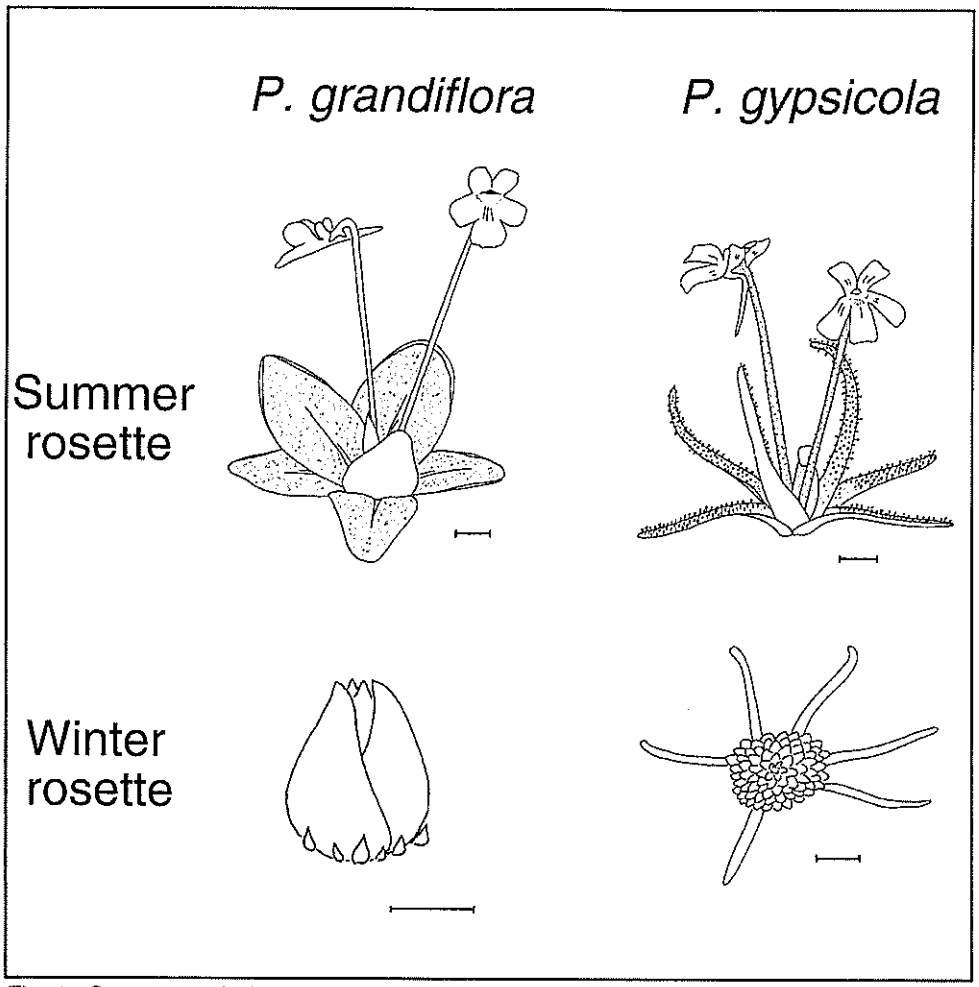

Fig. 1.- Summer and winter rosettes of *P. gypsicola* and *P. grandiflora*. *P. gypsicola* is a tropical growth type species, while *P. grandiflora* displays a temperate growth type cycle which differs from the previous growth type by the presence of an hibernaculum during the winter. As both species are heterophyllous, their summer (generative rosette) and winter (vegetative rosette for *P. gypsicola* or hibernaculum for *P. grandiflora*) leaves are different. The summer leaves of *P. gypsicola* are much longer than the winter ones and are often slow to die off. Some can thus be seen laying flat on the ground during part of the winter. The winter resting bud of *P. grandiflora* produces small gemmae at its base through the winter. Scale bars represent 1 cm.

Fig. 1.- Rosettes d'été et d'hiver de *P. gypsicola* et *P. grandiflora*. *P. gypsicola* a un cycle de croissance de type tropical, tandis que *P. grandiflora* a un cycle de croissance de type tempéré qui diffère du précédent par la présence d'un hibernacle en hiver. Comme ces deux espèces sont hétérophylles, leurs feuilles d'été (rosette générative) et d'hiver (rosette végétative dans le cas de *P. gypsicola* et hibernacle dans le cas de *P. grandiflora*) ne se ressemblent pas. Les feuilles d'été de *P. gypsicola* sont plus longues que celles d'hiver et meurent lentement. Quelques-unes peuvent ainsi être observées à plat sur le sol durant une partie de l'hiver. Le bourgeon hivernal de *P. grandiflora* produit des bulbilles à sa base l'hiver. Les indicateurs de taille représentent 1 cm.

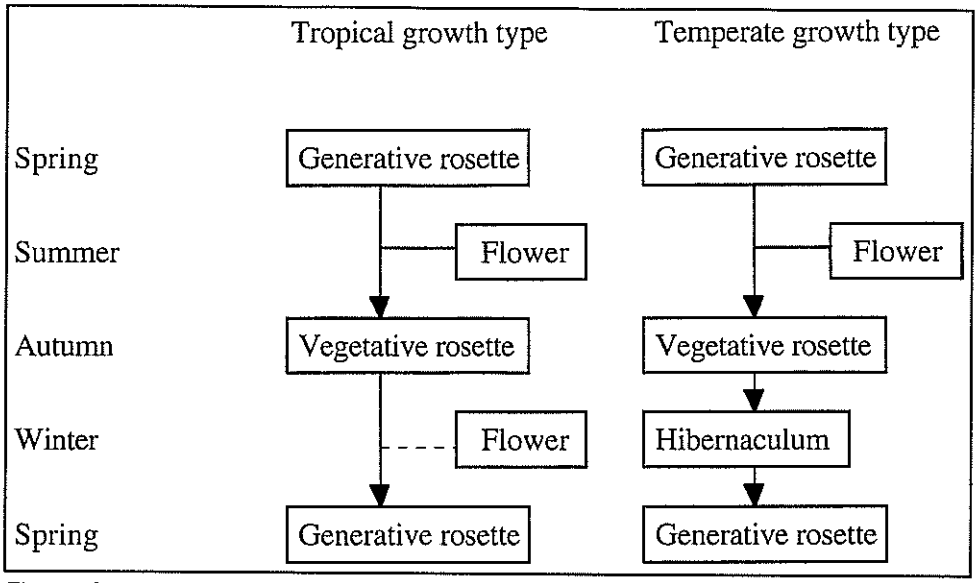

Fig. 2.- Growing cycles of *Pinguicula* species. *Pinguicula* species harbor either a tropical or a temperate growth type cycle. Even though the vegetative rosette of most *Pinguicula* species with a tropical growth type are not carnivorous, they carry photosynthesis over the winter season unlike the hibernaculum of temperate growth type species which will have very limited photosynthetic activity over this period. This will allow some tropical growth type species to bloom during the winter. Whatever growth type is considered, the generative and vegetative rosettes may either be similar (homophyllous type) or different (heterophyllous type).

Fig. 2.- Cycles de croissance d'espèces de *Pinguicula*. Les espèces de *Pinguicula* ont un cycle de croissance soit de type tropical, soit de type tempéré. Bien que les rosettes végétatives des espèces de *Pinguicula* de type tropical soient rarement carnivores, elles assurent la photosynthèse durant l'hiver contrairement aux hibernacles des espèces tempérées qui ont une activité photosynthétique très réduite durant cette période. Ceci permet à certaines espèces de type tropical de fleurir l'hiver. Quel que soit le cycle de croissance considéré, les rosettes génératives et végétatives sont soit identiques (homophylle), soit différentes (hétérophylle).

III. EVOLUTION AND TAXONOMY

It is always surprising to see that the currently accepted phylogenetic tree places the genus *Pinguicula* with its apparently simple-looking flypaper-type trap leaves in the same family, the *Lentibulariaceae*, as two other carnivorous plant genera, *Utricularia* and *Genlisea*, which produce highly complex underground suction-type traps. Furthermore, on this same phylogenetic tree, *Pinguicula* species are distant from other carnivorous plant genera with flypaper-type traps such as *Drosera, Byblis, Drosophyllum* and *Triphyophyllum.* While these apparent discrepancies have lead several researchers to move away from current taxonomic rules and yield schemes with a global integration of all carnivorous plant taxa originating from one common extinct and unknown ancestor (Markgraf, 1954, 1955; Croizat, 1961, in Heads *et al.*, 1984; Schmid, 1964), it should be noted that the careful study of the chemistry of the flavonoïds produced by these plants (Jay & Lebreton, 1972; Jay &

Table 1.- Growth type classification in the genus *Pinguicula*.
Tableau 1.- Types de croissance dans le genre *Pinguicula*.

Growth type	Tropical		Temperate
Homophyllous	*P. agnata*	*P. greenwoodii*	*P. algida*
	P. albida	*P. immaculata*	*P. alpina*
	P. antarctica	*P. involuta*	*P. corsica*
	P. benedicta	*P. ionantha*	*P. grandiflora*
	P. caerulea	*P. jackii*	*P. leptoceras*
	P. calyptrata	*P. lignicola*	*P. macroceras*
	P. casabitoana	*P. lilacina*	*P. nevadensis*
	P. chilensis	*P. lusitanica*	*P. ramosa*
	P. clivorum	*P. lutea*	*P. variegata*
	P. crenatiloba	*P. planifolia*	*P. villosa*
	P. crystallina	*P. primuliflora*	*P. vulgaris*
	P. emarginata	*P. pumila*	
	P. filifolia	*P. sharpii*	
	P. gigantea	*P. takakii*	
	P. gracilis		
Heterophyllous	*P. acuminata*	*P. laxifolia*	*P. balcanica*
	P. colimensis	*P. macrophylla*	*P. longifolia*
	P. crassifolia	*P. mesophytica*	*P. mundi*
	P. cyclosecta	*P. mirandae*	*P. vallisneriifolia*
	P. debbertiana	*P. moctezumae*	
	P. ehlersiae	*P. moranensis*	
	P. elongata	*P. oblongiloba*	
	P. esseriana	*P. orchidioides*	
	P. gypsicola	*P. rectifolia*	
	P. hemiepiphytica	*P. rotundiflora*	
	P. heterophylla	*P. stolonifera*	
	P. imitatrix	*P. utricularioides*	
	P. jaumavensis	*P. parvifolia*	
	P. kondoi	*P. potosiensis*	
	P. laueana	*P. zecheri*	

Gonnet, 1973, 1974), their C-4 carbon fixation cycle, their myrmecophily (does not concern *Pinguicula* species), the recent discovery of monocotyledonous carnivorous plant genera and the comparison of some of their DNA sequences (Albert *et al.*, 1992) have given little ground to these thoughts. Additionally, members of the *Lentibulariaceae* do share more features than it may seem at first glance. First of all, all members of the *Lentibulariaceae* bear zygomorphic flowers while other flypaper-type carnivorous plant genera develop actinomorphic flowers. Then, the digestive glands of *Pinguicula, Utricularia* and *Genlisea* species share common physiological features which are not found in other carnivorous plant genera (see below and Juniper *et al.*, 1989). Still, with no fossil record of *Pinguicula*, it is difficult to understand how and when these plants have evolved with the elaboration of characters so complex as traps or digestive glands which must inevitably derive from large clusters of genes. Current hypotheses are thus mostly based on their geographic distribution.

The genus *Pinguicula* currently consists of about 75 species. While many of them thrive in arctic, alpine or temperate regions of the northern hemisphere, quite a few favor the tropical regions of northern and central America as well as the Caribeans where they cross

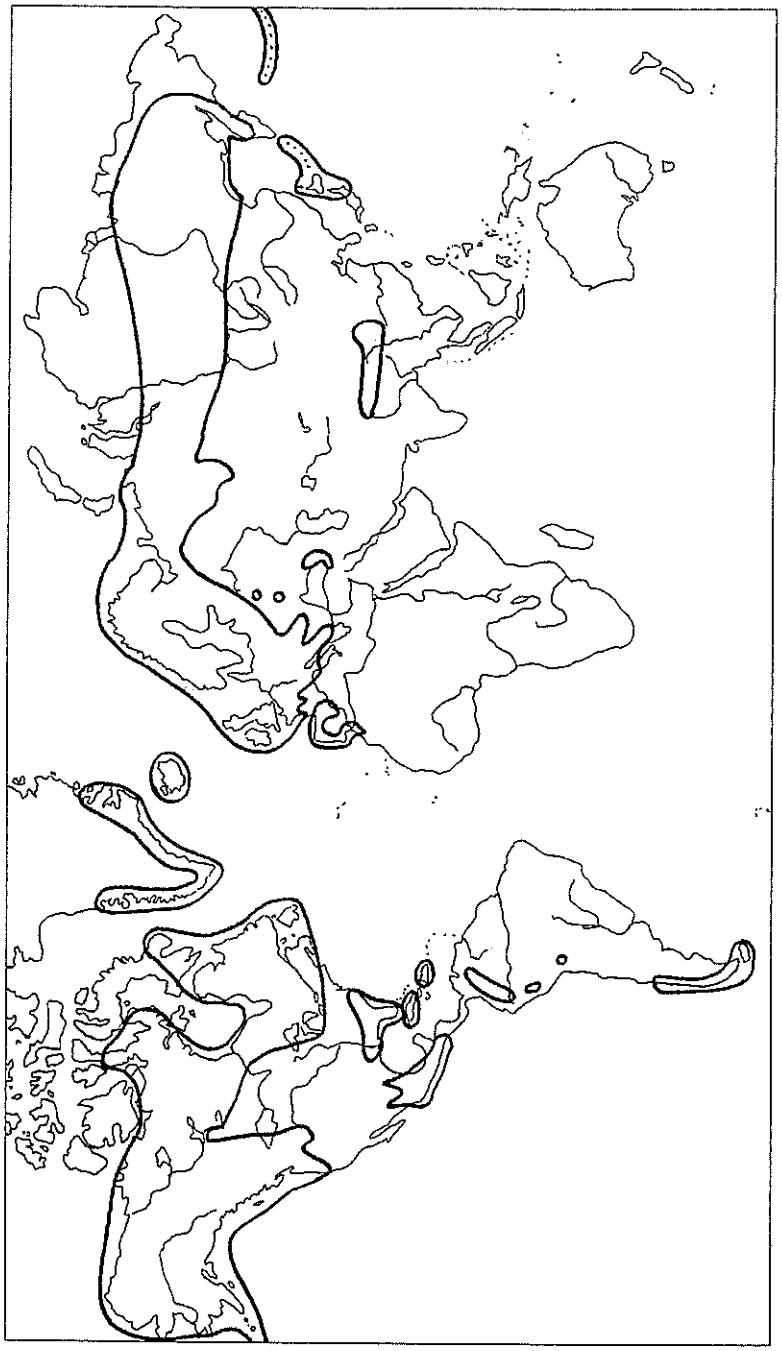

Fig. 3.- Geographical distribution of genus *Pinguicula*.
Fig. 3.- Distribution géographique du genre *Pinguicula*.

the equador, some members having established themselves on the western side of southern America all the way down to the southern tip of Chili (Fig. 3). It has thus been hypothesized that *Pinguicula* species may have existed at a time when the American and European continents were close enough to allow plants to move from one continent to the next (Steiger, 1998). According to this hypothesis, original plants would have been growing at and around what is currently known as the Caribean and the Mediterranean seas. They would have subsequently moved north and east in Eurasia and north and south in the Americas to colonize the vast surfaces of land unveiled after the retreival of glaciers during interglacial ages. Cytological studies conducted on a group of closely related European *Pinguicula* (*P. corsica, P. nevadensis, P. grandiflora, P. leptoceras* and *P. vulgaris*) have revealed that the number of chromosomes of the species found in northern regions is twice the one observed in the closely related species thriving more south (Casper, 1966; Steiger, 1998). *P. corsica* (endemic to the Corsica island) and *P. nevadensis* (endemic to the high bogs of the Sierra Nevada national park in southern Spain), which are among the southernmost species, indeed harbor the smallest chromosome count (2n = 16), while *P. grandiflora* (Pyrenees and Jura) and *P. leptoceras* (southern Alps) have double this number, 2n = 32. The northernmost species, *P. vulgaris* (Pyrenees, Alps up to Iceland and Greenland) exhibits 2n = 64. It is, therefore, possible that these European *Pinguicula* species have regularly evolved via a doubling of their number of chromosomes to settle under higher latitudes (Steiger, 1998). This is consistant with the "Hagerup-Tischler" rule which states that a higher chromosome count gives an adaptation advantage to plants thriving under highly changing climatic conditions (Hagerup, 1932). Over the past one million of years, environmental conditions have in fact always been more unstable under increasing latitudes in Europe. All of this reasoning leaves two major exceptions among European *Pinguicula* species: *P. villosa* and *P. lusitanica*. These two species, however, bear physiological characteristics which are very different from the species studied above (see Fig. 4). Moreover, *P. villosa* (2n = 16) seems to have followed the glaciers without changing too much, kind of like a sluggish, non-inquisitive concervative species (J. Steiger, personal communication). Growing conditions are anyhow very constant close to the north pole where it thrives. *P. lusitanica* (2n = 12) grows close to the Atlantic ocean and is thus also bathed by much more moderate climate conditions than species living inland. Similar studies will now have to be conducted on the American species to see whether this scheme of evolution can be applied to other sections of the genus.

All of the small differences in flower and leaf structure have helped scientists to subclassify the 74 known *Pinguicula* species (Fig. 4). Nevertheless, the naming of several species, such as the Italian *P. fiorii* (Tammaro & Pace, 1987), the Spanish *P. submediterranea* (Zamora *et al.*, 1996), the Moroccan *P. fontiqueriana* (Romo *et al.*, 1996) and the Mexican *P. jorgehintonii* (Turner, 1994), *P. hintoniorum* (Turner, 1994) and *P. reticulata* (Schlauer, 1991), is still a subject of debate (Schlauer, 1994; Luhrs, 1993; Gluch, 1997; Loyd, 1998; Steiger, 1998). None of these species has thus been taken into account in Fig. 4. Clearly, the latest monograph of the genus which was published by Casper in 1966, and which represented a really well-thought study of the 46 species known at that time, deserves to be updated.

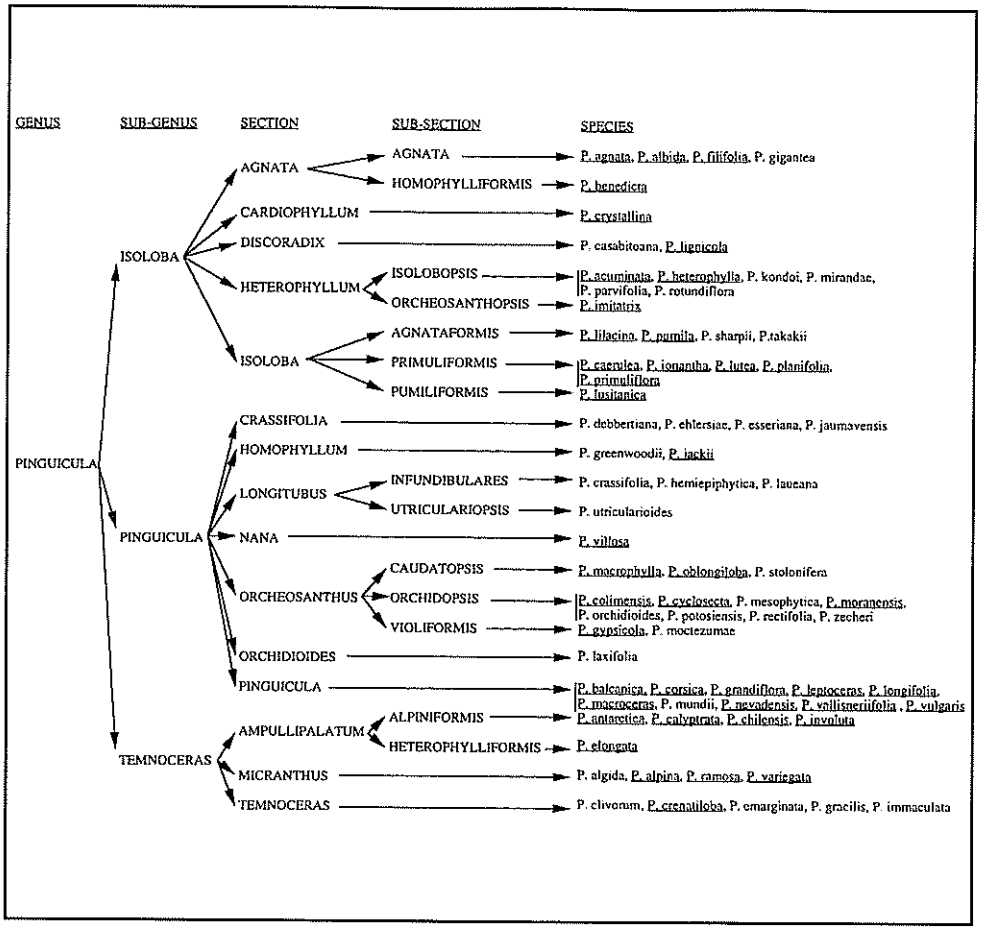

Fig. 4.- Sub-classification of *Pinguicula* species. This sub-classification of the genus *Pinguicula* is derived from Casper's monograph (1966), Schlauer (1986), Luhrs (1993), Gluch (1995, 1997) and the world carnivorous plant list maintained up-to-date by J. Schlauer on the carnivorous plant database web site at *http://www.hpl.hp.com/bot/cp_home*. All of the species which were present in the latest monograph of the genus (Casper, 1966) are underlined. Subgenera, sections, sub-sections and species have been organised in alphabetical order. Sub-species, forms and varieties have not been included. Species which are subject to debate have not been indicated either. As a complete taxonomic revision of the genus is beyong the scope of this review, readers are warmly refered to the litterature cited in the text.

Fig. 4.- Sous-classification des espèces de *Pinguicula*. Cette sous-classification du genre *Pinguicula* est dérivée des travaux de Casper (1966), Schlauer (1986) , Luhrs (1993), Gluch (1995, 1997) et la liste des plantes carnivores du monde maintenue à jour par J. Schlauer sur le site Internet "Carnivorous plant Database" à *http://www.hpl.hp.com/bot/cp_home*. Toutes les espèces présentes dans la dernière monographie (Casper, 1966) sont soulignées. Les sous-genres, sections et sous-sections ont été rangés par ordre alphabétique. Les sous-espèces, formes et variétés n'ont pas été inclues ainsi que toutes les espèces soumises à débat. Comme une révision taxonomique globale du genre est en dehors du champ d'intérêt de cette revue, les lecteurs sont cordialement invités à se référer à la littérature citée dans le texte.

IV. CARNIVORY

The idea that *Pinguicula* may be carnivorous most likely stems from a conversation held between W. Marshall and C. Darwin just a little bit before 1875, as reported by C. Darwin himself : « I was led to investigate the habits of this plant by being told by Mr. W. Marshall that on the mountains of Cumberland many insects adhere to the leaves ». This hypothesis was brillantly confirmed by this same author after a series of 17 experiments (Darwin, 1875). Despite the great debate generated by his observations (reviewed by Lloyd, 1942), most of them still hold true and do set most of the main features around the carnivory of *Pinguicula*. Basically, to make a long story short, *Pinguicula* are true carnivorous plants in the sense that they are able to attract, catch, digest and absorb the nutriments of small insects. It has later been shown that they do benificiate from the feeding with small diptorans for example (Aldenius *et al.*, 1983). Still, this same study suggested that the heterotrophic state of nutrition was not as effective as an autotrophic nutrition state (Aldenius *et al.*, 1983).

Only small flying insects such as Aphids, which leg diameter is no more than 3 to 5 times the one of the plant gland peduncles, are cought. Bigger ones easily fly off and would otherwise lead to the rotting of the leaves. Because of the open nature of the traps, pollen grains and seeds are also cought and digested making of these plants the only herbivorous plants.

V. ATTRACTION, MOUVEMENT AND TRAPPING

How insects are attracted to *Pinguicula* leaves is not clear. Nevertheless, the glistening effect of the many glands present at the surface of the leaf which is highly visible on the light-absorbing leaf surface has been suggested to participate in the attractive process (Juniper *et al.*, 1989). The scent of decaying animals already trapped on a leaf may also help as one leaf might take a long time to catch its first prey but is quickly covered by many soon after. No evidence of such a phenomenon has, however, yet been given. It is interesting to note that no reward is given to the attracted insect in contrast to many other carnivorous genera such as *Sarracenia, Heliamphora, Darlingtonia* and *Nepenthes.*

C. Darwin also demonstrated that the leaves are able to move. These movements are slow, taking a few hours to a few days to complete. Even though it has always been clear that such leaf mouvement cannot assist *Pinguicula* species in catching animals, Darwin's explanation of the role of these slow motions later turned out to be wrong. From his experiments on *P. vulgaris*, he concluded that leaf mouvement helps bring more glands into contact with the prey and helps push the captured animal to new positions. This was later corrected by Lloyd (1942) who, after a series of experiments conducted on what he thought was also *P. vulgaris* but is now known to be its Pacific coast relative *P. macroceras*, stated that the mouvements of the leaves only help to hold the secretions in place. These mouvements can be decomposed into several different events. First of all, as an insect is captured, the glands beneath the prey tend to lose turgor, placing the insect body in close contact with the leaf surface (Heslop-Harrison, 1970). At the same time, the epidermal cells below these glands also lose turgor forming a small bowl in which secretions accumulate and the prey is bathed (Batalin, 1877). If the prey is close enough to the leaf margin, a slow growth mouvement will cause the leaf edge to curve upward and sometimes roll around the insect body (Lloyd, 1942; Darwin, 1875). In the case of species with straight, long and nar-

row leaves such as *P. vallisneriifolia*, the entire leaf blade may even bend under the insect and form a 45 to 90° angle. After digestion is over, the leaf margins (or also the leaf blade) unfold back to their original position. Contrary to common belief, margins of *Pinguicula* species are not always upcurled as in the most studied species *P. vulgaris* and *P. grandiflora*. They may be flat or even curve downward as in *P. longifolia*. The trapping strategy is, however, always similar and solely relies on the thickness of the mucilage secreted by the leaf glands.

VI. DIGESTION

The final demonstration that *Pinguicula* species are able to digest captured matters on their own and benefit from the digestion products was obtained by Harder and Zemlin (1968) when they showed that axenic cultures of *Pinguicula* which do not develop well in the absence of nitrogen or phosphorus in their growing medium will resume growth and even set flowers when their leaves are supplemented with pinus pollen. This was later confirmed by Heslop-Harrison and Knox (1971) which fed ^{14}C-proteins to *Pinguicula* leaves and observed that this radioactive material will penetrate the plant at the inoculation point and later diffuse towards the growing center of the plant. However, these ^{14}C-proteins most likely do not enter the plant without being subject to some kind of transformation such as digestion beforehand. A 2 h delay was indeed necessary for the absorption of radioactive material from ^{14}C-proteins while only 2 min were sufficient when ^{3}H-asparagine was deposited.

The carnivory of *Pinguicula* heavily relies on the presence of two types of glands, sessile and stalked glands, on the surface of their leaves (Fig. 5). The relative number of these glands varies from species to species. In most species, they are only present on the upper surface (adaxial) of the leaves. But in several cases, they are also present on the flower scapes and sepals (abaxial face) as in the case of *P. primuliflora* and, in very few cases (*P. gigantea* for example), they are also present on the underside of the leaves (abaxial face). The stalked glands secrete a sticky mucilage which is responsible for the trapping of prey. They only play a minor role in digestion which is mostly carried out by the sessile glands.

The structure of the stalked glands has been well studied on *P. grandiflora* (Heslop-Harrison & Knox, 1971; Heslop-Harrison & Heslop-Harrison, 1981) and *P. vulgaris* (Vassilyev & Muravnik, 1988a,b). They display one of the most simple structure among carnivorous plants harboring stalked glands such as *Drosera* (Fig. 5, Juniper *et al.*, 1989). At their base, they possess a basal reservoir cell embedded in the epidermis. This cell is very prominent (Heslop-Harrison, 1975, 1976) and serves a major function in the rapid initiation of chloride effux during secretory activity (see below). It is also involved in the accumulation and distribution of solutes both from and towards the gland. The reservoir cell is positionned under a stalk cell bearing an endodermoid cell which holds 8 to 32 radiating head cells (Fig. 5). These head cells are responsible for the formation of a relatively large drop of mucilage which flows from the cells apoplast via cutin free wall regions. These have been called « cuticular gaps » by Joel and Juniper (1982) or « ill-defined cuticular discontinuities » by Heslop-Harrison (1975, 1976). In contrast to this thin, perforated, and thus permeable, protective cuticle cover, the endodermoïd cell has a thick cuticle and provides a zone of impregnated apoplast impermeable to the passage of small molecules as demonstrated with electron-dense tracer studies (Heslop-Harrison, 1976). It probably also represents a serious barrier to the passage of pathogenic microorganisms which

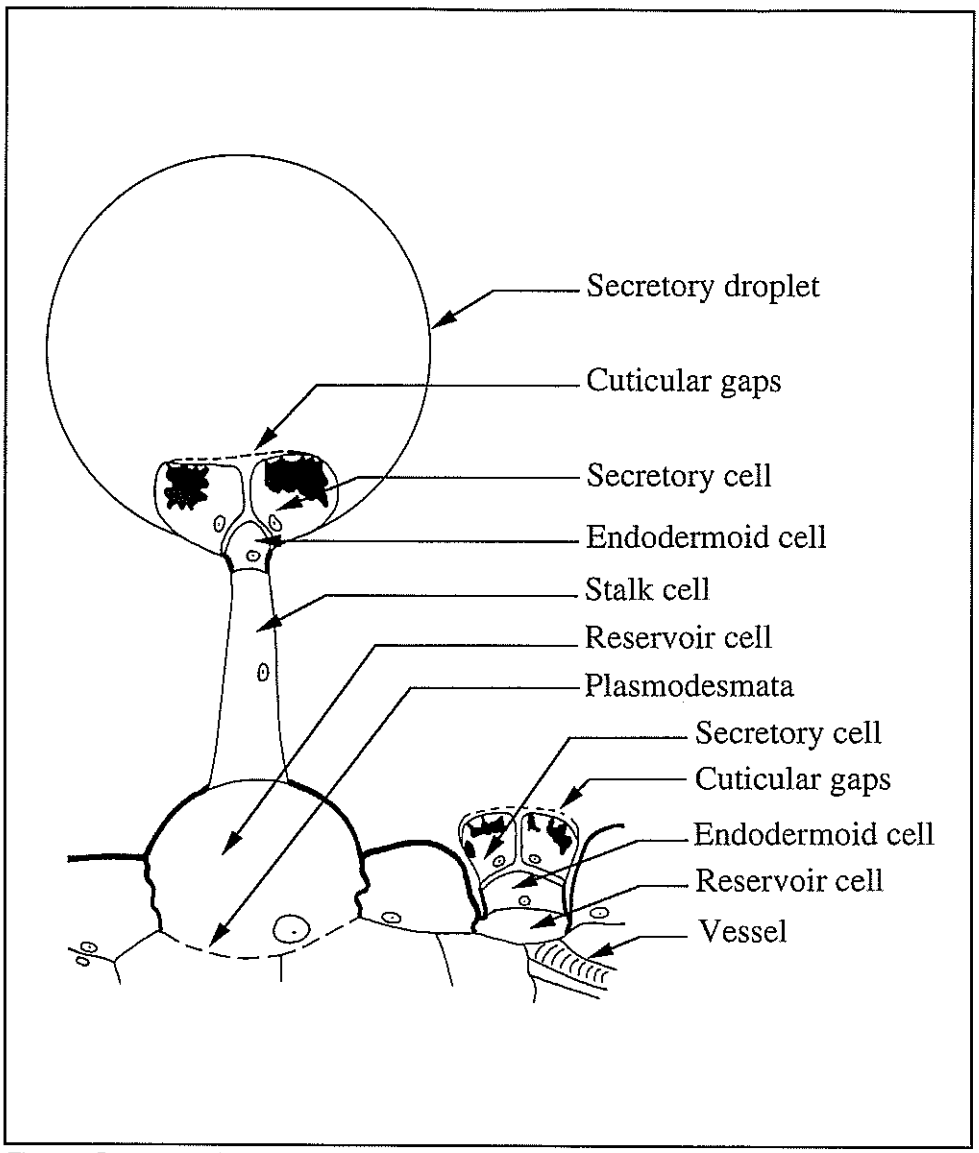

Fig. 5.- Structure of sessile and stalked glands of *Pinguicula*. The structure of a stalked gland and a sessile gland are respectively shown on the left- and right-hand side of the figure. This graph is adapted (with small modifications) from studies conducted on *P. grandiflora* by Heslop-Harrison and Knox (1971) and displays cuticule areas of different thickness. The vessel is connected to the vascular system.

Fig. 5.- Structure des glandes pédonculées et sessiles de *Pinguicula*. La structure d'une glande pédonculée et celle d'une glande sessile sont respectivement montrées sur le côté gauche et droit de la figure. Le shéma est tiré (avec quelques modifications) d'études conduites sur *P. grandiflora* par Heslop-Harrison et Knox (1971) et représente des zones de cuticule à épaisseur variable. Le vaisseau est connecté au système vasculaire.

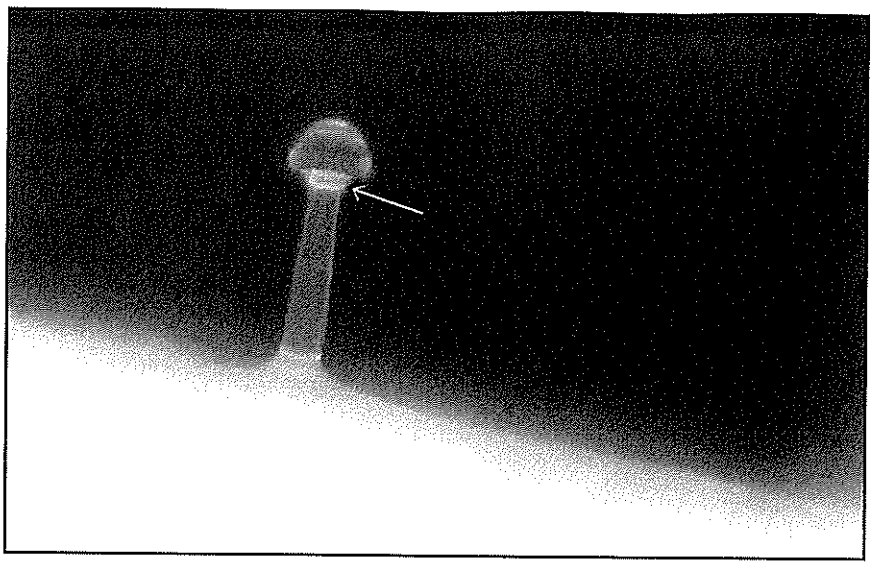

Fig. 6.- Autofluorescence of a stalked gland of *Pinguicula*. A flower stem of *P. primuliflora* was illuminated by UV light at 280 nm and observed under the microscope (x125). The round nature of the flower stem allowed stalked glands to be in one plane of focus. Emmited fluorescence was generally yellowish except at one area which was light blue (indicated by an arrow). Photograph by B. Letillois.

Fig. 6.- Autofluorescence d'une glande pédonculée de *Pinguicula*. Une hampe florale de *P. primuliflora* a été illuminée sous UV à 280 nm et observée sous le microscope (x125). La nature ronde de la hampe florale permettait d'observer la hampe florale dans un seul plan de netteté. La fluorescence émise était généralement jaune, sauf en une zone où elle était bleu clair (indiquée par une flèche). Photo de B. Letillois.

would otherwise take advantage of the cuticular gaps to invade the plant. Protection at the level of the endodermoid cell is strengthened by the heavy accumulation of phenolic compounds which can be seen via their light blue fluorescence emmission when illuminated at 280 nm (Fig. 6). The contact between the different cells of a gland is therefore only provided by symplasts and numerous plasmodesmata. The sessile glands only differ from the stalked glands by i/ their number of head cells which is comprised between 4 and 8, ii/ the size of their stalk which allows the gland to lie flush on the surface of the epidermis, iii/ a small reservoir cell and iv/ the presence of a vascular system under the gland. Stalked glands are not connected to the vascular system but their reservoir cell is in contact with 4 to 8 epidermal cells via plasmodesmata. None of these secretory cells displays any photosynthetic activity. Nevertheless, they possess plastids which are in fact considerably larged than in epidermal cells (Vogel, 1960; Schnepf, 1961; Heslop-Harrison, 1975). Their endoplasmic reticulum is extremely active (Heslop-Harrison & Knox, 1971; Heslop-Harrison, 1975), probably due to the need to produce mucilage or enzymes.

Unstimulated leaves present very weak hydrolytic activity. Within a few hours of entrapping an insect, the prey will be bathed in a small digestive pool. This secretory mechanism does not concern the whole leaf and will be just sufficient to cope with the particular prey

Table 2.- Enzymes detected in the digestive glands of *Pinguicula*.
Tableau 2.- Enzymes détectées dans les glandes digestives de *Pinguicula*.

Species	Gland type	Enzymes							Reference
		acid phosphatase	amylase	esterase	leucine aminopeptidase	peroxidase	protease	ribonuclease	
P. moranensis	stalked	+	+	+			+	+	a
	sessile	+		+	+				a, b
P. grandiflora	stalked	+	+	+		-	+	+	a, b
	sessile	++	-	++		-	++	++	a, b
P. ionantha	sessile	+		+					c
P. lusitanica	stalked	+	+	+			+	+	b
	sessile	+	+	+			+	+	b
P. moranensis	sessile	+		+					c
P. vulgaris	stalked	+	+	+			+	+	b
	sessile	+	+	+			+	+	b

Enzyme activities were detected by biochemical or substrate-film methods.
++: strongly detected; +: detected; -: not detected; space: not assayed.
a: Heslop-Harrison (1975); b: Heslop-Harrison & Knox (1971); c: Heslop-Harrison & Heslop-Harrison (1981).

that has been captured (Heslop-Harrison & Knox, 1971). It is stimulated by nitrogenous substances (ammonium ions or primary amino groups) originating from the prey (Heslop-Harrison & Knox, 1971; Heslop-Harrison & Heslop-Harrison, 1981). The basal level of hydrolytic activity of the leaf surfaces may help generate more of these substances. Interestingly, it has been shown that stimulated glands release their total load of hydrolases (Table 2) in a « one-off » secretory action and that, once fired, these glands will not synthesize more hydrolytic activity (Heslop-Harrison & Knox, 1971; Heslop-Harrison, 1975,1976; Heslop-Harrison & Heslop-Harrison, 1981). This response is thus rapid and esterase activity can be detected only 1 h post-stimulation (Heslop-Harrison & Knox, 1971; Heslop-Harrison & Heslop-Harrison, 1981). For comparison purposes, a 20 h delay was necessary for the detection of enhanced enzyme secretion by the fast-moving carnivorous plant genus *Dionaea* (Robins, 1978). *Pinguicula* leaf secretion can also be initiated by mechanical stimuli which may very well originate from the captured prey itself when it struggles to escape. The nature of the fluids produced under such circonstances has, however, never been clearly compared with the one obtained upon insect stimulation.

Vogel (1960) and later Heslop-Harrison and Heslop-Harrison (1981) observed that hydrolytic enzymes are stored in small vacuoles near the outer surface of resting glands. Upon stimulation, these vacuoles fuse to form larger ones which then merge with the plasmamembrane to release this load of hydrolytic power. This migration event towards the surface of the gland has been hypothesized to be initiated by the pumping of chloride ions into the subcuticular space causing, via osmotic forces, water to rush out of the head cell along with the secretory vacuoles (Heslop-Harrison & Heslop-Harrison, 1980). This scheme supposes chloride ions to move from the reservoir cell to the endodermoid cell and into the

head cells. Nevertheless, chloride pumps as well as receptors to the eliciting substances or transducing elements capable of transmitting the secretory signal to the reservoir cell have not yet been evidenced. The reabsorption of the digestive pool is even less understood. Even though the secretory mechanisms described above could very well be reversed via the pumping of the chloride ions back into the cells, the protoplasts of the head cells seem to be considerably degraded during the release of the digestive fluid (Heslop-Harrison, 1975, 1976). The endodermoid cell would thus have to do the job, a job that seems to require energy as many mitochondria remain active at this time (Juniper *et al.*, 1989).

VII. MUCILAGE AND SECRETIONS

Even though largely neglected in most studies, the mucilage secreted by the stalked glands is a key factor for the trapping of insects as well as a key ingredient to carry digestion at a place where a real digestive cavity is absent. Its exact chemical composition has most likely been subject to intense selection pressures to become finely tuned with all other digestive elements and the plant environment. Its viscosity will, indeed, define a cut-off limit in insect strength above which no insect can stay glued onto a leaf. This will thus fix a limit on the size of the insects which are cought to prevent a leaf from rotting under a piece of meat too large to be digested while still allowing big enough food elements to be cought. This same viscosity factor will also be linked to the water surface tension of the drops on top of the stalked glands. It will, therefore, be an important element, along with air humidity, in defining the size of the secretion droplets and in allowing the drops to stay fix on top of the stalk and not drip from the leaf. It will also reduce water evaporation from the secretions, a phenomenon which would otherwise lead to the dehydration of the plant since these secretions are in direct contact with the plant apoplast. Once an insect is cought, the mucilage will be diluted into the pool of digestive fluid which develops around the prey. This new fluid contains enzymes (Table 2) as well as wetting agents similar to the pitcher liquor found in the carnivorous plant genus *Nepenthes* (Heslop-Harrison & Knox, 1971). Acids are also released since the pH of the fluid has been shown to drop of two units from pH 5.0 down to 3.0 (Heslop-Harrison & Knox, 1971). Even under these new conditions, the mucilage will have the difficult task of holding all of the secretions in place on a leaf surface which is not always flat and horizontal. Additionally, it should not, by its presence, prevent the diffusion of substances through the digestive pool. To the contrary, it has been shown that besides its role in raising the overall viscosity, the mucilage actually acts as an ion exchanger to provide a more effective transportation medium (Juniper *et al.*, 1989) and thus makes a perfect bridge between the insect body and the plant apoplast. Finally, the viscous nature of the mucilage will prevent abrasive damage from the prey when it struggels to escape. Even though the mucilage seems to play such an important role in catching and digesting preys, its exact chemical nature remains unknown. Some studies conducted on *Drosera* species, however, suggest that it may contain polysaccharides (Gowda *et al.*, 1983).

VIII. ECOLOGY

Most *Pinguicula* species favour moist to very wet soils in open areas protected from direct sunshine. Even though some members can be found in acidic bogs (*P. lusitanica* for

example) or grow as epiphytes on trees (*P. lignicola* for example), most species prefer neutral to alkaline soils close to a spring or running water.

As many rosetted species, *Pinguicula* leaves exert a strong tension on the ground. This allows many species to stick on rocks with their roots in cavities. These species thus have a perfect adaptation to colonize vertical faces (or even sometimes sub-vertical cliffs as in the case of *P. alpina*) where water is permanently dripping. As quite a few *Pinguicula* survive frost periods, several species are found in montain areas at very high altitudes (up to 4100 m for *P. alpina* in the Himalayas and 3800 m for *P. involuta* in the Andes; see Casper, 1966).

There is no unique temperature requirement for all *Pinguicula* species as long as the air humidity is high enough. Species can thus be found from frost regions such as Iceland to the steamy savana of the south eastern United States or Cuba (Fig. 3).

Interestingly, the nature of the ecological niches colonized by *Pinguicula* can be partly related to their carnivorous character. First of all, the production of watery secretions is incompatible with the survival in an area where water is scarce and air humidity low. Then, potential preys are more numerous in humid and shaded areas even though photosynthesis would be favored in direct sunlight. An open area will additionally allow more preys to see the plant and more vegetable debris to fall accidentlally on the leaves. Finally, a recent study conducted on *P. vallisneriifolia* has shown that the number of prey that are cought results from a fine compromise between the number of preys available and the adhesiveness of the mucilage of the leaves (Zamora, 1995). If the plant lives in a sunny, rocky and dry area, the adhesiveness of the mucilage of its leaves and thus the effectiveness of its traps is great, but the number of preys available is weak. Inversely, if the plant lives in a shaded and wet area, the number of potential preys is high but the functionning of the trap is severely altered as the muscilage is not sticky enough. In this study, kleptoparasitism was found to be equal in both habitats.

Carnivory is not the only intriguing adaptative feature developped by *Pinguicula* to survive in their environment. Several species indeed posses unique means of mutiplying and scattering themselves. For example, the hibernaculum produced by temperate growth type species sets small gemmae at its base. These usually stay in close proximity to the mother bud but may be pushed away by a stolon as in the case of *P. vallisneriifolia.* Their number varies greatly from one species to the next and may be as high as 30 as in the case of *P. grandiflora*. Since the roots of these species often die off in the winter, two main modes of dispersal can be observed in nature. First, the action of snow, frost or running water may help some of the mother or doughter buds to loosen up and fall to new grounds. This is commonly observed with plants growing on vertical cliffs (Slack, 1979). Secondly, big herbivores such as horses, cows, deers or mountain goats may smash the mother bud. As *Pinguicula* species grow in damp areas, this event will split apart the doughter buds and allow some of them to hold temporarilly to the animal shoe in a mud ball before being detached on a new habitat. Species like *P. vulgaris* or *P. grandiflora* are thus often found growing in France on the sides of the holes made by these animals in the mud or along the trails they often create (personal observation on horses and J. Steiger personal communication on wild animals). If they are not detached from the mother bud, these gemmae will serve no purpose regarding the mutiplication of their species since the mother plant will outgrow them in the spring. Several Mexican tropical growth type species also seem to have adopted a similar strategy. Their succulent, non-carnivorous, winter-resting leaves indeed gain turgor when watered late in the winter and can thus be detached easily one

from each other under heavy rain fall or animal stepping. Each individual leaf is then capable of regenerating a new plant.

Another adaptative example concerns the scattering of seeds of *Pinguicula* species growing on vertical cliffs. These are normally scattered by the wind after the pods have opened. Yet, most *Pinguicula* species dislike being exposed to high winds which dry their secretions out and are usually found in close contact with the rock at places receiving protection from direct winds. Thus, some vertical cliffs loving species such as *P. ramosa* or *P. longifolia* subsp. *longifolia*, see their flower stems bend towards the cliff surface when the seed pods mature so that their seeds are deposited above the mother plant and do not always fall under it (Casper, 1966; Luhrs, 1998; Steiger, 1998).

IX. CULINARY AND PHARMACOLOGICAL USES

Pinguicula species seem to have a very limited secondary metabolism and have thus lead to very few pharmacological uses in the past (Baffray *et al.*, 1985; Juniper *et al.*, 1989) and none in modern medicine. While cinnamic acids are the main secondary metabolites found in *Pinguicula* leaves (Von Christen & Gordonoff, 1960; Von Christen, 1961; Banquis & Mirimanoff, 1970), some flavonoïds (Jay & Gonnet, 1973, 1974) and a large aray of carotenoïds (Neamtu & Bodea, 1972) have been detected (Tables 3 and 4). No alkaloid seems to accumulate.

In contrast to their limited pharmacological applications, *Pinguicula* leaves have long been utilized as food processing material (reviewed by Loyd, 1995, 1996). Most reports, which go back to the early 18th century, are dealing with dairy products. The many folk names given to *P. vulgaris* across north-western Europe (Table 5) suggest that such practices have been carried all over this geographic area. The main use of *Pinguicula* leaves in

Table 3.- Flavonoids in leaves of *P. vulgaris* (Jay & Gonnet, 1973, 1974).
Tableau 3.- Flavonoïdes des feuilles de *P. vulgaris* (Jay & Gonnet, 1973, 1974).

apigenin	++
6-hydroxyluteolin	+
hypolaetin[a]	+
isocutallarin[b]	+
luteolin	+
scutellarin[c]	+
malvidin-glycosides	P

++: major component; +: minor component; P: presence shown.
a: 8-hydroxyluteolin; b: 8-hydroxyapigenin; c: 6-hydroxyapigenin

Table 4.- Carotenoids in leaves and flowers of *Pinguicula* (Neamtu & Bodea, 1972); tr: trace.
Tableau 4.- Caroténoïdes des feuilles et fleurs de *Pinguicula* (Neamtu & Bodea, 1972); tr: trace.

Species	Part of plant	Carotenoids (mg/100 g dry wt)									
		α-ionines			β-ionines						
		α-carotene	lutein	lutein ester	β-carotene	cryptoxanthin	cryptoxanthin-ester	violaxanthin	violaxanthin-ester	neoxanthin	zeaxanthin-ester
P. alpina	leaf	tr	1.3		2.3	0.9		0.3		0.1	
	flower	0		1.8	1.0		0		0.1		0
P. vulgaris	leaf	0.2	1.2		2.1	0.7		0.2		0.1	
	flower	0.8		1.2	1.5		0.2		0.3		0.4

Table 5.- Folk names given to *P. vulgaris* in northern Europe (Loyd, 1995).
Tableau 5.- Noms vernaculaires de *P. vulgaris* en Europe du nord (Loyd, 1995).

Country	Folk name
England	earning-grass
Faroe Islands	undirlogugras
Finland	maitoruohu, maelkegraes
France	caya-lach, caille-lait
Germany	Fettkraut, Schmantblättchen
Iceland	lyfjagras, lobegras, kaesirgras
Northern Ireland	steepweed, steepgrass, steepwort
Norway	tette, tetteblomst, tettegraes, kjaesegraes, fjukkmolkgras
Orkney and Shetland Islands	yirnin-girse, ekkel-girse
Scotland	thickening-grass
Sweden	tätgräs, tätört, sätgräs, sätört, tätmjölksgräs, tätmjölksblad, skygräs, sköblad, sköblomma, löpegräs, stjirgräs

dairying leads to the production of a thick and ropy fermented milk, a scandinavian classic called Tätmjölk. The fermentation process is carried out by a bacteria naturally housed by the leaves of *Pinguicula* but which can also be found in *Drosera* mucilage or snail slime. Traditionaly, the milk is passed over the leaves to become inoculated by the bacteria. Previously inoculated milk can then serve as a new source of inoculum for a fresh batch of milk. An ancient belief, which has, however, never been supported by further scientific studies, even says that cows grazing on *Pinguicula* leaves would naturally produce thick milk. As the bacteria tend to adhere to each other, they form long strands or ropes which can be seen when lifting up part of the final product. This brings ropiness to the overall texture. These bacteria also release polysaccharides which generate a slimy texture. These fermentations are, nevertheless, unreliable since most of the useful genetic information is contained in the plastid DNA of the bacteria. Another dairying application of *Pinguicula* leaves leads to the production of curdled milk for the cheese industry. The active ingredients in this process are the proteases present in the leaf secretions. These are called vegetable rennet in comparison with the rennet enzyme extracted from the stomach of calf and which has been used for the same purpose. *Pinguicula* enzyme extracts have also been used in Germany at the beginning of the 20th century to tenderize freshly sloughtered or tough meat. Regrettable as it is, none of these receipes are any more in use in modern times.

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