Taxonomy and conservation ecology of the genus *Pinguicula* L. (Lentibulariaceae)

Volume 1.

Main text

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Errata

page	error	correction
14, 74, 115, 191, 194, 265, and elsewhere	intraspecific	infraspecific
114	Bayesian inference.....	omit this paragraph
120-121	Sierra Nevada	Sierra Madre
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Acknowledgements

My interest in the genus *Pinguicula* started when I saw *P. grandiflora*, a non-native to Britain, at Edale in the Peak District National Park, in May 1996. Since then, I tried to amass as much information on the genus as possible. The way forward has not always been straightforward having been interrupted many times. It took more than 20 years to reach the point of submitting this thesis. During this period, particularly in last a few years, a large number of people helped me to complete this study.

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Abstract

This thesis, "Taxonomy and conservation ecology of the genus *Pinguicula* L. (Lentibulariaceae)", consists of 4 chapters. An abstract for each chapter is as follows:

Chapter 1: Red List assessments of the genus Pinguicula L.

The genus *Pinguicula* L. (Lentibulariaceae), comprising of 91 taxa all of which are carnivorous, is repeatedly collected from the field and is grown by amateur collectors. The current status of many *Pinguicula* taxa in the wild is mostly unavailable due to little information although a number of taxa are endemic to a small area and those are thought to be threatened. The International Union for Conservation (IUCN) Red List Categories and Criteria is a standard for evaluating the risk of extinction. In this chapter, all the 91 taxa recognised were evaluated using the criteria, Extent of occurrence (EOO) and Area of Occupancy (AOO), based on herbarium specimens. The results suggest that at least 61 % of taxa are evaluated as threatened, and the risk is higher in "Mexico and Central America" than "Europe and Western Asia", both of which are *Pinguicula* biodiversity hotspots. Urgent action for the conservation of the taxa and their habitats will be necessary.

Chapter 2: Phylogenetic analyses of the genus Pinguicula L.

The current taxonomy of the genus *Pinguicula* is based on the flower morphology, and it is divided into three subgenera, *Isoloba, Pinguicula*, and *Temnoceras*. Some recent molecular analyses, however, suggest that the results do not agree with the current subgeneric classification based on the morphological characters. In this chapter, three DNA regions, *mat*K and *trn*K, *rpl32-trnL* in chloroplast DNA (cpDNA), and the internal transcribed spacer (ITS) in nuclear ribosomal DNA (nrDNA) from 81 *Pinguicula* taxa, were sequenced. The three results are inconsistent with the taxonomy based on floral morphology. The molecular results, particularly ITS, infer that most of *Pinguicula* taxa are monophyletic within each geographic area. Chromosome and basic numbers are also agreed well with their distributions. Concerning the same seasonal growth cycle, forming winter rosettes or hibernacula, it is not just simply ecologically convergent but the taxa within the same region are phylogenetically closely related to one another. Phylogenetic trees inferred from the three regions and combined genes are also somewhat different from one another. Further research with other genes will be necessary to support the theory discussed in this chapter.

Chapter 3: The effect of geographical and environmental factors on patterns of species richness in the genus Pinguicula L.

A number of *Pinguicula* species are confined to a small geographical area and those are often endemic to the area while only a few species are distributed widely. This chapter explored what geographical and environmental factors affect species richness of *Pinguicula*. Four geographical factors, land area (km^2), latitude of country centroid, mean elevation, mean distance to nearest coastline (km), and six Koeppen-Geiger climate categories, A (tropical-type climate category), B (dry-type climate category), C (temperate-type climate category), D (cold-type climate category), E (polar-type climate), and H (alpine-type climate) for each country were used for the analyses to determine whether the number of taxa in all countries, Europe and Western Asia, Northeastern Asia, and America were correlated with those factors. Overall, relatively weak positive correlations were found between the number of taxa and those factors. Remarkable results in this study have suggested that species richness is significantly correlated with land area, i.e. large countries have more species, probably due to diversity of climates. Furthermore the number of taxa is significantly correlated with climate B (dry) in all countries and America. The result implies that an impact of species richness in Mexico correlated with B (dry). Species richness of *Pinguicula* is particularly seen in small wet places surrounded by large dry areas. More detailed studies on local ecology will be necessary to consider the distribution of the genus.

Chapter 4: A revision of the genus Pinguicula L.

The most recent revision of the genus *Pinguicula* was attempted by Casper in 1966, but the number of species expanded from 46 to almost double with some new sectional delimitations. Taxonomic confusion is, however, often seen and therefore a revision with recent knowledge is necessary. In this study, a review of literature and over 6,800 herbarium specimens from 167 herbaria was performed, and as a result, 91 *Pinguicula* taxa (89 species and 2 varieties) have been recognised. Based on the phylogenetic analysis in Chapter 2, a new sectional delimitation of the genus is proposed. In this study, the 91 taxa were divided into 11 sections including newly proposed sections, *Alpinae, Andinae, Caribensis, Elongatae, Membraniformis, Mesoamericana*, and *Pumiliformis*, as well as existing sections, *Cardiophyllum, Isoloba, Nana*, and *Pinguicula*. Keys to section and species, a brief description, distribution maps, and line drawings for each taxon are provided. Due to limited availability of materials on this occasion, some Italian taxa newly described in the recent years were unable to be examined in this study.

General introduction

1. INTRODUCTION

Carnivorous plants

Approximately 352,000 to 391,000 species of flowering plants have been described so far (Paton et al. 2008, RBG Kew 2016). Most of these species produce chemical energy through photosynthesis, but nutrient poor soil may also restrict their growth. Amongst the flowering plants over 600 species have developed a strategy to overcome this limitation to growth whereby prey is captured, digested and nutrients are absorbed (Givnish 1989, Adamec 1997). These carnivorous plants can dominate nutrient poor soils where other plant species are often sparse. Carnivorous plants have a wide geographic distribution, from tropical to arctic climates, but are mostly restricted to sunny, wet, and nutrient poor acid soils (Givnish 1989). Environmental preference or tolerance, however, very much depends on species. The number of carnivorous plants conventionally recognised varies because of taxonomic treatment and the definitions of carnivory, e.g. 9 families and 19 genera (Juniper et al. 1989), 11 families and 19 genera (Heubl et al. 2006), or 12 families and 20 genera (Givnish 2015).

The term "carnivory" in plants is defined by Givnish (1989), Juniper et al. (1989), and Chase et al. (2009) as follows: 1) to attract prey to the traps by nectar, fragrance, colour, or ultra-violet reflection, 2) to capture, retain, and kill prey by the trapping mechanisms, 3) to digest them by secreted enzymes and/or bacterial activities, and 4) to absorb digested substance as potential nutrition usually through glands (Table 1). However, only five genera, *Drosera* L. (sundew), *Dionaea* Soland. ex Ellis (Venus flytrap), *Drosophyllum* Link, *Pinguicula* L. (butterwort), and *Nepenthes* L. (tropical pitcher plant), are experimentally confirmed to fulfill all four conditions (i.e. true carnivores) (Juniper et al. 1998), although there are different opinions (e.g. Givnish 2015). The other species lack one or more of the features. Some plant species possess only one or two of the conditions, such as *Erica tetralix* L., *Passiflora foetida* L., and *Plumbago capensis* Thunb., and are considered to be non-carnivorous (Chase et al. 2009). In other cases genera that fall between carnivorous and non-carnivorous are sometimes termed proto-carnivorous plants (Albert et al. 1992).

Some carnivorous plants obtain nutrition not only from animal substances, but from plant substances as well. Harder and Zemlin (1968) reported that more vigorous vegetative growth and flowering initiation was seen in *Pinguicula lusitanica* L., fed with pine pollens. Similarly *Nepenthes ampullaria* Jack, forming a cluster of pitchers on the forest floor, is adapted to trap leaf litter as a nutrient source (Moran et al. 2003).

Table 1. List of carnivorous, proto-carnivorous, and non-carnivorous plants. The data are taken from Juniper et al. (1989), Chase et al. (2009), and Givnish (2015). The number of species is shown only for carnivorous and proto-carnivorous plants. B = bladder trap, F = flypaper trap, HS = hooked spines, L = lobster-pots, P = pitcher trap, S = snap trap, + = positive, – = negative, ± = dubious, ? = not confirmed. Some scientists include proto-carnivorous plants into carnivorous plants.

	Family	Genus	Species no.	Trap	Attract	Trap & kill	Digest w/ enzyme	Absorb
Carnivorous	Bromeliaceae	*Brocchinia*	2	P	+	+	–	+
		Catopsis	1	P	+	+	–	+
	Byblidaceae	*Byblis*	6	F	+	+	±	+
	Cephalotaceae	*Cephalotus*	1	P	?	+	–	+
	Dioncophyllaceae	*Triphyophyllum*	1	F	+	+	–	+
	Droseraceae	*Aldrovanda*	1	S	–	+	+	+
		Dionaea	1	S	+	+	+	+
		Drosera	ca. 190	F	+	+	+	+
	Drosophyllaceae	*Drosophyllum*	1	F	+	+	+	+
	Lentibulaliaceae	*Genlisea*	ca. 30	L	?	+	+	+
		Pinguicula	ca. 90	F	+	+	+	+
		Utricularia	ca. 230	B	±	+	+	+
	Plantaginaceae	*Philcoxia*	7	F	?	+	+	+
	Nepenthaceae	*Nepenthes*	ca. 170	P	+	+	+	+
	Sarraceniaceae	*Darlingtonia*	1	P	+	+	–	+
		Heliamphora	ca. 20	P	+	+	–	+
		Sarracenia	8	P (L)	+	+	–	+
Proto	Eriocaulaceae	*Paepalanthus*	1	P	?	+	?	+
	Roridulaceae	*Roridula*	2	F	+	+	–	±
	Stylidiaceae	*Stylidium*	ca. 300	F	?	+	+	±
Non-carnivorous (or possibly proto-carnivorous)	Astaraceae	*Haplopappus*		F	?	+	–	–
	Brassicaceae	*Capsella* (seed)		F	+	+	+	+
	Bromeliaceae	*Puya*		HS	?	+	?	?
	Caryophyllaceae	*Cerastium*		F	?	+	+	?
		Lychnis		F	?	+	–	–
		Stellaria		F	?	+	+	?
	Ericaceae	*Erica*		F	?	+	?	±
	Geraniaceae	*Geranium*		F	?	+	±	±
		Pelargonium		F	?	+	±	±
	Lythraceae	*Cuphea*		F	?	+	?	?
	Martiniaceae	*Proboscidea*		F	?	+	±	–
	Nyctaginaceae	*Mirabilis*		F	?	+	±	–
	Orobanchaceae	*Lathraea*		F	?	+	±	±
	Passifloraceae	*Passiflora*		F	?	+	?	?
	Plumbaginaceae	*Plumbago*		F	?	+	±	±
	Primulaceae	*Primula*		F	?	+	±	?
	Rosaceae	*Potentilla*		F	?	+	–	±
	Saxifragaceae	*Saxifraga*		F	?	+	?	+
	Solanaceae	*Nicotiana*		F	?	+	±	–
		Petunia		F	?	+	–/±	–
		Solanum		F	?	+	+	–
	Capriofiaceae	*Dipsacus*		P	?	+	–	–

The trapping mechanisms with movement regardless of speed and without movement are called active traps and passive traps, respectively. The former contains *Aldrovanda* L., *Dionaea, Drosera*, and *Utricularia* L., while the latter contains the rest; *Byblis* Salisb., *Brocchinia* Schult. ex Schult. et Schult., *Catopsis* Griseb., *Cephalotus* Labill., *Drosophyllum, Genlisea* St.-Hil., *Heliamphora* Benth., *Nepenthes*, *Phylcoxia* Taylor et Souza, *Sarracenia* Dumort., and *Triphyophyllum* Airy Shaw. Inconsistent observations have been reported in *Pinguicula* indicating that it is active (Darwin 1875) or passive (Legendre 2000).

The largest carnivorous family is Lentibulariaceae, which comprises the genera *Utricularia* (ca. 210 species; Taylor 1989), *Pinguicula* (ca. 90 species; Cieslak et al. 2005), and *Genlisea* (ca. 30 species; Fleischmann 2012) followed by Droseraceae and Nepenthaceae. However, the numbers of species are gradually increasing due to new discoveries in recent years, notable species including *Nepenthes attenboroughii* Rob., McPherson et Heinrich, and *Drosera magnifica* Rivadavia et Gonella have attracted considerable attention.

Carnivorous plants have evolved a number of different mechanisms by which they trap their prey. Specifically, 1) snap traps, where lobes of a leaf lamina rapidly close to capture prey when the prey touches hairs on the inner surface (*Aldrovanda* and

Dionaea), 2) flypaper or adhesive traps involving secretion of a minute droplet of mucilage at the head of glandular hair (*Byblis*, *Drosera, Drosophyllum, Pinguicula* L., *Triphyophyllum*), 3) pitcher or pitfall traps, where a pitcher-like leaf containing fluid captures prey to fall into inside (*Brocchinia*, *Catopsis*, *Cephalotus*, *Darlingtonia* Torr., *Heliamphora, Sarracenia* except *S. psittacina* Michx., and *Nepenthes*), 4) bladder traps, a small bladder sucks tiny prey (*Utricularia*), and 5) lobster-pots or eel-traps, cylindrical chambers with bristles inside to prevent escape of prey (*Genlisea* and *Sarracenia psittacina*) (Givnish 1989, Juniper et al. 1989, Nolan 2015). Carnivorous syndromes may have arisen independently at least five or six times in their evolutionary history (Albert et al. 1992, Heubl et al. 2006). For this reason, not necessarily all carnivorous plants share a common ancestor (i.e. polyphyletic). For example, the structures of the glandular hairs of *Drosera* L. and *Pinguicula*, which secrete mucilage to capture prey, are anatomically and functionally different (it is called a tentacle with movement in *Drosera* and a stalked gland without movement in *Pinguicula*) (Darwin 1875, Lloyd 1942, Juniper 1989). Having the same trapping system, therefore, does not always infer evolution from a common ancestor, rather convergence on a similar strategy. Furthermore, in some cases more closely related taxa have developed radically different strategies, such as Lentibulariaceae, where *Genlisea, Pinguicula*, and *Utricularia* each possess a completely different trapping mechanism.

Many scientists have been attracted by the carnivorous nature of these plants. Darwin (1875) experimentally confirmed that some plants capture insects, digest prey, and absorb digested substances for their partial growth, calling them insectivorous plants (a subcategory of carnivorous plants). Darwin (1875) mostly used *Drosera rotundifolia* L., locally abundant in the Northern Hemisphere, for his experiments. Lloyd (1942) studied more than 10 carnivorous genera providing very detailed observations, and illustrated their morphology and trapping mechanisms through meticulous line drawings. Later, Heslop-Harrison (1970) added to this body of knowledge, using scanning electron microscopy to study gland structures of the genus *Pinguicula.*

The taxonomy of some carnivorous plant families and genera has been studied in depth. For example, Danser (1928) and more recently Jebb and Cheek (1997) reviewed the Nepenthaceae. A monograph of the genus *Drosera* was published by Diels (1909) but is in need of updating. Taxonomy in the family Lentibulariaceae based on morphological characters has been studied by a number of researchers, notably De Candolle (1844) and Barnhart (1916). *Utricularia* and *Genlisea* were more recently studied and revised by Taylor (1989) and Fleishmann (2012), respectively.

The genus Pinguicula L.

Casper (1966) recognised 46 species in *Pinguicula*, and divided them into three subgenera, *Isoloba* Barnhart, *Pinguicula* Casper, and *Temnoceras* Barnhart, according to the flower shape and colour. More recently, a number of *Pinguicula* species have been described (e.g. Speta and Fuchs (1982, 1989, 1992), Zamudio and Rzedowski (1986, 1991), Zamidio (1992, 1997, 1999), Casper and Steiger (2001), Casper and Urquiola (2003), Conti and Peruzzi (2006). As a result, the total number of species is approximately double that of Casper's (1966) monograph, with ca. 90 species recognised today (Cieslak et al. 2005). Those new species have been classified into one of the three subgenera proposed by Casper (1966). Recent phylogenetic studies (e.g. Cieslak et al. 2005, Shimai and Kondo 2007), however, do not support the subgeneric classification of Casper (1966).

Molecular techniques are now a standard in the inference of phylogenetic relationships among taxa. In the genus *Pinguicula*, earlier studies on the internal transcribed spacer (ITS) sequences in nuclear ribosomal DNA (nrDNA) used some taxa within limited geographical ranges to infer their phylogenetic relationships, e.g. 24-28 taxa from mild to cold regions of Eurasia and North America (Degtjareva et al. 2006, Kondo and Shimai 2006), and 36 taxa from Mexico and Central America (Shimai and

Kondo 2007). On the other hand, Cieslak et al. (2005), using 42 taxa covering all regions where *Pinguicula* occurs, suggested that the subgenera proposed by Casper (1966) were polyphyletic based on their *mat*K and *trn*K analysis in chloroplast DNA (cpDNA). Those results suggest that a revision of the genus *Pinguicula* based on phylogeny with more sampling is required to provide a better understanding of the phylogenetic relationships among the taxa.

Recently, Lampard et al. (2016) and Roccia et al. (2016) published two volumes on *Pinguicula* covering all taxa they recognised and divided them based on distributions; “the Temperate North” (Roccia et al. 2016) and “Latin America” (Lampard et al. 2016).

The genus *Pinguicula* is absent from Oceania, Antarctica, and the majority of Africa (Casper 1966). The International Plant Names Index database (2016) lists 147 *Pinguicula* taxon names, specific and intraspecific ranks, but it does not indicate synonyms. The number of accepted species varies among taxonomists, but normally between 85 (Cieslak et al. 2005) and 100 species (Peruzzi and Gestri 2013) in the recent literature. Over 40 species occur in Mexico alone (Zamudio 2005).

The distribution of many *Pinguicula* taxa is often restricted to a small area (Conti and Peruzzi 2006) and their microhabitats are disturbed by climate changes or environmental stress (Zamora et al. 1996). Therefore, the current conservation status of each *Pinguicula* taxon has to be carried out with scientific approaches for a subsequent possible conservation.

2. MORPHOLOGY

A general morphology of *Pinguicula* is presented in Fig. 1. The vegetative structure of *Pinguicula* consists of a very short stem, leaves, and roots, and the floral structure consists of a scape, a calyx, and a corolla. Each detail will be discussed later.

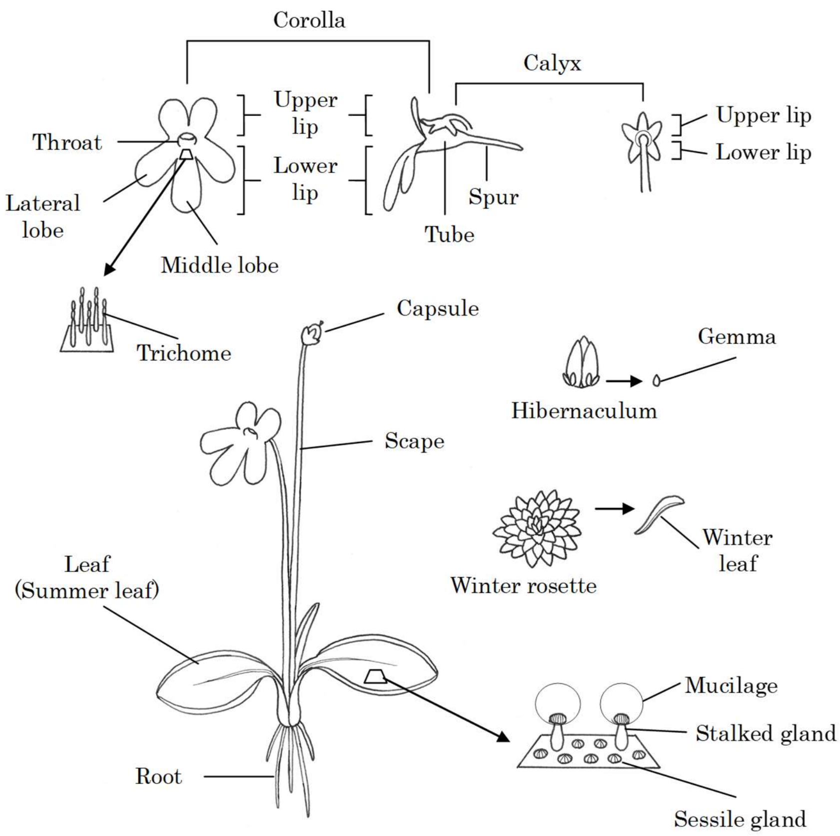

Fig. 1. General morphology of *Pinguicula.*

Vegetative Morphology

Cotyledons and eophylls

Cotyledons in *Pinguicula* are very small, often less than 1 mm long, non-carnivorous, and the shape is more or less cylindrical. Cotyledon number could be one of the most important morphological characters to distinguish angiosperms. Although Lentibulariaceae is dicotyledonous, a number of *Pinguicula* species possess a single cotyledon (Lloyd 1942). If two cotyledons are present in a *Pinguicula* seedling, both cotyledons are similar in size and those are arranged opposite each other on the extremely short node. Degtjareva et al. (2004) observed that only 5 taxa (*P. crystallina* Smith, *P. lusitanica* L., *P. moranensis* Kunth, *P. variegata* Turcz., and *P. villosa* L.) had two cotyledons out of 23 taxa that they examined. It appears that the cotyledon number does not present taxonomic features within the genus. Furthermore, the number of cotyledons seems to be not strictly fixed within each taxon (Haccius and Hartle-Baude 1957). For this reason, as Degtjareva et al. (2004) suggested, the number of cotyledon may not be a useful character for identification in *Pinguicula*.

The shape of eophyll, or primary leaf in seedlings, is more or less uniform among species, and it is much simpler than adult leaves. The leaf primordium occurs at the apex of the node. The first eophyll is often very small, less than 2 mm long, oblong to suborbicular. It possesses glands on the upper surface and is able to capture tiny prey. The second or third eophyll gradually increases its size and it may show morphological differences among species whereas the size is often still very small (less than 5 mm). In many species, the plants mature to produce flowers within the second or third growth season.

Stem

The stem of *Pinguicula* is basically very slender, abbreviated, cylindrical, and unbranched. In *P. vulgaris* L., a mean stem length may vary according to the habitat, but it is 2.1 ± 0.81 mm (Karlsson 1986). Usually the stem is covered by leaves arranged radially either in a clockwise or counterclockwise spiral obscuring the stem (Raju 1969). Grob et al. (2007) found that leaf arrangement of *P. moranensis* on the basal stem was a spiral phyllotaxis associated with Fibonacci numbers, an angle of ca. 137°. Due to the short stem, many species form a basal rosette and the leaves are extended radially on the ground, while some others extend their leaves upward or parabolically. Seasonal stem elongation is seen in *P. villosa*, which elongates its stem under a sphagnum mat when sprouting from a hibernaculum. In northern Sweden, a mean of 6.4 mm (up to 24 mm) stem elongation was observed in *P. villosa* and such a stem is termed a "subterranean stem" (Karlsson 1986). The subterranean stem might be seen in other species growing on moss carpets, but the elongation is not as obvious as that in *P. villosa*. Occasionally, the axis stem of some species may produce branches in the soil. The branched stems become daughter plants that subsequently detach from the axis stem. Some larger species (e.g. *P. gigantea* Luhrs and *P. moranensis*) have a somewhat thicker and rigid stem. Unlike some species of *Utricularia* or *Genlisea*, tubers are not formed by any species in the genus *Pinguicula*.

Leaf

All *Pinguicula* species are carnivorous for at least a part of the year and the leaf is densely covered by two types of minute glands, "stalked glands" and "sessile glands" (Lloyd 1942, Heslop-Harrison and Knox 1971, Givnish 1989, Juniper et al. 1989). The main role of stalked glands is to secrete sticky mucilage to capture prey, whereas that of sessile glands is to secrete digestive enzymes and to absorb digested fluid (Heslop-Harrison 1976, Heslop-Harrison and Heslop-Harrison 1981). The glands are densely developed on the upper leaf surface during their growth season, exceptions are *P. gigantea*, *P. jackii* Barnhart, and *P. longifolia* Ram. ex DC. that possess glands also on the lower surface, although very sparsely. Non-secretary hairs are seen in winter leaf of some Mexican and Central American taxa, and are also seen in near the base of the summer leaf in many taxa. Detailed structures and roles of the glands will be discussed later.

The leaf morphology is often a useful character for identification of *Pinguicula* though some species may present different shapes of the leaf from season to season. Two groups are recognized in relation to leaf polymorphisms: "dimorphic-leaved species" and "monomorphic-leaved species" (Casper 1966, Zamudio 2001). Within a total of 91 taxa recognised in this study, 62 taxa are dimorphic-leaved species and 29 taxa are monomorphic-leaved species. Dimorphic-leaved species produce different shapes and functions of leaves according to season, namely, "summer leaves" and "winter leaves" during the summer growth season and winter dormant season, respectively. On the other hand, monomorphic-leaved species produce the same shape of leaves regardless of seasons though they may be smaller during cooler seasons.

Among dimorphic-leaved species, summer leaves are larger than winter leaves in size and form more extended rosettes than those of winter leaves. Summer leaves exhibit wider range of shapes, from very narrow to broad leaves depending on species. Summer leaves are often somewhat fleshy in texture. The outer margin of the summer leaf is often slightly to strongly involute or revolute. The mid rib on the lower surface is longitudinally keeled, which is particularly prominent near the middle to the base but often obscure near the apex, while that on the upper is often somewhat hollowed and slightly paler in colour. The leaf colour is basically bright yellowish-green or pale green, but sometimes partly or entirely suffused with maroon by reddish pigments. In the shade, it may be darker green (Lloyed 1942). Zamora (1995) experimentally confirmed that leaf colour is one of the factors attracting insects to capture. The winter leaf is smaller and narrower than the summer leaf and they tightly form a winter rosette or a hibernaculum to endure the freezing or dry winter season.

In addition, the dimorphic-leaved species are further divided into two groups based on the arrangements and functions of winter leaves, i.e., forming "winter rosettes" or "hibernacula". The species forming winter rosettes are mostly found in Mexico and Central America when the winter rosettes endure a dryer winter season. The species forming hibernacula occur in higher altitudes or higher latitudes of the Northern Hemisphere, including Eurasia, North America, and the northern part of Africa. The hibernaculum consists of tightly clustered small scale leaves and endures temperatures below freezing (Heslop-Harrison 2004).

The monomorphic-leaved species (29 taxa), not forming winter rosettes or hibernacula, are mostly distributed in the southeastern USA, the Caribbean Islands and South America, and a few species are seen in Europe (Iceland, the British Isles, Portugal, and more east) to Anatolia and Cyprus. The monomorphic-leaved is categorized in the summer leaf in this study.

Dimorphic-leaved species and monomorphic-leaved species are sometimes called "temperate growth type" and "tropical growth type" respectively according to their growth cycles (Legendre 2000), but those terms do not necessarily refer to climate zones where the species actually occur.

Summer leaf

The summer leaf is produced in all species during their growth season, and the leaf shape is sometimes informative to identify species. Variations within an individual in these characteristics should also be considered. Some representative leaf shapes are presented in Fig. 2.

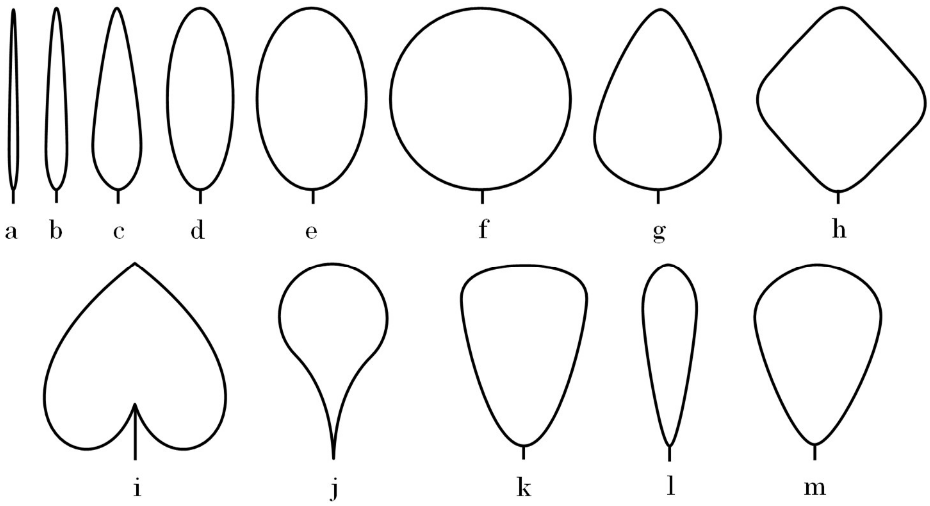

Fig. 2. Approximate leaf morphology of *Pinguicula*. a) filiform, b) linear-lanceolate, c) lanceolate, d) oblong, e) elliptic, f) orbicular, g) ovate, h) rhombate, i) cordate, j) spatulate, k) cuneate, l) oblanceolate, m) obovate. The illustrations shown above are examples of some representative leaf shapes of *Pinguicula*. The leaf shape in some species may not fit above, or some species may produce different shapes of leaves at different times of the year. Furthermore, the size of the leaf may vary significantly among species.

The shape of summer leaf could be roughly divided into two types, "narrow leaf type" and "broad leaf type". Species producing narrow leaves such as filiform, linear-lanceolate, or oblong-lanceolate are rather unusual in the genus. The size of narrow leaf depends on the species, but the length sometimes extends more than 200 mm. Most species have broad leaves such as elliptic, oblong, lanceolate, ovate, or orbicular. The size of broad leaf varies among species from less than 10 mm to more than 150 mm in length and the width is usually not greater than the length. Different shapes of leaves, particularly in broad-leaved species, however, may be produced among clone, individuals, or populations even within the same species. Some individuals produce oblong leaves but some others might produce ovate or obovate leaves within the same locality at the same time of the year. It is, therefore, somewhat difficult to define groups by leaf shape. The general appearance of the leaf is often affected by other factors including leaf thickness and/or the degree of marginal curl as well as its direction (inward or upward). Those characters are stated in a description of each species. Although some species have morphologically characteristic summer leaves, it is still difficult to identify them without observing the flowers.

The size of summer leaf (or rosette diameter) and the number of leaves produced during a growth season within the same species may depend on the duration of the growth season attributed to environmental factors, such as an altitudinal and/or climatic concerns. *P. macroceras* Link in Japan, for example, produces larger leaves, nearly 8 cm in length with flatter margins and a number of summer leaves are formed during the growth season at above the Haide-gawa Dam (ca. 250 m) in Niigata; in contrast, those produce much smaller leaves rarely exceeding 3 cm in length with strongly involute margins and only 4-6 leaves are formed during the growth season at above the Hakuba-ōhike Pond (ca. 2,500 m) in Nagano (per. observ., Shimai). Thus the environmental factors at the habitat may affect the leaf size.

Winter leaf of dimorphic-leaved species

The winter leaf is produced in some species during their dormant season mostly in winter. Thirty-eight species found in Mexico and Central America usually produce small, narrow and thick winter leaves, and those leaves endure a dryer season in winter. The shape of the winter leaf varies among the species, but it is often ovate, lanceolate, obovate, oblanceolate or spatulate. A number of winter leaves (sometimes more than 100) often tightly form a compact winter rosette and the shape is globose, subglobose, lenticular, or acetabuliform. In a few species (e.g. *P. debbertiana* Speta et Fuchs, *P. ehlersiae* Speta et Fuchs, and *P. esseriana* Kirchner), winter leaves can very easily detach from a winter rosette, and clonal plantlets are produced at the base of the detached leaves.

Twenty one species found in higher altitudes or higher latitudes in the Northern Hemisphere produce small concave scale leaves by autumn. Normally up to 15 scale leaves are tightly congested and develop a hibernaculum protecting the vegetative and floral buds from frost or snow (Heslop-Harrison 1962). The shape of hibernaculum is mostly ovoid, but is occasionally subglobose or ellipsoid. A few to numerous gemmae, or sometimes called brood-buds, are produced at the base of the hibernaculum, and they sprout to be clonal plantlets in spring.

While most of dimorphic-leaved species do not have a root system during the dormant season, two exceptions are known. The hibernaculum of *P. alpina* has long roots during a winter dormant season (Blanca et al. 1999). In addition, *P. elongata* Benjamin, found in Venezuela and Colombia form a winter rosette with roots and the leaves are very thin (in thickness), ovate and concave, and the appearance is very similar to a hibernaculum.

Spring leaf in dimorphic-leaved species

In dimorphic-leaved species, shorter leaves are often produced just before extending summer leaves, and those are sometimes called spring leaves (Blanca et al. 1999). Some species, such as *P. elongata*, *P. vallisneriifolia* Webb, and *P. heterophylla* Bentham, may produce distinctive spring leaves. In this work the morphology of spring leaf is not discussed further since the number of leaves is usually only a few and eventually and continuously summer leaves, more informative for taxonomy, will be produced. In each description; however, a term “spring rosette” may be used for some species to indicate a phase just before forming a summer rosette, since the scape may arise from spring rosette.

Gland

The detailed structures of the glands can be observed only microscopically. Although the glands of *Pinguicula* are a characteristic feature within the family, this is not an informative character for identifying species in *Pinguicula* since the shape and structure of the glands are essentially very similar among species (Heslop-Harrison and Knox 1971). There are two types of glands, stalked and sessile, densely covering the upper surface of the leaf except at the margin and near the base (Darwin 1875, Heslop-Harrison and Knox 1971). In fact, a much greater number of sessile glands can be observed than the number of stalked glands (Heslop-Harrison and Knox 1971). The two types of glands are different structurally and functionally while both of them are of epidermal origin and do not possess chlorophylls or colour pigments resulting in a colourless appearance (Lloyd 1942).

The stalked gland roughly consists of secretory, stalk, endodermal, and reservoir cells (Heslop-Harrison and Knox 1971, Heslop-Harrison 1975). The head, usually composed of 16 but occasionally 8 or 32 secretory cells, is arranged in single radial layer. The outer walls of the secretory cells are covered by a thin discontinuous cuticle, and discharge of secretion occurs irregularly on the surface of the head (Heslop-Harrison 1976). An endodermal cell is located at below the head and adjoining to a stalk. The stalk supports the head through the endodermal cell. A large basal reservoir cell is situated under the stalked cell. The head of stalked gland secretes a tiny droplet of mucilage, muco-polysaccharide, enabling to capture tiny prey like mites, gnats or small moths, but have only a partial role to digest them (Heslop-Harrison 1970, 1975, 1976, Heslop-Harrison and Knox 1971). Mucilage will be secreted by the stalked glands repeatedly even if it is washed away by water or rain.

The sessile gland roughly consists of secretory, endodermal, and reservoir cells, but it does not possess a stalk (Heslop-Harrison and Knox 1971, Heslop-Harrison 1975). The head composed of 2-8 cells, much fewer than that in the stalked gland, is arranged in single radial layer. An endodermal cell is situated between the head and a reservoir cell. The roles of the sessile glands are secreting digestive enzyme from the head to digest captured prey and absorbing the digested substance (Heslop-Harrison 1970). Unlike the stalked glands, the sessile glands remain dry on the unstimulated leaf.

Once prey adheres to the leaf and stimulation has taken place, digestive enzymes including esterase, acid phosphatase, protease, and ribonuclease are secreted from both glands (amylase seems to be secreted only from the stalked glands) within an hour to form a secretion pool on the leaf and digested substances from the prey will be absorbed through the sessile glands in two hours (Heslop-Harrison and Knox 1971, Heslop-Harrison 1975). Enzyme secretion may not be continuous, but depends upon the size of captured prey or degree of stimulation (Heslop-Harrison 1976, 1978). On the other hand, little or no secretion is observed against insoluble substances (Darwin 1875). The fluid pH changes dramatically from 5.0-5.5 on the unstimulated leaf to 3.1-3.4 on the stimulated leaf (Heslop-Harrison and Knox 1971). The fluid contains bactericide preventing prey from rotting while being digested (Chase et al. 2009).

Runner

The runners are very thin stems associated with asexual reproduction and are formed only in a few species of *Pinguicula*. There are two types of runners. One is an underground runner sprouting in the soil that is seen, for example, in *P. calyptrata* Kunth and *P. mirandae* Zamudio et Salinas. The other type is an aerial runner sprouting above the ground surface that is seen in *P. orchidioides* DC. and *P.*

vallisneriifolia. Few observations have been made; however, it has a few scale leaves without roots and a clonal plantlet is produced only at the apex of the runner. The clonal plantlet eventually develops roots in soil and detaches from the mother plant.

Root

The root systems in *Pinguicula* have been rarely studied. A primary stage of the seedling has a very short taproot, but it is soon replaced by roots arising from the stem (Lloyd 1942). Compared with many other plant species, the root of *Pinguicula* is very poorly developed. In most *Pinguicula* species, the root is slender, short, simple, fragile, and it shallowly lodges into the soil. During the growth season, the length of the root was ca. 3 cm in *P. vulgaris* (Darwin 1875), but often within 5 cm in most species. Although it may be of little relevance to the taxonomy of *Pinguicula*, a few noteworthy characters are seen. The number of root varies species to species, but is generally only a few to often less than 30. The species forming hibernacula loose the root during winter, except *P. alpina*, having the root throughout the year. Maximum total root length has been observed in July to August in *P. villosa* and *P. vulgaris*, while it was in June to July in *P. alpina* (Karlsson 1986). Species in Mexico also loose the root during winter, but it may not be all species. In some species, for example *P. alpina*, *P. antarctica* Vahl, *P.*

calyptrata, and *P. chilensis* Clos, the root is rather elastic, robust, and tough. The main purpose of the root system seems to be to absorb water and to anchor the plant to the soil. No mycorrhizal fungi associated with the root have been detected so far (Juniper et al. 1989, Heslop-Harrison 2004). According to Kirchoff et al. (2008), *P. vulgaris* has a root cap, but *P. moranensis* does not. Uniquely, epiphytic species of *P. casabitoana* Jiménez and *P. lignicola* Barnhart root directly on to the surface of tree twigs or branches.

Floral Morphology

Flower

The flower is hermaphrodite and mostly pollinated by insects. Two stamina and a stigma are furnished at an entrance or inside of the upper part of corolla. The stamina are hidden by a flap-like lower lip of stigma situated at below the stigma. Each stamen consists of an anther and an incurved short filament. The two anthers face each other at below the ovary. The stigma is very small, abbreviated, laterally oblong, bilabiate, and fringed. The ovary, up to ca. 2 mm in diameter, is globose to subglobose. The corolla is sympetalous and consists of a 2-lobed upper lip, a 3-lobed lower lip, a tube, and a spur. The corolla shows diversities in shapes, sizes, and colours among species which are often informative for species identification. The shape of corolla lobes varies from suborbicular, ovate, obovate, elliptic, oblong to subquadrate. The upper lip is often smaller and less complex than the lower lip. The lips form either a subactinomorphic or zygomorphic corolla. In many species having zygomorphic flowers, the base of lower lip often has a convex process and it is densely covered by trichomes or multicellular hairs. Trichomes often continue to the inside of tube and those also continue more sparsely to the middle (or the tip) of lower lip and the base of upper lip. Approximately 20 species have subactinomorphic corollas, in particular, all six species found in the southeastern USA (e.g. *P. caerulea* Walter, *P. lutea*, and *P. pumila* Michx.) have typically subactinomorphic corollas. The rest of approximately 70 species have zygomorphic corollas, including species from the Northern Hemisphere (e.g. *P. longifolia*, *P. macroceras*, and *P. vulgaris*).

The flower colour is also an important characteristic in species identification. The colour shows a wider range from white, lilac, pale pink, pink, red, reddish-purple, purple, bluish-purple, dark blue to yellow. Among the colour variation, many species have white, pink, or purple (including pale purple, reddish-purple, and bluish purple) flowers whereas being rare in other colours. Variations in flower colour are also recognised within a species: a remarkable example appears to be *P. pumila* exhibiting white, pale lilac, purple, cream, or yellow colour among strains. *P. emarginata* Zamudio et Rzedowski and *P. kondoi* Casper have prominent purple veins on white to pale purple corolla lobes. Roles of flower colour to attract pollinators remain unknown, but reflection and absorption patterns of ultraviolet on the corolla might have a correlation with flower colour (Gloßner 1992, Lunau 2007). The flower seems to be scentless, at least for the human's olfactories, except *P. agnata* Casper.

The corolla tube is located between lips and a spur. The shape of tube is usually conical, cylindrical, or subcylindrical. The tube is well-developed in many species while it is very short in some Mexican species (e.g. *P. cyclosecta* Casper, *P. gypsicola* Brandegee , *P. moctezumae* Zamudio et Ortega, and *P. moranensis*). The tube is dorsally compressed in most of species found in the Northern Hemisphere (e.g. *P. macroceras*, *P. vulgaris*, and *P. vallisneriifolia*). The inner surface of the tube is termed "throat" to distinguish from the outer surface. The base of lower lip and throat are often covered by trichomes. Although the trichomes show great morphological diversities on the floral organs, it sometimes considered an informative character for identifications (Godfrey and Stripling 1961, Casper 1966). Furthermore, the shape of trichomes is probably associated with a kind of pollinator visiting the flower (per. com., Cheek). All species found in the southeastern USA (e.g. *P. caerulea*, *P. ionantha* Godfrey, and *P. pumila*) characteristically have a hairy terete process prominently projecting from a lower throat. A few species such as European *P. lusitanica*, Mexican *P. lilacina* Schlecht. et Cham., *P. sharpii* Casper et Kondo, and *P. takakii* Zamudio et Rzedowski have a trapeziform convex process in a lower throat.

The spur holds nectar inside that may have a role to attract pollinators. All species have a spur which extends from the end of tube abruptly or vaguely with or without angle. Its shape is often cylindrical or subcylindrical, straight, or curved, and the length varies from 1 mm to 40 mm, while it may be occasionally saccate to conical (e.g. *P. alpina*, *P. antarctica*, and *P. elongata*). The apex of spur is very rarely bifid but often obscure. The *Pinguicula* flower is basically entomophilous (Wood and Godfrey 1957, Proctor et al. 1996) although a few species (e.g. *P. lusitanica* and *P. villosa*) are believed to be self-pollinating (Alm 2000, Heslop-Harrison 2004). For this reason, it is likely that the length of the spur depends on the kind of pollinator, but little has been documented. Heslop-Harrison (2004) stated that the flower of *P. vulgaris* is mostly pollinated by bees, while Proctor et al. (1996) suggested *P. alpina* is principally visited by flies. Other possible pollinators observed are thrips and beetles for *P. vallisneriifolia* (Zamora 1999), hoverflies for *P. macroceras* (per. observ., Shimai), or small butterflies for *P. moranensis* (Alcalá and Domínguez 2003). Some species or clones show self-incompatibility (per. observ., Shimai).

Scape

The scape arises from the axil of rosette in the flowering season. The scape in most species is simple, elect to subelect, and straight to arcuate. The length varies considerably among species ranging from ca. 15 mm in *P. nivalis* Luhrs et Lampard to 440 mm in *P. lutea* Walter (per. observ., Shimai). Bracts are always absent and the scape is often densely or sparsely covered by glands or hairs. The glands on the scape can also digest captured prey as those on leaves can (Thorén et al. 1996). In smaller species (e.g. *P. ramosa* Miyoshi and *P. villosa*) the scape plays a more important role in prey capture at least during their flowering season. The scape is basically unbranched and bears a single flower at the apex (Lloyd 1942). *P. ramosa* is an exception as it often produces a bifurcate or trifurcate scape, branching at below the middle or near the base of the scape under optimal conditions (n.b. unbranched scapes are also seen within the same population) (Miyoshi 1890). The number of scape produced during the flowering season in each year varies from one (e.g. *P. ramosa* and *P. villosa*) to more than ten (*P. hirtiflora* Tenore and *P. pumila*) depending on species or environmental factors. When pollination has been successful, the scape elects vertically and its length increases slightly. This extension is particularly remarkable in species growing on vertical to overhanging rock walls to attach a capsule directly to the rock walls and disperse seed; although only a small amount of seed is successfully deposited on the rock walls.

Calyx

The calyx is bilabiate with a 3-lobed upper lip and a 2-lobed lower lip. Lobes are ovate, elliptic, oblong, lanceolate, or broadly triangular, and lower lobes tend to be only slightly smaller and narrower than upper ones. The arrangement of the calyx lobes is either subactinomorphic or zygomorphic. The lower lobes are sometimes connate to middle or entirely. The calyx is sparsely or densely covered by glands secreting mucilage in most species, but it is glabrous in a few species, such as *P. debbertiana* and *P. gracilis* (Zamudio 1988, Speta et Fuchs 1992).

Capsule

The capsule, or the fruit, contains numerous tiny seed up to ca. 150 (Heslop-Harrison 2004). The shape of capsule is globose, subglobose, ellipsoid, ovoid, or obovoid, depending on the species. When the capsule is mature, it dries and the colour becomes yellowish-brown, brown, or dark brown. It eventually dehisces longitudinally from the top to base into bivalves, and then the seed is dispersed by wind, rain, or any vibrations.

Seed

The seed of *Pinguicula* is very tiny, mostly 0.4-1.2 mm long and the colour is usually black or brown. Among Swedish species, mean seed weight reported varies between 15.1 ± 2.5 μg in *P. alpina* and 28.7 ± 0.6 μg in *P. villosa* (Karlsson 1986). The shape also varies significantly among species, but mostly subglobose, pyriform, ellipsoid, fusiform, or narrowly so. The apex or both ends have an appendage which is often abruptly narrowed or is nearly acute. In a few species, the appendage is rather obscure (e.g. in *P. lutea*), or it is remarkably well-developed (e.g. in *P. vallisneriifolia*). The texture of outer surface is often densely and reticulately dimpled. The shape of dimples varies among species, but it is often narrowly rectangular, oblong, or nearly circular, and it is usually allied longitudinally parallel. The seed morphology may be helpful for taxonomy only in a few species but it is largely taxonomically uninformative (see Appendix I). On the other hand, it may be useful for grouping the taxa (per. com., Cheek). The seed requires light for germination (Gardner 1921). Unless it is sterile, the seed can germinate immediately when mature (Casper and Steiger 2001) or do so very well within one or two years, but the germination rate rapidly decreases after three years. Some seeds germinate within the same growth season (usually summer), but some others are stored on the soil surface and are preserved until next growth season for their germination (Shimai 2016).

Pollen grain

The size of pollen grain reported is 12.5-34.0 µm in polar axis diameter and 18.5-36.0 µm in equatorial diameter (Ikuse 1956, Sohma 1975). Rodoni et al. (2010) observed 4-10 (but more often 5-9) zonocolporate in nine European *Pinguicula* taxa. Consistent observations have been reported by Casper (2007a, 2007b) from European taxa, Ansaldi and Casper (2009) from Cuban taxa, and Shimai (2016) from *P. ramosa*. Espinosa-Matías et al. (2005), who studied pollen grains of Mexican species, concluded that the result did not support the three subgeneric divisions in terms of the pollen morphology.

3. DISTRIBUTION AND HABITAT

Geographical distribution area

Geographical distribution of *Pinguicula* can be found in all continents except

Oceania, Antarctica, and a majority of Africa (Casper 1966, Givnish 1989). The general outline of the distribution is seen in Europe, not only Continental Europe but also the British Isles, Iceland, and Corsica, and it continues to Asia extending from Anatolia and Cyprus to the Russian Far East, Sakhalin, the Kuril Islands, Japan (Hokkaidō, Honshū, and Shikoku), the Himalayas and Southwest China. Only three species reach to Northern Africa (Morocco). The genus is also found in North America, including Greenland, the Aleutian Islands, and stretches to Mexico, Central America, the Bahamas, Cuba, the Dominican Republic, down the Andes and into the Patagonian region of South America; as far south as the vicinity of Tierra del Fuego. The geographical distribution of *Pinguicula* can, therefore, be approximately divided into two areas through a disjunction in its range (Fig. 3); one is higher altitudes or higher latitudes (arctic) of the Northern Hemisphere, and the other is in the southeastern parts of the USA to the southern tip of South America, extending to Tierra del Fuego. The climate of the former range is mostly temperate or alpine whereas the latter is temperate, subtropical, or tropical.

Twenty-four species are distributed in temperate regions of the Northern Hemisphere including Eurasia, Morocco, and the northern part of North America. Twenty of the 24 species are found in Europe to Anatolia, Cyprus, and the Caucasus, while 7 species occur in North America or Eastern Asia including the Russian Far East and the Himalayas. A majority of species in this group form hibernacula by the end of summer to protect vegetative and floral buds from frost and/or snow. Three species (*P. crystallina*, *P. hirtiflora*, and *P. lusitanica*) are exceptions to this rule ranging from Europe to Cyprus through to Anatolia, and survive the winter season without forming hibernacula.

Sixty-six taxa are distributed through the southeastern part of the USA to South America including the Caribbean. Mexico, in particular, harbors 46 taxa with considerable morphological diversities among the species, most of which are endemic (Zamudio 2005). Twenty-one taxa out of 66 are found outside of Mexico and Central America, i.e. in the southeastern USA, Cuba, and the Andes through to southern Patagonian region of South America. Most of the Mexican and Central American species form winter rosettes to survive the arid winter season while other species do not form any winter rosettes. One exception appears to be *P. elongata* distributed in Venezuela and Colombia, which forms a winter bud that resembles a hibernaculum.

Most species tend to be confined to small geographical areas, such as a specific region, gorge, or a mountain, while only a few species (e.g. *P. alpina*, *P. macroceras*, *P. vulgaris*, and *P. villosa*) exhibit much wider distributions. Thus, the high levels of endemism have resulted in high numbers being threatened with extinct due to environmental stress, climate changes, and/or human activities. A few species (e.g. *P. greenwoodii* Cheek, *P. sharpii*, and *P. utricularioides* Zamudio et Rzedowski) are known only from the type locality with a single collection record, and their current status within the habitat and their actual distribution remain unknown.

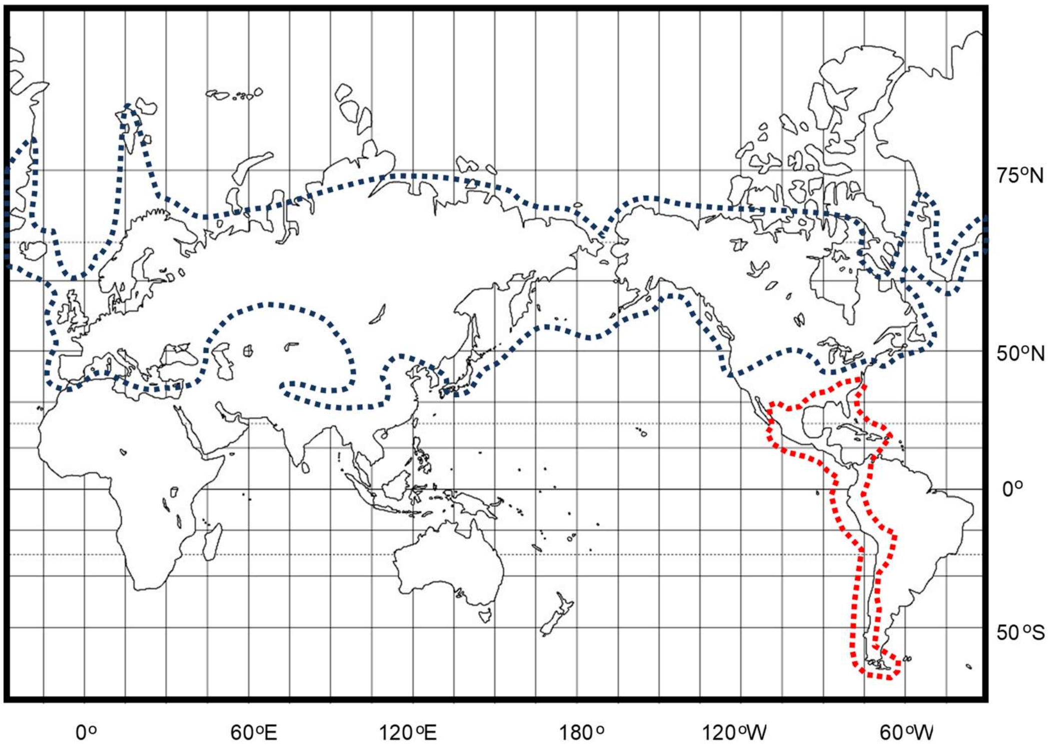

Fig. 3. Approximate distribution areas of the genus *Pinguicula.* The figure shows a rough image of distribution areas of the genus *Pinguicula*. There are two major distribution areas; one is northern Eurasia and northern North America shown in a blue dot line and the other one is the southeastern USA to South America shown in a

red dot line. In this figure, some minor distributional gaps are ignored to present approximate distribution areas, and the northern limit may not be accurate since exact northern limits of the distribution are poorly known. The latitudinal distribution in the northernmost range is ca. 79°20'N in Svalbard and in the southernmost range is ca. 55°30'S in the Tierra del Fuego region.

Only a few species (e.g. *P. alpina*, *P. macroceras*, *P. villosa*, and *P. vulgaris*) are widely distributed. Such wider distributions are rare in the genus. *P. alpina* can be found in Europe, through Siberia, and into China. *P. macroceras* is distributed in the northern Pacific Rim regions including Japan, Sakhalin, the Kuril Islands, Kamchatka, the Aleutians, Alaska, the Pacific region of Canada and the USA as far south as the Oregon and California state border. *P. villosa* and *P. vulgaris* show much wider distributions than other species. *P. villosa* is distributed in circumpolar regions of the Northern Hemisphere, but its actual distribution boundaries remains unclear since most of the areas are inaccessible and plant itself is tiny with a very limited growth season; often only 2 months. *P. vulgaris* is distributed in North America, Eurasia and Morocco and it is regionally very abundant. It is interesting to note that within each species they are largely uniform in terms of their morphology in spite of the wider geographical distribution.

The largest number of species occurs in Mexico (46 taxa), followed by France (10), Spain (9), USA including Alaska (9), Italy (8), and Cuba (8). Natural hybridizations may occur in sympatric habitats in Europe (e.g. *P. leptoceras* X *P. vulgaris* in the Alps and *P. grandiflora* X *P. vulgaris* in the Pyrenees) and possibly in Mexico (per. com., Zamudio). In contrast, natural hybridization is unlikely to occur in Florida, where two or more species are found sympatrically (Wood and Godfrey 1957).

Altitudinal distribution

Altitudinal range of suitable habitat is one of the major factors that is likely to constrain the distribution of *Pinguicula* although a species can range in altitude from 0 m to over 4,500 m above sea level. Six species are mostly found at less than 50 m above sea level in the Coastal Plain region of the southeastern USA. Also, *P. albida* Wright ex Griseb. and *P. filifolia* Wright ex Griseb. occur at the forest margin of coastal regions of western Cuba. *P. villosa* is often found at slightly higher altitudes of the circumpolar region, mostly between 350 m and 550 m (Alm 2000). Although *P. grandiflora*, *P. macroceras*, *P. vulgaris*, and *P. hirtiflora* are more commonly found at a higher altitude, they also occur near coastal areas. These species tend to grow in higher mountains in lower latitudes, and also at lower altitudes in higher latitudes. The distribution of some species stretches above 4,000 m, e.g. *P. calyptrata* in the Andes and *P. alpina* in the Himalayas and southwestern China. Most species are, however, found in mountains or gorges at altitudes between 1,000 m and 3,000 m.

Habitat

Many species of *Pinguicula* prefer calcareous soils. The soil types where *Pinguicula* is more commonly found in are limestone, lime-rich sand/sandstone, or gypsum, but occasionally in silty soil, serpentine, peat, or sphagnum; mostly soils are between weak acid and weak alkaline. Heslop-Harrison (2004) summarised minimum and maximum soil pH in different *Pinguicula* habitats, ranging pH 3.1 to 8.0, though some may represent extremes. Generally, a higher calcareous content in soil increases a pH level (i.e. more alkaline). Preference of soil types is different among species, although *P. grandiflora* and *P. vulgaris* are rather indifferent to soil types (Blanca et al. 1999). The soil is often permanently or seasonally wet, in which typical stream sides, pond margins, bogs, marshes, sphagnum mats, wet slopes and rock walls (Lloyd 1942, Givnish 1989, Juniper et al. 1989). For this reason, *Pinguicula* is often regarded as wetland plants (Darwin 1875, Lloyd 1942, Juniper et al. 1989, Adlassnig et al. 2005).

Even in cases were the soil is dry, high air humidity, fog, and/or precipitation may supply enough moisture to maintain plants. In the higher mountains in Europe and Asia, *Pinguicula* is more commonly found on limestone outcrops, gravelly ridges, near glacier, or snow patch margins.

In terms of hydrology, water is often moving either slowly or rapidly on slopes, cliffs, streamside, or bogs of very wet habitats, at least during their growing season. The water may be oozing, running, dripping, or flashing, from above or in the habitat. In a rare case, immersion of plants (e.g. *P. planifolia* Chapman) can occur in shallow pools in the southeastern USA. Thus the regular water supply, either permanently or seasonally, at least to the root system is necessary in some species. According to Heslop-Harrison (2004), water pH was approximately 4.14-8.22 including some extremes and the dissolved calcium level was 60-200 mg L^{-1} at sampled European habitats. A number of *Pinguicula* species are to be found as a predominant vascular plant at an ecological micro niche. From a phytosociological point of view, a specific vegetation and soil type, where a *Pinguicula* species is predominantly present on limestone slopes or cliffs with water flushes involving tufa travertines has been termed "*Pinguiculion*" particularly for the plant communities in the Iberian Peninsula (Jiménez-Alfaro et al. 2013). *Pinguiculion* is characterized by the presence of a *Pinguicula* species often restricted to a specific ecological niche in small geographical areas. For example, habitats of *P. longifolia*, *P. mundi* Blanca, Jamilena, Ruiz-Rejón et Zamora, and *P. vallisneriifolia* could be typical *Pinguiculion* vegetation, while those of *P. dertosensis* (Cañigueral) Mateo et Crespo and *P. grandiflora* are not necessarily restricted to only such a specific habitat but can also be found in various wet places (e.g. pond margins or streamsides), and other types of vegetation (per. com., Jiménez-Alfaro).

Karlsson et al. (1987) and Givnish (1989) have mentioned that the habitat of *Pinguicula* is exposed to sunlight; however, its habitats are usually north-facing or located within a forest or a gorge to avoid direct sunlight. Thus, a number of *Pinguicula* species are intolerant of strong light intensity (Cheek 1994, Zamudio 1997, 1999, Zamudio and Studnička 2000). A possible reason why the habitats of *Pinguicula* species are often restricted under shade could be that evaporation occurs much faster than water supply at sunny places (Heslop-Harrison 2004). Another possible reason could be that direct sunlight causes reflected heat on a rock surface. Although there are no data on light intensity from each habitat, a relatively low photosynthetic photon density (PPFD), with a maximum of 416 µmol m^{-2} s^{-1} was recorded at a *P. ramosa* habitat in a mountain forest (Oba et al. 2013). The definition of light tolerance in the current work is roughly as follows, "High light intensity" means the plants are often exposed to direct sun light or nearly so during daytime in their growth season, "Low light intensity" means the plants are exposed to direct sun light only for a very short time, exposed to weak sun light filtering through tree leaves, or are not exposed to direct sunlight due to their location in a forest or deep gorge.

Such soils and light environments could be restricting factors for growth of other plants (including tree species), whereas *Pinguicula* species alone often form large communities in such environment to avoid growth competition with other plant species. In addition, exposed vertical or overhanging rocks might be an appropriate microhabitat for *Pinguicula*, while other vascular plants find it difficult to grow. A few species (*P. casabitoana* and *P. lignicola*) are unique in that they are epiphytic, growing on tree stems or twigs (Jiménez 1960, Casper 1987). *P. hemiepiphytica* Zamudio et Rzedowski and *P. mesophytica* Zamudio also grow on mossy tree trunks as epiphytes though they may also be found on rocks (Zamudo 1991, 1997).

Climate at habitats

As mentioned earlier, *Pinguicula* has a large geographical range although many species can be generally seen in cooler areas, at least seasonally. Even though a few species can be found south of the equator, their distribution is restricted to higher altitudes. As such there are few tropical species preferring higher temperature, except for several species found in the Caribbean and lower altitudinal ranges of Mexico to Central America. With suitable habitats, average monthly precipitation, maximum, and/or minimum temperatures often show seasonal changes. Those climates sometimes related to annual growth cycles of *Pinguicula* species. Some representative habitats of *Pinguicula* have been shown in Fig. 4.

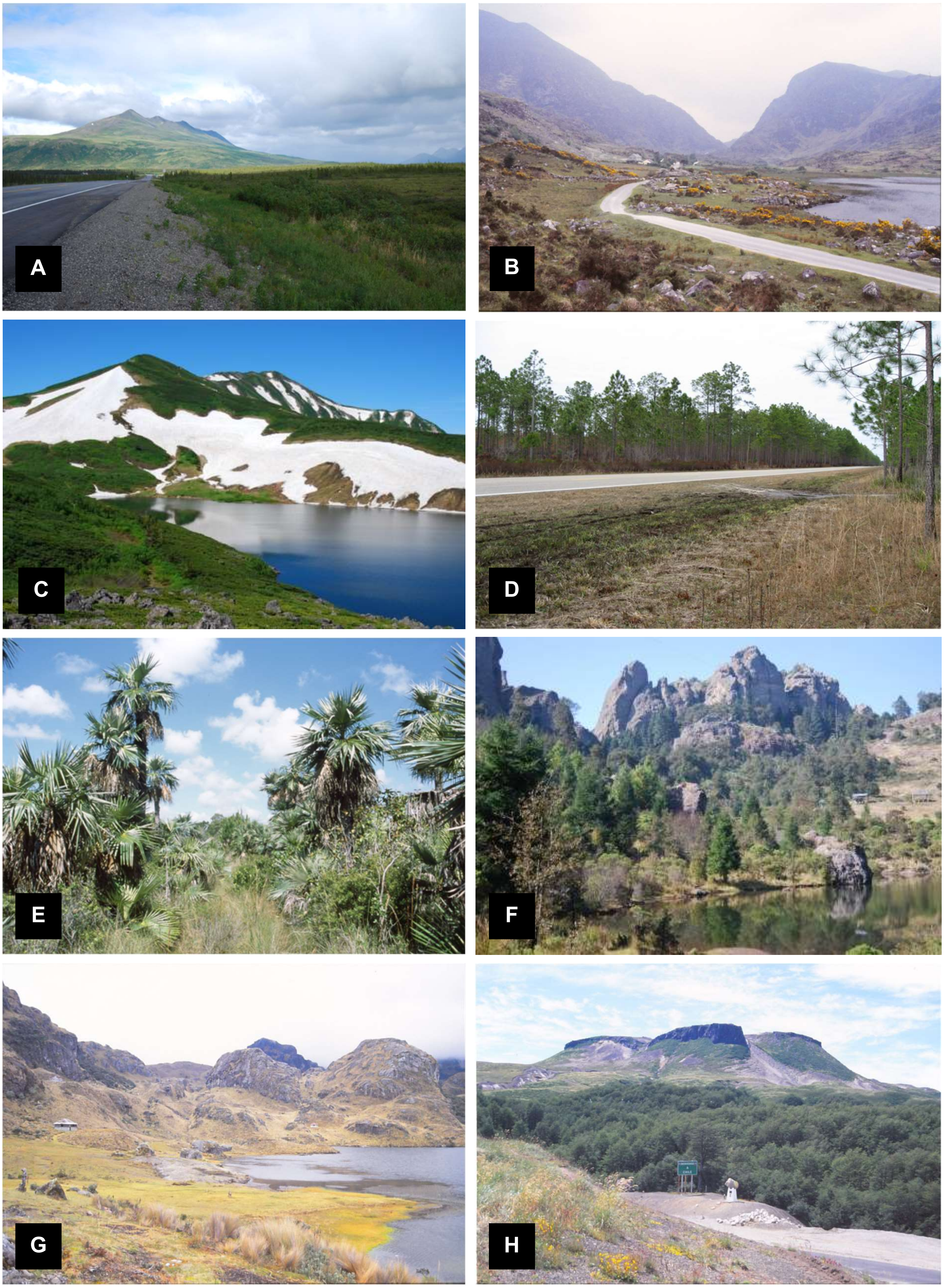
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Fig. 4. Some representative habitats of *Pinguicula.* A: Arctic habitat (Broad Pass, Alaska, USA; ca. 63°18'N, 730 m). B: Higher latitude in Europe (Gap of Dunloe, Kerry Co., Ireland; ca. 52°01'N, 120 m). C: Alpine habitat in Asia (Hakuba-ōike Pond, Nagano, Japan; ca. 36°47'N, 2,380 m). D: Coastal habitat in the southeastern USA (Apalachicola National Forest, Florida, USA; ca. 30°05'N, 10 m). E: Subtropical habitat in the Caribbean (Pinar del Río, Cuba; ca. 22°04'N, 5 m). F: Highland habitat in Mexico (El Chico National Park, Hidalgo, Mexico; ca. 20°11'N, 2,900 m). G: Andean habitat in tropical South America (Cajas National Park, Azuay, Ecuador; ca. 02°47'S, 3,920 m). H: Patagonian habitat in South America (Puyehue National Park, Los Lagos, Chile; ca. 40°42'S, 1,300 m). Photo by H. Shimai.

In this thesis, Chapter 1 deals with Red List assessments in each taxon to evaluate a current status based on the criterion by the International Union for Conservation of Nature (IUCN 2012). The current web site of the IUCN Red List of Threatened Species (http://www.iucnredlist.org/) has listed only 7 *Pinguicula* taxa. Chapter 2 focuses on the phylogenetic analyses to infer the relationships among *Pinguicula* taxa and their phylogeography. As mentioned earlier, the three subgenera are not supported by phylogeny which needs to further investigation with more samples.

Chapter 3 explores which geographical or environmental factor affects patterns of species richness in *Pinguicula*. Chapter 4 is a revision of the genus *Pinguicula* mainly based on the phylogenetic analyses discussed in the phylogeny chapter. This chapter will propose new sectional delimitations and describe the characteristics of each taxon. To clarify the taxonomy is an important process to assess the Red List categories and subsequent conservation of the taxa.

4. SUMMARY

The genus *Pinguicula* is a well-defined taxonomic group within Lentibulariaceae due to their morphological features and means of prey capture (a key to genus is shown below). The distribution area of most taxa in the genus is restricted to a small area but their current status in nature is often poorly known. In addition, there is disagreement between the current taxonomy based on the morphology and phylogeny. The samples used for phylogenetic studies in the earlier studies are limited to infer their relationships. Only a few works covering all taxa and a revision of the genus have been published, often resulting in taxonomic confusions. Here, these questions are investigated.

Key to genus

Leaves forming a basal rosette

Scape w/o bracts, simple, flower solitary --- ***Pinguicula***

Scape w/ bracts, racemose --- ***Genlisea***

Leaves alternate --- ***Utricularia***

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CHAPTER 1

Red List assessments of the genus *Pinguicula* L.

1.1. INTRODUCTION

The International Union for Conservation of Nature (IUCN) Red List Categories and Criteria (IUCN 2012) is the main assessment mechanism by which the threat status of a species is determined. The categories are Critically Endangered (CR), Endangered (EN), Vulnerable (VU), Near Threatened (NT), and Least Concern (LC). Within the categories, CR, EN, and VU are considered to be facing a high risk of extinction in the wild. By incorporating those species assessed through the Sampled Red List Index (SRLI) for Plants and those species yet to be discovered (RBG Kew 2010, Brummitt et al. 2015a), Joppa et al. (2011) estimate that 27-33 % of flowering plant species are threatened with extinction. In contrast, Davies et al. (2011) estimated that approximately 70 % of flowering plant species are threatened with extinction, although very limited numbers of species, 19,738 out of ca. 380,000 plant species (Brummitt et al. 2015a), have been assessed using the criteria. Whatever the case it is clear that a significant number of flowering plants are under threat of extinction.

Knowledge of the current conservation status is of clear importance, but it has to be evaluated under the same standard (Brummitt et al. 2015b). The IUCN Red List forms a stable, scientific-based framework by which species can be assessed; however, earlier assessments may need to be re-assessed with expert knowledge on taxonomy in a specific plant group (Willis et al. 2003, Newton and Oldfield 2008, Brummitt et al. 2015a). Although Red List assessments in plants gain less impact and financial support than those in animals (Goettsch at al. 2015), subsequent conservation programs certainly require the assessments (Hoffmann et al. 2008).

There are a range of approaches to accumulate datasets for the Red List assessments. For example, 1) to visit the habitat for direct observations (Rivers et al. 2010, Romeiras et al. 2014), 2) to study literature on regional floras (Brummitt et al. 2015a), 3) to utilize external data and internet sources (Bachman et al. 2011, Brummitt 2015a), 4) to study voucher specimens deposited in museums (Rivers et al. 2010, 2011, Brummitt et al. 2015b, Roberts et al. 2016). There are, however, issues with all these approached that need to be considered. For 1), it is not always possible to visit each locality and there may be limited factors such as the phenological state (e.g. dormant season), safety, or limited means of transportation to access the locality. For 2), the information source is often unclear with lack of detailed locality names. Regarding 3), writers may be anonymous and information is not always reliable. Some issues with specimens related to 4) are discussed in detail by Roberts et al. (2016) such as accuracy of information on labels, information gaps in time, sampling gaps, subsequent taxonomic revisions, and the habitat has already been lost.

Despite the issues with museum specimens, they can be biologically informative and provide objective evidence that other information sources may lack; geographical details (e.g. exact locality name, latitude and longitude coordinates, locality map), date of collection, altitude, and ecological observations (Romeiras et al. 2014). Specimens are regarded as the best available evidence, and often the only available evidence in little known taxa, for the Red List assessment (Willis et al. 2003, Brummitt et al. 2015a, 2015b).

It has been hypothesised that species discovered earlier are more likely to have wider distribution ranges, and therefore a higher chance of being encountered resulting in more information being accumulated (Collen et al. 2004). In theory, more recently discovered species with fewer specimen records infer smaller distribution ranges and such species consequently have a higher risk of extinction (Roberts et al. 2016). Those are not just simply because they are more recently described, but because they are actually rare (Collen et al. 2004). The year of description may be used as a surrogate of species discovery; i.e. the date a species was formally described and given a scientific name under the rules of the International Code of Nomenclature for algae, fungi, and plants (McNeill et al. 2012).

For some species, particularly plants, Area of Occupancy (AOO) and Extent of

Occurrence (EOO) are the primary measures of their threat status, and are applied under criterion B of the IUCN Red List guidelines. AOO can be simply defined as the sum of the site occupied (the guidelines recommend 2 km X 2 km square grid be used). Whereas EOO is an area encompassing all known sites of a taxon (IUCN 2012). For a full Red List assessment, additional criteria are required, although the data for which are often more difficult to obtain and at times somewhat subjective. They include population size reduction over any 10 years or 3 generations, estimated population size smaller than a specific number of mature individuals, or quantitative analysis showing the probability of extinction in the wild (IUCN 2012). The IUCN SRLI does not require full assessment for all species since in many cases species that are going to assessed are expected to be rare or already threatened (Brummitt et al. 2015a).

In some particular plant groups, such as the family Cactaceae, 31 % of 1,478 evaluated species are reported to be threatened (Goettsch et al. 2015). In the case of carnivorous plants, only 20% (mostly *Nepenthes* spp.) have been currently assessed by the Carnivorous Plant Specialist Group according to the IUCN website (http://www.iucnredlist.org/) and little published information is yet available. Among the carnivorous genera, the patchy distribution of *Pinguicula* L. (Lentibulariaceae), often having a very narrow environmental preference, is reported particularly from semiarid regions such as Mediterranean and Mexico, and resulting in small population sizes within a highly restricted distribution area (Zamora et al. 1996). Particularly in Mexico a higher proportion of endemism is seen (Shimai and Kondo 2007). The IUCN Red List of Threatened Species™ database (2016) currently list only 7 taxa from the 91 taxa of *Pinguicula* L. (Lentibulariaceae), 4 of which are evaluated as Least Concern, this is clearly not representative of the genus as a whole.

The geographical distribution of the genus *Pinguicula* have been studied by scientists, for example, throughout the genus by Casper (1966), or locally by Casper (1962) for Eurasia, Godfrey and Stripling (1961) for North America, Blanca et al. (1999) for the Iberian Peninsula, and Heslop-Harrison (2004) for the British Isles, but it is still lacking in some areas. Due to increasing the number of taxa, a review of the distribution range for each taxon will be necessary.

A number of taxa in the genus *Pinguicula* are highly restricted to a small geographical area, such as a specific mountain range or gorge, except for a few taxa which have wider distribution ranges, e.g. *P. alpina* L., *P. villosa* L., and *P. vulgaris* L. However, for those species with narrow distribution ranges, their current threat status is poorly known as to whether or not they are actually threatened (Simpson 1994). What we do know is that a number of species of *Pinguicula* have been over-collected in the field because of their horticultural values as carnivorous plants. No species of *Pinguicula* are currently listed in the appendices of the Conservation on International Trade in Endangered Species of Wild Fauna and Flora (CITES) for commercial trade (von Arx et al. 2001; also see the CITES website for an up to date checklist). The habitats of *Pinguicula* are often found within national parks or natural reserves, but some of them are likely disturbed repeatedly.

Due to questions over the threat status of the genus *Pinguicula*, an understanding of the distribution of threats is required for their effective conservation. In this chapter, the main questions are: 1) whether more recently described *Pinguicula* taxa have fewer numbers of specimens (or localities) that may be threatened with extinction, 2) how many taxa in the genus are actually threatened, 3) whether extinction risk of endemic taxa is higher than that of non-endemic taxa in the *Pinguicula* biodiversity hotspots of Mexico and Central America, Europe and Western Asia, and the Caribbean Islands.

1.2. MATERIALS AND METHODS

Data collection

The year of description referred the original publications where each taxon was officially described with a valid scientific name.

Although Rivers et al. (2011) critically estimated that the minimum of 15 specimens (or 10 specimens for rare species presenting sparse distributions, such as orchids) are required to detect whether a species is threatened, a total of over 6,800 *Pinguicula* specimens were examined to minimize sampling gaps. Specimens represent an important resource for primary assessments; however, some specimens may have been misidentified and furthermore the cumulative number of taxa has increased since the monograph by Casper (1966). Therefore, it is important to review as many specimens as possible. During the examinations geographic information was gathered for the taxon from existing herbarium specimens deposited at 167 herbaria; A, AAU, ABS, ACAD, ALA, AMD, AO, APP, ARIZ, ASU, BAA, BABY, BASSA, BC, BEI, BEO, BERN, BIRM, BKL, BM, BOLO, BP, BR, BUF, BVS, CGE, CHRB, CINC, CLF, CLU, CONN, CR, DBN, DES, E, EAP, EGE, ENCB, FCO, FIAF, FLAS, FRP, GAZI, GBH, GDAC, G-DC, GMNHJ, GOET, GR, GZU, HAJU, HAL, HAM, HAST, HEM, HUB, I, ID, IEB, IJ, ISKW, ISTF, JACA, JE, JEPS, K, KANA, KMN, KWHU, KYO, LAGU, LE, LEA, LI, LINN, LISU, LJS, LJU, LUG, MAK, MANCH, MARS (General herb.), MARY, MASS, MERL, MEXU, MGC, MHA, MKNH, MMMN, MO, MONTU, MRSN, MSC, MSNM, MU, MW, NAP, NCY, NHA, NHMF, NMW, NSPM, NY, NYS, O, OLYM, OXF, P, PAD, PE, PH,

PLU, PRA, QCA, QFA, QK, REG, RO, S, SAPS, SAV, SB, SHIN, SNU, SO, SOC, SOM, SRP, STR, STU, TAA, TEX, TI, TL, TNS, TSM, TUS, UBC, UDM, UM, UNA, UPA, UPS, US, USF, UTC, UWSP, VAL, VM, VT, WA, WI, WIN, WIS, WTU, WU, WVA, WWB, ZA, ZAHO, ZT, Eastern Washington University, Fukui City Museum of Natural History, Nippon Dental University, Slater Museum of Natural History (University of Puget Sound), Tochigi Prefectural Museum, and herb. Dr Garrett Crow. The code for each herbarium follows Index Herbariorum (Holmgren et al. 1981, Thiers; continuously updated). The accepted 91 taxa according to this study (see Chapter 4) are shown in Table 1.2 and those specimens examined are listed in Appendix II. The term "taxon" can be used for any taxonomic units and also those not formally described, but the term in this work refers to a specific or intraspecific (subspecies and variety) rank as treated in the IUCN Red List Categories and Criteria version 3.1, second edition (IUCN 2012). In this study, the definition of "endemic" is a taxon confined to one country.

Only information on labels on existing voucher sheets from the herbaria listed was collected for this study. Information available from external sources such as Global Biodiversity Information Facility (GBIF) or in the literature was excluded due to misleading data except the type records with specific locality information. Specimens with no locality or incomplete locality information showing only a regional name, e.g.

Florida, Lapland, Transylvania, Tyrol, or Yorkshire, were excluded. Based on the specimen labels, the unique locality of each specimen in each taxon was plotted on a map of Geospatial Conservation Assessment Tool (GeoCAT) following the instruction available online (http://geocat.kew.org/help) to present an outline of distribution area.

GeoCAT, an open source web tool that harnesses primary biological data for semi-automated IUCN Red List assessment and analysis to support the threat assessments, was developed by the Royal Botanic Gardens, Kew. The tool performs rapid geospatial analysis on two aspects of a taxon, EOO and AOO, the foundation of criteria B of the IUCN Red List system, were evaluated using GeoCAT as described by Bachman et al. (2011).

During the analysis duplicate specimens were excluded to remove the issue of non-independence. Introduced populations, e.g. *P. grandiflora* Lam. in Britain, *P. vallisneriifolia* Webb in Switzerland, or *P. primuliflora* Wood et Godfrey in Japan have also been excluded for the analysis. An area in square kilometres (km^2) and a category, Critically Endangered (CR), Endangered (EN), Vulnerable (VU), Near Threatened (NT), or Least Concern (LC), for EOO and AOO in each taxon were automatically assessed using GeoCAT based on the threshold shown in Table 1.1. Among the five categories, CR, EN, and VU are recognised as threatened with extinction. For AOO, the default value of

2 km (i.e. 4 km² in a grid square) was applied for each analysis as recommended by the IUCN (2012). In extreme cases, only type specimens from a single locality are known (e.g. *P. greenwoodii* Cheek, *P. sharpii* Casper et Kondo, and *P. utricularioides* Zamudio et Rzedowski); however, it is still possible to calculated the AOO value (Brummitt et al. 2015a) although if the sampling number was 1 or 2; EOO value was not calculated since at least 3 unique localities are required for creating the minimum convex polygon (Brummitt et al. 2015a). In such a case, the category might be Data Deficient (DD); however, GeoCAT assigns the taxon the threat category of CR; therefore, CR was adopted in this work. The reason for this treatment was discussed by the IUCN (2012) as liberal use of DD should be avoided. In *P. cubensis* Uruquiola et Casper and *P. jarmilae* Halda et Malina, different locality names or altitudes are recorded in specimen labels; however, those are likely identical or are subpopulations within the same area (Beck et al. 2008).

Table 1.1. Threshold categories by IUCN (2012). CR = Critically Endangered, EN = Endangered, VU = Vulnerable. EOO = Extent of occurrence, AOO = Area of occupancy.

	Threatened (km²)			Not threatened (km²)
	CR	EN	VU	
EOO	< 100	< 5,000	< 20,000	> 20,000
AOO	< 10	< 500	< 2,000	> 2,000

Data analyses

Spearman's rank correlation was used for analyses between distribution range in km^2, the natural logarithms (NL), IUCN Red List categories, the number of specimens and the year of description.

For the correlation between the Red List categories (CR, EN, VU, NT, and LC) and endemic taxa in the three *Pinguicula* biodiversity hotspots, Spearman's rank correlation was applied. A chi-square test was used to determine if endemic taxa have a statistically higher risk of extinction than non-endemics. Due to zero values in some cases, the Red List categories were divided into two, threatened (CR, EN, and VU) and not threatened (NT and LC), and the relationship between the Red List categories and endemic or non-endemic for EOO and AOO were analysed by the 2 X 2 contingency test.

1.3. RESULTS

There are no *Pinguicula* taxa that are evaluated as Extinct (EX), Extinct in the Wild (EW), or DD, although *P. greenwoodii, P. sharpii,* and *P. utricularioides*, collected in 1987, 1972, and 1956 respectively, are hitherto known only from the type specimens with no recent information regarding the status of their habitats. The year of description, EOO, AOO, and the number of localities on the distribution map in each taxon are shown in Table 1.2.

Table 1.2. Described year, endemism, threat categories in EOO and AOO, and the number of localities on the distribution map of each taxon. Endemic = restricted to one country. CR = Critically Endangered, EN = Endangered, VU = Vulnerable, NT = Near Threatened, LC = Least Concern. NL = Natural logarithm. P.P. = precautionary principles, the higher threat level used for each taxon between EOO and AOO.

Taxa	Year	Endemic	EOO	EOO km^2 (LN)	AOO	AOO km^2 (LN)	P.P.	Locality no. (LN)
P. acuminata	1839	Yes	NT	22,817 (10.04)	EN	100 (4.62)	EN	28 (3.33)
P. agnata	1963	Yes	VU	10,543 (9.26)	EN	64 (4.17)	EN	22 (3.09)
P. albida	1866	Yes	EN	4,238 (8.35)	EN	52 (3.97)	EN	13 (2.56)
P. algida	1966	Yes	LC	4,176,757 (15.25)	EN	148 (5.00)	EN	38 (3.64)
P. alpina	1753	No	LC	30,265,929 (17.31)	NT	2,736 (7.91)	NT	1,398 (7.24)
P. antarctica	1805	No	LC	650,340 (13.39)	EN	84 (4.44)	EN	21 (3.04)
P. balcanica	1962	No	LC	1,336,820 (14.11)	VU	584 (6.37)	VU	174 (5.16)
P. benedicta	1910	Yes	EN	1,149 (7.05)	EN	76 (4.34)	EN	20 (3.00)
P. caerulea	1788	Yes	LC	342,551 (12.74)	EN	464 (6.14)	EN	117 (4.76)
P. calderoniae	2001	Yes	CR	0 (0.00)	CR	8 (2.20)	CR	2 (0.69)
P. calyptrata	1817	No	LC	66,175 (11.10)	EN	244 (5.50)	EN	69 (4.23)
P. casabitoana	1960	Yes	EN	2,498 (7.82)	EN	28 (3.37)	EN	7 (1.95)
P. caussensis	2016	Yes	EN	2,110 (7.65)	EN	48 (3.89)	EN	14 (2.64)
P. chilensis	1849	No	LC	87,289 (11.38)	EN	56 (4.04)	EN	14 (2.64)
P. clivorum	1944	No	CR	0 (0.00)	CR	8 (2.20)	CR	2 (0.69)
P. colimensis	1963	Yes	CR	38 (3.66)	EN	12 (2.56)	CR	3 (1.10)
P. conzattii	2003	Yes	CR	0 (0.00)	CR	8 (2.20)	CR	2 (0.69)
P. corsica	1850	Yes	EN	765 (6.64)	EN	72 (4.29)	EN	20 (3.00)
P. crassifolia	1988	Yes	CR	3 (1.39)	EN	20 (3.04)	CR	6 (1.79)
P. crenatiloba	1844	No	LC	1,368,009 (14.13)	EN	256 (5.55)	EN	63 (4.14)
P. crystallina	1806	No	LC	184,257 (12.12)	EN	124 (4.83)	EN	37 (3.61)
P. cubensis	2003	Yes	CR	0 (0.00)	CR	8 (2.20)	CR	3 (1.10)
P. cyclosecta	1963	Yes	VU	7,594 (8.94)	EN	36 (3.61)	EN	10 (2.30)
P. debbertiana	1992	Yes	CR	0 (0.00)	CR	4 (1.61)	CR	1 (0.00)
P. dertosensis	1995	Yes	LC	45,792 (10.73)	EN	56 (4.04)	EN	15 (2.71)
P. ehlersiae	1982	Yes	EN	1,843 (7.52)	EN	36 (3.61)	EN	10 (2.30)
P. elizabethiae	1999	Yes	CR	43 (3.78)	EN	16 (2.83)	CR	5 (1.61)
P. elongata	1847	No	LC	142,533 (11.87)	EN	68 (4.23)	EN	17 (2.83)
P. emarginata	1986	Yes	EN	130 (4.88)	EN	16 (2.83)	EN	4 (1.39)
P. esseriana	1981	Yes	NT	37,958 (10.54)	EN	56 (4.04)	EN	15 (2.71)
P. filifolia	1866	Yes	VU	7,540 (8.93)	EN	100 (4.62)	EN	25 (3.22)
P. fiorii	1987	Yes	CR	28 (3.37)	EN	20 (3.04)	CR	5 (1.61)
P. gigantea	1995	Yes	CR	0 (0.00)	CR	4 (1.61)	CR	2 (0.69)
P. gracilis	1988	Yes	VU	7,491 (8.92)	EN	20 (3.04)	EN	5 (1.61)
P. grandiflora	1789	No	LC	1,330,923 (14.10)	VU	832 (6.73)	VU	219 (5.39)
P. greenwoodii	1994	Yes	CR	0 (0.00)	CR	4 (1.61)	CR	1 (0.00)
P. gypsicola	1911	Yes	CR	13 (2.64)	EN	24 (3.22)	CR	6 (1.79)
P. hemiepiphytica	1991	Yes	EN	1,351 (7.21)	EN	72 (4.29)	EN	22 (3.09)
P. heterophylla	1839	Yes	LC	86,894 (11.37)	EN	168 (5.13)	EN	43 (3.76)

Table 1.2 (continued)

P. hirtiflora	1811	No	LC	379,204 (12.85)	EN	436 (6.08)	EN	119 (4.78)
P. ibbarae	2005	Yes	EN	129 (4.87)	EN	12 (2.56)	EN	5 (1.61)
P. immaculata	1992	Yes	EN	739 (6.61)	EN	24 (3.22)	EN	6 (1.79)
P. involuta	1798	No	LC	250 (5.53)	EN	40 (3.71)	EN	10 (2.30)
P. ionantha	1961	Yes	EN	2,466 (7.81)	EN	60 (4.11)	EN	15 (2.71)
P. jackii var. *jackii*	1930	Yes	CR	6 (1.95)	EN	16 (2.83)	CR	4 (1.39)
P. jackii var. *parviflora*	1961	Yes	CR	4 (1.61)	CR	12 (2.56)	CR	3 (1.10)
P. jaraguana	2003	Yes	CR	7 (2.08)	EN	16 (2.83)	CR	4 (1.39)
P. jarmilae	2007	Yes	CR	0 (0.00)	CR	4 (1.61)	CR	1 (0.00)
P. kondoi	1974	Yes	VU	6,568 (8.79)	EN	48 (3.89)	EN	13 (2.56)
P. laueana	1989	Yes	CR	0 (0.00)	CR	8 (2.20)	CR	2 (0.69)
P. laxifolia	1995	Yes	CR	0 (0.00)	CR	8 (2.20)	CR	2 (0.69)
P. leptoceras	1823	No	LC	96,114 (11.47)	VU	632 (6.45)	VU	164 (5.10)
P. lignicola	1920	Yes	EN	744 (6.61)	EN	36 (3.61)	EN	10 (2.30)
P. lilacina	1830	No	LC	985,037 (13.80)	EN	180 (5.20)	EN	48 (3.87)
P. longifolia	1805	No	EN	916 (6.82)	EN	112 (4.73)	EN	30 (3.40)
P. lusitanica	1753	No	LC	1,629,156 (14.30)	VU	1,116 (7.02)	VU	286 (5.66)
P. lutea	1788	Yes	LC	563,490 (13.34)	VU	544 (6.30)	VU	137 (4.92)
P. macroceras	1820	No	LC	10,530,758 (16.17)	VU	1,524 (7.33)	VU	402 (6.00)
P. macrophylla	1817	Yes	NT	31,633 (10.36)	EN	192 (5.26)	EN	53 (3.97)
P. martinezii	2005	Yes	CR	4 (1.61)	EN	16 (2.83)	CR	6 (1.79)
P. medusina	2000	Yes	VU	7,319 (8.90)	EN	32 (3.50)	EN	8 (2.08)
P. mesophytica	1997	No	NT	39,401 (10.58)	EN	72 (4.29)	EN	21 (3.04)
P. mirandae	1996	Yes	CR	14 (2.71)	CR	8 (2.20)	CR	3 (1.10)
P. moctezumae	1994	Yes	CR	2 (1.10)	EN	16 (2.83)	CR	5 (1.61)
P. moranensis var. *moranensis*	1817	No	LC	499,901 (13.12)	VU	1,764 (7.48)	VU	487 (6.19)
P. moranensis var. *neovolcanica*	1999	Yes	LC	57,533 (10.96)	EN	136 (4.92)	EN	37 (3.61)
P. mundi	1996	Yes	CR	0 (0.00)	CR	8 (2.20)	CR	2 (0.69)
P. nevadensis	1962	Yes	CR	11 (2.48)	EN	24 (3.22)	CR	7 (1.95)
P. nivalis	2006	Yes	CR	0 (0.00)	CR	8 (2.20)	CR	2 (0.69)
P. oblongiloba	1844	Yes	LC	346,536 (12.76)	EN	472 (6.16)	EN	125 (4.83)
P. orchidioides	1844	No	LC	63,771 (11.06)	EN	128 (4.86)	EN	37 (3.61)
P. parvifolia	1894	Yes	LC	178,612 (12.09)	EN	168 (5.13)	EN	43 (3.76)
P. pilosa	2004	Yes	CR	0 (0.00)	CR	4 (1.61)	CR	1 (0.00)
P. planifolia	1897	Yes	NT	32,886 (10.40)	EN	128 (4.86)	EN	33 (3.50)
P. poldinii	2001	Yes	EN	2,202 (7.70)	EN	32 (3.50)	EN	8 (2.08)
P. potosiensis	1989	Yes	CR	0 (0.00)	CR	4 (1.61)	CR	1 (0.00)
P. primuliflora	1957	Yes	NT	42,748 (10.66)	EN	132 (4.89)	EN	35 (3.56)
P. pumila	1803	No	LC	1,144,425 (13.95)	VU	672 (6.51)	VU	169 (5.13)
P. ramosa	1890	Yes	CR	67 (4.22)	EN	40 (3.71)	CR	18 (2.89)
P. rectifolia	1989	Yes	CR	0 (0.00)	CR	4 (1.61)	CR	1 (0.00)
P. reichenbachiana	1908	No	CR	1 (0.69)	CR	8 (2.20)	CR	4 (1.39)
P. rotundiflora	1985	Yes	EN	156 (5.06)	EN	16 (2.83)	EN	5 (1.61)
P. sharpii	1977	Yes	CR	0 (0.00)	CR	4 (1.61)	CR	1 (0.00)
P. spathulata	1840	Yes	LC	4,449,021 (15.31)	EN	224 (5.42)	EN	57 (4.04)
P. takakii	1986	Yes	CR	3 (1.39)	EN	16 (2.83)	CR	4 (1.39)
P. utricularioides	1991	Yes	CR	0 (0.00)	CR	4 (1.61)	CR	1 (0.00)
P. vallisneriifolia	1853	Yes	EN	1,533 (7.34)	EN	32 (3.50)	EN	11 (2.40)
P. vallis-regiae	2006	Yes	CR	0 (0.00)	CR	4 (1.61)	CR	1 (0.00)
P. villosa	1753	No	LC	9,165,438 (16.03)	VU	1,400 (7.24)	VU	354 (5.87)
P. vulgaris	1753	No	LC	32,447,567 (17.30)	LC	5,988 (8.70)	LC	1,524 (7.33)
P. zecheri	1982	Yes	VU	6,451 (8.77)	EN	36 (3.61)	EN	12 (2.48)

The distribution area of *Pinguicula* was divided into 9 regions, concerning geographical barriers and/or distributions of taxa, and the number of taxa in each region is shown in Table 1.3; some taxa are found in two or more regions; therefore, the total number exceeds the 91 taxa accepted in this study. There are three regions of

Pinguicula biodiversity hotspots; Mexico and Central America with 46 taxa, Europe and Western Asia with 20 taxa, and the Caribbean Islands with 10 taxa. Only 10 taxa are found in the Caribbean Islands but all taxa except *P. pumila* are endemic; therefore, it is recognised as a biodiversity hotspot in this study.

Spearman's rank correlation suggested that there were significant correlations between EOO, AOO, the number of localities, and the year of description (Table 1.4).

Year of description

The earliest species, *P. alpina* L., *P. lusitanica* L., *P. villosa* L., and *P. vulgaris* L., were described in 1753 by Linnaeus (1753). The number of described taxa gradually increased to 1979 except 1960-1969 when Casper (1962, 1963, 1966) described a number of species, then rapidly increased further between 1980 and 2009 (Fig. 1.1). Two *Pinguicula* biodiversity hotspots, "Mexico and Central America (46 taxa)" and "Europe and Western Asia (20 taxa)", were selected to examine the cumulative patterns of taxa described (Fig. 1.2). The number of described taxa in Mexico and Central America sharply increased after 1980 while those in Europe and Western Asia only gradually increased. A large lag, between 1753 and 1817 (64 years), is seen in the first descriptions from the two regions.

Table 1.3. Number of taxa in each IUCN Red List category in each distribution areas of *Pinguicula*. Some species occur in two or three areas; therefore, the total number of taxa is more than 91. The numbers show precautionary principle, a higher thread level of extinction between EOO and AOO. NAF = North Africa; EUR = Europe, west of the Urals, including the British Isles and Iceland; WAS = Western Asia, including Cyprus, Anatolia, and the Caucasus; NAS = Northeastern Asia, east of the Urals, including Siberia, Kamchatka, Sakhalin, the Kuril Islands, Mongolia, China, the Himalayas, and Japan; NAM = North America, including Alaska, the Aleutians, Greenland, but excluding Mexico; MEX = Mexico; CAM = Central America, including Guatemala to Panama, but excluding Mexico; CRB = the Caribbean Islands, including the Bahamas, Cuba, and Hispaniola; SAM = South America, from the Venezuelan Andes to Tierra del Fuego. % indicates the percentage of threatened categories (a total number of taxa in CR, EN, and VU) in each distribution area.

IUCN Red List Category	Distribution areas								
	NAF	EUR	WAS	NAS	NAM	MEX	CAM	CRB	SAM
CR	0	5	0	1	0	22	1	4	1
EN	0	7	1	2	4	23	4	5	5
VU	2	5	1	2	4	1	1	1	0
NT	0	1	0	1	0	0	0	0	0
LC	1	1	0	0	1	0	0	0	0
% threatened	66.7	89.5	100	83.3	88.9	100	100	100	100
Total	3	19	2	6	9	46	6	10	6

Table 1.4. Spearman's rank correlation between range in km^2, natural logarithm, IUCN Red List categories, number of specimens, and the year of description.

	Year of description	
Variable	r_s	d.f.
EOO (km^2)	–0.708**	89
EOO (LN)	–0.708**	89
EOO (RL categories)	–0.687**	89
AOO (km^2)	–0.767**	89
AOO (LN)	–0.767**	89
AOO (RL categories)	–0.630**	89
Number of localities	–0.757**	89
Precautionary principles	–0.641**	89

** = $P < 0.01$, d.f. = degree of freedom

The number of taxa in EOO and AOO

The number of taxa in the Red List categories is shown in Table 1.5 and the proportion of each Red List categories in EOO and AOO are shown in Fig. 1.3. Based on EOO, 61.1 % of taxa were threatened. In particular, the percentage of CR (36.3 %) was much higher than that of EN (17.6 %) and VU (3.3 %). AOO resulted in a much higher extinction risk (97.8 %) than that of EOO. The proportion of EN (65.9 %) was much higher than that of others (22.0-1.1 %).

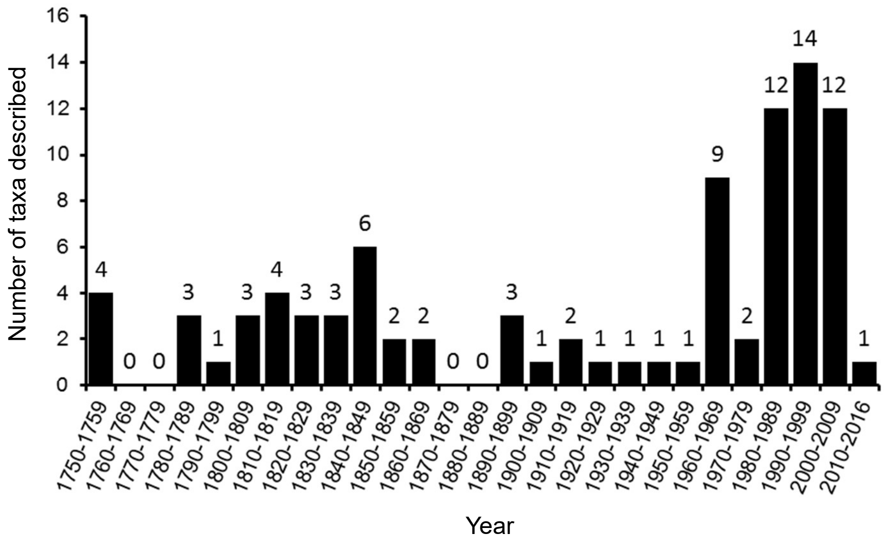

Fig. 1.1. The number of taxa described. The numbers above bars indicate the total number of taxa described in each decade. Synonyms are excluded.

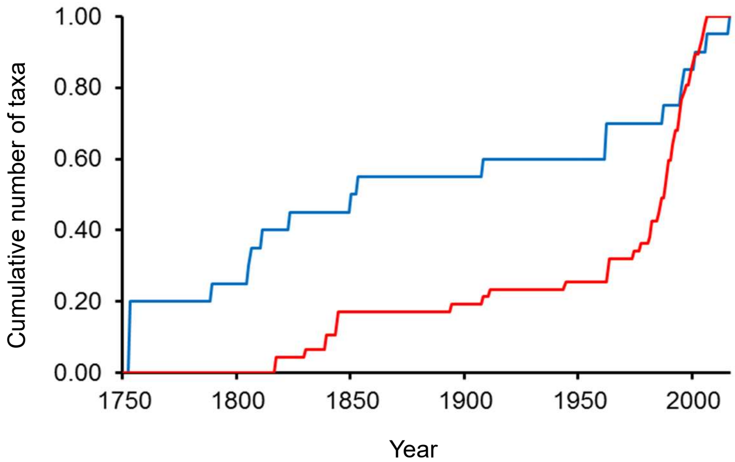

Fig. 1.2. Cumulative trend in described taxa in two *Pinguicula* hotspots. Blue line = Europe and Western Asia. Red line = Mexico and Central America.

Table 1.5. The number of taxa in each IUCN Red List categories in EOO and AOO, and the percentage of the values. GeoCAT analyses show that 56 taxa (61.6 %) in EOO and 89 taxa (97.8 %) in AOO are threatened.

	EOO		AOO	
Category	No. of taxa	%	No. of taxa (AOO)	%
CR	33	36.3	20	22.0
EN	16	17.6	60	65.9
VU	7	7.7	9	9.9
NT	6	6.6	1	1.1
LC	29	31.9	1	1.1
Total	91	100	91	100

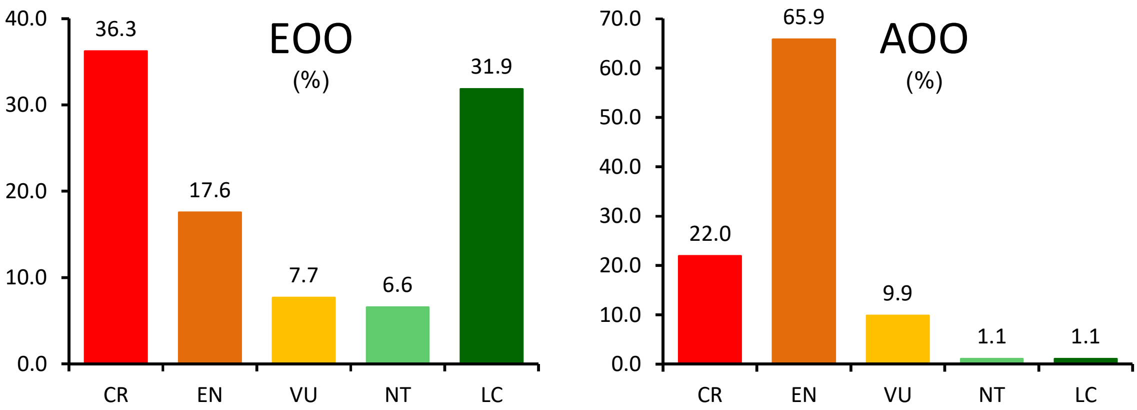

Fig. 1.3. Percentage of Red List categories in *Pinguicula*. Percentage of five categories (CR, EN, VU, NT, and LC) of the IUCN for EOO (left) and AOO (right) are shown. CR, EN, and VU are threat categories. The data are from the GeoCAT analyses.

Correlation between year of description and distribution area

More recently described taxa tend to have fewer occurrences. Correlation (R^2 = 0.631) was found between the year of description and the number of localities (Fig. 1.4). Spearman's rank correlation showed higher correlation ($r_s = -0.757$) with significance at $P < 0.01$ (Table 1.4) than the correlation presented in Fig. 1.4. There were a few exceptions that more recently described taxa had higher numbers of occurrences. For example, *P. balcanica* Casper was described in 1962 with 174 localities on the distribution map, but the populations had been known for long time and were divided from *P. vulgaris* by Casper (1962).

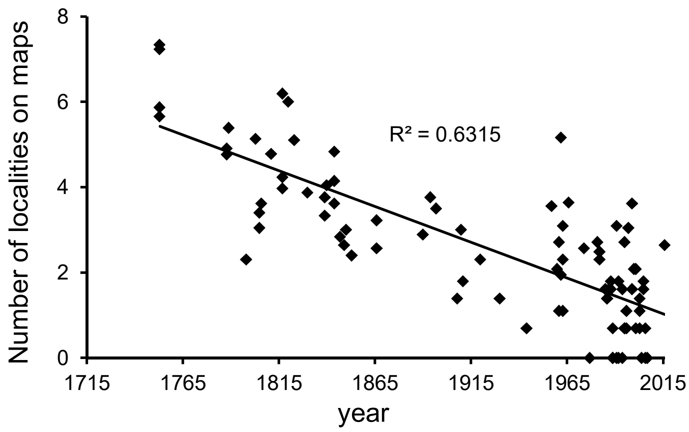

Fig. 1.4. Correlation between the year of description in each taxon and the number of localities on a distribution map of the taxon. Only taxa recognised in this study were shown. The year of description and the number of localities on the distribution maps are listed in Table 1.2.

Correlation between the year of description and values in EOO/AOO

Weak negative correlation between the year of description in each taxon and the value (NL) of the taxon in AOO was suggested, but no correlation was seen in EOO (Fig 1.5). In contrast, Spearman's correlations showed the correlation both in EOO and AOO with significance at $P < 0.01$ (Table 1.4). There are tendencies that more recently described taxa have smaller values of distribution areas.

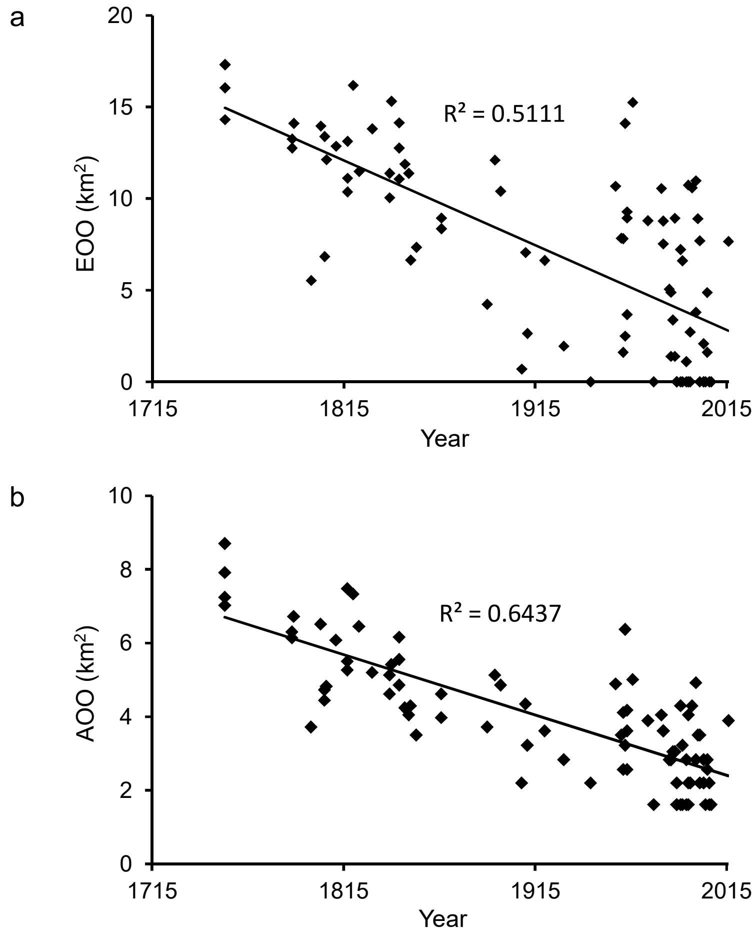

Fig. 1.5. Correlations between described year and NL in km² for EOO or AOO. a: EOO, b: AOO. The year of description and the NL in km² are listed in Table 1.2.

Correlation between EOO/AOO and endemic/non-endemic taxa in biodiversity hotspots

The number of endemic and non-endemic taxa in the three *Pinguicula* hotspots is presented in Table 1.6. A higher proportion of endemism in two hotspots, Mexico and Central America (87 % are endemic) and the Caribbean Islands (90 % are endemic), were seen.

Table 1.6. The number of endemic and non-endemic taxa in three *Pinguicula* hotspots. Mex = Mexico and Central America, Euro = Europe and Western Asia, Carib = the Caribbean Islands. end. = endemic taxa, n.e. = non-endemic taxa

	EOO						AOO					
	Mex		Euro		Carib		Mex		Euro		Carib	
	end.	n.e.	end.	n.e.	end.	n.e.	end.	n.e.	end.	n.e.	end.	n.e.
CR	21	1	4	1	4	0	14	1	2	1	2	0
EN	6	0	4	1	4	0	26	4	7	3	7	0
VU	6	0	0	0	1	0	0	1	0	5	0	1
NT	3	1	0	0	0	0	0	0	0	1	0	0
LC	4	4	1	9	0	1	0	0	0	1	0	0
Total	40	6	9	11	9	1	40	6	9	11	9	1

Negative correlations were found in all results between the Red List categories (CR, EN, VU, NT, and LC) and the number of endemic taxa in the three *Pinguicula* hotspots for both EOO and AOO tested by the Spearman's rank correlation (Table 1.7). In endemic taxa, all results, except the Caribbean taxa in EOO, showed a significant difference, i.e. endemic taxa have a higher risk of extinction.

Table 1.7. Spearman's rank correlations between Red List categories and endemic taxa in EOO/AOO. Mex = Mexico and Central America, Euro = Europe and Western Asia, Carib = the Caribbean Islands. * = $P < 0.05$.

	EOO			AOO		
	Mex	Euro	Carib	Mex	Euro	Carib
R^2	–0.872*	–0.632*	–0.949	–0.783*	–0.783*	–0.783*
P-value	0.054	0.252	0.014	0.118	0.118	0.118
d.f.	3	3	3	3	3	3

All chi-square test results, except endemic taxa in Europe and the Caribbean in EOO, showed significant difference, i.e. endemic taxa have a higher risk of extinction (Table 1.8). Due to some zero values, it was not possible to test for non-endemic taxa.

Table 1.8. Chi-square test (χ^2) between endemic taxa and Red List categories in EOO/AOO. Mex = Mexico and Central America, Euro = Europe and Western Asia, Carib = the Caribbean Islands. * = $P < 0.05$, the χ^2 value exceeding the critical value of 9.49 for d.f. = 4.

	EOO			AOO		
	Mex	Euro	Carib	Mex	Euro	Carib
χ^2	27.25*	9.33	9.33	69.00*	20.44*	20.44*
d.f.	4	4	4	4	4	4

A highly significant difference was seen between the two Red List categories, threatened/non-threatened and endemic/non-endemic taxa in EOO, i.e. endemic taxa have higher risk of extinction, but non-endemic taxa have low risk. There was no significance in European taxa in AOO, but not possible to test for the Mexican and Caribbean taxa due to zero values (Table 1.9).

Table 1.9. 2 X 2 contingence test between threatened/non-threatened and endemic/non-endemic taxa in EOO/AOO. Mex = Mexico and Central America, Euro = Europe and Western Asia, Carib = the Caribbean Islands. ** = $P < 0.01$, the χ^2 value exceeding the critical value of 6.63 for d.f. = 1.

	EOO			AOO		
	Mex	Euro	Carib	Mex	Euro	Carib
χ^2	11.73**	9.90**	10.00**	n.a.	1.82	n.a.
d.f.	1	1	1	1	1	1

To compare extinction risk between Mexican threatened taxa and European taxa using the contingency table, there was no significant difference in EOO (Table 1.10). However, in AOO, it was significantly higher ($P < 0.01$) in Mexican taxa than European taxa.

Table 1.10. Frequencies of threatened *Pinguicula* taxa in Mexico and Europe. CR = Critically Endangered, EN = Endangered, VU = Vulnerable. Mex = the number of taxa in Mexico and Central America, Euro = the number of taxa in Europe and Western Asia. ** = $P < 0.01$.

	EOO				AOO			
IUCN RL categories	CR	EN	VU	Total	CR	EN	VU	Total
Mex	22	6	6	34	15	30	1	46
Euro	5	5	0	10	3	10	5	18
Total	27	11	6	44	18	40	6	64
x^2	5.27				10.41**			
d.f.	2				2			

1.4. DISCUSSION

The results demonstrated that more recently described taxa tended to have a small distribution range and are known from fewer localities, and therefore have limited information documented. Subsequently, such taxa had higher extinction risk status.

Only preliminary analyses, EOO and AOO, were attempted in this work, but the results suggested that at least 61.1 % of *Pinguicula* taxa are likely to be facing the threat of extinction. A number of specimens were collected from localities only once and some time ago. Such localities without recent collection records might have been lost while more localities not yet recorded may be exist. A further critical study is necessary if the data shown in this chapter correspond to actual status of each taxon in the wild. As a result of careful taxonomic studies by Zamudio (1988, 1994, 1997, 1999a, 1999b) and Speta and Fuchs (1982, 1989) the number of species in Mexico and Central America have largely increased after 1980s. There are a few more new species to be described in those areas (per. com., Zamudio). In Europe, some recently described taxa had been collected many years ago and were identified as already known taxa, but were later described as new species. For example, *P. mundi* Blanca, Jamilena, Ruiz-Rejón et Zamora was described by Blanca et al. (1996) but it had been repeatedly collected since the 19th century as *P. longifolia* Ram. ex DC. or others.

As discussed earlier, a taxon confined to one country is defined as endemic in this work. Among 91 *Pinguicula* taxa recognised in this study, 67 taxa (74 %) are endemic and only 24 taxa (26 %) are non-endemic (Table 1.2). Within Mexico and Central America, 40 taxa (87 %) out of 46 are endemic.

In *Pinguicula* biodiversity hotspots, endemic taxa basically have higher extinction risk than non-endemic taxa. There are a few taxa occurring in two or more countries but which still have a restricted range (e.g. *P. leptoceras* in the Alps or *P. longifolia* in the Pyrenees). In Europe and Western Asia, the proportion of endemic taxa is lower than that of non-endemic taxa (Table 1.6). In general, non-endemic *Pinguicula* taxa are locally common or wide spread (Blanca et al. 1999). In this work, the definition of endemic is a taxon that occurs within one country. There could be two types of endemic taxa; one (neo-endemic) is relatively new in the evolutionary history and potentially expanding its distribution area, and the other one (paleo-endemic) is more ancient and contracting its area. It is probably likely that a number of *Pinguicula* taxa are relatively new (see Chapter 2), but their distribution area is contracting.

Although yet very small numbers of species have been assessed, it is unclear how adequately the species currently listed in the IUCN Red List of Threatened Species™ database have been evaluated. In this study, while only primary Red List assessments were conducted, all recognised taxa were assessed; according to Chapter 4. Other factors, which data are far more difficult to obtain, are necessary for the full Red List assessments.

There could be a possible issue for a full Red List assessment. Firstly, if the number of localities is one or two, EOO shows 0 km^2. EOO requires at least three localities. The results therefore look as though there is no distribution area, and it may affect further analyses. In this study, 16 taxa (*P. calderoniae* Zamudio, *P. clivorum* Standley et Steyermark, *P. conzattii* Zamudio et van Marm, *P. debbertiana* Speta et

Fuchs, *P. gigantea* Luhrs, *P. greenwoodii*, *P. laueana* Speta et Fuchs, *P. laxifolia* Luhrs, *P. mundi*, *P. nivlais* Luhrs et Lampard, *P. pilosa* Luhrs, Studnička et Gluch, *P. potosiensis* Speta et Fuchs, *P. rectifolia* Speta et Fuchs, *P. sharpii*, *P. utricularioides*, and *P. vallis-regiae* Conti et Peruzzi) had one or two localities that were evaluated as 0 km^2 in EOO.

Secondly, the percentage of taxa in the threatened categories (CR, EN, and VU) is sometimes higher in AOO than that in EOO. AOO covers the area in which the taxon actually occurs while EOO covers the whole geographic range size of the taxon with no internal angle exceeding 180^o (Bachman et al. 2011). In *P. macroceras* Link, for example, AOO is 1,524 km^2 (VU) while EOO is 10,530,758 km^2 (LC), but the covered area is mostly on the ocean. Thus it should be recognised that EOO may overestimate the distribution area, and as a result, the category in EOO shows a lower risk of extinction.

The rapid and accelerating loss of biodiversity is chiefly caused by human action (Vitousek et al. 1997). As discussed, a number of *Pinguicula* taxa are threatened globally although how much environmental stress by human affects this is unclear. Even so, an urgent plan of action will be necessary to protect them from extinction in the wild. A number of *Pinguicula* taxa have a very narrow ecological preference (Blanca et al. 1999). It is important to protect not only the populations but their ecosystem as well as to control trades. Finally Red List assessments are not the final goal, but a gateway for effective conservation.

1.5. CONCLUSION

At least 60 % of *Pinguicula* taxa are threatened with extinction. In particular, endemic taxa have higher risk of extinction than non-endemic taxa, and it is significantly higher in the *Pinguicula* biodiversity hotspots, Mexico and Europe. Although data shown here are not full Red List assessments, it suggests that urgent action for conservation planning are required.

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CHAPTER 2

Phylogenetic analyses of the genus *Pinguicula* L.

2.1. INTRODUCTION

Carnivorous plants are not a monophyletic taxonomic group, rather they possess features 1) to attract prey to the traps, 2) to capture, retain, and kill them, 3) digest them by secreting enzymes and/or bacterial activities, and 4) to absorb the digested substance; although they do not necessarily possess all of them. As a result, carnivorous plant families evolved these mechanisms independently during their evolutionary history (Albert et al. 1992, Heubl et al. 2006).

While molecular analyses have been applied to various carnivorous plant genera they have been either limited in the coverage of taxa and/or gene regions sequenced. The gene regions *rbcL* and 18S were sequenced for 59 species (31 % out of ca. 190 species) of *Drosera* L. (Droseraceae) (Rivadavia et al. 2003). The analysis of Meimberg et al. (2001) sequenced the *trn*K regions of 71 taxa (42 % out of ca. 170 species) from the genus *Nepenthes* L. (Nepenthaceae). The results differed from the taxonomy of Danser (1928). A total of 199 nuclear gene sequences of the genus *Sarracenia* Dumort. (Sarraceniaceae) resulted in 8-11 species with 8 subspecies/varieties (covering all known species) (Stephens et al. 2015). In the Lentibulariaceae, the *trn*K region has been sequenced for 31 species (13 % of ca. 230 species) of *Utricularia* L. and ca. 22 species (70 % of ca. 30 species) of *Genlisea* St.-Hil.

by Müller and Borsch (2005) and Fleischmann et al. (2010) respectively. The results were well resolved and in agreement with the taxonomy based on morphology by Taylor (1989) for *Utricularia* and by Fleischmann (2012a, 2012b) for *Genlisea*.

The most recent taxonomic work on the genus *Pinguicula* L. (Lentibulariaceae Rich.) was carried out by Casper (1966), who recognised 46 species divided between 3 subgenera, *Isoloba*, *Pinguicula*, and *Temnoceras*, and 12 sections (see Table 4.1 in Chapter 4). After the taxonomic work by Casper (1966), eighty four taxon names have been additionally listed in the International Plant Names Index (2016). The number of species within the genus is estimated to be over 85 (Cieslak et al. 2005) and as high as 100 (Beck et al. 2008) although some taxa appear to be synonymous with other species already known (e.g. Luhrs 1995, Zamudio 1997, 1998). However, it is safe to assume that there are approximately 90 valid species. Hence, the number of species has almost doubled since Casper's (1966) taxonomic monograph. In association with new species discoveries, new sections have been established: sections *Classifolia* (Speta and Fuchs 1982), *Longitubus* (Zamudio and Rzedowski 1991), *Orchidioides* (Luhrs 1995), and *Microphyllum* (Luhrs and Lampard 2006).

Molecular systematics is now a standard in the inference of phylogenetic relationships among plant taxa. A molecular-based plant taxonomy, the Angiosperm

Phylogeny Group (APG) system, has been published regularly since 1998 (e.g. APG 1998, APG II 2003, APG III 2009) and higher taxonomic ranks have been revised from the traditional taxonomies based on morphological characteristics. Many regions of DNA sequences have been examined; however, *mat*K in chloroplast DNA (cpDNA) or the internal transcribed spacer (ITS) regions, between 18S and 26S, in nuclear ribosomal DNA (nrDNA) is often used to infer phylogenetic relationships at a specific rank (Steele and Vilgalys 1994, Johnson and Soltis 1995, Yukawa et al. 2002). Johnson and Soltis (1995) suggested that *mat*K sequence was more useful within plant families or genera.

Few have examined the phylogenetic relationships within the genus *Pinguicula*; however, these have largely been sparse in terms of taxa sampled and/or phylogenetic regions examined. For example Degtjareva et al. (2006) and Kondo and Shimai (2006) mainly sampled taxa from mild to cold regions of the Northern Hemisphere, and analysed only the ITS region to infer their phylogenetic relationships. Their data indicated that most of the taxa forming hibernacula, particularly belonging to the section *Pinguicula,* were likely monophyletic. Shimai and Kondo (2007) analysed ITS regions in 36 species from Mexico and Central America and suggested they were likely to be monophyletic, although Casper (1966) divided them into 3 subgenera. Cieslak et al. (2005) used 42 *Pinguicula* taxa from wider regions to analyse *mat*K and *trn*K. Cieslak et al. (2005) showed that the three subgenera could be polyphyletic. Thus there is a disagreement between the current taxonomy and the phylogeny. Degtjareva et al. (2006) stated that ITS was slightly more informative than *mat*K. It seems that those results are still fragmental, both in DNA regions and samplings, and therefore it would be valuable to sequence more regions with more samples for a further evaluation of the phylogenetic relationships among *Pinguicula* taxa. In this work, two regions, *mat*K and *trn*K and *rpl32-trnL*, in cpDNA and one region, ITS (including ITS1, 5.8S, and ITS2) in nrDNA were sequenced using up to 80 *Pinguicula* taxa.

2.2. MATERIALS AND METHODS

Plant materials

Total genomic DNA was extracted for sequencing from 81 taxa of *Pinguicula*. Those taxa sampled are summarised in Table 2.1. Thirty eight sequences were cited from Cieslak et al. (2005) and Beck et al. (2008) registered at the GenBank database; therefore, a total number of taxa in the table are 83. Some taxa may be synonymous with other taxa but original sample names were adopted in this work (the taxonomy is discussed in Chapter 4). For DNA isolation, either fresh leaves or dried leaves were used. The fresh leaves were obtained from live plants. The dried leaves were collected from herbarium specimens. The voucher specimens used for those samples have been deposited at herbaria recognized internationally (Table 2.1.).

DNA isolation from fresh plant materials

Digestive enzyme, believed to hinder DNA amplification, was secreted from the fresh leaf under 10% milk diluted with distilled water for 30-40 min, and then the leaf was washed by running water to remove milk. After washing the leaves, water was removed completely using Kimwipes. Total genomic DNA was isolated from 0.07-0.1 g of fresh leaves per sample and ground in liquid nitrogen. DNA isolation from the samples was carried out using ISOPLANT II (Nippon Gene, Tokyo, Japan) kits following the manufacture's protocol.

DNA isolation from dried plant materials

Dust or insects stuck on the dried leaf were carefully removed using cotton buds moistened by 70% ethanol. Total genomic DNA was isolated from 0.020-0.025 g of dried leaves per sample and the leaf was ground in liquid nitrogen. DNA isolation from the samples was carried out using the DNeasy Plant Mini Kit (Quiagen, Tokyo, Japan) following the manufacture's protocol.

Table 2.1. List of *Pinguicula* taxa used for phylogenetic analyses. Accession numbers for the GenBank database and specimen records are shown. Sequence data not yet available from the database are indicated TBA. The specimens deposited at HIRO (Hiroshima University) were transferred to TNS (National Museum of Nature and Science, Tsukuba, Japan) in 2013. (d) = DNA from dried leaves, (f) = DNA from fresh leaves.

	Taxa	ITS	*mat*K	*rpl32*	Specimens	Source
1	*P. acuminata*	AB199751	DQ010652	TBA	5757-LPCGS (HIRO)	cultivated material (f)
2	*P. agnata*	AB199752	AF531782	—	5758-LPCGS (HIRO)	cultivated material (f)
3	*P. albida*	AB212095	TBA	TBA	5788-LPCGS (HIRO)	Pinar del Rio, Cuba (d)
4	*P. alpina*	AB198341	AF531783	TBA	5734-LPCGS (HIRO)	Zilina, Slovakia (d)
5	*P. antarctica*	AB212096	DQ010653	TBA	716-LPCGS (HIRO)	cultivated material (f)
6	*P. balcanica* subsp. *balcanica*	AB198342	—	—	5738-LPCGS (HIRO)	Fokida, Greece (d)
7	*P. balcanica* subsp. *pontica*	TBA	—	TBA	*Shimai s.n.*, TNS, UPS	Bursa, Turkey (d)
8	*P. benedicta*	AB212097	TBA	TBA	715-LPCGS (HIRO)	Holguin, Cuba (d)
9	*P. bissei*	AB212098	TBA	TBA	5790-LPCGS (HIRO)	Guantanamo, Cuba (d)
10	*P. bohemica*	AB198343	TBA	TBA	5739-LPCGS (HIRO)	Liberec, Czech R. (d)
11	*P. caerulea*	AB212099	—	TBA	5791-LPCGS (HIRO)	cultivated material (f)
12	*P. calyptrata*	AB212100	FM200225	TBA	717-LPCGS (HIRO)	Azuay, Ecuador (d)
13	*P. chilensis*	AB212101	—	TBA	718-LPCGS (HIRO)	Los Lagos, Chile (d)
14	*P. colimensis*	AB199753	TBA	TBA	5759-LPCGS (HIRO)	cultivated material (f)
15	*P. conzattii*	AB199754	TBA	TBA	709-LPCGS (HIRO)	cultivated material (f)
16	*P. corsica*	AB198344	AF531784	TBA	5740-LPCGS (HIRO)	Corsica, France (d)
17	*P. crassifolia*	AB199755	TBA	TBA	5760-LPCGS (HIRO)	cultivated material (f)
18	*P. crenatiloba*	TBA	—	TBA	*Shimai s.n.*, LE, TNS	Michoacan, Mexico (d)
19	*P. crystallina*	AB198363	—	TBA	5753-LPCGS (HIRO)	Cyprus (d)
20	*P. cubensis*	AB212102	TBA	TBA	5794-LPCGS (HIRO)	Pinar del Rio, Cuba (d)
21	*P. cyclosecta*	AB199756	TBA	TBA	5761-LPCGS (HIRO)	cultivated material (f)
22	*P. debbertiana*	AB199757	TBA	—	5762-LPCGS (HIRO)	cultivated material (f)
23	*P. dertosensis*	AB198345	—	TBA	5741-LPCGS (HIRO)	Tarragona, Spain (d)
24	*P. ehlersiae*	AB199758	TBA	TBA	5763-LPCGS (HIRO)	cultivated material (f)
25	*P. elongata*	AB212103	FM200224	TBA	718-LPCGS (HIRO)	cultivated material (f)
26	*P. emarginata*	AB199759	AF531785	TBA	5764-LPCGS (HIRO)	cultivated material (f)
27	*P. esseriana*	AB199760	DQ010656	TBA	5765-LPCGS (HIRO)	cultivated material (f)
28	*P. filifolia*	AB212104	AF531786	TBA	5795-LPCGS (HIRO)	cultivated material (f)
29	*P. fiorii*	AB198346	AF531787	TBA	5742-LPCGS (HIRO)	Pescara, Italy (d)
30	*P. gigantea*	AB199761	AF531789	TBA	5766-LPCGS (HIRO)	cultivated material (f)
31	*P. gracilis*	AB199762	AF531790	TBA	5767-LPCGS (HIRO)	cultivated material (f)
32	*P. grandiflora* ssp. *grandiflora*	AB198347	AF531791	TBA	701-LPCGS (HIRO)	Pyrenees-Atlant., Fr. (d)
33	*P. grandiflora* ssp. *rosea*	AB198348	—	—	5743-LPCGS (HIRO)	Isere, France (d)
34	*P. gypsicola*	AB199763	TBA	—	5768-LPCGS (HIRO)	cultivated material (f)
35	*P. hemiepiphytica*	AB199764	TBA	TBA	5769-LPCGS (HIRO)	cultivated material (f)
36	*P. heterophylla*	AB199765	—	TBA	5770-LPCGS (HIRO)	cultivated material (f)
37	*P. hirtiflora*	AB198364	DQ010654	—	5754-LPCGS (HIRO)	Salerno, Italy (d)
38	*P. ibarrae*	AB251603	TBA	TBA	5771-LPCGS (HIRO)	cultivated material (f)
39	*P. immaculata*	AB199766	TBA	TBA	5772-LPCGS (HIRO)	cultivated material (f)
40	*P. involuta*	—	FM200226	—	—	
41	*P. ionantha*	AB212105	TBA	TBA	5796-LPCGS (HIRO)	cultivated material (f)
42	*P. jackii* var. *jackii*	AB212106	—	—	5797-LPCGS (HIRO)	Cienfuegos, Cuba (d)
43	*P. jackii* var. *parviflora*	AB212107	TBA	TBA	5798-LPCGS (HIRO)	Cienfuegos, Cuba (d)

Table 2.1 (continued)

44	*P. jarmilae*	—	FM200223	—	—	
45	*P. jaumavensis*	AB199767	TBA	TBA	5773-LPCGS (HIRO)	cultivated material (f)
46	*P. laueana*	AB199768	DQ010659	TBA	5774-LPCGS (HIRO)	cultivated material (f)
47	*P. leptoceras*	AB198349	AF531792	TBA	5744-LPCGS (HIRO)	Bern, Switzeralnd (d)
48	*P. lignicola*	AB300151	—	—	5803-LPCGS (HIRO)	Guantanamo, Cuba (d)
49	*P. lilacina*	AB199769	TBA	TBA	5775-LPCGS (HIRO)	cultivated material (f)
50	*P. longifolia* subsp. *caussensis*	AB198350	AF531794	TBA	5745-LPCGS (HIRO)	Aveyron, France (d)
51	*P. longifolia* subsp. *longifolia*	AB198351	—	TBA	702-LPCGS (HIRO)	Huesca, Spain (d)
52	*P. longifolia* subsp. *reichenbachiana*	AB198352	DQ010660	TBA	5746-LPCGS (HIRO)	Alpes Maritimes, Fr. (d)
53	*P. lusitanica*	AB198365	DQ010661	TBA	5752-LPCGS (HIRO)	Hampshire, UK (d)
54	*P. lutea*	AB212108	DQ010662	TBA	5799-LPCGS (HIRO)	cultivated material (f)
55	*P. macroceras*	AB198353	AF531796	TBA	5747-LPCGS (HIRO)	Nagano, Japan (f)
56	*P. macrophylla*	AB199770	TBA	TBA	5776-LPCGS (HIRO)	cultivated material (f)
57	*P. medusina*	AB199771	TBA	TBA	710-LPCGS (HIRO)	cultivated material (f)
58	*P. mesophytica*	AB251604	—	—	5777-LPCGS (HIRO)	cultivated material (f)
59	*P. mirandae*	AB251605	TBA	TBA	5778-LPCGS (HIRO)	cultivated material (f)
60	*P. moctezumae*	AB199772	AF531797	TBA	5779-LPCGS (HIRO)	cultivated material (f)
61	*P. moranensis*	AB199773	AF531798	TBA	5780-LPCGS (HIRO)	cultivated material (f)
62	*P. mundi*	AB198354	AF531800	TBA	5748-LPCGS (HIRO)	Albacete, Spain (d)
63	*P. nevadensis*	AB198355	DQ010664	TBA	5749-LPCGS (HIRO)	Granada, Spain (d)
64	*P. nivalis*	AB199774	TBA	TBA	5781-LPCGS (HIRO)	cultivated material (f)
65	*P. oblongiloba*	AB199775	TBA	TBA	712-LPCGS (HIRO)	cultivated material (f)
66	*P. parvifolia*	AB199777	—	—	713-LPCGS (HIRO)	cultivated material (f)
67	*P. pilosa*	AB199778	—	TBA	714-LPCGS (HIRO)	cultivated material (f)
68	*P. planifolia*	AB212109	TBA	TBA	5800-LPCGS (HIRO)	cultivated material (f)
69	*P. poldinii*	AB198356	AF531804	TBA	702-LPCGS (HIRO)	Pordenone, Italy (d)
70	*P. potosiensis*	AB199779	TBA	TBA	5728-LPCGS (HIRO)	cultivated material (f)
71	*P. primuliflora*	AB212110	DQ010666	TBA	5801-LPCGS (HIRO)	cultivated material (f)
72	*P. pumila*	AB212111	TBA	TBA	5802-LPCGS (HIRO)	cultivated material (f)
73	*P. ramosa*	AB198357	DQ010667	TBA	5735-LPCGS (HIRO)	Tochigi, Japan (d)
74	*P. rectifolia*	AB199780	AF531801	—	5783-LPCGS (HIRO)	cultivated material (f)
75	*P. reticulata* (*P. kondoi*)	AB199781	TBA	—	5784-LPCGS (HIRO)	cultivated material (f)
76	*P. rotundiflora*	AB199782	AF531802	TBA	5785-LPCGS (HIRO)	cultivated material (f)
77	*P. sharpii*	AB199783	AF531803	TBA	5786-LPCGS (HIRO)	cultivated material (f)
78	*P. vallisneriifolia*	AB198358	AF531805	TBA	5750-LPCGS (HIRO)	Jaen, Spain (d)
79	*P. vallis-regiae*	—	—	TBA	719-LPCGS (HIRO)	cultivated material (f)
80	*P. variegata* (*P. spathulata*)	AB198359	DQ010668	TBA	5736-LPCGS (HIRO)	Sakhalin, Russia (d)
81	*P. villosa*	AB198360	DQ010669	TBA	5737-LPCGS (HIRO)	Alaska, USA (d)
82	*P. vulgaris*	AB198361	AF531806	TBA	5751-LPCGS (HIRO)	Zilina, Slovakia (d)
83	*P. zecheri*	AB199784	TBA	TBA	5787-LPCGS (HIRO)	cultivated material (f)

Polymerase chain reaction (PCR)

ITS sequences

The ITS region of nrDNA isolated from fresh or dried materials was amplified by polymerase chain reaction (PCR) using TaKaRa *LA Taq*™ (Takara Bio Inc., Shiga, Japan) with GC buffer II included in the kit. The concentration of template DNA used was 10 µg/µl per sample. Forward primer was 20 pmol/µl of ITS5 and reverse primer was 20 pmol/µl of ITS4 (White et al. 1990). The samples were incubated for an initial 2 min at 94°C and then 33 cycles of 50 sec denaturation at 94°C, 1 min annealing at 48°C and 30 sec extension at 72°C. If the amplification was insufficient, 20 pmol/µl of AB101 for forward and AB102 primers for reverse (Douzery et al. 1999) were used instead of ITS5 and ITS4. The samples were incubated for an initial 2 min at 94°C and then 33 cycles of 50 sec denaturation at 94°C, 1 min annealing at 60°C, and 30 sec extension at 72°C.

ITS5 (forward primer): 5'-GGAAGTAAAAGTCGTAACAAGG-3'

ITS4 (reverse primer): 5'-TCCTCCGCTTATTGATATGC-3'

AB101 (forward primer): 5'-ACGAATTCATGGTCCGGTGAAGTGTTCCG-3'

AB102 (reverse primer): 5'-GAATTCCCCGGTTCGCTCGCCGTTAC-3'

For cycle sequencing, PCR products were purified from collected agarose gels using GFX PCR DNA and Gel Band Purification Kit (Amersham Biosciences, NJ, USA) following the manufacture's protocol. Cycle sequencing conditions regardless of the type of primer were as follows: incubation for an initial 1 min at 96°C, and then 35 cycles of 10 sec denaturation at 96°C, 5 sec annealing at 50°C, and 80 sec extension at 72°C. In some cases, up to 2 µl of DMSO per sample was added for GC rich samples.

matK and trnK

The basic protocol used was that mentioned in Cieslak et al. (2005). The primers used were also identical with those cited in Cieslak et al. (2005) and Beck et al. (2008). One forward primer "Ping_trnK-F2" was designed in this study. Apart from the sequence data (38 taxa) cited from Cieslak et al. (2005) and Beck et al. (2008), additional DNA from 29 taxa were sampled and amplified at Kyoto University to add to this study.

(Forward primers)

trnK-F: 5'-CTC AAC GGT AGA GTA CTC G-3' (Steele and Vilgalys 1994)

Ping_trnK-F2: 5'-TCC CCT CCA TCA GGG GAT TCT-3' (this study)

trnK 8F: 5'-TTG CTC ATG ATG GTG GTT TC-3' (Cieslak et al. 2005)

ACmatK500F: 5'-TTC TTC TTT GCA TTT ATT ACG-3' (Beck et al. 2008)

trnK 10F: 5'-TGG TCA AGG AAC CTT GCA TAC-3' (Cieslak et al. 2005)

trnK 12F: 5'-CTT ACC CGT TGA GGG CAG TA-3' (Cieslak et al. 2005)

(Reverse primers)

trnK-2R: 5'-AAC TAG TCG GAT GGA GTA G-3' (Steele and Vilgalys 1994)

trnK 13R: 5'-TAC TGC CCT CAA CGG GTA AG-3' (Cieslak et al. 2005) trnK 1R: 5'-CGG CTT ACT AAT GGG ATG CC-3' (Cieslak et al. 2005)

Le 1: 5'- ATA GAA ATA GAT TCG TTC-3' (Beck et al. 2008)

trnK 9R: 5'-GAA ACC ACG ATC ATG AGC AA-3' (Cieslak et al. 2005)

trnK 4R: 5'-CGG ATC CTC ATT CCA TGA TA-3' (Cieslak et al. 2005)

rpl32-trnL

The *rpl32-trnL* region in cpDNA was amplified using Phusion Green Hot Start II High-Fidelity DNA Polymerase (Thermo Scientific, MA, USA) with 0.6 µl of DMSO per sample following the manufacture's protocol at the University of Florida. The primers used for *rpl32-trnL* (Shaw et al. 2007) are shown below. The samples were incubated for an initial 45 sec at 98°C and then 32 cycles of 10 sec denaturation at 98°C, 30 sec annealing at 55°C, and 40 sec extension at 72°C. Finally it was kept 72°C for 5 min.

rpL32–F (forward primer): 5'-CAGTTCCAAAAAAACGTACTTC-3'

trnL$^{(UAG)}$ (reverse primer): 5'-CTGCTTCCTAAGAGCAGCGT-3'

Data matrices

The DNA data matrix was aligned by Genetyx-Win Version 5.2 (Software

Development Co., LTD., Tokyo, Japan) using 'Multiple Alignment' function and was then adjusted manually. The edited and manually adjusted alignments of each gene were then concatenated into a single supermatrix using FASconCAT v.1.0 (Kück and Meusemann 2010). In the concatenated matrix, at least one gene was sampled per species; if no gene sequence was available, the FASconCAT software treated it as missing data in the supermatrix. For the accuracy of phylogenetic reconstruction, independent models of molecular evolution for all the single-gene and combined-gene alignments were conducted using PartitionFinder (Lanfear et al. 2012).

The sequence data reported are available in the DDBJ/EMBL/GenBank databases under the accession numbers summarised in Table 2.4. Some data not yet registered at the database (shown as TBA) will be available in the near future. When the sequences were identical between the two taxa, these were treated as one operational taxonomic unit (OTU). Sequence data in 38 taxa for the *mat*K and *trn*K analysis were cited from Cieslak et al. (2005) and Beck et al. (2008), and 29 additional taxa obtained in this work were added to the analysis. Some sequences, particularly in *mat*K, were only partially readable. If the data were insufficient for alignments or subsequent analyses, they were omitted.

Phylogenetic analyses

Maximum likelihood (ML). Giving the best fit partitioning schemes identified by PartitionFinder for all the datasets were equivalent (nst = 6, tare = gamma), ML analyses for each individual gene alignment and the combined supermatrix were conducted using RAxML ver. 8.1.12 (Stamatakis 2014), with 1,000 replicates under the GTRGAMMA model as implemented on the HiPerGator 2.0 at the University of Florida. Up to 5 *Genlisea* or 3 *Utricularia* species were selected for outgroup taxa. All the trees were manipulated by MEGA (Tamura et al. 2013).

Bayesian inference. Bayesian approaches using Bayes 3.2.5 (Ronquist and Huelsenbeck 2003) were also employed for combined genes. The alignment was partitioned under the GTR + G + I model of evolution by PartitionFinder, but allowed different overall evolutionary rates for each partition. The default prior probabilities were used for the model. Trees were sampled per 1,000 generations under two MCMC runs each of 2,000,000 generations. The first 25% trees were discarded as burn-in, with the remaining trees being used to generate the consensus tree. In each analysis, it was estimated that the MCMC converged to the stationary distribution, defined by the average standard deviation of the split frequencies of the runs being less than 0.01, after around ca. 1,000,000 generations.

2.3. RESULTS

Here, taxonomy based on morphology refers to Casper (1966) and some other taxonomists who established new sections within Casper's three subgenera (Table 2.2).

Table 2.2. Taxonomic treatment based on morphology. Species normally recognised are listed although there are some disagreements among taxonomists. Intraspecific ranks are ignored in this table. Not necessarily all species are accepted in this work.

I. Subgenus *Isoloba*
- 1. Sect. *Isoloba*
  - 1. *P. lusitanica*
  - 2. *P. pumila*
  - 3. *P. lilacina*
  - 4. *P. sharpii*
  - 5. *P. takakii*
  - 6. *P. ionantha*
  - 7. *P. primuliflora*
  - 8. *P. planifolia*
  - 9. *P. caerulea*
  - 10. *P. lutea*
- 2. Sect. *Agnata*
  - 11. *P. agnata*
  - 12. *P. gigantea*
  - 13. *P. ibarrae*
  - 14. *P. martinezii*
  - 15. *P. pilosa*
  - 16. *P. albida*
  - 17. *P. jaraguana*
  - 18. *P. filifolia*
  - 19. *P. cubensis*
  - 20. *P. benedicta*
  - 21. *P. bissei*
- 3. Sect. *Discoradix*
  - 22. *P. lignicola*
  - 23. *P. casabitoana*
- 4. Sect. *Heterophyllum*
  - 24. *P. acuminata*
  - 25. *P. heterophylla*
  - 26. *P. medusina*
  - 27. *P. parvifolia*
  - 28. *P. conzattii*
  - 29. *P. mirandae*
  - 30. *P. kondoi*
  - 31. *P. reticulata*
  - 32. *P. rotundiflora*
  - 33. *P. imitatrix*
- 5. Sect. *Cardiophyllum*
  - 34. *P. hirtiflora*
  - 35. *P. crystallina*

II. Subgenus *Temnoceras*
- 6. Sect. *Temnoceras*
  - 36. *P. crenatiloba*
  - 37. *P. clivolum*
  - 38. *P. emarginata*
- 7. Sect. *Microphyllum*
  - 39. *P. immaculata*
  - 40. *P. gracilis*
  - 41. *P. nivalis*
- 8. Sect. *Ampullipalatum*
  - 42. *P. elongata*
  - 43. *P. calyptrata*
  - 44. *P. involuta*
  - 45. *P. jarmilae*
  - 46. *P. chilensis*
  - 47. *P. antarctica*
- 9. Sect. *Micranthus*
  - 48. *P. alpina*
  - 49. *P. variegata*
  - 50. *P. ramosa*

III. Subgenus *Pinguicula*
- 10. Sect. *Homophyllum*
  - 51. *P. jackii*
  - 52. *P. lithophytica*
  - 53. *P. greenwoodii*
- 11. Sect. *Orcheosanthus*
  - 54. *P. gypsicola*
  - 55. *P. moctezumae*
  - 56. *P. cyclosecta*
  - 57. *P. mesophytica*
  - 58. *P. colimensis*
  - 59. *P. elizabethiae*
  - 60. *P. moranensis*
  - 61. *P. potosiensis*
  - 62. *P. rectifolia*
  - 63. *P. zecheri*
  - 64. *P. macrophylla*
  - 65. *P. oblongiloba*
  - 66. *P. orchidioides*
- 12. Sect. *Longitubus*
  - 67. *P. crassifolia*
  - 68. *P. calderoniae*
  - 69. *P. hamiepiphytica*
  - 70. *P. laueana*
  - 71. *P. utricularioides*
- 13. Sect. *Orchidioides*
  - 72. *P. laxifolia*
- 14. Sect. *Crassifolia*
  - 73. *P. esseriana*
  - 74. *P. jaumavensis*
  - 75. *P. ehlersiae*
  - 76. *P. debbertiana*
- 15. Sect. *Pinguicula*
  - 77. *P. vallisneriifolia*
  - 78. *P. mundi*
  - 79. *P. longifolia*
  - 80. *P. nevadensis*
  - 81. *P. corsica*
  - 82. *P. leptoceras*
  - 83. *P. poldinii*
  - 84. *P. grandiflora*
  - 85. *P. dertosensis*
  - 86. *P. balcanica*
  - 87. *P. fiorii*
  - 88. *P. vallis-regiae*
  - 89. *P. vulgaris*
  - 90. *P. bohemica*
  - 91. *P. macroceras*
- 16. Sect. *Nana*
  - 92. *P. villosa*

ITS

The length of the ITS region (ITS1, 5.8S, and ITS2) was between 573 and 717 (base pairs) bp. The ITS tree could be divided into 9 clades although some nodes are weakly supported by bootstrap support (BS) particularly near the base of the tree (Fig. 2.1). Clade I (67 % BS) consists of 5 species, distributed in the southeastern USA, all of which are classified into the subgenus *Isoloba*. Clade II (< 50 % BS) consists of 2 Mediterranean species, *P. crystallina* Smith and *P. hirtiflora* Tenore, in the subgenus *Isoloba* and 1 Mexican species, *P. crenatiloba* DC. in the subgenus *Temnoceras*. Clade III (99 % BS) comprises 3 species, *P. antarctica* Vahl, *P. calyptrata* Kunth, and *P. chilensis* Clos in the subgenus *Temnoceras*. Clade IV (100 % BS) consists of 3 species, *P. ramosa* Miyoshi, *P. variegata* Turcz., in the subgenus *Temnoceras* and *P. villosa* L. in the subgenus *Pinguicula*. The former two species are restricted to eastern Asia while *P. villosa* is very widely distributed in the circumpolar regions of Eurasia and North America. Clade IV appears to be a sister of Clade V. Clade V (63 % BS) is encompassing 18 taxa (e.g. *P. grandiflora* Lam. subsp. *grandiflora* Lam., *P. vulgaris* L. etc.) in the subgenus *Pinguicula*. Those are mostly found in the mild to cold regions of the Northern Hemisphere. All the taxa in Clades IV and V form hibernacula to resist low temperature in winter. Clade VI (100 % BS) includes only 2 morphologically very similar species, *P.*

lilacina Schlecht. et Cham. and *P. sharpii* Casper et Kondo in the subgenus *Isoloba*. *P. lilacina* is very widely distributed in Mexico and Central America. *P. sharpii* is recorded from a single locality in Chiapas, Mexico. Clade VI could be closely related to Clades VII and VIII. Clade VII (99 % BS) encompasses 18 species in Casper's three subgenera, *Isoloba, Pinguicula*, and *Temnoceras*. This group is mostly found in the mountain ranges of Sierra Madre Occidental and Sierra Madre del Sur in Mexico and Central America with the exception of *P. moranensis* Kunth, which extends also to the Sierra Madre Oriental. Clade VIII (98 % BS) includes 16 taxa in the three subgenera. The taxa in Clade VIII are mostly found in the Sierra Madre Oriental in Mexico although conjunctions between Clades VII and VIII are seen in Central Mexico. Most of them in the two clades form winter rosettes during winter to survive the dry season. Clade IX (100 % BS) consists of 7 Cuban taxa in the subgenera *Isoloba* and *Pinguicula*. *P. pumila* Michx, distributed in the southeastern USA and the Bahamas, does not form a clade with other taxa, but it is closely related to Clade I. The other three species, *P. lusitanica* L., *P. alpina* L., and *P. elongata* Benjamin, did not form any clades with other taxa.

matK and trnK

The length of *mat*K and *trn*K was approximately 2,500 bp. The *mat*K tree could be divided into at least to 4 clades (Fig. 2.2). Clade I (89 % BS) includes 12 taxa, classified in the three subgenera, from Mexico and Cuba. Clade II (99 % BS), the largest clade, may be divided to 3 or 4 subclades, is formed by 26 taxa in the three subgenera found in Mexico and Central America. Clade III (96 % BS) comprises 13 taxa distributed in mild to cold regions of the Northern Hemisphere. All taxa in Clade III belonging to the subgenus *Pinguicula* and forming hibernacula could be the most well-defined group in this analysis. Clade IV (47 % BS) with 14 species in the three subgenera is rather a miscellaneous group in terms of the geographical distribution and taxonomy. *P. ramosa, P. variegata*, and *P. villosa*, forming hibernacula are small species mostly found in cold regions. Homophyllous *P. hirtiflora* and *P. lusitanica* are found in Europe. The rest of species in this clade are found in southeastern USA or South America.

In some cases, sequence results are fragmental and those are not useful for a subsequent analysis. Alternative primer designs will be necessary for the region.

rpl32-trnL

The length of sequence including *prl32-trnL* was between 319 and 695 bp. The *rpl32-trnL* tree consists of 4 clades (Fig. 2.3). Some basal nodes are weakly supported with low bootstrap support. Clade I (81 % BS) encompasses 18 taxa in the subgenera

Temnoceras and *Pinguicula*. All the taxa, forming hibernacula in winter, in this clade are distributed in mild to cold regions of the Northern Hemisphere. Clade II (75 % BS) is rather a miscellaneous group that includes 11 taxa in the subgenera *Isoloba* and *Temnoceras*, distributed in Europe to Anatolia, southeastern USA or South America. Clade III (< 50 % BS), divided to 3 or 4 subclades, includes 31 species distributed in Mexico to Central America except South American *P. elongata*. Clade IV (< 50 % BS) includes 6 Cuban taxa in the subgenera *Isoloba* and *Pinguicula*. Three species, *P. ramosa, P. variegata*, and *P. villosa* do not belong to any clades.

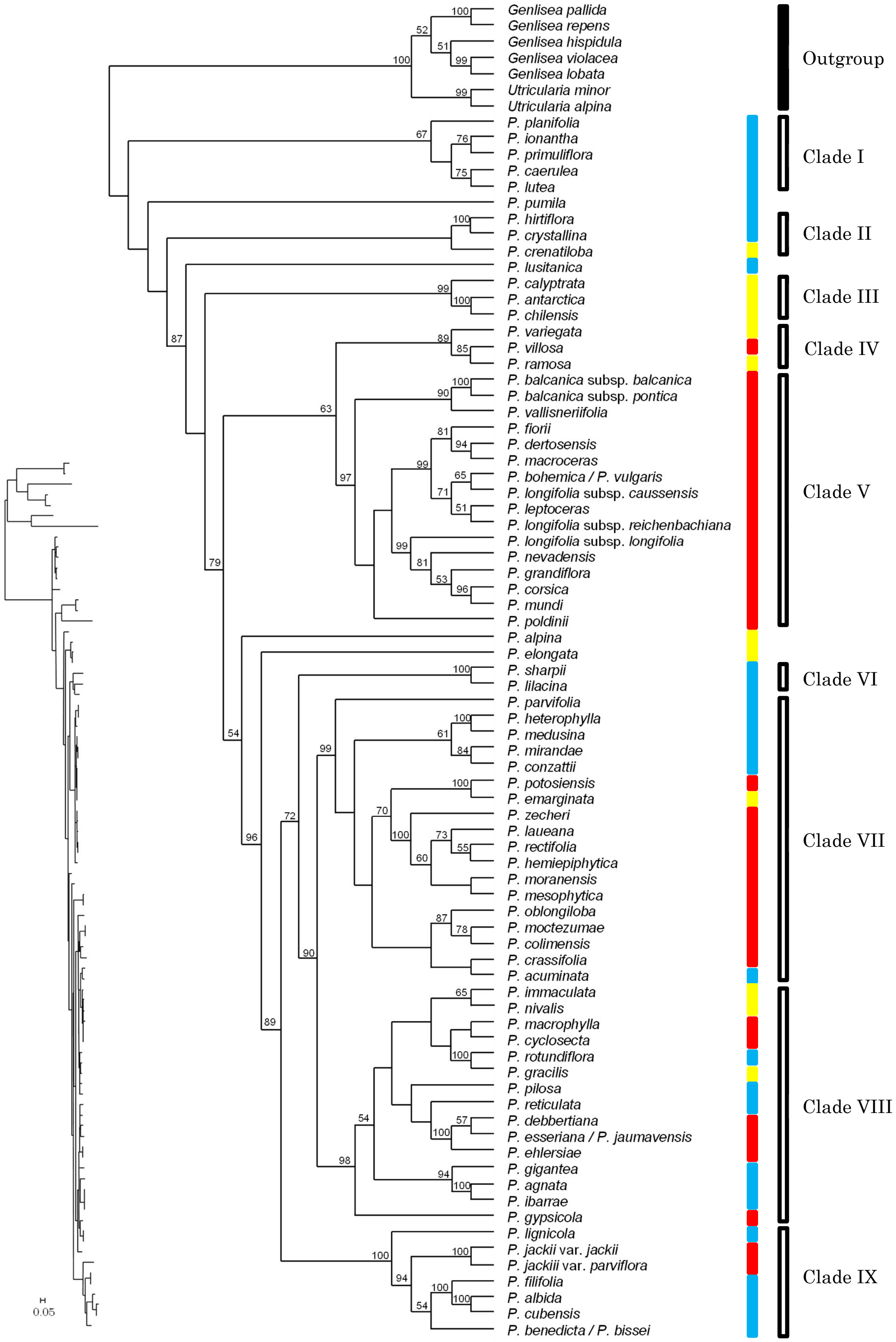
Combined cpDNA (matK and trnK + rpl32-trnL)

The genus *Pinguicula* was divided to 4 clades (Fig. 2.4) mostly with low bootstrap support (< 50 %). Clade I (61 % BS) consists of 17 taxa that contradict both geographical distributions and taxonomy by Casper (1966). Clade II (< 50 % BS) with 16 taxa is well-defined group. All taxa forming hibernacula in winter belong to the section *Pinguicula* although the relationships among the taxa are mostly supported with low bootstrap support (< 50 % BS). Clade III (< 50 % BS) with 13 taxa, distributed in Mexico and Central America or Cuba, belonging to Casper's 3 subgenera, is rather miscellaneous. Clade IV (< 50 % BS) basically consists of taxa from Mexico and Central

America except one Spanish species, *P. dertosensis* (Cañigueral) Mateo et Crespo.

Combined nrDNA and cpDNA (ITS + matK and trnK + rpl32-trnL)

Divisions of clades are somewhat vague; however, at least 7 clades are apparent (Fig. 2.5). Clade I (92 % BS) contains only 3 species, *P. ramosa, P. variegata*, and *P. villosa*. Clade II (91 % BS) with 14 rather miscellaneous species in the subgenera *Isoloba* and *Temnoceras* may be divided to a number of subclades. The species in this clade are distributed through the southeastern USA, South America, Europe and Anatolia. Clade III (100 % BS) includes 18 taxa in the subgenus *Pinguicula* distributed in mild to cold regions of the Northern Hemisphere. The taxa in Clade III is a well-defined group both phylogenetically and morphologically (forming hibernacula). Clade IV (100 % BS) is comprised of 8 Cuban taxa classified in the subgenera *Isoloba* and *Pinguicula*. Clade V (< 50 % BS) includes only 3 species, *P. crenatiloba* in Mexico and Central America, *P. crystallina* and *P. hirtiflora* in the Mediterranean region. Clade VI (85 % BS) includes 16 Mexican taxa in the three subgenera. Most of them are found in the Sierra Nevada Oriental region. Clade VII (79 % BS) includes 18 species in the three subgenera. Most of them are found in the Sierra Nevada Occidental, Sierra Nevada del Sur, or Central America. *P. moranensis,* shows much wider distribution, extending to the Sierra Nevada Oriental. Two species, *P. alpina* and *P. elongata* do not form any clades with others.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Genlisea repens
Genlisea hispidula
Genlisea violacea
Genlisea lobata
Utricularia minor
Utricularia alpina
P. planifolia
P. ionantha
P. primuliflora
P. caerulea
P. lutea
P. pumila
P. hirtiflora
P. crystallina
P. crenatiloba
P. lusitanica
P. calyptrata
P. antarctica
P. chilensis
P. variegata
P. villosa
P. ramosa
P. balcanica subsp. balcanica
P. balcanica subsp. pontica
P. vallisneriifolia
P. fiorii
P. dertosensis
P. macroceras
P. bohemica / P. vulgaris
P. longifolia subsp. caussensis
P. leptoceras
P. longifolia subsp. reichenbachiana
P. longifolia subsp. longifolia
P. nevadensis
P. grandiflora
P. corsica
P. mundi
P. poldinii
P. alpina
P. elongata
P. sharpii
P. lilacina
P. parvifolia
P. heterophylla
P. medusina
P. mirandae
P. conzattii
P. potosiensis
P. emarginata
P. zecheri
P. laueana
P. rectifolia
P. hemiepiphytica
P. moranensis
P. mesophytica
P. oblongiloba
P. moctezumae
P. colimensis
P. crassifolia
P. acuminata
P. immaculata
P. nivalis
P. macrophylla
P. cyclosecta
P. rotundiflora
P. gracilis
P. pilosa
P. reticulata
P. debbertiana
P. esseriana / P. jaumavensis
P. ehlersiae
P. gigantea
P. agnata
P. ibarrae
P. gypsicola
P. lignicola
P. jackii var. jackii
P. jackiii var. parviflora
P. filifolia
P. albida
P. cubensis
P. benedicta / P. bissei
Outgroup
Clade I
Clade II
Clade III
Clade IV
Clade V
Clade VI
Clade VII
Clade VIII
Clade IX
0.05

Fig. 2.1. Phylogenetic relationships of *Pinguicula* taxa in ITS inferred by the ML trees. Numbers on nodes show bootstrap support (%), but those 50 % or less are not shown. Coloured bars indicate the three subgenera *sensu* Casper (1966); blue = *Isoloba*, red = *Pinguicula*, and yellow = *Temnoceras*. Black and white bars indicate outgroup taxa and possible clade divisions, respectively. Phylogram is shown on the left.

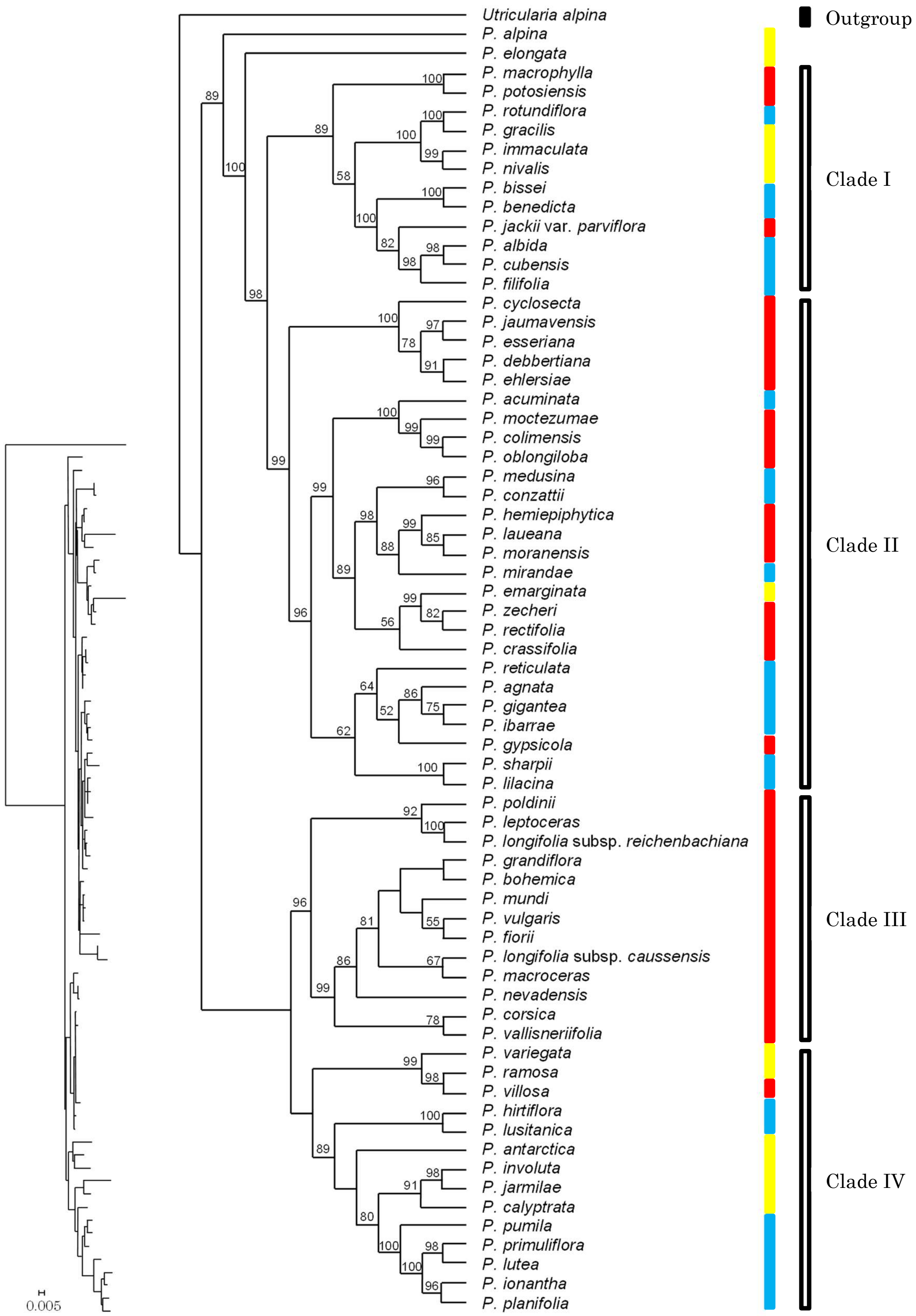
Utricularia alpina
P. alpina
P. elongata
P. macrophylla
P. potosiensis
P. rotundiflora
P. gracilis
P. immaculata
P. nivalis
P. bissei
P. benedicta
P. jackii var. parviflora
P. albida
P. cubensis
P. filifolia
P. cyclosecta
P. jaumavensis
P. esseriana
P. debbertiana
P. ehlersiae
P. acuminata
P. moctezumae
P. colimensis
P. oblongiloba
P. medusina
P. conzattii
P. hemiepiphytica
P. laueana
P. moranensis
P. mirandae
P. emarginata
P. zecheri
P. rectifolia
P. crassifolia
P. reticulata
P. agnata
P. gigantea
P. ibarrae
P. gypsicola
P. sharpii
P. lilacina
P. poldinii
P. leptoceras
P. longifolia subsp. reichenbachiana
P. grandiflora
P. bohemica
P. mundi
P. vulgaris
P. fiorii
P. longifolia subsp. caussensis
P. macroceras
P. nevadensis
P. corsica
P. vallisneriifolia
P. variegata
P. ramosa
P. villosa
P. hirtiflora
P. lusitanica
P. antarctica
P. involuta
P. jarmilae
P. calyptrata
P. pumila
P. primuliflora
P. lutea
P. ionantha
P. planifolia
Outgroup
Clade I
Clade II
Clade III
Clade IV
0.005

Fig. 2.2. Phylogenetic relationships of *Pinguicula* taxa in *mat*K and *trn*K inferred by the ML trees. Numbers on nodes show bootstrap support (%), but those 50 % or less are not shown. Coloured bars indicate the three subgenera *sensu* Casper (1966); blue = *Isoloba*, red = *Pinguicula*, and yellow = *Temnoceras*. Black and white bars indicate outgroup taxa and possible clade divisions, respectively. Phylogram is shown on the left.

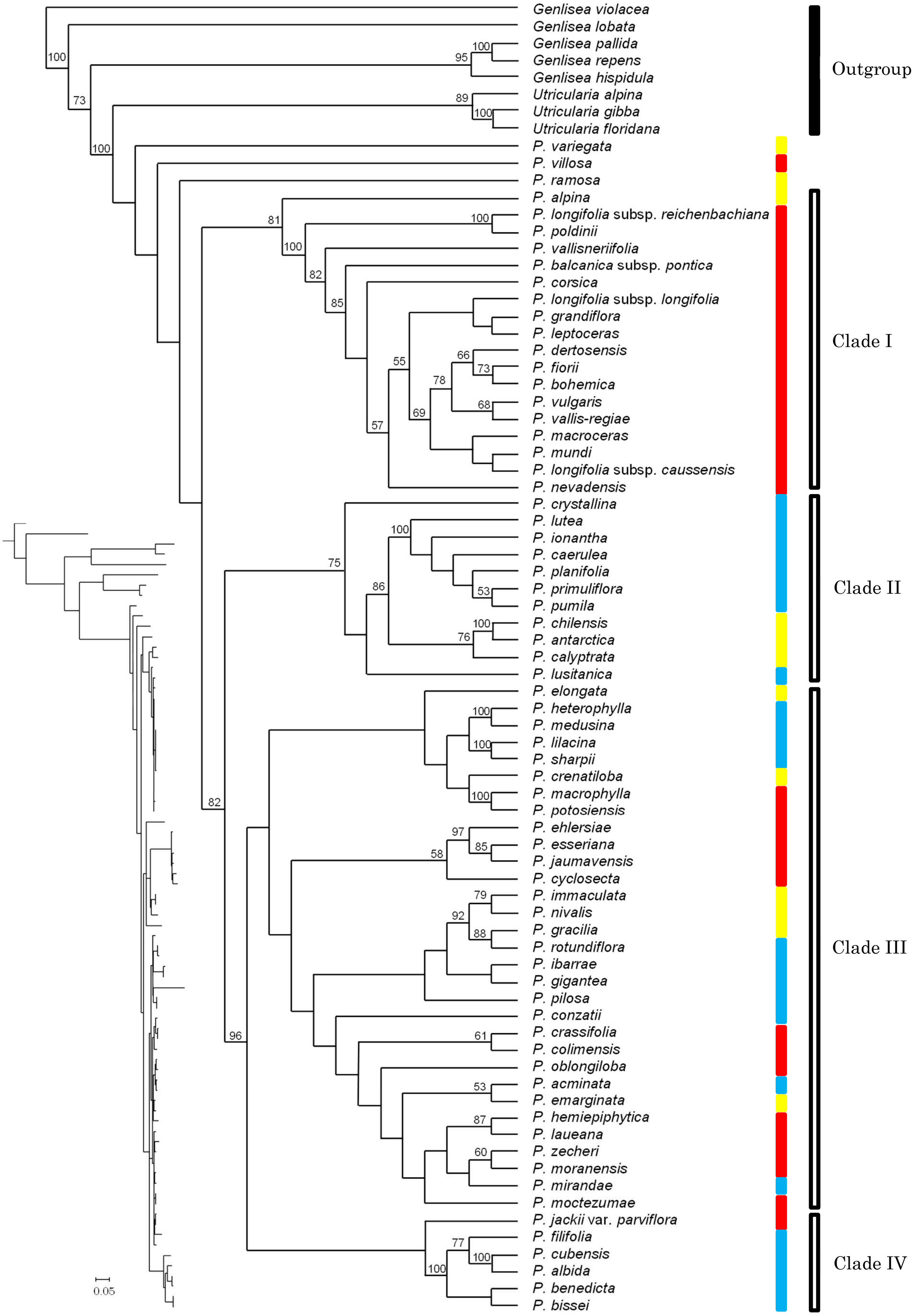
Genlisea violacea
Genlisea lobata
Genlisea pallida
Genlisea repens
Genlisea hispidula
Utricularia alpina
Utricularia gibba
Utricularia floridana
P. variegata
P. villosa
P. ramosa
P. alpina
P. longifolia subsp. reichenbachiana
P. poldinii
P. vallisneriifolia
P. balcanica subsp. pontica
P. corsica
P. longifolia subsp. longifolia
P. grandiflora
P. leptoceras
P. dertosensis
P. fiorii
P. bohemica
P. vulgaris
P. vallis-regiae
P. macroceras
P. mundi
P. longifolia subsp. caussensis
P. nevadensis
P. crystallina
P. lutea
P. ionantha
P. caerulea
P. planifolia
P. primuliflora
P. pumila
P. chilensis
P. antarctica
P. calyptrata
P. lusitanica
P. elongata
P. heterophylla
P. medusina
P. lilacina
P. sharpii
P. crenatiloba
P. macrophylla
P. potosiensis
P. ehlersiae
P. esseriana
P. jaumavensis
P. cyclosecta
P. immaculata
P. nivalis
P. gracilia
P. rotundiflora
P. ibarrae
P. gigantea
P. pilosa
P. conzatii
P. crassifolia
P. colimensis
P. oblongiloba
P. acminata
P. emarginata
P. hemiepiphytica
P. laueana
P. zecheri
P. moranensis
P. mirandae
P. moctezumae
P. jackii var. parviflora
P. filifolia
P. cubensis
P. albida
P. benedicta
P. bissei
Outgroup
Clade I
Clade II
Clade III
Clade IV
0.05

Fig. 2.3. Phylogenetic relationships of *Pinguicula* taxa in *rpl32-trnL* inferred by the ML trees. Numbers on nodes show bootstrap support (%), but those 50 % or smaller are not shown. Coloured bars indicate the three subgenera *sensu* Casper (1966); blue = *Isoloba*, red = *Pinguicula*, and yellow = *Temnoceras*. Black and white bars indicate outgroup taxa and possible clade divisions, respectively. Phylogram is shown on the left.

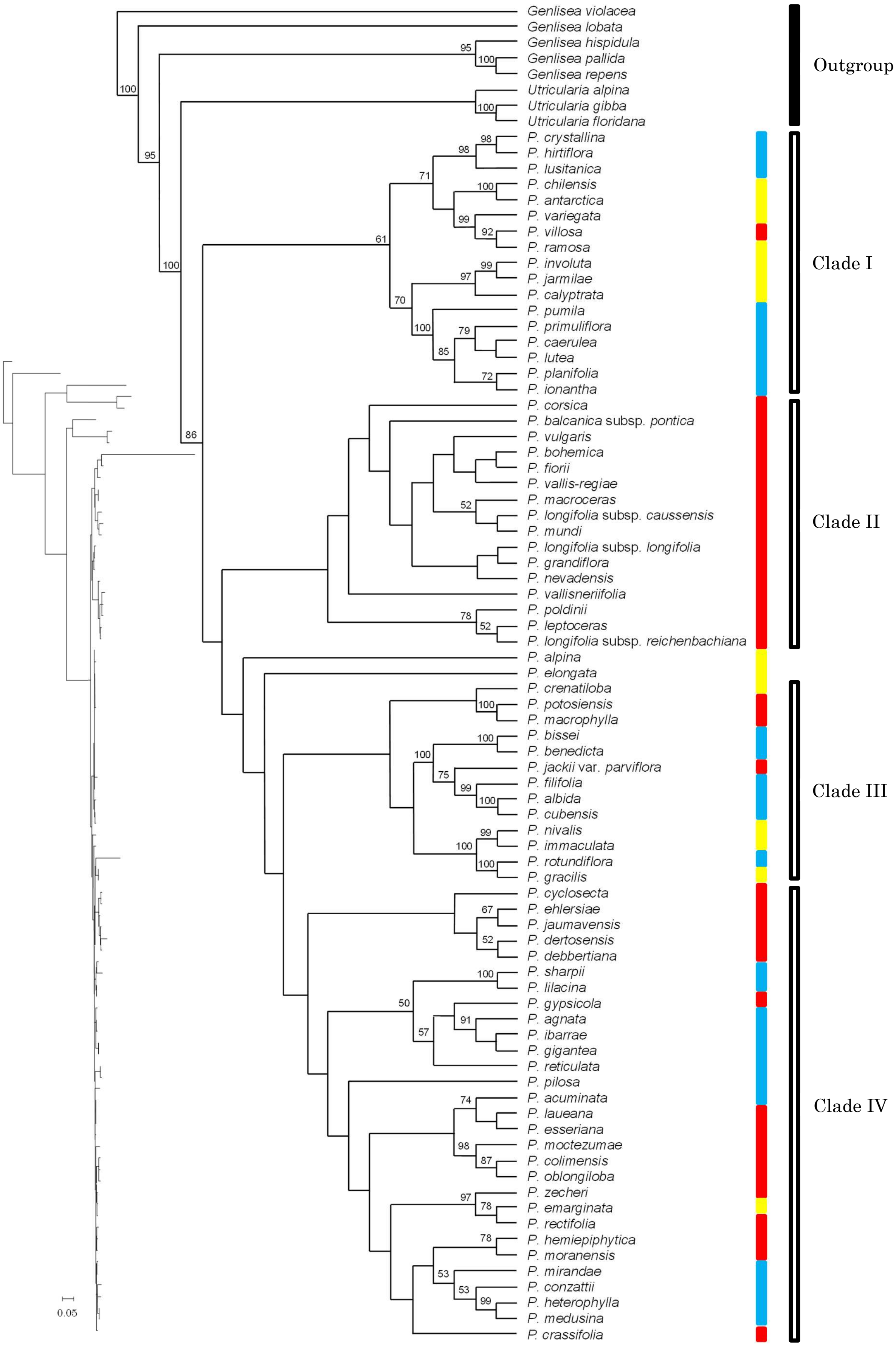
Genlisea violacea
Genlisea lobata
Genlisea hispidula
Genlisea pallida
Genlisea repens
Utricularia alpina
Utricularia gibba
Utricularia floridana
P. crystallina
P. hirtiflora
P. lusitanica
P. chilensis
P. antarctica
P. variegata
P. villosa
P. ramosa
P. involuta
P. jarmilae
P. calyptrata
P. pumila
P. primuliflora
P. caerulea
P. lutea
P. planifolia
P. ionantha
P. corsica
P. balcanica subsp. pontica
P. vulgaris
P. bohemica
P. fiorii
P. vallis-regiae
P. macroceras
P. longifolia subsp. caussensis
P. mundi
P. longifolia subsp. longifolia
P. grandiflora
P. nevadensis
P. vallisneriifolia
P. poldinii
P. leptoceras
P. longifolia subsp. reichenbachiana
P. alpina
P. elongata
P. crenatiloba
P. potosiensis
P. macrophylla
P. bissei
P. benedicta
P. jackii var. parviflora
P. filifolia
P. albida
P. cubensis
P. nivalis
P. immaculata
P. rotundiflora
P. gracilis
P. cyclosecta
P. ehlersiae
P. jaumavensis
P. dertosensis
P. debbertiana
P. sharpii
P. lilacina
P. gypsicola
P. agnata
P. ibarrae
P. gigantea
P. reticulata
P. pilosa
P. acuminata
P. laueana
P. esseriana
P. moctezumae
P. colimensis
P. oblongiloba
P. zecheri
P. emarginata
P. rectifolia
P. hemiepiphytica
P. moranensis
P. mirandae
P. conzattii
P. heterophylla
P. medusina
P. crassifolia
Outgroup
Clade I
Clade II
Clade III
Clade IV
0.05

Fig. 2.4. Phylogenetic relationships of *Pinguicula* taxa based on the combined cpDNA (*mat*K and *trn*K + *rpl32-trnL*) dataset inferred by the Bayesian trees. Numbers on nodes show bootstrap support (%), but those 50 % or less are not shown. Coloured bars indicate the three subgenera *sensu* Casper (1966); blue = *Isoloba*, red = *Pinguicula*, and yellow = *Temnoceras*. Black and white bars indicate outgroup taxa and possible clade divisions, respectively. Phylogram is shown on the left.

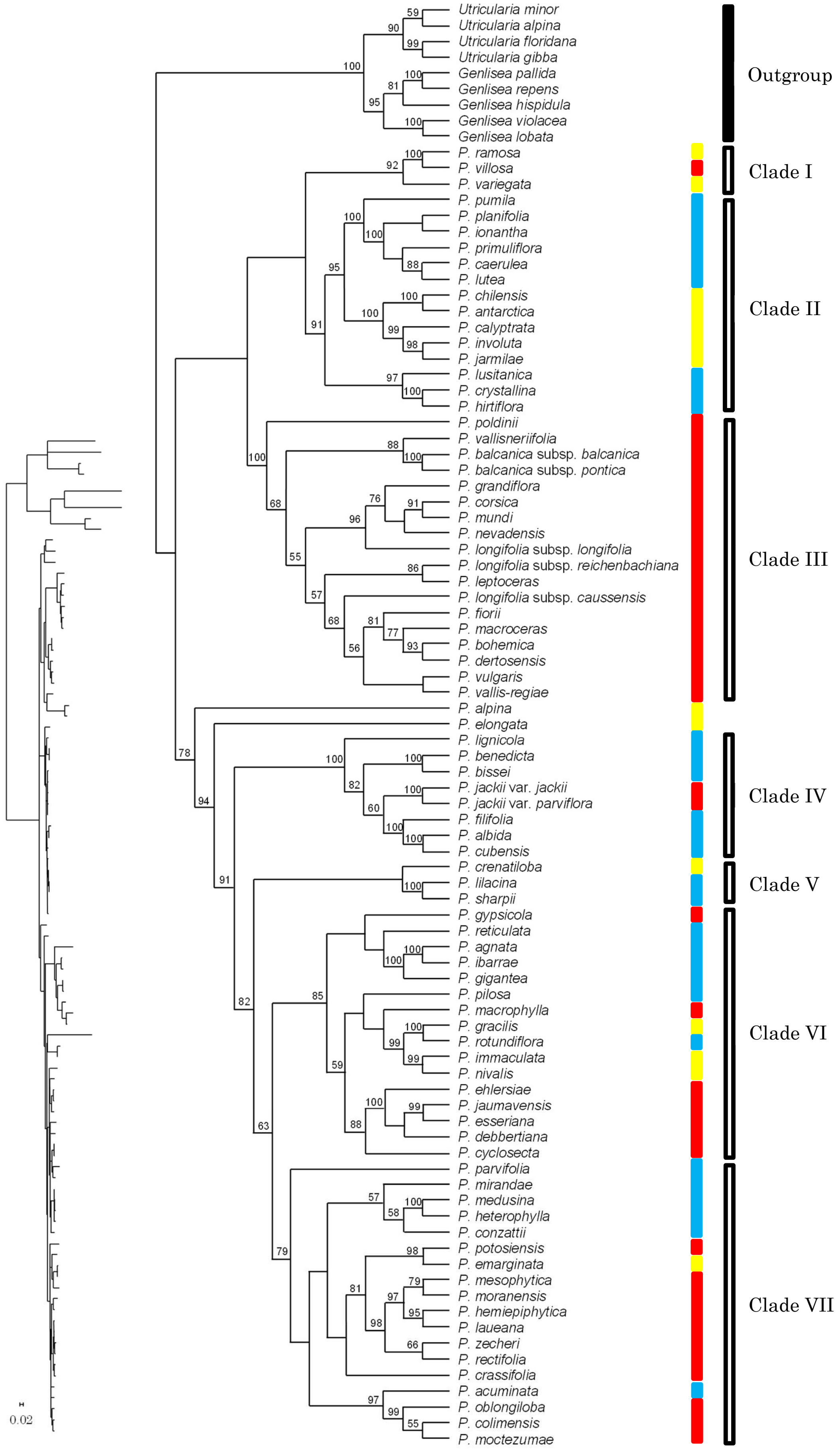
Utricularia minor
Utricularia alpina
Utricularia floridana
Utricularia gibba
Genlisea pallida
Genlisea repens
Genlisea hispidula
Genlisea violacea
Genlisea lobata
Outgroup
P. ramosa
P. villosa
P. variegata
Clade I
P. pumila
P. planifolia
P. ionantha
P. primuliflora
P. caerulea
P. lutea
P. chilensis
P. antarctica
P. calyptrata
P. involuta
P. jarmilae
P. lusitanica
P. crystallina
P. hirtiflora
Clade II
P. poldinii
P. vallisneriifolia
P. balcanica subsp. balcanica
P. balcanica subsp. pontica
P. grandiflora
P. corsica
P. mundi
P. nevadensis
P. longifolia subsp. longifolia
P. longifolia subsp. reichenbachiana
P. leptoceras
P. longifolia subsp. caussensis
P. fiorii
P. macroceras
P. bohemica
P. dertosensis
P. vulgaris
P. vallis-regiae
Clade III
P. alpina
P. elongata
P. lignicola
P. benedicta
P. bissei
P. jackii var. jackii
P. jackii var. parviflora
P. filifolia
P. albida
P. cubensis
Clade IV
P. crenatiloba
P. lilacina
P. sharpii
Clade V
P. gypsicola
P. reticulata
P. agnata
P. ibarrae
P. gigantea
P. pilosa
P. macrophylla
P. gracilis
P. rotundiflora
P. immaculata
P. nivalis
P. ehlersiae
P. jaumavensis
P. esseriana
P. debbertiana
P. cyclosecta
Clade VI
P. parvifolia
P. mirandae
P. medusina
P. heterophylla
P. conzattii
P. potosiensis
P. emarginata
P. mesophytica
P. moranensis
P. hemiepiphytica
P. laueana
P. zecheri
P. rectifolia
P. crassifolia
P. acuminata
P. oblongiloba
P. colimensis
P. moctezumae
Clade VII
0.02

Fig. 2.5. Phylogenetic relationships of *Pinguicula* taxa based on the combined nrDNA and cpDNA (ITS + *mat*K and *trn*K + *rpl32-trnL*) dataset inferred by the Bayesian trees. Numbers on nodes show bootstrap support (%), but those 50 % or less are not shown. Coloured bars indicate the three subgenera *sensu* Casper (1966); blue = *Isoloba*, red = *Pinguicula*, and yellow = *Temnoceras*. Black and white bars indicate outgroup taxa and possible clade divisions, respectively. Phylogram is shown on the left.

2.4. DISCUSSION

Samples used in the earlier studies sequenced *mat*K and *trn*K (Cieslak et al. 2005, Beck et al. 2008) and ITS (Degtjareva 2006, Shimai and Kondo 2007) were limited. However, the results suggested that they partially disagreed with Casper's (1966) subgeneric classification. In this study, additional taxa (a total of 83 taxa) and gene region (*rpl32-trnL*) were sequenced to infer phylogenetic relationships within the genus.

Phylogenetic analyses, distribution areas, and morphology

There are some disagreements between the phylogenetic analyses and the current taxonomy *sensu* Casper (1966). According to the analyses, taxa in the section *Pinguicula* distributed in the mild to cold region of the Northern Hemisphere seem to be phylogenetically the most well-defined group. Those taxa form a clade in each tree with one exception, which is a clade in the *rpl32-trnL* tree contains *P. alpina* in the subgenus *Temnoceras*. Taxa in Mexico could also be phylogenetically more or less a well-defined group although Casper (1966) divided them into 3 subgenera, *Isoloba, Pinguicula* and *Temnoceras*. An exception is seen that *P. crenatiloba* is a sister taxon with Mediterranean *P. crystallina* and *P. hirtiflora* in ITS. One morphological commonality between *P. crenatiloba* and the two Mediterranean species is that they have monomorphic leaves, but they are very different in terms of morphology. In contrast, the *rpl32-trnL* indicates that *P. crenatiloba* is closely related to other Mexican taxa, such as *P. macrophylla* Kunth and *P. potosiensis* Speta et Fuchs. A South American *P. elongata* has formed a clade together with the Mexican and Central American group in *rpl32-trnL*. Unlike the other South American species, *P. elongata* forms a winter rosette like most of Mexican and Central American taxa do. Cuban taxa are also well-defined except in *mat*K and *trn*K, where Cuban taxa and Mexican and Central American taxa form the same clade. Similarly, Cieslak et al. (2005) and Beck et al. (2008), using only one Cuban species, *P. filifolia* Wright ex Griseb. also demonstrated that it formed a clade with Mexican taxa in their *mat*K and *trn*K analysis.

In each phylogenetic tree, the morphology based taxonomy by *sensu* Casper (1966) is not supported. Regardless of growth cycles or geographical distributions, Casper (1966) focused mainly on the floral morphology; i.e. the subgenus *Isoloba* has more or less equal shapes of five corolla lobes, the subgenus *Pinguicula* possesses zygomorphic corollas with usually darker color, while the subgenus *Temnoceras* are paler colour or white. In contrast, Legendre (2000), without taxonomic revisions, categorized the genus *Pinguicula* by growth cycles, a “Homophyllous type”, having the same shapes of leaves throughout the year, and a “Heterophyllous type”, having the different types of leaves in the different times of the year. The latter type was further divided to a "Tropical growth type" and "Temperate growth type" although those do not exactly correspond with the climate zones (i.e. some Tropical-growth-type species occur in the Temperate zone). Similar categories have often been applied to the cultivation of *Pinguicula* in horticulture (Huxley et al. 1992).

Legendre (2000) also used growth cycles in order to explain their ecological adaptation; however, it could be better interpreted by geographical regions, partially corresponding with climates, according to the phylogeny. Namely, taxa forming hibernacula is restricted to the mild to cold regions and higher mountains of the temperate Northern Hemisphere. Similarly, taxa forming winter rosettes are found in Mexico and Central America.

In comparison to the tree generated by individual gene datasets, ITS, *mat*K, and *rpl32-trnL*, the ITS result is potentially more informative than others as Degtjareva et al. (2006) suggested. The cladistics divisions in *mat*K or *rpl32-trnL* do not clearly support those in ITS, probably due to the different evolutionary histories of the organelles. This work agrees with that of Degtjareva et al. (2006), and hereafter the ITS results are used to explain phylogenetic relationships.

Chromosome numbers

Recently, chromosome numbers of *Pinguicula* taxa have been extensively studied by Casper and Stimper (2009). Chromosome numbers vary among taxa, normally between $2n = 16$ and $2n = 64$, but up to $2n = 128$ in an unidentified taxon (Casper and Stimper 2009). Most of the taxa possess a basic number of $x = 8$ or 11. Relationships between the basic number and the current taxonomy at the subgeneric rank showed no clear tendencies; however, applying the number of chromosomes to the ITS tree shows a clearer tendencies. This may imply a correlation between chromosome numbers and phylogenetic evolution (Fig. 2.6). Within a taxon, chromosome evolution generally increases the number of chromosomes, which may subsequently result in morphological evolution (Imai et al. 1986), but reduction of the number is rather rare (Schubert 2007). In this study, however, chromosome evolution and phylogenetic evolution cannot be equally compared due to weak bootstrap support at some basal nodes.

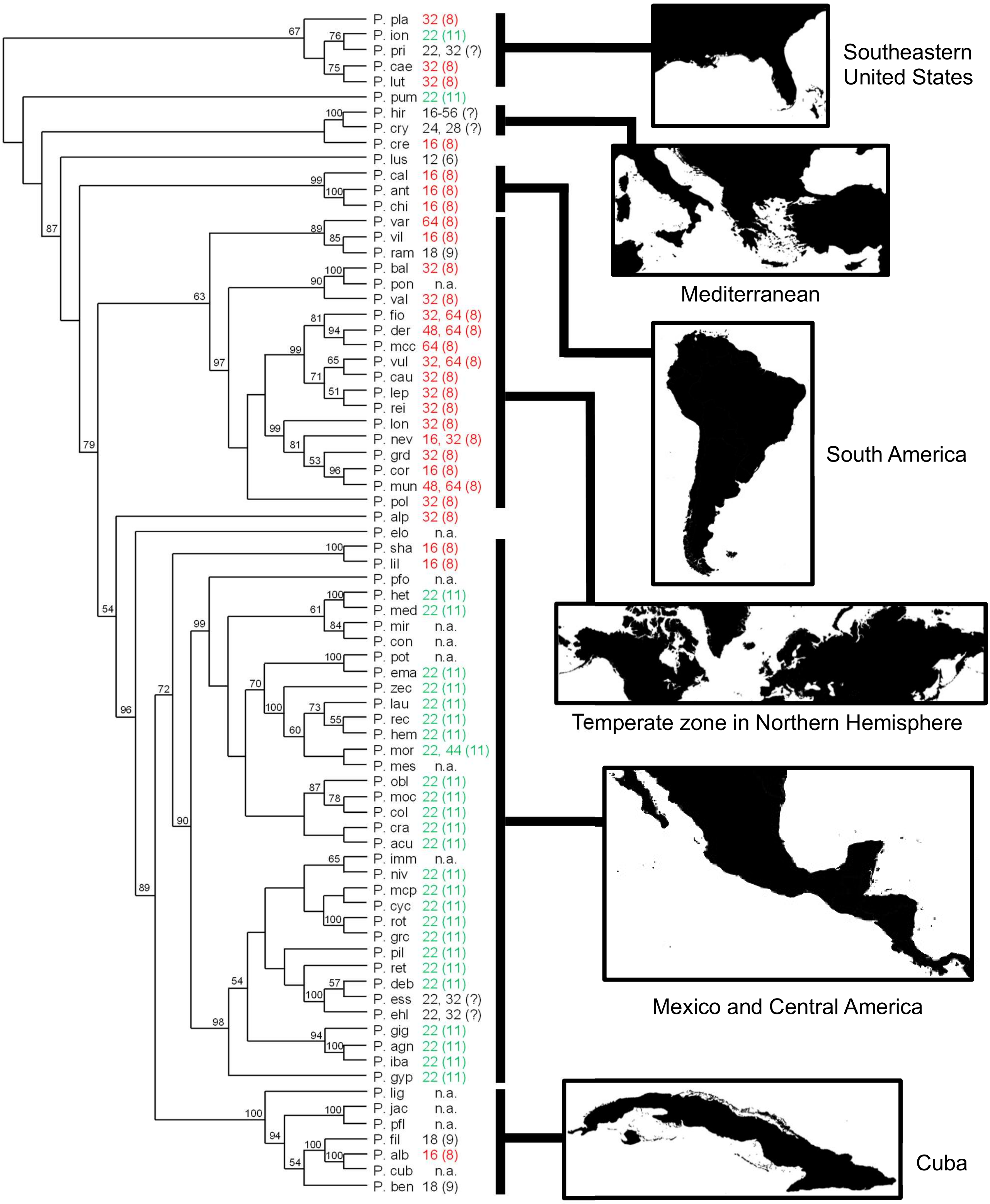
P. pla 32 (8)
P. ion 22 (11)
P. pri 22, 32 (?)
P. cae 32 (8)
P. lut 32 (8)
P. pum 22 (11)
P. hir 16-56 (?)
P. cry 24, 28 (?)
P. cre 16 (8)
P. lus 12 (6)
P. cal 16 (8)
P. ant 16 (8)
P. chi 16 (8)
P. var 64 (8)
P. vil 16 (8)
P. ram 18 (9)
P. bal 32 (8)
P. pon n.a.
P. val 32 (8)
P. fio 32, 64 (8)
P. der 48, 64 (8)
P. mcc 64 (8)
P. vul 32, 64 (8)
P. cau 32 (8)
P. lep 32 (8)
P. rei 32 (8)
P. lon 32 (8)
P. nev 16, 32 (8)
P. grd 32 (8)
P. cor 16 (8)
P. mun 48, 64 (8)
P. pol 32 (8)
P. alp 32 (8)
P. elo n.a.
P. sha 16 (8)
P. lil 16 (8)
P. pfo n.a.
P. het 22 (11)
P. med 22 (11)
P. mir n.a.
P. con n.a.
P. pot n.a.
P. ema 22 (11)
P. zec 22 (11)
P. lau 22 (11)
P. rec 22 (11)
P. hem 22 (11)
P. mor 22, 44 (11)
P. mes n.a.
P. obl 22 (11)
P. moc 22 (11)
P. col 22 (11)
P. cra 22 (11)
P. acu 22 (11)
P. imm n.a.
P. niv 22 (11)
P. mcp 22 (11)
P. cyc 22 (11)
P. rot 22 (11)
P. grc 22 (11)
P. pil 22 (11)
P. ret 22 (11)
P. deb 22 (11)
P. ess 22, 32 (?)
P. ehl 22, 32 (?)
P. gig 22 (11)
P. agn 22 (11)
P. iba 22 (11)
P. gyp 22 (11)
P. lig n.a.
P. jac n.a.
P. pfl n.a.
P. fil 18 (9)
P. alb 16 (8)
P. cub n.a.
P. ben 18 (9)
Southeastern United States
Mediterranean
South America
Temperate zone in Northern Hemisphere
Mexico and Central America
Cuba

Fig. 2.6. Phylogenetic relationships with chromosome numbers, basic numbers, and geographical distributions based on the ITS. Epithets are abbreviated in this figure (see Fig. 2.1 for the names). Numbers show chromosome numbers ($2n$ =) and those in bracts are the basic number (x =) (Casper and Stimper 2009). The numbers indicated in red are the basic number of 8, and those in green are the basic number of 11. Other basic numbers and chromosome number unidentified taxa (n.a.) are shown in black.

Possible molecular evolution

Within Lentibulariaceae, the genus *Pinguicula* is a well-defined group both morphologically (Lloyd 1942) and phylogenetically (Jobson et al. 2004, Müller et al. 2004). In this study, some basal nodes have relatively low bootstrap support and therefore potential relationships are difficult to infer. Although morphological diversity is seen for example in Mexican and Central American taxa, the data suggests that those are more or less monophyletic. Shorter branch lengths shown in each phylogram (Figs. 2.1 to 2.5) imply either rapid speciation or slow molecular evolution, but as shown by Müller et al. (2004) longer branch length in the genera *Genlisea* and *Utricularia* (Lentibulariaceae) could suggest the former. It is likely that rapid speciation occurred in each geographical region. Similar examples have been reported in *Gaertnera* Lam.

(Rubiaceae) (Malcomber 2002) or the taxa in the Valerianaceae (Hidalgo et al. 2004). Therefore, the morphological diversities within such geographical regions are probably adaptation to their environment and pollination strategy resulting in radial speciation. Similar morphological characters (e.g. flowers) among some taxa in different regions are likely a result of convergent evolution (Fleischmann 2012a), which has likewise been reported elsewhere such as in cichlid fish between isolated lakes (Kocher et al. 1993). Fossil records of *Pinguicula* are hitherto not reported; therefore, it was not possible to estimate evolutionary time in this study.

As discussed, there is little alignment between the phylogenetic analyses and the morphological-based taxonomy of Casper (1966). A revision of the genus *Pinguicula* based on the phylogeny is proposed in Chapter 4.

2.5. CONCLUSION

There was low congruence between the nrDNA of the ITS and the cpDNA of *mat*K and *trn*K and *rpl32-trnL*. While the divisions of clades did not agree with the current sectional divisions based on morphology, they agreed with geographical distribution areas and to a certain extent with chromosome basic numbers. The same growth style within a region (e.g. taxa forming a winter rosette in Mexico) may not be simply as a result of ecological convergence but they are phylogenetically close to one another while their floral morphology is diverse. The data suggest that a taxonomic revision of the genus *Pinguicula* based on phylogeny with more sampling of other informative gene regions may be required.

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CHAPTER 3

The effect of geographical and environmental factors on patterns of species richness in the genus *Pinguicula* L.

3.1. INTRODUCTION

The distribution of plant species is significantly impacted by climatic variables while other factors such as soil type affect patterns of species richness at more local scales (Bakkenes et al. 2002). A definition of species richness depends on the nature of research that may use geographic distribution, abundance of species, or uncommon species found in a particular area (Prendergast et al. 1993). How many plant species occur in a region or country, species richness, is a major concern for conservations; however, hotspots have to be correctly defined (Schödelbauerová et al. 2009). Approximately 44 % of all vascular plant species are confined to one of 25 biodiversity hotspots as defined by Myers et al. (2000). Apart from the 25 biodiversity hotspots, variation in species richness is also seen more locally (Prendergast et al. 1993, Pillon et al. 2006).

The relationships between the number of plant species and land area have been discussed over many years (Gleason 1922, Johnson and Simberloff 1974). There is a positive correlation between species number, the land area, and the number of habitat types: larger areas contain more habitat types and therefore more species (Kohn and Walsh 1994, Ackerman et al. 2007). Species confined to small areas in a rare climate are likely to be threatened, while those occurring in wide diversity climates are more likely, from a conservation point of view, to be of least concern (Ohlemüller et al. 2008).

In carnivorous plants, most of genera consist of only a few species. All species (8-11) of *Sarracenia* L. (Sarraceniaceae) are found in the USA and one species in Canada. Among the more speciose carnivorous plant genera, the areas of highest species richness in the genus *Drosera* L. (Droseraceae) are in Australia, Africa, and South America (Rivadavia et al. 2003), whereas for the genus *Nepenthes* L. (Nepenthaceae) the highest level of species richness is in Southeast Asia (Jebb and Cheek 1997).

The genus *Pinguicula* L. (Lentibulariaceae) occurs in the Americas, Europe, temperate Asia, and North Africa (Casper 1966, Juniper et al. 1989, Legendre 2000, Kondo and Shimai 2006). The distribution of *Pinguicula* covers at least 68 countries and stretches from ca. 79°20'N in Svalbard to ca. 55°30'S in Tierra del Fuego, and ranging in altitude from the sea level to over 4,600 m (Chapters 1 and 4). The distribution of the genus is geographically and climatically diverse although a number of the taxa have small distributions. Although wet places isolated by large arid areas are ecologically rare, a number of *Pinguicula* species are restricted such environments (Blanca et al. 1999).

Casper (1966) studied the distribution of all 46 species known at that time, but the number of known species has almost doubled (Zamudio 2005, Conti and Peruzzi 2006, Chapter 4 revision). The distribution has also been studied regionally by many botanists, often as a part of regional floras; some representatives cover, at least in part, Eurasia (Casper 1962, 1972, Mill 1978, Taylor 1985, Blanca et al. 2001, Heslop-Harrison 2004, Li and Cheek 2011), North America (Godfrey and Stripling 1961, Hultén 1968), Mexico (Zamudio 2005), and South America (Reiche 1910, Fernández-Pérez 1946).

In temperate regions of the Northern Hemisphere such as Eurasia and North America, *Pinguicula* is more commonly found at higher altitudes in the south and at lower altitudes in the north correlated with seasonal temperature, and many taxa found in such a region form hibernacula during winter (Heslop-Harrison 2004). In the mountain ranges of Mexico, the climate is relatively mild even though frost and low precipitation may occur during winter and thus most taxa in Mexico form winter rosettes during this period (Zamudio 2001). On the other hand, a number of species are also found in subtropical and tropical regions, but here their distribution is restricted to higher elevations, often 2,500 m or higher, under and near the equator in South America (Fernández-Pérez 1946, Taylor 1975). Although a number of scientists suggested that the occurrence of *Pinguicula* may be correlated with latitude and altitude, such a correlation has not been previously studied in detail.

As shown in the General Introduction of this thesis, Mexico, having 46 taxa (45 species and 1 variety recognised in this study; see Chapter 4), is the most species rich country in terms of *Pinguicula* biodiversity. After Mexico, there is an almost five fold drop in species richness with France having 10 taxa, 9 taxa in Spain and also in the USA including Alaska. In contrast, only *P. alpina* L. is found in Bhutan, India, Liechtenstein, Myanmar, and Nepal, and only *P. vulgaris* L. occurs in Belarus, Belgium, Czech Republic, Denmark, Iceland, Latvia, and the Netherlands.

At the regional level, Mexico and Central America has 46 taxa (40 taxa are endemic to Mexico and 6 taxa are found in Mexico and other Central American countries), Europe and Western Asia has 20 taxa, and the Caribbean has 10 taxa. An endemic taxon defined in this work is one that is confined to a single country. In those regions, endemism is 87 % (40 taxa), 45 % (9 taxa), and 90 % (9 taxa) respectively (Chapter 1). It is, however, unclear what factors influence species diversity within the genus.

3.2. MATERIALS AND METHODS

The number of *Pinguicula* taxa in each country was extracted from over 6,800 herbarium specimens from 167 herbaria, as described in Chapters 1 and 4. Physical geography data and Koeppen-Geiger climate data for each country were downloaded from the website of the Department of Economics, Portland University (https://www.pdx.edu/econ/country-geography-data). Here the source datasets of three countries, Andorra, the Bahamas, and Liechtenstein were not available; therefore, these were not included in the analyses. The dataset of Serbia containing that of Kosovo was treated as one area with two species (Table 3.2).

A number of geographic and Koeppen-Geiger climate datasets are available by country in the Portland University's website. Variables that may be informative and require consideration when studying their correlation with the distribution of plant species are presented in Table 3.1; these are land area (km^2), latitude of country centroid, mean elevation (meters above sea level), and mean distance to nearest coastline (km), and the Koeppen-Geiger climate system were divided to six categories; A (tropical-type climate category), B (dry-type climate category), C (temperate-type climate category), D (cold-type climate category), E (polar-type climate), and H (alpine-type climate). Latitude was considered as degrees from the equator, i.e. the absolute value of latitude. Other geography data were log transformed (LN). The climate in each country as a percentage (%) was converted using arcsin (ASIN) transformation. Correlations between each of those and the number of taxa were performed for each region using the Pearson's correlation. Similarly correlations between each of those and LN of the number of taxa were analysed. All datasets are shown in Table 3.2.

A global analysis was performed covering all countries in which *Pinguicula* is known to occur, and three subregions; Europe and Western Asia (37 countries including whole European countries in which *Pinguicula* occurs and Cyprus, Turkey, and Georgia, but excluding Russia), Northeastern Asia (9 countries including China, India, and Russia; excluding *P. balcanica* Casper in the Caucasus), America (18 countries including North America, Greenland, Mexico, the Caribbean, Central and South America) were used (Table 3.2). The analysis was repeated but excluding Mexico due to the extremely high *Pinguicula* diversity; i.e. for all countries and America.

As each analysis involved 10 variables Bonferroni's correlation was applied. When significant difference was seen in two or more variables within each region, multiple regression analysis was performed to determine which variable more strongly affected the species richness of *Pinguicula*.

Table 3.1. Variables used for geographical and environmental analyses for species richness of *Pinguicula*. Data were obtained from the Portland University website (https://www.pdx.edu/econ/country-geography-data). More detailed descriptions for the Koeppen's climate systems were listed in Kalvová et al. (2003).

Variable	Description
country	Country name (as of 1996)
area (km^2)	Land area (km^2)
cen_lat	Latitude of country centroid
elev	Mean elevation (metres above sea level)
distc	Mean distance to nearest coastline (km)
A	Koeppen-Geiger climate zone: Tropical (Af+Am+Aw), mean temperature of the coldest month exceeding +18°C Af = Tropical rainforest (average ≥ 6 cm rain in driest month) Am = Tropical monsoon (average < 6 cm rain in driest month, allowing forest growth) Aw = Savannah (average < 6 cm rain in driest month)
B	Koeppen-Geiger climate zone: Dry (Bs+Bw) Bs = Steppe (bush to grassland) Bw = Desert
C	Koeppen-Geiger climate zone: Temperate (Cf+Cs+Cw), mean temperature of the coldest month between –3 and +18°C Cf = Without dry season Cs = Dry Summer Cw = Dry Winter
D	Koeppen-Geiger climate zone: Cold (Dw+Df), mean temperature of the warmest month > 10°C and the coldest month < –3°C Dw = Dry Winter Df = Without dry season
E	Koeppen-Geiger climate zone: Polar (E), mean temperature of the warmest month < 10°C.
H	Koeppen-Geiger climate zone: Alpine (H)

Table 3.2. Geography and Koeppen-Geiger climate data used for analyses.

area	wbcode	country	taxa	taxa (LN)	area (km2)	area (LN)	cen_lat	elev (m)	elev (LN)	distc (km)	distc (LN)
EUR	ALB	Albania	2	0.693	27899.96	10.236	41.143	911.4	6.815	76.04	4.331
EUR	AUT	Austria	3	1.099	84905.64	11.349	47.598	898.8	6.801	263.15	5.573
EUR	BEL	Belgium	1	0	31318.33	10.352	50.662	181.8	5.203	123.76	4.818
EUR	BGR	Bulgaria	1	0	119438.6	11.691	42.791	421.2	6.043	158.61	5.066
EUR	BIH	Bosnia Herz.	2	0.693	51385.29	10.847	44.175	702.2	6.554	136.69	4.918
EUR	BLR	Belarus	1	0	205718.3	12.234	53.547	160.8	5.080	687.56	6.533
EUR	CHE	Switzerland	4	1.386	41452.37	10.632	46.839	1369.6	7.222	279.26	5.632
EUR	CZE	Czech Repub.	1	0	80164.98	11.292	49.779	433.0	6.071	434.55	6.074
EUR	DEU	Germany	2	0.693	349898	12.765	51.083	270.8	5.602	255.97	5.545
EUR	DNK	Denmark	1	0	32407.53	10.386	56.114	34.3	3.534	22.52	3.114
EUR	ESP	Spain	9	2.197	485472.7	13.093	40.402	704.6	6.558	141.56	4.953
EUR	EST	Estonia	2	0.693	38744.69	10.565	58.632	61.9	4.126	507.83	6.230
EUR	FIN	Finland	3	1.099	333517.9	12.717	64.430	164.5	5.103	494.86	6.204
EUR	FRA	France	10	2.303	550787.7	13.219	46.531	375.1	5.927	183.88	5.214
EUR	GBR	United Kingdom	3	1.099	219140.8	12.297	53.887	162.6	5.091	45.02	3.807
EUR	GRC	Greece	2	0.693	105139.9	11.563	39.163	498.6	6.212	41.41	3.724
EUR	HRV	Croatia	2	0.693	53732.65	10.892	45.110	331.6	5.804	146.43	4.987
EUR	HUN	Hungary	2	0.693	95568.61	11.468	47.209	143.6	4.967	507.23	6.229
EUR	IRL	Ireland	3	1.099	67816.94	11.125	53.163	112.4	4.722	43.66	3.776
EUR	ISL	Iceland	1	0	100376.3	11.517	64.920	557.4	6.323	46.32	3.836
EUR	ITA	Italy	8	2.079	296127.4	12.599	42.880	538.7	6.289	64.64	4.169
EUR	LVA	Latvia	1	0	62352.89	11.041	56.850	95.9	4.563	409.48	6.015
EUR	MKD	Macedonia	2	0.693	25823	10.159	41.574	741.5	6.609	142.50	4.959
EUR	MON	Montenegro	1	0	13995.82	9.547	42.789	1086.7	6.991	84.83	4.441
EUR	NLD	Netherlands	1	0	32983.36	10.404	52.209	30.1	3.405	67.31	4.209
EUR	NOR	Norway	3	1.099	349504.6	12.764	67.470	566.8	6.340	89.30	4.492
EUR	POL	Poland	2	0.693	305676.3	12.630	52.136	171.7	5.146	279.24	5.632
EUR	PRT	Portugal	2	0.693	93102.51	11.441	39.689	372.5	5.920	104.74	4.651
EUR	ROM	Romania	2	0.693	231660.4	12.353	45.913	414.1	6.026	389.89	5.966
EUR	SRB	Serbia	2	0.693	88010.47	11.385	44.047	442.1	6.091	297.91	5.697
EUR	SVK	Slovakia	2	0.693	47843.81	10.776	48.785	458.6	6.128	577.93	6.359
EUR	SVN	Slovenia	2	0.693	20440.81	9.925	46.128	492.6	6.200	112.12	4.720
EUR	SWE	Sweden	3	1.099	433618.7	12.980	62.746	320.1	5.769	210.72	5.351
EUR	UKR	Ukraine	2	0.693	586548.7	13.282	49.062	176.8	5.175	343.38	5.839
WAS	CYP	Cyprus	1	0	9181.428	9.125	35.031	9.2	2.216	10.94	2.392
WAS	GEO	Georgia	1	0	72279.36	11.188	42.181	1432.4	7.267	239.98	5.481
WAS	TUR	Turkey	2	0.693	790418.8	13.580	39.019	1167.0	7.062	160.19	5.076
NAS	BTN	Bhutan	1	0	38303.91	10.553	27.395	2220.2	7.705	506.89	6.228
NAS	CHN	China	2	0.693	9344594	16.050	36.591	1840.0	7.517	1090.58	6.994
NAS	IND	India	1	0	3151251	14.963	22.932	621.8	6.433	463.79	6.139
NAS	JPN	Japan	3	1.099	358359	12.789	36.955	438.3	6.083	39.74	3.682
NAS	MMR	Myanmar	1	0	656424.2	13.395	21.169	702.4	6.555	347.74	5.851
NAS	MNG	Mongolia	2	0.693	1558417	14.259	46.853	1528.0	7.332	1855.69	7.526
NAS	NPL	Nepal	1	0	147402.7	11.901	28.299	2565.4	7.850	825.38	6.716
NAS	PRK	Korea, DPR	1	0	126959.7	11.752	40.128	599.3	6.396	70.20	4.251
NAS	RUS	Russia	7	1.946	16600000	16.625	61.699	372.5	5.920	2325.40	7.752
NAM	CAN	Canada	3	1.099	9590309	16.076	61.063	487.6	6.190	1567.98	7.358
NAM	USA	United States	9	2.197	9400722	16.056	45.625	725.7	6.587	761.91	6.636
NAM	GRL	Greenland	1	0	2089010	14.552	74.703	1792.6	7.491	1919.15	7.560
MEX	MEX	Mexico	46	3.829	1923122	14.469	23.921	1110.9	7.013	207.17	5.334
CRB	CUB	Cuba	8	2.079	100428.7	11.517	21.698	108.2	4.684	21.24	3.056
CRB	DOM	Dominican Repub.	1	0	45356.82	10.722	18.952	424.9	6.052	30.18	3.407
CAM	CRI	Costa Rica	1	0	50525.34	10.830	10.012	746.2	6.615	35.48	3.569
CAM	GTM	Guatemala	5	1.609	108418.3	11.594	15.742	759.6	6.633	105.10	4.655
CAM	HND	Honduras	2	0.693	113208	11.637	14.837	684.9	6.529	79.36	4.374
CAM	PAN	Panama	1	0	73322.34	11.203	8.572	359.7	5.885	20.49	3.020
CAM	SLV	El Salvador	1	0	20886.14	9.947	13.783	442.0	6.091	44.68	3.799
SAM	ARG	Argentina	2	0.693	2775401	14.836	35.387	595.6	6.390	388.41	5.962
SAM	BOL	Bolivia	2	0.693	1090806	13.902	16.726	1192.6	7.084	743.67	6.612
SAM	CHL	Chile	2	0.693	668868.7	13.413	35.816	1871.1	7.534	111.60	4.715
SAM	COL	Colombia	2	0.693	1153540	13.958	3.881	593.1	6.385	422.65	6.047
SAM	ECU	Ecuador	1	0	248705.8	12.424	1.463	1117.2	7.019	188.69	5.240
SAM	PER	Peru	1	0	1302897	14.080	9.184	1555.3	7.349	368.05	5.908
SAM	VEN	Venezuela	1	0	929507.1	13.742	7.076	448.7	6.106	322.41	5.776

Table 3.2 (continued)

area	wbcode	country	A (%)	A (ASIN)	B (%)	B (ASIN)	C (%)	C (ASIN)	D (%)	D (ASIN)	E (%)	E (ASIN)	H (%)	H (ASIN)
EUR	ALB	Albania	0	0	0	0	100	1.571	0	0	0	0	0	0
EUR	AUT	Austria	0	0	0	0	88.17	1.080	0	0	0	0	11.83	0.119
EUR	BEL	Belgium	0	0	0	0	100	1.571	0	0	0	0	0	0
EUR	BGR	Bulgaria	0	0	0	0	100	1.570	0	0	0	0	0	0
EUR	BIH	Bosnia Herz.	0	0	0	0	100	1.571	0	0	0	0	0	0
EUR	BLR	Belarus	0	0	0	0	0	0	100	1.571	0	0	0	0
EUR	CHE	Switzerland	0	0	0	0	0.44	0.004	0	0	0	0	0.56	0.006
EUR	CZE	Czech Repub.	0	0	0	0	98.78	1.415	0.31	0.003	0	0	0.91	0.009
EUR	DEU	Germany	0	0	0	0	94.73	1.245	0	0	0	0	5.27	0.053
EUR	DNK	Denmark	0	0	0	0	100	1.571	0	0	0	0	0	0
EUR	ESP	Spain	0	0	9.144	0.092	88.87	1.095	0	0	0	0	1.98	0.020
EUR	EST	Estonia	0	0	0	0	0	0	100	1.571	0	0	0	0
EUR	FIN	Finland	0	0	0	0	0.60	0.006	92.68	1.186	6.71	0.067	0.00	0
EUR	FRA	France	0	0	0	0	99.29	1.451	0	0	0	0	0.71	0.007
EUR	GBR	United Kingdom	0	0	0	0	100	1.571	0	0	0	0	0	0
EUR	GRC	Greece	0	0	0	0	100	1.571	0	0	0	0	0	0
EUR	HRV	Croatia	0	0	0	0	100	1.571	0	0	0	0	0	0
EUR	HUN	Hungary	0	0	0	0	72.99	0.818	27.01	0.273	0	0	0	0
EUR	IRL	Ireland	0	0	0	0	100	1.571	0	0	0	0	0	0
EUR	ISL	Iceland	0	0	0	0	100	1.571	0	0	0	0	0	0
EUR	ITA	Italy	0	0	0	0	96.94	1.323	0	0	0	0	3.06	0.031
EUR	LVA	Latvia	0	0	0	0	16.31	0.164	83.69	0.992	0	0	0	0
EUR	MKD	Macedonia	0	0	0	0	100	1.571	0	0	0	0	0	0
EUR	MON	Montenegro	0	0	0	0	100	1.571	0	0	0	0	0	0
EUR	NLD	Netherlands	0	0	0	0	100	1.571	0	0	0	0	0	0
EUR	NOR	Norway	0	0	0	0	56.69	0.603	16.94	0.170	18.44	0.185	7.94	0.079
EUR	POL	Poland	0	0	0	0	40.13	0.413	56.44	0.600	0	0	3.43	0.034
EUR	PRT	Portugal	0	0	0	0	100	1.571	0	0	0	0	0	0
EUR	ROM	Romania	0	0	0.31	0.003	26.68	0.270	57.76	0.616	0	0	15.26	0.153
EUR	SRB	Serbia	0	0	0	0	99.72	1.495	0.28	0.003	0	0	0	0
EUR	SVK	Slovakia	0	0	0	0	40.08	0.412	35.48	0.363	0	0	24.44	0.247
EUR	SVN	Slovenia	0	0	0	0	100	1.571	0	0	0	0	0	0
EUR	SWE	Sweden	0	0	0	0	26.03	0.263	68.97	0.761	5.00	0.050	0.00	0
EUR	UKR	Ukraine	0	0	41.00	0.422	1.46	0.015	55.18	0.585	0	0	2.36	0.024
WAS	CYP	Cyprus	0	0	0	0	100	1.571	0	0	0	0	0	0
WAS	GEO	Georgia	0	0	0	0	23.43	0.237	1.87	0.019	0	0	74.70	0.843
WAS	TUR	Turkey	0	0	16.88	0.170	50.41	0.528	0	0	0	0	32.70	0.333
NAS	BTN	Bhutan	0	0	0	0	68.16	0.750	0	0	0	0	31.84	0.324
NAS	CHN	China	0.31	0.003	33.69	0.344	23.79	0.240	17.14	0.172	0	0	25.07	0.253
NAS	IND	India	34.10	0.348	27.72	0.281	31.55	0.321	0	0	0	0	6.64	0.066
NAS	JPN	Japan	0	0	0	0	57.01	0.607	42.99	0.444	0	0	0	0
NAS	MMR	Myanmar	40.04	0.412	0	0	35.76	0.366	0	0	0	0	24.20	0.244
NAS	MNG	Mongolia	0	0	73.64	0.828	0	0	17.05	0.171	0	0	9.31	0.093
NAS	NPL	Nepal	0	0	0	0	62.68	0.677	0	0	0	0	37.32	0.382
NAS	PRK	Korea, DPR	0	0	0	0	0	0	100	1.571	0	0	0	0
NAS	RUS	Russia	0	0	2.87	0.029	0.36	0.004	86.75	1.050	7.76	0.078	2.26	0.023
NAM	CAN	Canada	0	0	2.15	0.022	1.19	0.012	70.55	0.783	22.69	0.229	3.42	0.034
NAM	USA	United States	0.13	0.001	21.98	0.222	37.97	0.389	26.25	0.266	2.67	0.027	11.01	0.110
NAM	GRL	Greenland	0	0	0	0	0	0	0	0	100	1.571	0	0
MEX	MEX	Mexico	20.18	0.203	52.56	0.553	3.73	0.037	0	0	0	0	23.53	0.237
CRB	CUB	Cuba	100	1.571	0	0	0	0	0	0	0	0	0	0
CRB	DOM	Dominican Repub.	100	1.571	0	0	0	0	0	0	0	0	0	0
CAM	CRI	Costa Rica	100	1.570	0	0	0	0	0	0	0	0	0	0
CAM	GTM	Guatemala	67.50	0.741	0	0	0	0	0	0	0	0	32.50	0.331
CAM	HND	Honduras	63.98	0.694	0	0	0	0	0	0	0	0	36.02	0.368
CAM	PAN	Panama	100	1.571	0	0	0	0	0	0	0	0	0	0
CAM	SLV	El Salvador	98.05	1.373	0	0	0	0	0	0	0	0	1.95	0.020
SAM	ARG	Argentina	0.005	0.00004	44.42	0.460	38.71	0.398	0	0	0.11	0.001	16.74	0.168
SAM	BOL	Bolivia	47.30	0.493	0	0	16.99	0.171	0	0	0	0	35.71	0.365
SAM	CHL	Chile	0	0	31.35	0.319	30.82	0.313	0	0	2.89	0.029	34.94	0.357
SAM	COL	Colombia	83.12	0.981	1.40	0.014	0	0	0	0	0	0	15.48	0.155
SAM	ECU	Ecuador	51.26	0.538	0	0	0	0	0	0	0	0	48.74	0.509
SAM	PER	Peru	45.91	0.477	11.84	0.119	8.55	0.086	0	0	0	0	33.69	0.344
SAM	VEN	Venezuela	80.22	0.931	15.39	0.155	0	0	0	0	0	0	4.38	0.044

(Table 3.2) EUR = Europe, WAS = Western Asia, NAS = Northeastern Asia, NAM = North America, Mex = Mexico, CRB = Caribbean, CAM = Central America, SAM = South America. LN = natural log. areakm2 = land area (km^2), cen_lat = latitude of country centroid, elev = mean elevation (meters above sea level), distc = mean distance to nearest coastline (km), A = tropical-type climate category (Af + Am + Aw), B = dry-type climate category (Bs + Bw), C = temperate-type climate category (Cf + Cs + Cw), D = cold (Dw + Df), E = polar-type climate, H = alpine-type climate. ASIN = arcsin. Variables not converted to LN or ASIN are also presented.

3.3. RESULTS

Correlation

A positive correlation were found between species richness and all variables; however, most were weak or very weak ($r^2 < 0.40$). A modest to very strong positive correlation ($r^2 > 0.40$) was seen in four cases which were between latitude, E (polar) and the number of taxa in Northeastern Asia, between B (dry) and the number of taxa in America, and between latitude and the number of taxa (LN) in Northeastern Asia (Table 3.3).

Significant Pearson's correlations were found in 14 cases out of 120 ($P < 0.05$)

as shown in Table 3.3. Those were between area, B (dry climate) and the number of taxa in all countries, between land area and the number of taxa in all countries without Mexico, between land area and the number of taxa in Europe & Western Asia, between latitude, E (polar) and Northeastern Asia, between B (dry) and the number of taxa in America, between land area, B (dry) and the number of taxa (LN) in all countries, between land area and the number of taxa (LN) in all countries without Mexico, between land area and the number of taxa (LN) in Europe and Western Asia, between latitude, E (polar) and the number of taxa (LN) in Northeastern Asia, and between B (dry) and the number of taxa (LN) in America. No significance was seen in other combinations.

When Bonferroni's correlation was applied this fell to only 8 cases and significant correlations, which were between B (dry) and the number of taxa in all countries, between land area and the number of taxa in Europe and Western Asia, between latitude, E (polar) and the number of taxa in Northeastern Asia, between B (dry) and the number of taxa in America, between land area and the number of taxa (LN) in all countries, between land area and the number of taxa (LN) in Europe and Western Asia, and between latitude and the number of taxa (LN) in Northeastern Asia (Table 3.3). Graphs showing the correlations with significance are presented in Fig 3.1.

Table 3.3. Correlations between number of taxa and each value and significance.

a) the number of taxa in all countries

all countries							
	variable	taxa	r	r^2	P-value	Sig.	Sig. Bonf.
area (km^2) (LN)	65	91	0.271	0.073	0.029	*	ns
cen_lat	65	91	0.060	0.004	0.632	ns	ns
elev (LN)	65	91	0.102	0.010	0.418	ns	ns
distc (LN)	65	91	0.022	0.000	0.864	ns	ns
A (Af+Am+Aw)	65	91	0.020	0.000	0.875	ns	ns
B (Bs+Bw)	65	91	0.358	0.128	0.003	**	*
C (Cf+Cs+Cw)	65	91	0.104	0.011	0.411	ns	ns
D (Dw+Df)	65	91	0.055	0.003	0.664	ns	ns
E	65	91	0.041	0.002	0.748	ns	ns
H	65	91	0.049	0.002	0.699	ns	ns

b) the number of taxa in all countries without Mexico

all countries without Mexico							
	variable	taxa	r	r^2	P-value	Sig.	Sig. Bonf.
area (km^2) (LN)	64	45	0.328	0.107	0.008	**	ns
cen_lat	64	45	0.131	0.017	0.303	ns	ns
elev (LN)	64	45	0.007	0.000	0.953	ns	ns
distc (LN)	64	45	0.029	0.001	0.819	ns	ns
A (Af+Am+Aw)	64	45	0.051	0.003	0.687	ns	ns
B (Bs+Bw)	64	45	0.022	0.000	0.861	ns	ns
C (Cf+Cs+Cw)	64	45	0.019	0.000	0.880	ns	ns
D (Dw+Df)	64	45	0.006	0.000	0.963	ns	ns
E	64	45	0.055	0.003	0.667	ns	ns
H	64	45	0.134	0.018	0.293	ns	ns

c) the number of taxa in Europe and Western Asia

Europe and Western Asia							
	variable	taxa	r	r^2	P-value	Sig.	Sig. Bonf.
area (km^2) (LN)	37	20	0.480	0.231	0.003	**	*
cen_lat	37	20	0.116	0.014	0.493	ns	ns
elev (LN)	37	20	0.235	0.055	0.161	ns	ns
distc (LN)	37	20	0.008	0.000	0.961	ns	ns
A (Af+Am+Aw)	37	20	0.046	0.002	0.788	ns	ns
B (Bs+Bw)	37	20	0.054	0.003	0.753	ns	ns
C (Cf+Cs+Cw)	37	20	0.021	0.000	0.900	ns	ns
D (Dw+Df)	37	20	0.138	0.019	0.414	ns	ns
E	37	20	0.062	0.004	0.715	ns	ns
H	37	20	0.105	0.011	0.536	ns	ns

Table 3.3 (continued)

d) the number of taxa in Northeastern Asia

Northeastern Asia							
	variable	taxa	r	r^2	P-value	Sig.	Sig. Bonf.
area (km^2) (LN)	9	7	0.612	0.375	0.080	ns	ns
cen_lat	9	7	0.841	0.707	0.005	**	*
elev (LN)	9	7	0.529	0.280	0.143	ns	ns
distc (LN)	9	7	0.328	0.108	0.389	ns	ns
A (Af+Am+Aw)	9	7	0.320	0.102	0.402	ns	ns
B (Bs+Bw)	9	7	0.068	0.005	0.862	ns	ns
C (Cf+Cs+Cw)	9	7	0.389	0.151	0.301	ns	ns
D (Dw+Df)	9	7	0.423	0.179	0.256	ns	ns
E	9	7	0.933	0.871	0.000	***	**
H	9	7	0.455	0.207	0.219	ns	ns

e) the number of taxa in America

America							
	variable	taxa	r	r^2	P-value	Sig.	Sig. Bonf.
area (km^2) (LN)	18	70	0.239	0.057	0.340	ns	ns
cen_lat	18	70	0.065	0.004	0.797	ns	ns
elev (LN)	18	70	0.081	0.007	0.750	ns	ns
distc (LN)	18	70	0.034	0.001	0.895	ns	ns
A (Af+Am+Aw)	18	70	0.226	0.051	0.367	ns	ns
B (Bs+Bw)	18	70	0.648	0.419	0.004	**	*
C (Cf+Cs+Cw)	18	70	0.006	0.000	0.981	ns	ns
D (Dw+Df)	18	70	0.013	0.000	0.959	ns	ns
E	18	70	0.100	0.010	0.693	ns	ns
H	18	70	0.078	0.006	0.759	ns	ns

f) the number of taxa in America without Mexico

America without Mexico							
	variable	taxa	r	r^2	P-value	Sig.	Sig. Bonf.
area (km^2) (LN)	17	24	0.242	0.059	0.349	ns	ns
cen_lat	17	24	0.250	0.062	0.333	ns	ns
elev (LN)	17	24	0.394	0.155	0.117	ns	ns
distc (LN)	17	24	0.024	0.001	0.927	ns	ns
A (Af+Am+Aw)	17	24	0.122	0.015	0.641	ns	ns
B (Bs+Bw)	17	24	0.112	0.012	0.670	ns	ns
C (Cf+Cs+Cw)	17	24	0.336	0.113	0.187	ns	ns
D (Dw+Df)	17	24	0.268	0.072	0.299	ns	ns
E	17	24	0.142	0.020	0.588	ns	ns
H	17	24	0.087	0.008	0.740	ns	ns

Table 3.3 (continued)

g) the number of taxa (LN) in all countries

all countries							
	variable	taxa (LN)	r	r^2	P-value	Sig.	Sig. Bonf.
area (km^2) (LN)	65	91	0.375	0.140	0.002	**	*
cen_lat	65	91	0.116	0.013	0.358	ns	ns
elev (LN)	65	91	0.078	0.006	0.535	ns	ns
distc (LN)	65	91	0.068	0.005	0.590	ns	ns
A (Af+Am+Aw)	65	91	0.123	0.015	0.328	ns	ns
B (Bs+Bw)	65	91	0.256	0.066	0.039	*	ns
C (Cf+Cs+Cw)	65	91	0.052	0.003	0.679	ns	ns
D (Dw+Df)	65	91	0.005	0.000	0.966	ns	ns
E	65	91	0.078	0.006	0.535	ns	ns
H	65	91	0.059	0.003	0.641	ns	ns

h) the number of taxa (LN) in all countries without Mexico

all countries without Mexico							
	variable	taxa (LN)	r	r^2	P-value	Sig.	Sig. Bonf.
area (km^2) (LN)	64	45	0.344	0.118	0.005	*	ns
cen_lat	64	45	0.208	0.043	0.099	ns	ns
elev (LN)	64	45	0.027	0.001	0.835	ns	ns
distc (LN)	64	45	0.073	0.005	0.569	ns	ns
A (Af+Am+Aw)	64	45	0.144	0.021	0.258	ns	ns
B (Bs+Bw)	64	45	0.076	0.006	0.553	ns	ns
C (Cf+Cs+Cw)	64	45	0.011	0.000	0.929	ns	ns
D (Dw+Df)	64	45	0.044	0.002	0.730	ns	ns
E	64	45	0.078	0.006	0.538	ns	ns
H	64	45	0.134	0.018	0.292	ns	ns

i) the number of countries (LN) in Europe and Western Asia

Europe and Western Asia							
	variable	taxa (LN)	r	r^2	P-value	Sig.	Sig. Bonf.
area (km^2) (LN)	37	20	0.522	0.273	0.001	***	**
cen_lat	37	20	0.057	0.003	0.738	ns	ns
elev (LN)	37	20	0.306	0.094	0.065	ns	ns
distc (LN)	37	20	0.062	0.004	0.714	ns	ns
A (Af+Am+Aw)	37	20	0.110	0.012	0.516	ns	ns
B (Bs+Bw)	37	20	0.083	0.007	0.625	ns	ns
C (Cf+Cs+Cw)	37	20	0.071	0.005	0.674	ns	ns
D (Dw+Df)	37	20	0.095	0.009	0.577	ns	ns
E	37	20	0.169	0.029	0.317	ns	ns
H	37	20	0.126	0.016	0.456	ns	ns

Table 3.3 (continued)

j) the number of taxa (LN) in Northeastern Asia

Northeastern Asia							
	variable	taxa (LN)	r	r^2	P-value	Sig.	Sig. Bonf.
area (km^2) (LN)	9	7	0.639	0.408	0.064	ns	ns
cen_lat	9	7	0.850	0.722	0.004	**	*
elev (LN)	9	7	0.476	0.227	0.195	ns	ns
distc (LN)	9	7	0.270	0.073	0.483	ns	ns
A (Af+Am+Aw)	9	7	0.404	0.164	0.280	ns	ns
B (Bs+Bw)	9	7	0.089	0.008	0.819	ns	ns
C (Cf+Cs+Cw)	9	7	0.379	0.144	0.314	ns	ns
D (Dw+Df)	9	7	0.353	0.125	0.352	ns	ns
E	9	7	0.794	0.630	0.011	*	ns
H	9	7	0.490	0.240	0.181	ns	ns

k) the number of taxa (LN) in America

America							
	variable	taxa (LN)	r	r^2	P-value	Sig.	Sig. Bonf.
area (km^2) (LN)	18	70	0.346	0.120	0.159	ns	ns
cen_lat	18	70	0.199	0.040	0.428	ns	ns
elev (LN)	18	70	0.104	0.011	0.682	ns	ns
distc (LN)	18	70	0.092	0.008	0.717	ns	ns
A (Af+Am+Aw)	18	70	0.305	0.093	0.218	ns	ns
B (Bs+Bw)	18	70	0.549	0.301	0.018	*	ns
C (Cf+Cs+Cw)	18	70	0.203	0.041	0.420	ns	ns
D (Dw+Df)	18	70	0.179	0.032	0.476	ns	ns
E	18	70	0.173	0.030	0.492	ns	ns
H	18	70	0.095	0.009	0.708	ns	ns

l) the number of taxa (LN) in America without Mexico

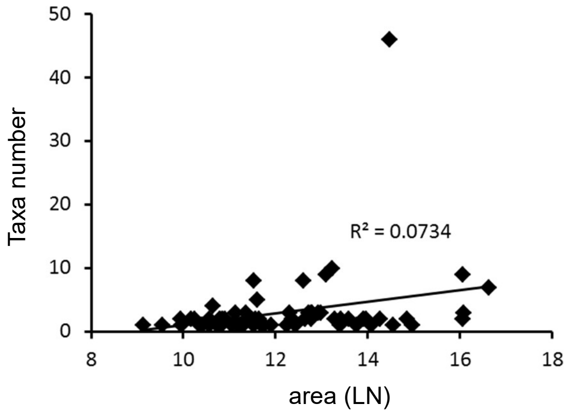
America without Mexico							
	variable	taxa (LN)	r	r^2	P-value	Sig.	Sig. Bonf.
area (km^2) (LN)	17	24	0.309	0.095	0.228	ns	ns
cen_lat	17	24	0.280	0.078	0.277	ns	ns
elev (LN)	17	24	0.337	0.114	0.186	ns	ns
distc (LN)	17	24	0.103	0.011	0.695	ns	ns
A (Af+Am+Aw)	17	24	0.233	0.054	0.369	ns	ns
B (Bs+Bw)	17	24	0.156	0.024	0.550	ns	ns
C (Cf+Cs+Cw)	17	24	0.370	0.137	0.144	ns	ns
D (Dw+Df)	17	24	0.340	0.116	0.182	ns	ns
E	17	24	0.178	0.032	0.494	ns	ns
H	17	24	0.033	0.001	0.901	ns	ns

Significance (* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$). Sig. Bonf. (* = 0.005, ** = 0.0001). ns = not significant.

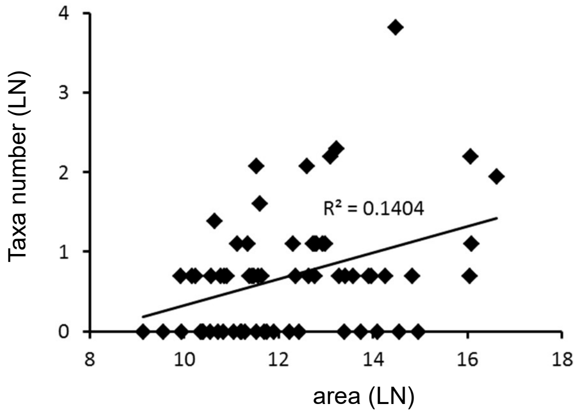
Fig. 3.1. Correlations between the number of taxa and variables with significance.

a) area in all countries, b) area in all countries (LN), c) B (dry) in all countries, d) B (dry) in all countries (LN), e) area in all countries without Mexico, f) area in all countries without Mexico (LN), g) area in Europe and Western Asia, h) area in Europe and Western Asia (LN), i) latitude in Northeastern Asia, j) latitude in Northeastern Asia (LN), k) E (polar) in Northeastern Asia, l) E (polar) in Northeastern Asia (LN), m) B (dry) in America, n) B (dry) in America (LN)

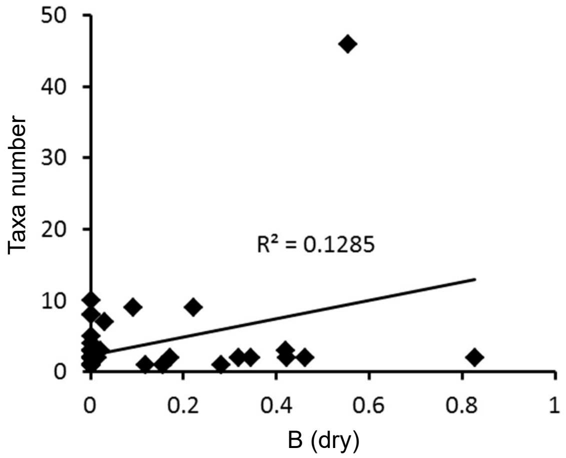
a) area in all countries



b) area in all countries (LN)



c) B (dry) in all countries



d) B (dry) in all countries (LN)

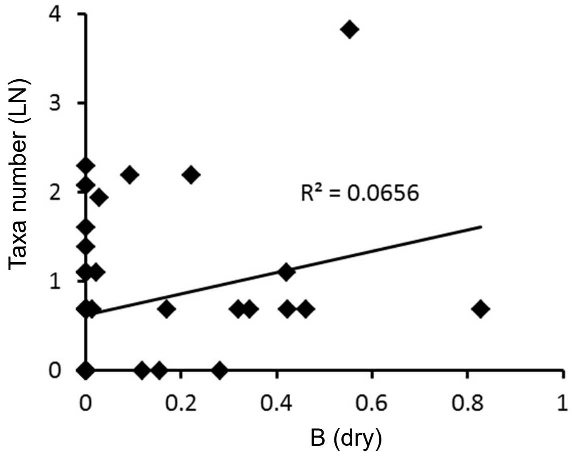


Fig. 3.1 (continued)

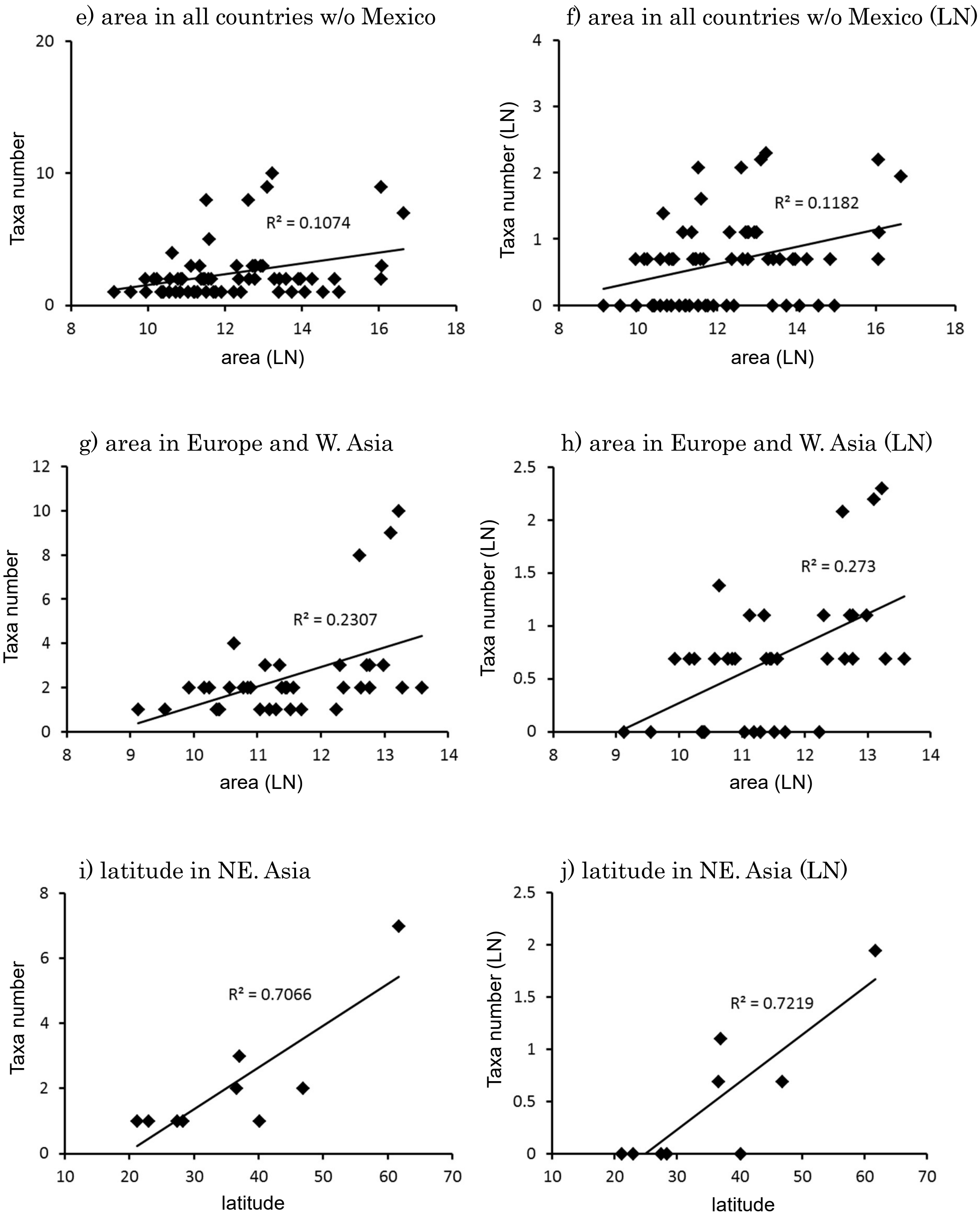
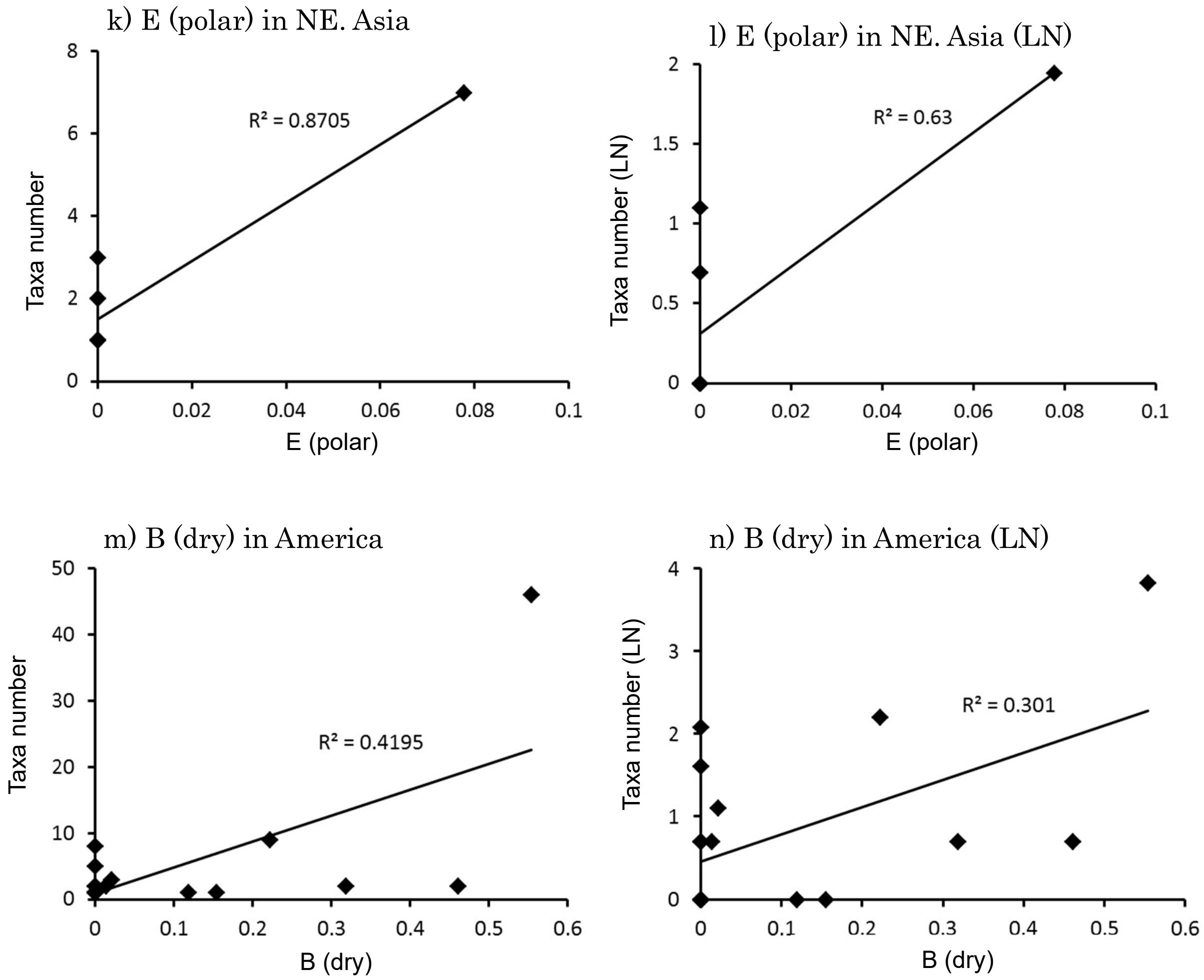


Fig. 3.1 (continued)



Impact of Mexican taxa

When Mexico was removed from the analysis due to the extremely high species diversity (nearly five times greater than the next most specious country, France with 10 taxa), the correlation between the number of taxa in all countries and B (dry) was weaker with no significance ($P > 0.05$). Similarly, when it was removed, the correlation between the number of taxa in America and B (dry) was weaker with no significance. It was also seen in the same pairwise comparison when the number of taxa was logged.

Multiple correlations

Only 4 cases of multiple correlations were tested as shown in Table 3.4 when two values showed significance (Table 3.3a, d, g, and j). Among land area, B (dry), and the number of taxa in all countries, very weak positive multiple correlations (r^2 = 0.139) were seen with a significance or $P < 0.01$, but only B (dry) was significantly correlated with the number of taxa ($P < 0.05$) (Table 3.4a). Among land area, B (dry), and the number of taxa (LN) in all countries, very weak positive correlations (r^2 = 0.146) were seen with a significance of $P < 0.01$, but only the land area was significantly correlated with the number of taxa ($P < 0.05$) (Table 3.4b). Among latitude, E (polar), and the number of taxa in Northeastern Asia, a very strong correlation (r^2 = 0.913) was seen with a high significance of $P < 0.001$; however, only E (polar) was significantly correlated with the number of taxa ($P < 0.01$) (Table 3.4c). Among latitude, E (polar), and the number of taxa (LN) in Northeastern Asia, strong positive correlations (r^2 = 0.775) with a significance of $P < 0.05$; however, each individual value did not show any significance for correlations (Table 3.4d).

Table 3.4. Multiple regression analyses between environmental factors and the number of *Pinguicula* taxa. a) multiple regression among the number of taxa in all countries, land area, and B (dry), b) multiple regression among the number of taxa (LN) in all countries, land area, and B (dry), c) multiple regression among the number of taxa in Northeastern Asia, latitude, and E (polar), d) multiple regression among the number of taxa in Northeastern Asia (LN), latitude, and E (polar)

a)

land area, B (dry), and number of taxa in all countries				
Regression statistics			Coeffic.	P-value
r	0.373	Intercept	–2.512	0.653
r^2	0.139**	land area	0.401	0.391
Observ.	65	B (dry)	10.681	0.034

** = $P < 0.01$ (Sign. F = 0.0097)

b)

land area, B (dry), and number of taxa (LN) in all countries				
Regression statistics			Coeffic.	P-value
r	0.387	Intercept	–1.109	0.129
r^2	0.146**	land area	0.145	0.019
Observ.	65	B (dry)	0.408	0.526

** = $P < 0.01$ (Sign. F = 0.008)

c)

latitude, E (polar), and number of taxa in NE. Asia				
Regression statistics			Coeffic.	P-value
r	0.955	Intercept	–0.068	0.945
r^2	0.913***	latitude	0.048	0.138
Observ.	9	E (polar)	52.689	0.009

*** = $P < 0.001$ (Sign. F = 0.0007)

d)

latitude, E (polar), and number of taxa (NL) in NE. Asia				
Regression statistics			Coeffic.	P-value
r	0.880	Intercept	–0.703	0.235
r^2	0.775*	latitude	0.031	0.097
Observ.	9	E (polar)	9.356	0.278

* = $P < 0.05$ (Sign. F = 0.011)

3.4. DISCUSSION

Here, it is aimed to determine which geographical and environmental factors (i.e. land area, latitude, elevation, distance to nearest coastline, or climates) best explain patterns of species richness in *Pinguicula* and if such factors consistently characterise the distribution of *Pinguicula* in different regions.

The results suggested overall very weak or weak positive correlation that proved to be non-significant, with only a few cases of significant correlations. There could be a few possible reasons, in particular the number of countries having only one or two species may have affected the analysis. If this is the case, larger geographical units may be more appropriate or alternatively the analysis should concentrate on smaller geographical areas such as Mexico. Another reason for the lack of significant correlation could be that the wide distribution range of the genus, from the equator to the polar regions, and sea level to over 4,500 m altitude (Casper 1966, Heslop-Harrison 2004, Chapter 4), may present less clear correlations.

Although the number of taxa was only weakly and positively correlated with land area, it was significantly ($P < 0.05$ to $P < 0.001$) supported in all countries and in Europe and Western Asia. While larger areas may be able to hold more species, larger areas potentially have a more diverse range of habitats or ecological heterogeneity resulting in greater species richness (Johnson and Simberloff 1974, Kohn and Walsh 1994). This theory is likely true also for the case of species richness in *Pinguicula*; however, the correlation is not seen in Northeastern Asia and America. It is potentially due to large distribution gaps (e.g. deserts) in those regions thus affecting the number of species.

In the main, absolute latitude was not found to be significantly correlated with species richness. However, there was a significant correlation ($P < 0.01$) between species richness and latitude in Northeastern Asia. In this region, six species (*P. algida* Malyschev, *P. alpina* L., *P. macroceras* Link, *P. spathulata* Ledeb., *P. villosa* L., and *P. vulgaris*) are found in Siberia and the Russian Far East, while only one species (*P. alpina*) is found in Bhutan, India, Myanmar, and Nepal, located at more south (Casper 1966). *P. alpina* is regarded as one of the glacial relics (Turesson 1927), and the populations in the Himalayas and southwestern China are isolated from those in Russia and Europe (Casper 1962, 1966, Chapter 4).

Species richness was not found to be correlated with altitude. Casper (1966) discussed the altitudinal distribution of *Pinguicula*, and a number of *Pinguicula* taxa are confined to a specific altitudinal range that is considered as one of the important distribution factors (Casper 1966, Zamudio 2001, Heslop-Harrison 2004). The altitudinal factor may be important for the distribution of each species; however, the results suggest that species richness of the genus is relatively constant regardless of altitudes. It is also possible that countries having only one or two species may affect the result.

The number of taxa is not correlated with distance to nearest coastline, suggesting that species richness of *Pinguicula* can be found regardless of distance to coastline. A number of taxa are confined to higher elevation (Zamudio 2001), while some other taxa are found in only coastal regions or islands (Wood and Godfrey 1957).

Significant positive correlations were found between the number of *Pinguicula* taxa and two climate categories. Firstly, the number of taxa in all countries was significantly correlated with climate B (dry) with a significance of $P < 0.01$ (Table 3.3a), and it was significantly correlated when the number of taxa was log transformed (LN) ($P < 0.05$) (Table 3.3g). The number of taxa in America was also significantly correlated with B (dry) (Table 3.3e). This suggests that species richness in *Pinguicula* is seen in arid regions as suggested by Blanca et al. (1999).

Species richness is strongly affected by the diversity of habitats which may be associated with various environmental or ecological factors (Traxmandlová et al. in press). Ohlemüller et al. (2008) demonstrated that species richness with small geographical ranges are frequently seen in wet areas surrounded by dry climate, often confined to higher elevations, or rare climates. It should be noted that approximately 53 % of Mexico is covered by dry climate (B) particularly in the north as shown by Peel et al. (2007). The habitat of *Pinguicula* in Mexico is, however, more often found in the central and southern part of Mexico but it is sparse in the north (Zamudio 2001, 2005, Chapter 4). Therefore, a more detailed study is needed to provide an understanding of the environmental factors that drive species richness in *Pinguicula* in Mexico. It is possible that the habitats of *Pinguicula* stand in a very specific environment and ecosystem in a wide climate area (Blanca et al. 1999, Heslop-Harrison 2004).

Secondly, the number of taxa in Northeastern Asia was positively correlated with climate E (polar) with a high significance of $P < 0.001$ (Table 3.3d), and when the number of taxa was log transformed with E (polar) it was $P < 0.05$ (Table 3.3j). In Northeastern Asia, the southern half is mostly very dry (deserts); only *P. alpina* is found in the higher elevations of the Himalayas and southwestern China (Casper 1962, 1966). Due to the large distribution gaps in this region, as mentioned, the distribution of *Pinguicula* is mostly found in Siberia to the Russian Far East. All species in this region form hibernacula to resist the harsh winter (Legendre 2000).

The hibernacula formed in some *Pinguicula* are small dormant buds (up to 20 mm long) tightly formed by 12-15 small leaves to survive the winter (Heslop-Harrison 1962). The formation of a hibernaculum is induced by a combination of short day length and low night temperature (Heslop-Harrison 1962). This strategy is probably as a result of adaptation to the cold winter and such species could have colonised the north or cold regions with subsequent speciation. Due to warm periods in the last ca. 10,000 years, a number of plant species are confined to higher elevations under a rare climate (Ohlemüller et al. 2008).

There were no significant correlations between the number of taxa and other climate types in the other regions. Although Bakkenes et al. (2002) suggested that the species richness in plants was correlated with climate, the number of taxa in *Pinguicula* is not absolutely correlated with each climate. A possible reason could be that the genus is wide spread and it is difficult to generalise the climatic preference. A number of *Pinguicula* taxa are, however, found only under specific environments such as seasonal temperatures, precipitations, soil types, and light intensity (Blanca 2001, Zamudio 2001, Heslop-Harrison 2004). In some large areas, uniform climate and simpler geography associate with small biodiversity in plant species (Qian and Ricklefs 2000).

Further detailed studies are needed particularly within centres of diversity such as Mexico and Europe, to provide an understanding of the factors that influence species richness. In climate B (dry), for example, what variables specifically affect species richness is less clear in the current study. If speciation and biodiversity of *Pinguicula* are apparently correlated with small wet areas in a large dry environment, i.e. isolation of habitats by ecological barriers, those are assumed to be as a result of adaptation to a localized climate or very narrow ecological niche. Using more detailed and small scale variables, such as a trait analysis, may elucidate the factors influencing species richness of the genus instead of large scale criteria used in this study.

Legendre (2000) hypothesised that *Pinguicula* originated in either the Mediterranean or the Caribbean region, and spread to neighbouring areas. Possessing heterophyllous (summer and winter leaves) characteristics in some taxa may be as a result of adaptation to an unfavourable season and may have originated independently in the two regions, “Mexico and Central America” and the “temperate regions of

Northern Hemisphere".

Only 4 multiple correlations were analysed in this study. In general, more species are found in dry areas in larger countries. In Northeastern Asia, more species are found at colder regions in the north. Although significant multiple correlations were suggested in all cases, not necessarily each variable significantly affects the number of taxa. It is probable that smaller scales, such as protected areas or island, instead of whole land areas, are more strongly affected species richness (Kohn and Walsh 1994, Schödelbauerová et al. 2009). Again, more detailed studies are needed for the multiple correlations which correlated factors influence species richness in *Pinguicula*.

3.5. CONCLUSION

In general, the number of *Pinguicula* taxa was positively correlated with land area in all countries and Europe and Western Europe; however, no correlations were found in Northeastern Asia and America. The number of taxa was also positively correlated with climate B (dry) in all countries and in America. The results suggested that the Mexican taxa had a great impact for the species richness. Climate E (polar) affects species richness only in Northeastern Asia. A number of *Pinguicula* are often found in small wet places in a large dry region. It is likely that small environmental variables should be more useful for analysing factors affecting species richness in *Pinguicula* that may result speciation in rare climates. A further detailed study will be needed to evaluate the correlation between species richness and environmental factors.

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CHAPTER 4

A revision of the genus *Pinguicula* L.

4.1. INTRODUCTION

Taxonomy based on morphology

In the Pre-Linnaean literatures, *Pinguicula* was already documented in the 16th century in Europe. Clusius (1585) was aware of at least two flower colours, white and purple, of the populations in the Austrian Alps. Later, Linnaeus (1737) recognised at least three species in his "Flora Lappland". Linnaeus (1753) first established the genus *Pinguicula* L. (spelled as *Pingvicula* in the original publication), one of the genera in Lentibulariaceae Rich., in his "Species Plantarum" on the basis of primary plant nomenclature and taxonomy. At that time, Linnaeus (1753) recognised only four European *Pinguicula* species (*P. alpina* L., *P. lusitanica* L., *P. vulgaris* L., and *P. villosa* L.). The scientific name *Pinguicula* has been attributed to the Latin word *pinguis* or fat because of greasy-looking or oily-texture leaves densely covered by mucilage (Lloyd 1942, Juniper et al. 1989). It was originally derived from "*De raris et admirandis herbis*" by Gesner in 1555 (Blanca 2001).

Du Mortier (1829) established Pinguiculaceae Du Mort. but it was basically a synonym of Lentibulariaceae. Most taxonomists are adopted Lentibulariaceae, incorporating the three carnivorous plant genera *Pinguicula*, *Genlisea* St.-Hil., and *Utricularia* L. (two genera, *Biovularia* Kamieński and *Polypompholyx* Lehm. have recently been often included in *Utricularia*, e.g. Taylor 1989) in their classifications. The genus *Isoloba* Raf., having five almost equally divided corolla lobes, including four species from the southeastern United States was divided from the genus *Pinguicula* by Rafinesque (1836); however, the genus *Isoloba* is currently not recognised. Some taxonomical works of the genus *Pinguicula* has been chronologically summarised in Table 4.1.

An earlier subgeneric taxonomical treatment was carried out by De Candolle (1844), who recognised three sections (*Orcheosanthus*, *Pionophyllum*, and *Brandonia*) including 30 species from all regions where *Pinguicula* occur. This classification was based on morphology and flower colour. Hence, the section *Orcheosanthus* bears a large purplish flower with a very short tube resembling an orchid flower, the section *Pionophyllum* has a wider variation in flower colours (e.g. blue, purple, or white) with a cylindrical or conical tube, and the section *Brandonia* comprises only one yellow campanulate-flowered species (*P. lutea* Walter).

Barnhart (1916) separated the genus into four subgenera (i.e. *Isoloba*, *Pionophyllum*, *Orcheosanthus*, and *Temnoceras*). Although the actual number of species in each subgenus is not specified, except the subgenus *Temnoceras* (comprising only one species: *P. crenatiloba* DC.), approximately 33 species were included in the genus. Those are subgenera *Isoloba* with almost equally divided corolla lobes (ca. 11 species), *Pionophyllum*, (ca. 15 species), *Orcheosanthus* (ca. six species), and *Temnoceras* having deeply divided corolla lips (one species).

Table 4.1. Taxonomic treatments of the genus *Pinguicula.* Some representative taxonomic treatments are listed in the table.

De Candolle (1844)	**Barnhart** (1916)	**Ernst** (1961)
[3 sections, 30 species]	[4 subg., ca. 33 species]	[3 sections, 35 species]
1. Sect. *Orcheosanthus*	1. Subg. *Isoloba*	1. Sect. *Temnoceras*
P. oblongiloba	*P. pumila*	*P. crenatiloba*
P. orchidioides	*P. lutea*	2. Sect. *Orcheosanthus*
P. moranensis	*P. lusitanica*	*P. caudata*
P. caudata	(total ca.11 species)	3. Sect. *Pionophyllum*
2. Sect. *Pionophyllum*	2. Subg. *Pionophyllum*	*P. vulgaris*
P. acuminata	*P. vulgaris*	*P. leptoceras*
P. acutifolia	(total ca. 15 species)	*P. corsica*
P. heterophylla	3. Subg. *Orcheosanthus*	*P. longifolia*
P. vulgaris	*P. caudata*	*P. vallisneriaefolia*
P. gypsophila	(total ca. 6 species)	*P. reichenbachiana*
P. leptoceras	4. Subg. *Temnoceras*	*P. grandiflora*
P. grandiflora	*P. crenatiloba*	*P. villosa*
P. involuta	(total 1 species)	*P. benedicta*
P. australis		*P. jackii*
P. calyptrata		*P. albida*
P. lusitanica		*P. filifolia*
P. crystallina		*P. heterophylla*
P. crenatiloba		*P. parvifolia*
P. obtusiloba		*P. acuminata*
P. villosa		*P. obtusiloba*
P. microceras		*P. lignicola*
P. macroceras		*P. cladophila*
P. daurica		*P. alpina*
P. antarctica		*P. variegata*
P. pumila		*P. antarctica*
P. elatior		*P. chilensis*
P. lilacina		*P. involuta*
P. alpina		*P. calyptrata*
P. variegata		*P. elongata*
P. spathulata		*P. hirtiflora*
3. Sect. *Brandonia*		*P. crystallina*
P. lutea		*P. lusitanica*
		P. lilacina
		P. pumila
		P. planifolia
		P. coerulea
		P. lutea

Table 4.1 (continued)

Casper (1966a)
[3 subg., 12 sections, 46 species]

I. Subgenus *Isoloba*
  1. Sect. *Isoloba*
    Subsect. *Pumiliformis*
      P. lusitanica
    Subsect. *Agnatiformis*
      P. pumila
      P. lilacina
    Subsect. *Primuliformis*
      Ser. *Pumilioideae*
        P. ionantha
      Ser. *Emarginatae*
        P. primuliflora
        P. planifolia
        P. caerulea
        P. lutea
  2. Sect. *Agnata*
    Subsect. *Agnata*
      Ser. *Agnatae*
        P. agnata
      Ser. *Albidae*
        P. albida
        P. filifolia
    Subsect. *Homophylliformis*
      P. benedicta
  3. Sect. *Discoradix*
      P. lignicola
      P. cladophila
  4. Sect. *Heterophyllum*
    Subsect. *Isolobopsis*
      P. heterophylla
      P. acuminata
      P. parvifolia
    Subsect. *Orcheosanthopsis*
      P. imitatrix
  5. Sect. *Cardiophyllum*
      P. hirtiflora
      P. crystallina

II. Subgenus *Temnoceras*
  6. Sect. *Temnoceras*
      P. crenatiloba
  7. Sect. *Ampullipalatum*
    Subsect. *Heterophylliformis*
      P. elongata
    Subsect. *Alpiniformis*
      Ser. *Andinae*
        P. calyptrata
        P. involuta
        P. chilensis
      Ser. *Antarcticae*
        P. antarctica
  8. Sect. *Micranthus*
      Ser. *Alpinae*
        P. alpina
      Ser. *Variegatae*
        P. variegata
        P. ramosa

III. Subgenus *Pinguicula*
  9. Sect. *Homophyllum*
      P. jackii
  10. Sect. *Orcheosanthus*
    Subsect. *Violiformis*
      P. gypsicola
    Subsect. *Orchidopsis*
      Ser. *Cyclosectae*
        P. cyclosecta
        P. colimensis
      Ser. *Caudatae*
        P. moranensis
    Subsect. *Caudatopsis*
        P. macrophylla
        P. oblongiloba
  11. Sect. *Pinguicula*
      Ser. *Longifoliae*
        P. vallisneriifolia
        P. longifolia
      Ser. *Hispanicae*
        P. nevadensis
      Ser. *Montanae*
        P. corsica
        P. leptoceras
      Ser. *Grandiflorae*
        P. grandiflora
      Ser. *Balcanicae*
        P. balcanica
      Ser. *Septentrionales*
        P. vulgaris
        P. macroceras
  12. Sect. *Nana*
        P. villosa

Newly proposed subfamily and sections after Casper (1966a)

Komiya (1972)
[1 subfamily, 4 sections]

Subfamily Pinguiculoideae
  1. Sect. *Isoloba*
      P. elatior (type)
  2. Sect. *Pionophyllum*
      P. vulgaris (type)
  3. Sect. *Orcheosanthus*
      P. caudata (type)
  4. Sect. *Temnoceras*
      P. crenatiloba (type)

Speta and Fuchs (1982)
  Sect. *Crassifolia*
    P. ehlersiae
    P. esseriana

Zamudio and Rzedowski (1991)
  Sect. *Longitubus*
    P. crassifolia
    P. hemiepiphytica
    P. utricularioides

Luhrs (1995a)
  Sect. *Orchidioides*
    P. laxifolia

Blanca, Ruiz-Rejón and Zamora (1999)
  Sect. *Longifoliae*
    P. vallisneriifolia
    P. longifolia
    P. mundi

Luhrs and Lampard (2006)
  Sect. *Microphyllum*
    P. immaculata
    P. nivalis
    P. gracilis

Ernst (1961) did not recognise subgenera, rather three sections and 35 species. Those were the monotypic sections *Temnoceras* (*P. crenatiloba*) and *Orcheosanthus* (*P. caudata* Schlecht.), and the section *Pionophyllum* with the remaining 33 species. Thus, intrageneric classifications by the three taxonomists (De Candolle 1844, Barnhart 1916, and Ernst 1961) were inconsistent.

Casper (1962a) reviewed *Pinguicula* species in Eurasia and listed 16 species in the continent. The most recent taxonomic work covering the entire genus was that of Casper (1966a), who recognised three subgenera, 12 sections and 46 species based on morphological characteristics derived from herbarium studies. The three subgenera were *Isoloba*, having almost equally divided corolla lobes (i.e. subactinomorphic corollas), *Temnoceras,* with more or less white to pale coloured zygomorphic corollas, and *Pinguicula,* with darker coloured zygomorphic corollas.

Komiya (1972) divided Lentibulariaceae into three subfamilies, Pinguiculoideae, Genliseoideae, and Utricularioidae, which are at present considered equivalent to the genera *Pinguicula*, *Genlisea* and *Utricularia*, respectively. Pinguiculoidae consisted of the genus *Pinguicula* alone. Komiya (1972) recognised a further four sections likewise Barnhart's (1916) subgenera; *Isoloba*, *Pionophyllum*, *Orcheosanthus*, and *Temnoceras*.

After Casper (1966a), a number of species have been described mostly from Europe (e.g. Tammaro and Pace 1987, Zamora et al. 1996, Casper and Steiger 2001, Conti and Peruzzi 2006), Mexico (e.g. Speta and Fuchs 1982, 1989, 1992, Zamudio 1988, 1997a, 1999a, 2001a, Cheek 1994) and Cuba (e.g. Casper 2003, Casper and Urquiola 2003). At the same time, several sections have been established by various researchers, such as the sections *Crassifolia* (Speta and Fuchs 1982), *Orchidioides* (Luhrs 1995a), *Longitubus* (Zamudio and Rzedowski 1991), and *Microphyllum* (Luhrs and Lampard 2006).

In 2010, Schlauer has recognised 94 species and 8 intraspecific taxa in his database available at the website (http://www.omnisterra.com/bot/cp_home.cgi). To date while there may be some differences of opinions amongst taxonomists, the genus basically comprises three subgenera, 16 sections and approximately 90 species based on morphology. Therefore, the number of species has almost doubled since Casper's (1966a) revision of the genus. The current classification and distribution areas are summarised in Table 4.2.

In some species (e.g. *P. moranensis* sl., *P. crystallina* – *P. hirtiflora* complex), great morphological diversities are seen, and has caused much taxonomical confusion. Intraspecific ranks are sometimes applied; however, it is difficult to distinguish one from another because of continuous morphological characters. In spite of enormous morphological diversities in *P. moranensis* Kunth, Zamudio (1999b) attempted to divide the species into two varieties. It is common that Mexican taxa morphologically similar to *P. moranensis* have been temporally added to *P. moranensis*. Therefore, *P. moranensis* is somewhat a 'dumping ground' for miscellaneous taxon. Further investigation involving molecular methods may lead to a clearer understanding of the relationships within the genus.

Cytology

Chromosome number can be useful in taxonomic studies. Chromosome numbers of *Pinguicula* have been reported in many species and those are $2n = 12$, 16, 18, 22, 24, 27, 28, 32, 48, 56, 64, and 128 (Table 4.3). The possible basic chromosome numbers are speculated to be $x = 6$, 8, 9, 11, and 14 ($x = 9$ may need a critical review). Possible ploidy levels are either $2n$ (diploid), $3n$ (triploid), $4n$ (tetraploid), $6n$ (hexaploid), $8n$ (octoploid), and $16n$ (hexadecaploid). Unfortunately, most of the earlier works reporting chromosome numbers did not present photographic evidence and it is impossible to reconfirm the number visually. More recently, Casper and Stimper (2009) observed chromosome numbers in 82 taxa and presented photographs for most of them.

In their work, the chromosome number in some species (e.g. *P. dertosensis* (Cañig.) Mteo et Crespo, *P. fiorii* Tammaro et Pace, *P. mundi* Blanca, Jamilena, Ruiz-Rejón et Zamora, and *P. primuliflora* Wood et Godfrey) disagreed with those previously reported by various authors.

Karyotype studies within the genus are difficult since the length of chromosomes is very short, 0.5-4.0 µm (Yoshimura 1973, Uchiyama 1990). Furthermore, the basic chromosome numbers speculated by Casper and Stimper (2009) in each subgenus varies greatly, for example $x = 6$, 8, 9, 11, and 14 for the subgenus *Isoloba*, $x = 8$, 9, and 11 for the subgenus *Temnoceras*, and $x = 8$ and 11 for the subgenus *Pinguicula*. The basic number and the taxonomy by Casper (1966a) do not show clear correlations.

Table 4.2. Morphological Classification and distribution areas in *Pinguicula*. *Pinguicula* species normally considered valid are listed (not necessarily all of them are accepted in this work), but intraspecific taxa are not shown. The classification follows Casper (1966a), Luhrs (1995a), Luhrs and Lampard (2006), Speta and Fuchs (1982), and Zamudio and Rzedowski (1991). Subsections are ignored in this table. Abbreviations for the geographical areas are; NAF = North Africa; EUR = Europe, west of the Urals, including the British Isles and Iceland; WAS = Western Asia, including Cyprus, Anatolia, and the Caucasus; NAS = Northeastern Asia, east of the Urals, including Siberia, the Russian Far East, Kamchatka, Sakhalin, the Kuril Islands, China, the Himalayas, and Japan; NAM = North America, including Canada, USA, Alaska, the Aleutians, Greenland, but excluding Mexico; MEX = Mexico; CAM = Central America including Guatemala to Panama, but excluding Mexico; CRB = the Caribbean Islands, including the Bahamas, Cuba, and Hispaniola; SAM = South America, from the Venezuelan Andes to Tierra del Fuego.

	NAF	EUR	WAS	NAS	NAM	MEX	CAM	CRB	SAM
I. Subgenus *Isoloba*	X	X	X		X	X	X	X	
1. Sect. *Isoloba*	X	X			X	X	X	X	
1. *P. lusitanica*	X	X							
2. *P. pumila*					X			X	
3. *P. lilacina*						X	X		
4. *P. sharpii*						X			
5. *P. takakii*						X			
6. *P. ionantha*					X				
7. *P. primuliflora*					X				
8. *P. planifolia*					X				
9. *P. caerulea*					X				
10. *P. lutea*					X				
2. Sect. *Agnata*						X		X	
11. *P. agnata*						X			
12. *P. gigantea*						X			
13. *P. ibarrae*						X			
14. *P. martinezii*						X			
15. *P. pilosa*						X			
16. *P. albida*								X	
17. *P. jaraguana*								X	
18. *P. filifolia*								X	
19. *P. cubensis*								X	
20. *P. benedicta*								X	
21. *P. bissei*								X	
3. Sect. *Discoradix*								X	
22. *P. lignicola*								X	
23. *P. casabitoana*								X	
4. Sect. *Heterophyllum*						X			
24. *P. acuminata*						X			
25. *P. heterophylla*						X			
26. *P. medusina*						X			
27. *P. parvifolia*						X			
28. *P. conzattii*						X			
29. *P. mirandae*						X			
30. *P. kondoi*						X			
31. *P. reticulata*						X			
32. *P. rotundiflora*						X			
33. *P. imitatrix*						X			
5. Sect. *Cardiophyllum*		X	X						
34. *P. hirtiflora*		X							
35. *P. crystallina*			X						
II. Subgenus *Temnoceras*		X		X		X	X		X
6. Sect. *Temnoceras*						X	X		
36. *P. crenatiloba*						X	X		
37. *P. clivolum*						X	X		
38. *P. emarginata*						X			
7. Sect. *Microphyllum*						X			
39. *P. immaculata*						X			
40. *P. gracilis*						X			
41. *P. nivalis*						X			
8. Sect. *Ampullipalatum*									X
42. *P. elongata*									X
43. *P. calyptrata*									X
44. *P. involuta*									X
45. *P. jarmilae*									X
46. *P. chilensis*									X
47. *P. antarctica*									X
9. Sect. *Micranthus*		X		X					
48. *P. alpina*		X		X					
49. *P. variegata*				X					
50. *P. ramosa*				X					

Table 4.2 (continued)

	NAF	EUR	WAS	NAS	NAM	MEX	CAM	CRB	SAM
III. Subgenus *Pinguicula*	X	X	X	X	X	X	X	X	
10. Sect. *Homophyllum*						X		X	
51. *P. jackii*								X	
52. *P. lithophytica*								X	
53. *P. greenwoodii*						X			
11. Sect. *Orcheosanthus*						X	X		
54. *P. gypsicola*						X			
55. *P. moctezumae*						X			
56. *P. cyclosecta*						X			
57. *P. mesophytica*						X	X		
58. *P. colimensis*						X			
59. *P. elizabethiae*						X			
60. *P. moranensis*						X	X		
61. *P. potosiensis*						X			
62. *P. rectifolia*						X			
63. *P. zecheri*						X			
64. *P. macrophylla*						X			
65. *P. oblongiloba*						X			
66. *P. orchidioides*						X	X		
12. Sect. *Longitubus*						X			
67. *P. crassifolia*						X			
68. *P. calderoniae*						X			
69. *P. hamiepiphytica*						X			
70. *P. laueana*						X			
71. *P. utricularioides*						X			
13. Sect. *Orchidioides*						X			
72. *P. laxifolia*						X			
14. Sect. *Crassifolia*						X			
73. *P. esseriana*						X			
74. *P. jaumavensis*						X			
75. *P. ehlersiae*						X			
76. *P. debbertiana*						X			
15. Sect. *Pinguicula*	X	X	X	X	X				
77. *P. vallisneriifolia*		X							
78. *P. mundi*		X							
79. *P. longifolia*		X							
80. *P. nevadensis*		X							
81. *P. corsica*		X							
82. *P. leptoceras*		X							
83. *P. poldinii*		X							
84. *P. grandiflora*	X	X							
85. *P. dertosensis*		X							
86. *P. balcanica*		X	X						
87. *P. fiorii*		X							
88. *P. vallis-regiae*		X							
89. *P. vulgaris*	X	X	X	X	X				
90. *P. bohemica*		X							
91. *P. macroceras*				X	X				
16. Sect. *Nana*		X		X	X				
92. *P. villosa*		X		X	X				

Table 4.3. Chromosome number of *Pinguicula*. Basic chromosome numbers, ploidy levels, and chromosome numbers reported are shown in the table. * = photograph is presented in the original reference. Casper and Stimper (2006, 2009) also reported $2n = 128$ for *P.* cf. *vulgaris*.

Taxon	Basic chromosome number & ploidy level	Chromosome number & reference	
Subg. *Isoloba*			
P. lusitanica	$x = 6$ ($2n$)	$2n = 12$	Casper (1962a, 1966a), Contandriopoulos (1962), Kondo (1969), Casper and Stimper (2006*, 2009*)
P. pumila	$x = 11$ ($2n$)	$2n = 22$	Godfrey and Stripling (1961), Casper and Stimper (2009*)
P. lilacina	$x = 8$ ($2n$)	$2n = 16$	Casper and Stimper (2009*)
P. sharpii	$x = 8$ ($2n$)	$2n = 16$	Casper and Kondo (1977*), Casper and Stimper (2009*)
P. ionantha	$x = 11$ ($2n$)	$2n = 22$	Godfrey and Stripling (1961)
P. primuliflora	$x = 11$ ($2n$)	$2n = 22$	Casper and Stimper (2006*, 2009*)
	$x = 8$ ($4n$)	$2n = 32$	Godfrey and Stripling (1961)
P. planifolia	$x = 8$ ($4n$)	$2n = 32$	Godfrey and Stripling (1961), Casper and Stimper (2009*)
P. caerulea	$x = 8$ ($4n$)	$2n = 32$	Godfrey and Stripling (1961), Kondo (1969), Casper and Stimper (2009*)
P. lutea	$x = 8$ ($4n$)	$2n = 32$	Godfrey and Stripling (1961), Kondo (1969), Casper and Stimper (2006, 2009*)
P. agnata	$x = 11$ ($2n$)	$2n = 22$	Casper and Stimper (2006*, 2009*)
P. gigantea	$x = 11$ ($2n$)	$2n = 22$	Casper and Stimper (2006*, 2009*)
P. ibarrae	$x = 11$ ($2n$)	$2n = 22$	Casper and Stimper (2009*)
P. pilosa	$x = 11$ ($2n$)	$2n = 22$	Casper and Stimper (2006, 2009*)
P. albida	$x = 8$ ($2n$)	$2n = 16$	Casper and Stimper (2009*)
P. filifolia	$x = 9$ ($2n$)	$2n = 18$	Casper and Stimper (2006*, 2009*)
P. bissei	$x = 9$ ($2n$)	$2n = 18$	Casper and Stimper (2006*, 2009*)
P. acuminata	$x = 11$ ($2n$)	$2n = 22$	Casper and Stimper (2009*)
P. heterophylla	$x = 11$ ($2n$)	$2n = 22$	Casper and Stimper (2006, 2009*)
P. medusina	$x = 11$ ($2n$)	$2n = 22$	Casper and Stimper (2006*, 2009*)
P. kondoi	$x = 11$ ($2n$)	$2n = 22$	Casper (1974), Casper and Stimper (2006, 2009*)
P. rotundiflora	$x = 11$ ($2n$)	$2n = 22$	Casper and Stimper (2006*, 2009*)
P. hirtiflora	$x = 8$ ($2n$)	$2n = 16$	Honsell (1959), Casper (1962a, 1966a), Contandriopoulos and Quézel (1974)
	$x = 8$ ($3n$)?	$2n = 24$	Contandriopoulos and Quézel (1974)

Table 4.3 (continued)

	$x = 9$ ($3n$)?	$2n = 27$	Strid and Franzen (1981), Peruzzi et al. (2004*)
	$x = 14$ ($2n$)	$2n = 28$	Mikeladze and Casper (1997), Casper and Stimper (2004*, 2006*, 2009*)
	$x = 8$ ($4n$)	$2n = 32$	Contandriopoulos and Quézel (1974)
	$x = 8$ ($6n$)	$2n = 48$	Contandriopoulos and Quézel (1974)
	$x = 14$ ($4n$)	$2n = 56$	Casper and Stimper (2009*)
P. crystallina	$x = 8$ ($3n$)?	$2n = 24$	Contandriopoulos and Quézel (1974)
	$x = 14$ ($2n$)	$2n = 28$	Casper and Stimper (2004*, 2006, 2009*)
Subg. *Temnoceras*			
P. crenatiloba	$x = 8$ ($2n$)	$2n = 16$	Casper (1966a)
P. emarginata	$x = 11$ ($2n$)	$2n = 22$	Casepr and Stimper (2006*, 2009*)
P. gracilis	$x = 11$ ($2n$)	$2n = 22$	Casper and Stimper (2009*)
P. nivalis	$x = 11$ ($2n$)	$2n = 22$	Casper and Stimper (2009*)
P. calyptrata	$x = 8$ ($2n$)	$2n = 16$	Casper and Stimper (2009*)
P. chilensis	$x = 8$ ($2n$)	$2n = 16$	Casper and Stimper (2009*)
P. antarctica	$x = 8$ ($2n$)	$2n = 16$	Casper and Stimper (2006*, 2009*)
P. alpina	$x = 8$ ($4n$)	$2n = 32$	Doulat (1947), Sokolovskaja and Strelkova (1960), Casper (1966a), Murín (1976)
P. variegata	$x = 8$ ($8n$)	$2n = 64$	Zhukova and Tikhonova (1971), Casper and Stimper (2009*)
P. ramosa	$x = 9$ ($2n$)	$2n = 18$	Yoshimura (1973*), Casper and Stimper (2009*)
Subg. *Pinguicula*			
P. gypsicola	$x = 11$ ($2n$)	$2n = 22$	Casper (1966a), Kondo (1969), Casper and Stimper (2009*)
P. moctezumae	$x = 11$ ($2n$)	$2n = 22$	Casper and Stimper (2006*, 2009*)
P. cyclosecta	$x = 11$ ($2n$)	$2n = 22$	Casper and Stimper (2006, 2009*)
P. colimensis	$x = 11$ ($2n$)	$2n = 22$	Casper and Stimper (2006, 2009*)
P. elizabethiae	$x = 11$ ($2n$)	$2n = 22$	Casper and Stimper (2009*)
P. moranensis	$x = 11$ ($2n$)	$2n = 22$	Kondo (1969)
	$x = 11$ ($4n$)	$2n = 44$	Casper (1966), Kondo (1969), Casper and Stimper (2009*)
P. rectifolia	$x = 11$ ($2n$)	$2n = 22$	Casper and Stimper (2009*)
P. zecheri	$x = 11$ ($2n$)	$2n = 22$	Speta and Fuchs (1982), Casper and Stimper (2009*)
P. macrophylla	$x = 11$ ($2n$)	$2n = 22$	Greilhuber et al. (2006*)
P. oblongiloba	$x = 11$ ($2n$)	$2n = 22$	Zamudio (2001b), Casper and Stimper (2009*)
P. orchidioides	$x = 11$ ($2n$)	$2n = 22$	Casper and Stimper (2006*, 2009*)
P. crassifolia	$x = 11$ ($2n$)	$2n = 22$	Casper and Stimper (2006, 2009*)
P. calderoniae	$x = 11$ ($2n$)	$2n = 22$	Casper and Stimper (2009*)
P. hemiepiphytica	$x = 11$ ($2n$)	$2n = 22$	Kondo (1969; see Zamudio 2001b)
P. laueana	$x = 11$ ($2n$)	$2n = 22$	Casper and Stimper (2009*)
P. esseriana	$x = 8$ ($4n$)	$2n = 32$	Speta and Fuchs (1982), Casper and Stimper (2006, 2009*)

Table 4.3 (continued)

P. jaumavensis	$x = 11$ ($2n$)	$2n = 22$	Casper and Stimper (2006, 2009*)
P. ehlersiae	$x = 11$ ($2n$)	$2n = 22$	Casper and Stimper (2006)
	$x = 8$ ($4n$)	$2n = 32$	Speta and Fuchs (1982)
P. debbertiana	$x = 11$ ($2n$)	$2n = 22$	Casper and Stimper (2006, 2009*)
P. vallisneriifolia	$x = 8$ ($4n$)	$2n = 32$	Zamora et al. (1996), Casper and Stimper (2006, 2009*)
P. mundi	$x = 8$ ($6n$)	$2n = 48$	Zamora et al. (1996)
	$x = 8$ ($8n$)	$2n = 64$	Casper and Stimper (2009*)
P. longifolia			
subsp. *longifolia*	$x = 8$ ($4n$)	$2n = 32$	Casper (1966a), Zamora et al. (1996)
subsp. *caussensis*	$x = 8$ ($4n$)	$2n = 32$	Casper and Stimper (2009)
subsp. *reichenbachiana*	$x = 8$ ($4n$)	$2n = 32$	Doulat (1947), Casper (1962a), Contandriopoulos (1962)
P. nevadensis	$x = 8$ ($2n$)	$2n = 16$	Zamora et al. (1996)
	$x = 8$ ($4n$)	$2n = 32$	Casper and Stimper (2009*)
P. corsica	$x = 8$ ($2n$)	$2n = 16$	Contandriopoulos (1962), Casper and Stimper (2009)
P. leptoceras	$x = 8$ ($4n$)	$2n = 32$	Casper (1962a), Contandriopoulos (1962)
P. poldinii	$x = 8$ ($4n$)	$2n = 32$	Casper and Stimper (2006, 2009)
P. grandiflora			
subsp. *grandiflora*	$x = 8$ ($4n$)	$2n = 32$	Doulat (1947), Casper (1962a, 1966a), Contandriopoulos (1962), Zamora et al. (1996), Casper and Stimper (2009*)
subsp. *rosea*	$x = 8$ ($4n$)	$2n = 32$	Contandriopoulos (1962)
P. dertosensis	$x = 8$ ($6n$)	$2n = 48$	Zamora et al. (1996)
	$x = 8$ ($8n$)	$2n = 64$	Casper and Stimper (2009)
P. balcanica	$x = 8$ ($4n$)	$2n = 32$	Casper (1966a), Casper and Stimper (2006)
P. fiorii	$x = 8$ ($4n$)	$2n = 32$	Tammaro & Pace (1987)
		$2n = 64$	Casper and Stimper (2009*)
P. vulgaris	$x = 8$ ($8n$)	$2n = 64$	Doulat (1947), Contandriopoulos (1962), Murín (1976), Löve and Löve (1982), Krahulcová & Jarolímová (1991), Casper and Stimper (2006*, 2009*)
f. *bicolor*	$x = 8$ ($8n$)	$2n = 64$	Zurzycki (1953)
P. bohemica	$x = 8$ ($4n$)	$2n = 32$	Casper and Stimper (2006, 2009*)
	$x = 8$ ($8n$)	$2n = 64$	Casper and Stimper (2009), Krahulcová and Jarolímová (1991)
P. macroceras	$x = 8$ ($8n$)	$2n = 64$	Uchiyama (1990*)
P. villosa	$x = 8$ ($2n$)	$2n = 16$	Löve and Löve (1982), Casper and Stimper (2009)

Phylogenetic analysis

In recent years, phylogenetic analysis of the genus has been conducted by a number of researchers, including Cieslak et al. (2005) for *mat*K and Shimai and Kondo (2007) for ITS. The results clearly presented disagreements between the phylogeny and morphological classification proposed by Casper (1966a). Taking account of those results, a revision of the genus will be necessary. Cieslak et al. (2005) conducted *mat*K analysis using 42 taxa and most of clades agreed with geographical distribution patterns. In their study, however, materials that might be important to consider phylogeography, in particular Cuban and South American species, were limited. Here, a revision is presented of the genus *Pinguicula* covering all taxa recognised based on all available evidence including herbarium specimens and the original descriptions.

4.2. MATERIALS AND METHODS

To study morphologies and distribution areas, 167 herbaria from across the geographical range of the genus *Pinguicula* were accessed; A, AAU, ABS, ACAD, ALA, AMD, AO, APP, ARIZ, ASU, BAA, BABY, BASSA, BC, BEI, BEO, BERN, BIRM, BKL, BM, BOLO, BP, BR, BUF, BVS, CGE, CHRB, CINC, CLF, CLU, CONN, CR, DBN, DES, E, EAP, EGE, ENCB, FCO, FIAF, FLAS, FRP, GAZI, GBH, G-DC, GDAC, GMNHJ,

GOET, GR, GZU, HAJU, HAL, HAM, HAST, HEM, HUB, I, ID, IEB, IJ, ISKW, ISTF, JACA, JE, JEPS, K, KANA, KMN, KWHU, KYO, LAGU, LE, LEA, LI, LINN, LISU, LJS, LJU, LUG, MAK, MANCH, MARS (General herb.), MARY, MASS, MERL, MEXU, MGC, MHA, MKNH, MMMN, MO, MONTU, MRSN, MSC, MSNM, MU, MW, NAP, NCY, NHA, NHMF, NMW, NSPM, NY, NYS, O, OLYM, OXF, P, PAD, PE, PH, PLU, PRA, QCA, QFA, QK, REG, RO, S, SAPS, SAV, SB, SHIN, SNU, SO, SOC, SOM, SRP, STR, STU, TAA, TEX, TI, TL, TNS, TSM, TUS, UBC, UDM, UM, UNA, UPA, UPS, US, USF, UTC, UWSP, VAL, VT, WA, WI, WIN, WIS, WTU, WU, WVA, WWB, ZA, ZAHO, ZT, Eastern Washington University, Fukui City Museum of Natural History, Nippon Dental University, Slater Museum of Natural History (University of Puget Sound), Okayama University, Tochigi Prefectural Museum, and herb. Dr Garrett Crow. The code for each herbarium follows that of Index Herbariorum (Holmgren 1981, Thiers; continuously updated). In this study, localities shown in the text and distribution maps are based only on the specimen records apart from the type locality, information from the literature or personal observation were not included. Flowering months were also recorded from the specimens. Previously, there are no published taxonomic works thoroughly presenting illustrations of each *Pinguicula* species; therefore, taxa accepted in this study as valid were illustrated. Each illustration was drawn by pencil and inked by 0.35 mm and 0.13 mm Rapidograph pens (rOtring, Hamburg, Germany) based on the living material or herbarium specimens. When the materials were not available, the illustrations were drawn from drawings or photos of publications. A stereomicroscope was used to draw seeds. To assist the identification, a concise description has been added. The descriptions in the previous publications, such as Godfrey and Stripling (1961), Casper (1962a, 1966a), Blanca et al. (1999), Zamudio (2001b), and the original Latin diagnosis by various authors cited elsewhere in this study, have been reviewed. Also the author's observations were added into the description.

DNA has been sampled from 81 taxa, and three DNA regions, ITS, *mat*K, and *rpl32-trnL*, were sequenced (see Chapter 2) to infer phylogenetic relationships among taxa.

4.3. RESULTS AND DISCUSSION

Classification of Pinguicula in this study

Conventionally, current classification of the genus *Pinguicula* largely follows a system proposed by Casper (1966a), which depends on morphological characteristics. In addition, four other sections have been established by several authors (Speta and Fuchs 1982, Zamudio and Rzedowski 1991, Luhrs 1995a, and Blanca et al. 1999), and the system has also been generally accepted (e.g. Legendre 2000, Cieslak et al. 2005). According to this system, the genus is divided to three subgenera and a further 16 sections as summarised in Table 4.1.

However, phylogenetic relationships obtained from phylogenetic analyses are inconsistent with the morphology based classification (Cieslak et al. 2005, Shimai and Kondo 2007). Their data suggest that the phylogeny and geographical distributions tend to show agreements. In particular, all species in Mexico and Central America are likely monophyletic, implying rapid speciation may have led to high levels of endemism. Thus, the classification of *Pinguicula* has to be revised here according to the phylogenetic analysis presented in Chapter 2, in particular the ITS sequence and taking account of morphological features. *Pinguicula* can, therefore, be divided into the following nine major groups based on the analysis result.

Clade I consists of 5 species (*P. caerulea* Walter, *P. ionantha* Godfrey, *P. lutea*, *P. planifolia* Chapman, and *P. primuliflora* Wood et Godfrey) mainly distributed in the coastal regions of the southeastern United States.

Clade II consists of 2 species (*P. crystallina* and *P. hirtiflora*) distributed in the

Mediterranean regions.

Clade III consists of 3 species (*P. calyptrata* Kunth, *P. chilensis* Clos, and *P. antarctica* Vahl) distributed in the Andean to Patagonian regions of South America.

Clade IV consists of 3 species (*P. ramosa* Miyoshi, *P. spathulata* Ledeb., and *P. villosa*) distributed in the circumpolar regions and Eastern Asia. This clade is a sister clade of Clade V.

Clade V consists of 17 taxa (including *P. grandiflora* Lam., *P. macroceras* Link, and *P. vulgaris*) distributed in mild to cold or alpine regions of the Northern Hemisphere.

Clade VI consists of 2 taxa (*P. lilacina* Schlecht. et Cham. and *P. sharpii* Casper et Kondo) distributed in Mexico and Central America.

Clade VII consists of 18 taxa (including *P. heterophylla* Bentham, *P. moranensis*, and *P. oblongiloba* DC.) distributed from northwestern Mexico to Central America.

Clade VIII consists of 16 taxa (including *P. agnata* Casper, *P. gypsicola* Brandegee, and *P. macrophylla* Kunth) mostly distributed in northeastern Mexico.

Clade IX consists of 7 taxa (including *P. albida* Wright ex Griseb., *P. benedicta* Barnhart, and *P. jackii* Barnhart) confined to Cuba.

The final three species (*P. alpina*, *P. lusitanica*, and *P. elongata*) remain unplaced.

In this study, eleven sections are proposed without any subgeneric ranks based mostly on the ITS phylogeny. Four sections have been diverted from the previous sections, one section has been elevated from a subsection, three sections have been elevated from series, and three sections have been newly established. The newly established sections are the sections *Caribensis* distributed in Cuba and the Dominican Republic, *Membraniformis*, and *Mesoamericana* distributed in Mexico and the latter extending to Central America. The geographical distributions of the latter two sections are more or less overlapped each other in Mexico. However, the species in the sect. *Membraniformis* have membranaceous leaves without forming any winter rosettes, while the species in sect. *Mesoamericana* have more fleshy leaves and most of the species form winter rosettes.

Although great morphological diversities are apparently seen within the sect. *Mesoamericana* (i.e. Clade VII and Clade VIII), monophyly and genetic homogeneity of this section are well-agreed with absence of reproductive barrier among species: i.e., artificial hybrids can be easily produced among the species (per. com., Shintani). Therefore, the species in the two clades have been treated as a single section here. Several species were unable to obtain for the phylogenetic analyses, so they have been temporary placed into the sect. *Mesoamericana*. In particular, *P. clivorum* and *P. greenwoodii* characteristically do not form winter rosettes, while the other species in the clades form winter rosettes. A phylogenetic relationship between *P. crenatiloba* and other taxa is also unclear. A further examination may be required to verify the phylogenetic relationships of the three species.

Cieslak et al. (2005) and Beck et al. (2008) inferred phylogenetic relationships in *Pinguicula* (42 taxa and 46 taxa respectively) using the chloroplast gene of *trn*K intron including *mat*K. Their data have presented that the phylogeny and the geographical distributions as well as growth cycles are agreed. Due to their limited number of samples, Cuban species (*P. filifolia*) form a clade with Mexican species. In this study, 6 Cuban taxa were used for *mat*K analysis and the data infer that Cuban and some Mexican taxa are likely monophyletic. Clades in the data of *rpl32-trnL* were also basically agreed with distribution areas but a few clades include species geographically isolated. ITS phylogeny provided clearer relationship between clades and geographical distributions. Taking account of the following reasons, sectional delimitations will be newly proposed mainly based on the ITS phylogeny: 1) more samples were used for the ITS analysis, 2) most of the major clades were well-agreed with geographical distributions, and 3) it is normally considered that ITS is a good method to infer relationships at a specific rank.

Classification and accepted taxa in this study

1. Sect. *Alpinae* (Casper) Shimai, comb. nov.

1. *P. alpina* L.

2. Sect. *Andinae* (Casper) Shimai, comb. nov.

2. *P. antarctica* Vahl

3. *P. calyptrata* Kunth

4. *P. chilensis* Clos

5. *P. involuta* Ruíz et Pavón

6. *P. jarmilae* Halda et Malina

3. Sect. *Cardiophyllum* Casper (1962) Feddes. Repert. 66, 34.

7. *P. crystallina* Smith

8. *P. hirtiflora* Tenore

4. Sect. *Caribensis* Shimai, sect. nov.

9. *P. albida* Wright ex Griseb.

10. *P. benedicta* Barnhart

11. *P. casabitoana* Jiménez

12. *P. cubensis* Urquiola et Casper

13. *P. filifolia* Wright ex Griseb.

14. *P. jackii* Barnhart

    a. *P. jackii* Barnhart var. *jackii* Barnhart

    b. *P. jackii* Barnhart var. *parviflora* Ernst

15. *P. jaraguana* Casper

16. *P. lignicola* Barnhart

5. Sect. *Elongatae* (Capser) Shimai, comb. nov.

17. *P. elongata* Benjamin

6. Sect. *Isoloba* Casper (1963) Bot. Jb. 82, 330.

18. *P. caerulea* Walter

19. *P. ionantha* Godfrey

20. *P. lutea* Walter

21. *P. planifolia* Chapman

22. *P. primuliflora* Wood et Godfrey

23. *P. pumila* Michx.

7. Sect. *Membraniformis* Shimai, sect. nov.

24. *P. crenatiloba* DC.

25. *P. lilacina* Schlecht. et Cham.

26. *P. sharpii* Casper et Kondo

27. *P. takakii* Zamudio et Rzedowski

8. Sect. *Mesoamericana* Shimai, sect. nov.

28. *P. acuminata* Bentham

29. *P. agnata* Casper

30. *P. calderoniae* Zamudio

31. *P. clivorum* Standley et Steyermark

32. *P. colimensis* McVaugh et Mickel

33. *P. conzattii* Zamudio et van Marm

34. *P. crassifolia* Zamudio

35. *P. cyclosecta* Casper

36. *P. dbbertiana* Speta et Fuchs

37. *P. ehlersiae* Speta et Fuchs

38. *P. elizabethiae* Zamudio

39. *P. emarginata* Zamudio et Rzedowski

40. *P. esseriana* Kirchner

41. *P. gigantea* Luhrs

42. *P. gracilis* Zamudio

43. *P. greenwoodii* Cheek

44. *P. gypsicola* Brandegee

45. *P. hemiepiphytica* Zamudio et Rzedowski

46. *P. heterophylla* Bentham

47. *P. ibarrae* Zamudio

48. *P. immaculata* Zamudio et Lux

49. *P. kondoi* Casper

50. *P. laueana* Speta et Fuchs

51. *P. laxifolia* Luhrs

52. *P. macrophylla* Kunth

53. *P. martinezii* Zamudio

54. *P. medusina* Zamudio et Studničika

55. *P. mesophytica* Zamudio

56. *P. mirandae* Zamudio et Salinas

57. *P. moctezumae* Zamudio et Ortega

58. *P. moranensis* Kunth

   a. *P. moranensis* Kunth var. *moranensis* Kunth

   b. *P. moranensis* Kunth var. *neovolcanica* Zamudio

59. *P. nivalis* Luhrs et Lampard

60. *P. oblongiloba* DC.

61. *P. orchidioides* DC.

62. *P. parvifolia* Robinson

63. *P. pilosa* Luhrs, Studničika et Gluch

64. *P. potosiensis* Speta et Fuchs

65. *P. rectifolia* Speta et Fuchs

66. *P. rotundiflora* Studničika

67. *P. utricularioides* Zamudio et Rzedowski

68. *P. zecheri* Speta et Fuchs

9. Sect. *Nana* Casper (1962) Feddes. Repert. 66, 41.

69. *P. algida* Malyschev

70. *P. ramosa* Miyoshi

71. *P. spathulata* Ledeb.

72. *P. villosa* L.

10. Sect. *Pinguicula* Casper (1963) Bot. Jb. 82, 327.

73. *P. balcanica* Casper

74. *P. caussensis* (Casper) Innangi, De Castro et Peruzzi

75. *P. corsica* Bernard et Gren. ex Gren. et Godr.

76. *P. dertosensis* (Cañigueral) Mateo et Crespo

77. *P. fiorii* Tammaro et Pace

78. *P. grandiflora* Lam.

79. *P. leptoceras* Reichenbach

80. *P. longifolia* Ram. ex DC.

81. *P. macroceras* Link

82. *P. mundi* Blanca, Jamilena, Ruiz-Rejón et Zamora

83. *P. nevadensis* (Lindberg) Casper

84. *P. poldinii* Steiger et Casper

85. *P. reichenbachiana* Schindler

86. *P. vallisneriifolia* Webb

87. *P. vallis-regiae* Conti et Peruzzi

88. *P. vulgaris* L.

11. Sect. *Pumiliformis* (Casper) Shimai, sect. nov.

89. *P. lusitanica* L.

Key to section

1. Forming hibernaculum

 2. Hibernaculum with roots -- Sect. *Alpinae*

 2. Hibernaculum without roots

  3. Scape often >2; summer rosette diam. usually >3 cm across ------- Sect. *Pinguicula*

  3. Scape 1; summer rosette diam. usually <3 cm across ----------------------- Sect. *Nana*

1. Not forming hibernaculum

 4. Forming winter rosette

  5. Winter rosette w/ roots; roots elastic -------------------------------------- Sect. *Elongatae*

  5. Winter rosette often w/o roots; roots fragile --------------------- Sect. *Mesoamericana*

4. Not forming winter rosette, i.e. homophyllous throughout the year

6. Flower shape often monstrous within the same individual; lower half of lips white, upper half of lips pale purple, throat yellow ----------- Sect. *Cardiophyllum*

6. Flower shape uniform within the same individual; colour varies among taxa

7. Plants often forming runners, producing plantlet at the tip ----- Sect. *Andenae*

7. Plants not forming runners

8. Corolla subactinomorphic w/ terete process at lower lip --------- Sect. *Isoloba*

8. Corolla shape diverse among taxa w/o terete process at lower lip

9. Corolla subactinomorphic, pale lilac or white, often with trapeziform process at lower throat ---------------------------------- Sect. *Membraniformis*

9. Corolla shape and colour diverse; leaf shape diverse

10. Corolla white to faintly pale lilac or pink, yellow at base of lips, emarginate at tip of lobes, w/ trapeziform process in lower throat --- Sect. *Pumiliformis*

10. Morphological characters not falling above; corolla colour diverse, obtuse to truncate at tip of lobes, w/o trapeziform process in lower throat -- Sect. *Caribensis*

Key to species

1. Corolla lobes ± equal in size and shape, and forming a subactinomorphic corolla

 2. Corolla w/ hairy terete process at lower throat; lobes notched or bifid at tip

  3. Corolla diam. often <20 mm across; rosette diam. usually <4 cm --------- *P. pumila*

  3. Corolla diam. often >20 mm across; rosette diam. usually >4 cm

   4. Corolla yellow -- *P. lutea*

   4. Corolla bluish-purple, pale purple, or nearly white

    5. Corolla bluish-purple w/ prominent darker veins; scape hairy at base and glandulous above -- *P. caerulea*

    5. Corolla pale purple or nearly white w/o prominent veins

     6. Leaves frequently producing clonal plantlets near the tip --- *P. primuliflora*

     6. Leaves never producing clonal plantlet

      7. Corolla lobes emarginate at tip; leaves yellowish-green-------- *P. ionantha*

      7. Corolla lobes deeply emarginate or bifid at tip; leaves reddish-yellow to maroon --- *P. planifolia*

 2. Corolla w/ single trapezoiform process or no process in lower throat; lobes rounded or emarginate to shallowly emarginate at tip

  8. Corolla w/ single trapeziform process in lower throat

9. Corolla lobes emarginate or shallowly notched at tip ------------------*P. lusitanica*

9. Corolla lobes ± orbicular to obtuse at tip

10. Corolla white, diam. 5-8 mm across -- *P. sharpii*

10. Corolla pale purple to faintly pale lilac or rarely white

11. Corolla diam. 5-10 mm across; leaf obovate to spatulate w/ cuneate base, 5-16 mm long --- *P. takakii*

11. Corolla diam. 10-13 mm across; leaf obovate to suborbicular, 15-35 mm long -- *P. lilacina*

8. Corolla w/o trapeziform process at lower throat

12. Corolla white to faintly pale purple w/ prominent purple veins ---------*P. kondoi*

12. Corolla white to faintly pale purple w/o prominent veins

13. Corolla diam. mostly 5-12 mm across

14. Corolla colour diverse (white to faintly pale purple or faintly pale yellow); leaf filiform, <200 mm long --- *P. filifolia*

14. Corolla white; leaf broader (not filiform)

15. Corolla lobes obovate; leaf ovate to suborbicular ------------------ *P. albida*

15. Corolla lobes oblong-ovate; leaf obovate to spatulate ---------*P. jaraguana*

13. Corolla diam. mostly >10 mm across

16. Corolla lobes broadly obovate and often overlapping ---------*P. rotundiflora*

16. Corolla lobes well-divided and often not overlapping

17. Corolla white, pale lilac to pale purple or faintly so w/o darker spots at base of lobes

18. Corolla lobes often densely pilose entirely ------------------------ *P. pilosa*

18. Corolla lobes pilose ± only lower half

19. Corolla tube cylindrical w/o angle; summer leaf very large, 60-165 mm long --- *P. gigantea*

19. Corolla tube cylindrical to cylindrically-conical w/ angle

20. Summer leaf obovate to ligulate or suborbicular, 20-40 mm long --- *P. mirandae*

20. Summer leaf ovate to orbicular, 20-90 mm, w/ petiole 10-80 mm long

21. Scape covered by glands only upper part, base of leaf often cordate ---*P. acuminata*

21. Scape covered by glands entirely, base of leaf broadly cuneate --- *P. conzattii*

17. Corolla white, pale lilac to pale purple or faintly so w/ darker purple or

reddish-purple spots at base of lobes

22. Summer leaf obovate to ligulate ----------------------------------- *P. ibarrae*

22. Summer leaf ± oblanceolate to spatulate

23. Summer leaf margin rather flat, sometimes slightly revolute -- *P. agnata*

23. Summer leaf margin revolute and upper surface ± convex --- *P. martinezii*

1. Corolla lobes unequal in size and shape, and forming a zygomorphic corolla

24. Corolla tube conical, very short and small, often inconspicuous

25. Corolla lobes white to pale purple w/ prominent purple veins entirely --- *P. emarginata*

25. Corolla colour diverse (white, pale purple, purple, reddish-purple etc.) but basically monochrome, sometimes w/ a white spot or stripes at base of lower lip or slightly darker veins on corolla lobes

26. Summer leaf linear-lanceolate

27. Corolla diam. 13-20 mm across, ± oblong w/ ± truncate tip ------ *P. gypsicola*

27. Corolla diam. 28-40 mm across, ± rounded ---------------------- *P. moctezumae*

26. Summer leaf diverse in shapes and sizes but mostly oblong, obovate,

spatulate, elliptic

28. Corolla white and middle lobe of lower lip much wider than laterals w/ emarginate tip

29. Upper lip very small compared w/ lower one, 1:4 to 1:6 in length -- *P. immaculata*

29. Upper lip slightly smaller than lower one

30. Lower half of lips w/ very fine purple veins ---------------------- *P. gracilis*

30. Lips w/o purple veins --- *P. nivalis*

28. Corolla w/ colour (pale purple, purple, reddish-purple etc.)

31. Corolla tube dorsally compressed, 2-yellow trichome crests at base of lower lip --- *P. debbertiana*

31. Corolla tube not compressed, w/o yellow crest at base of lower lip

32. Corolla lobes ± obovate or orbicular and often overlapping

33. Corolla lobes ± truncate and irregularly serrate and undulate at tip -- *P. zecheri*

33. Corolla lobe rounded at tip

34. Corolla glossy, bluish-purple to purple; summer leaf usually <35 mm long, outer margin sometimes suffused w/ maroon

-- *P. cyclosecta*

34. Corolla pinkish-purple; summer leaf usually >35 mm long, yellowish-green

35. Summer leaf margin slightly revolute ----------------*P. colimensis*

35. Summer leaf margin only slightly involute --------*P. elizabethiae*

32. Corolla lobes ± oblong to obovate or elliptic; lower lip lobes usually well-divided

36. Corolla lobes rather rectangular to cuneate w/ truncate to shallowly emarginate tip

37. Summer leaf obovate to spatulate, usually <25 mm long, thick -- *P. ehlersiae*

37. Summer leaf ± rounded (ovate, elliptic, oblong, cordate suborbicular etc.), sometimes >100 mm long

38. Corolla lobes often irregularly undulate at tip --------*P. rectifolia*

38. Corolla lobes entire at tip

39. Corolla deep reddish-purple or bluish-purple w/ white spots or stripes at base -- *P. potosiensis*

39. Corolla colour diverse (purple, pinkish-red, reddish-purple)

but usually not deep colour, or entirely white ---*P. moranensis*

a. Winter rosette lenticular or acetabuliform ------------------

-- var. *moranensis*

b. Winter rosette subglobose ------------------ var. *neovolcanica*

36. Corolla lobes ± oblong to suborbicular w/ rounded tip

40. With runners producing clonal plantlets at tip ------- *P. orchidioides*

40. Without runners

41. Corolla bluish-purple; leaf <135 mm long, petiole <60 mm long

--- *P. macrophylla*

41. Corolla reddish-purple; leaf <75 mm long, petiole <40 mm long

42. Winter rosette subglobose ------------------------- *P. oblongiloba*

42. Winter rosette lenticular --------------------------*P. mesophytica*

24. Corolla tube cylindrical to subcylindrical or conical and well-developed

43. Spur cylindrical to subcylindrical

44. Corolla tube dorsally compressed

45. Corolla diameter usually <10 mm across

46. Scape often bifurcate or trifurcate; corolla faintly pale purple ----- *P. ramosa*

46. Scape not bifurcate; corolla purple--- *P. villosa*

45. Corolla diameter usually >10 mm across

47. Corolla bluish-purple entirely, w/o white spot or gradation ------------ *P. fiorii*

47. Corolla w/ white spot or gradation, or faintly pale purple entirely

48. Summer leaf ± oblong-oblanceolate to liner-lanceolate, linear-oblanceolate

49. Summer leaf linear-oblanceolate, <250 mm long; with runners producing clonal plantlets at tip --------------------------- *P. vallisneriifolia*

49. Summer leaf <200 mm long; w/o runners

50. Summer leaf narrowly oblong to oblong-oblanceolate, <200 mm long; lower surface of leaf very sparsely glandulous ---------------*P. longifolia*

50. Summer leaf <120 mm long; lower surface of leaf not glandulous

51. Summer leaf linear-lanceolate and margin rather revolute -- *P. reichenbachiana*

51. Summer leaf oblong to oblong-lanceolate and margin sometimes slightly involute --- *P. mundi*

48. Summer leaf ± elliptic, oblong, ovate, or suborbicular

52. Corolla colour basically paler (pale purple, pale lilac, or faintly so)

53. Summer leaf oblong to oblong-ovate, margin irregularly undulate,

<75 mm long -- *P. corsica*

53. Summer leaf ovate to suborbicular, <50 mm long, but often much smaller -- *P. nevadensis*

52. Corolla colour basically darker (purple, reddish-purple, bluish-purple)

54. Lower lip w/ 6-8 white stripes at base, lobes often undulate at margin -- *P. grandiflora*

54. Lower lip white to paler colour at base or w/ white spot

55. Corolla lobes often overlapping or touching

56. Lobes of lower lip often overlapping -------------------- *P. dertosensis*

56. Lobes of lower lip often touching but usually not overlapping

57. Lobes of lower lip rounded at tip ------------------------ *P. leptoceras*

57. Lobes of lower lip rather truncate at tip ---------------*P. balcanica*

55. Corolla lobes often not overlapping or touching

58. Corolla diameter usually <15 mm across ----------------- *P. vulgaris*

58. Corolla diameter usually >15 mm across

59. Middle lobe of lower lip ± spatulate -----------------*P. vallis-regiae*

59. Middle lobe of lower lip ± ovate to obovate-oblong or suborbicular

60. Base of lower lip to throat w/ prominent purple veins -- *P. poldinii*

60. Base of lower lip to throat w/o prominent veins

61. Middle lobe of lower lip ± truncate to shallowly emarginate at tip ---------------------------------- *P. caussensis*

61. Middle lobe of lower lip ± rounded at tip ----- *P. macroceras*

44. Corolla tube not compressed

62. Spur obscurely continuing from thick corolla tube

63. Summer leaf ± elliptic to suborbicular

64. Middle lobe and lateral lobes of lower lip not overlapping or touching at base -- *P. crassifolia*

64. Middle lobe and lateral lobes of lower lip often overlapping or touching at base

65. Corolla pink to pinkish-purple w/ white stripes at base of lower lip -- *P. hemiepiphytica*

65. Corolla colour diverse (red, reddish-orange or reddish-pink) w/ small white spot or often w/o spot at base of lower lip ------------------*P. laueana*

63. Summer leaf very narrow

66. Summer leaf narrowly linear-lanceolate, <260 mm long ---- *P. calderoniae*

66. Summer leaf deeply concave to saccate, petiole <25 mm long -- *P. utricularioides*

62. Super ± abruptly narrowed from corolla tube

67. Lower surface of leaf sparsely glandulous ---------------------------------- *P. jackii*

a. Corolla dark blue, corolla diam. 20-35 mm across ------------------ var. *jackii*

b. Corolla white to faintly pale blue, corolla diam. 18-20 mm across --- var. *parviflora*

67. Lower surface of leaf not glandulous

68. Summer leaf very narrow or thread-like (narrowly linear-lanceolate to filiform)

69. Summer leaf often producing clonal plantlets at tip ----------*P. medusina*

69. Summer leaf not producing clonal plantlet at tip ----------*P. heterophylla*

68. Summer leaf ± broad to rounded but not too narrow

70. Corolla diam. often less <10 mm across

71. Corolla white

72. Corolla ± translucent white, corolla lobes notched at tip; leaf ovate to obovate, margin involute, <14 mm long --------------- *P. crenatiloba*

72. Corolla lobes rounded at tip; leaf linear-lanceolate, margin strongly revolute, <30 mm long ------------------------ *P. casabitoana*

71. Corolla purple to faintly pale purple

73. Corolla purple, middle lobe of lower lip ± oblong w/o yellow spot at base

74. Corolla purple w/ darker veins at base of lips, w/o yellow spot at base of lower lip -- *P. greenwoodii*

74. Corolla purple w/ yellow spot at base of lower lip -------- *P. algida*

73. Corolla faintly pale purple, middle lobe of lower lip ± suborbicular w/ yellow spot at base

75. Lobes of lower lip connate to middle; leaf yellowish-green, 18-46 mm long -- *P. clivorum*

75. Lobes of lower lip well-divided; leaf often suffused w/ maroon, <20 mm long --- *P. spathulata*

70. Corolla diam. often >10 mm across

76. Corolla throat w/ yellow trichomes

77. Leaf linear-lanceolate --- *P. cubensis*

77. Leaf ± oblong-elliptic to oblong-oblanceolate

78. Leaf often <20 mm long -------------------------------------- *P. lignicola*

78. Leaf often >20 mm long

79. Middle lobe of lower lip ± orbicular to cuneate at tip -- *P. crystallina*

79. Middle lobe of lower lip ± often emarginate ----------*P. hirtiflora*

76. Corolla throat w/o yellow trichomes

80. Corolla colour reddish-purple to dark pink

81. Leaf ovate to obovate, 10-20 mm long ----------------- *P. benedicta*

81. Leaf elliptic to oblanceolate, 32-68 mm long ----------- *P. laxifolia*

80. Corolla usually pale pink to pale purple

82. Summer leaf w/o petiole, thick --------------------------- *P. esseriana*

82. Summer leaf w/ short petiole ---------------------------- *P. parvifolia*

43. Spur ± conical to saccate, often obscurely continuing from corolla tube

83. Corolla lobes ± emarginate to deeply notched at tip

84. Leaf <110 mm long, margin slightly revolute --------------------------- *P. jarmilae*

84. Leaf <35 mm long, margin strongly involute

85. Leaf often suffused w/ maroon

86. Corolla lobes deeply notched to bifid at tip ----------------------- *P. calyptrata*

86. Corolla lobes shallowly emarginate to emarginate ---------------- *P. involuta*

85. Leaf yellowish-green

87. Corolla tube w/ dark purple veins ----------------------------------- *P. antarctica*

87. Corolla tube w/o darker veins --- *P. chilensis*

83. Corolla lobes rounded to truncate or rather acute at tip

88. Corolla white w/ yellow spots on lower lip; leaf ± ovate to oblong ------ *P. alpina*

88. Corolla white to faintly pale purple w/o yellow spots on lower lip; leaf linear-lanceolate --- *P. elongata*

Abbreviations: > = more than, < = less than, ± = more or less, w/ = with, w/o = without, diam. = diameter

Genus *Pinguicula* L., Sp. Pl. 1 (1753) 17.

TYPE: *Pinguicula vulgaris* L.

SYNONYMS: *Brandonia* Reichenbach, *Isoloba* Rafinesque

DESCRIPTION: Perennial (or annual to biannual) herbs. Terrestrial, lithophytic, or epiphytic. Root usually not too many, filiform, short, and fragile, but occasionally long and elastic, often absent during dormant season. Stem very short, forming leaves radially. Leaf yellowish green, whitish green, or partially to entirely suffused with maroon, monomorphic or seasonally dimorphic, often forming basal rosette, diverse in shape, upper surface densely covered by very tiny glands secreting mucilage, usually thin but sometimes thick, margin often involute or occasionally revolute, winter leaf much smaller than summer one, often scale-like, without secreting mucilage. Winter rosette or hibernaculum formed in dimorphic-leaved species, winter leaf 12 to more than 100, densely imbricate. Scape 1 to more than 10, straight or curved, basically unbalanced, bractless, densely or sparsely glandulous or pilose, but rarely glabrous, terminally forming single flower. Calyx bilabiate, upper lip 3-lobed, lobes ± ovate, lower lip 2-lobed, lobes usually slightly smaller than upper ones, sometimes connate at base or entirely, often covered by glands. Flower diverse in colour. Corolla bilabiate, upper lip 2-lobed, lower lip

3-lobed, upper lip usually smaller than lower one, lips fused at base and forming corolla, base of lips to throat often densely covered by trichomes, lobes usually entire but sometimes emarginate or deeply notched at tip, tube usually well-developed but occasionally very short, cylindrical to conical, sometimes dorsally compressed, spur cylindrical to saccate. Stamen 2, located at entrance or inside of upper throat, externally covered by lower lip of stigma, stigma very small. Capsule usually globose to subglobose or ovoid, dehiscing longitudinally. Seed numerous (up to ca. 150), 400-1,200 μm long, diverse in shape, surface often reticulate texture.

DISTRIBUTION: Eurasia excluding tropical regions, Africa (Morocco), North America, Caribbean, Mexico, Central America and the Andean and Patagonian regions of South America.

Sect. *Alpinae* (Casper) Shimai, comb. nov.

TYPE: *Pinguicula alpina* L.

SYNONYMS: Sect. *Pionophyllum* DC., Ser. *Alpinae* Casper

1. ***Pinguicula alpina*** L., Spec. Pl. 1 (1753) 17.

TYPE: in Flora Lapponica 11, t. 12, f.3 (Linnaeus 1737!), (lectotype: designated by Blanca et Jarvis in Blanca et al. 1999).

SYNONYMS: *P. alba* Kuchl, *P. albiflora* Cariot et St. Lager, *P. albiflora* Cariot et St. Lager var. *villosa* Cariot et St. Lager, *P. alpestris* Persoon, *P. alpina* L. subsp. *gavei* Beauverd, *P. alpina* L. var. *bimaculata* Wahlenberg, *P. alpina* L. var. *flavescens* Steudel et Hochstetter, *P. alpina* L. var. *lendneri* Beauverd, *P. alpina* L. var. *lendneri* Perrier, *P. alpina* L. var. *villosa* Villars, *P. auricolor* Arv. Touv., *P. brachyloba* Ledebour, *P. flavescens* Floerke, *P. gelida* Schur, *P. hyperborea* Gandoger, *P. lusitanica* Allioni, *P. pallida* Turczaninov, *P. purpurea* Willdenow, *P. villosa* Villars

DESCRIPTION: Perennial herb. Root filiform, elastic. Stem very short. Leaf dimorphic, summer leaf 5-8, yellowish-green or maroon, ovate to elliptic-oblong or lanceolate-oblong, margin involute, 15-60 mm long, apex rather acute, 8-20 mm wide, winter leaf up to 15, ovate, acute, concave, small. Hibernaculum ovoid with roots. Scape 1-13, glabrous or rather sparsely glandulous, 30-130 mm long. Calyx bilabiate, upper lip 3-lobed, lobes oblong-ovate, 2-3 mm long, lower lip 2-lobed, lobes smaller than uppers. Flower white, 1-5 yellow spots on middle lobe of lower lip. Corolla bilabiate, 8-15 mm across, zygomorphic, 8-21 mm long including spur, upper lip 2-lobed, lobes suborbicular to ovate, lower lip 3-lobed, lobes larger than uppers, lateral lobes similar to uppers but oblique and larger, middle lobe cuneate to broadly oblong, tip truncate to shallowly emarginate, tube white with pale purple veins, shortly cylindrical, spur yellowish-green, saccate to conical, 2-5 mm long. Capsule ovoid, acute. Seed ellipsoid, 700-1,000 × 200-160 µm. $2n = 32$. (Plate 4.1).

PHENOLOGY: IV, V, VI, VII, VIII

ETYMOLOGY: alpine or native of the Alps

HABITAT: Various soil types (limestone, tufa, gravel, fine sand, peat, or sphagnum) in many wet places including open flat areas, slopes, or cliffs. Tolerant to various light intensities.

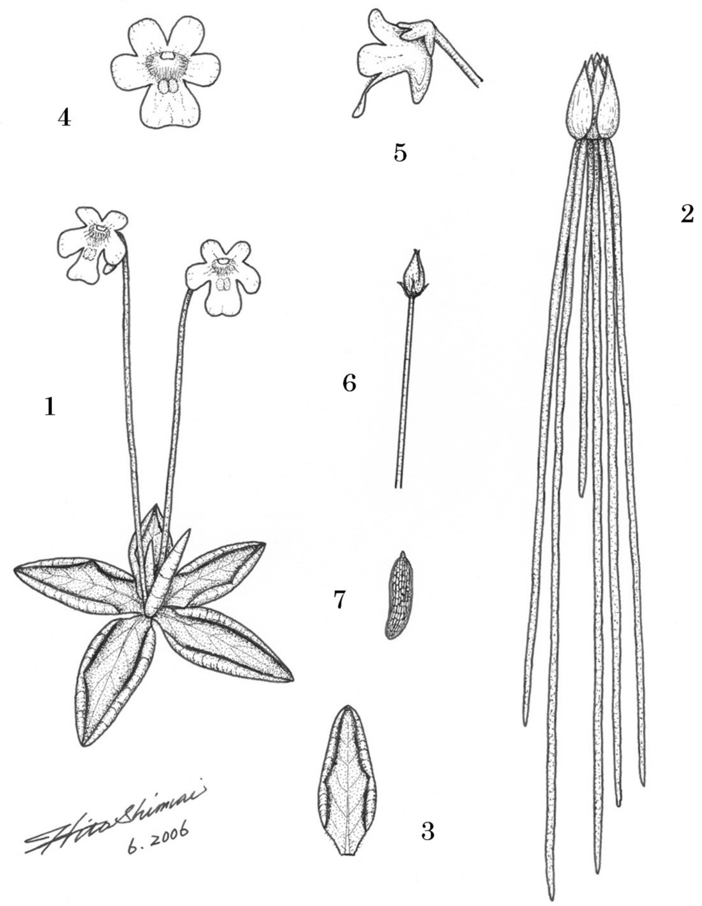
NATURAL HYBRID: × *P. vulgaris* (= *P.* × *hybrida* Wettstein)?

DISTRIBUTION: Very widely distributed in Eurasia. AUSTRIA (Kärnten, Niederösterreich, Oberösterreich, Salzburg, Steiermark, Tirol, Vorarlberg); BHUTAN (Bumthang, Lhuntse, Paro, Thimpu, Trashiyangtse); CHINA (Chongqing, Gansu, Guizhou, Hubei, Qinghai, Shaanxi, Sichuan, Yunnan, Xizang); CROATIA (Karlovac, Primorje-Gorski Kotar); ESTONIA (Harju maakond, Saare maakond, Tartu maakond); FINLAND (Lappi, Pohjois-Pohjanmaa); FRANCE (Ain, Haute-Garonne, Haute-Savoie, Hautes-Alpes, Hautes-Pyrénées, Isère, Pyrénées-Orientales, Savoie); GERMANY (Barden-Württemberg, Bayern); HUNGARY (Veszprém); INDIA (Arunachal Pradesh, Assam, Sikkim, Uttarakhand); ITALY (Friuli-Venezia Giulia, Lombardia, Piemonte, Trentino-Alto Adige, Valle d'Aosta, Veneto); LIECHTENSTEIN (Triesenberg); MONGOLIA (Khövsgöl); MYANMAR (Kachin); NEPAL (Bagmati, Dhawalagiri, Gandaki, Karnali, Kosi, Mahakali); NORWAY (Finnmark, Nordland, Oppland, Sør-Trøndelag, Svalbard, Troms); POLAND (Małopolskie); ROMANIA (Alba, Argeş, Bistrița-Năsăud, Braşov, Caraş-Severin, Dâmbovița, Maramureş, Neamț, Prahova, Sibiu, Suceava); RUSSIA (Buryatia, Irkutsk, Khanty-mansi, Komi, Krasnoyarsk, Leningrad, Murmansk, Nenetsia, Sakha, Yamalo-Nenets); SLOVAKIA (Prešovský kraj, Žilinský kraj); SLOVENIA (Bled, Bloke, Bojinj, Borovnica, Bovec, Brezovica, Cerklje na Gorenjskem, Cerknica, Črna na Koroškem, Dobrna, Idrija, Jesenice, Jezersko, Kamnik, Kranj, Kranjska Gora, Ljubljana, Nova Gorica, Radece, Sodražica, Solčava, Tržič, Velike Lašče, Vojnik, Železniki, Žirovnica); SPAIN (Huesca, Lleida, Navarra); SWEDEN (Gotland, Jämtland, Norrbotten, Västerbotten); SWITZERLAND (Appenzell-Innerrhoden, Bern, Fribourg, Genève, Graubünden, Obwalden, Schwyz, Ticino, Uri, Valais, Vaud, Zürich); UKRAINE (Zakarpattia Oblast); UNITED KINGDOM ([SCOTLAND] Highland). 0-4,600 m.

DISCUSSION: *Pinguicula alpina*, is very widely distributed in cold regions of Eurasia. The northernmost population is recorded from Svalbard. Populations in Scotland, locally extinct today, might have been introduced (Heslop-Harrison 2004). Despite its wider distribution with many synonyms, *P. alpina* is morphologically uniform except the number of yellow spot(s) on the middle lobe of the lower lip varying from 1 to 5 depending on the strains. It is particularly abundant in the Alps and sometimes grows together with *P. leptoceras* and/or *P. vulgaris* within the same microhabitat. The white flower is hardly confused with other purple-flowered species during the flowering season. Without flowers, however, it is morphologically difficult to distinguish from the other species, but

P. alpina has thick, long, and elastic root systems throughout the year while *P. leptoceras* and *P. vulgaris* have thin, short, and fragile root systems only during the growth season. In southwestern China, it is occasionally misidentified as *P. vulgaris*, but it seems only *P. alpina* is found there. It is also locally sympatric, for example, with *P. poldinii* in northeastern Italy, and with *P. villosa* in Northern Europe. A natural hybrid with *P. vulgaris* (i.e. *P.* X *hybrida*) has been reported, but it is questionable whether or not they can produce the hybrid (Heslop-Harrison 2004).

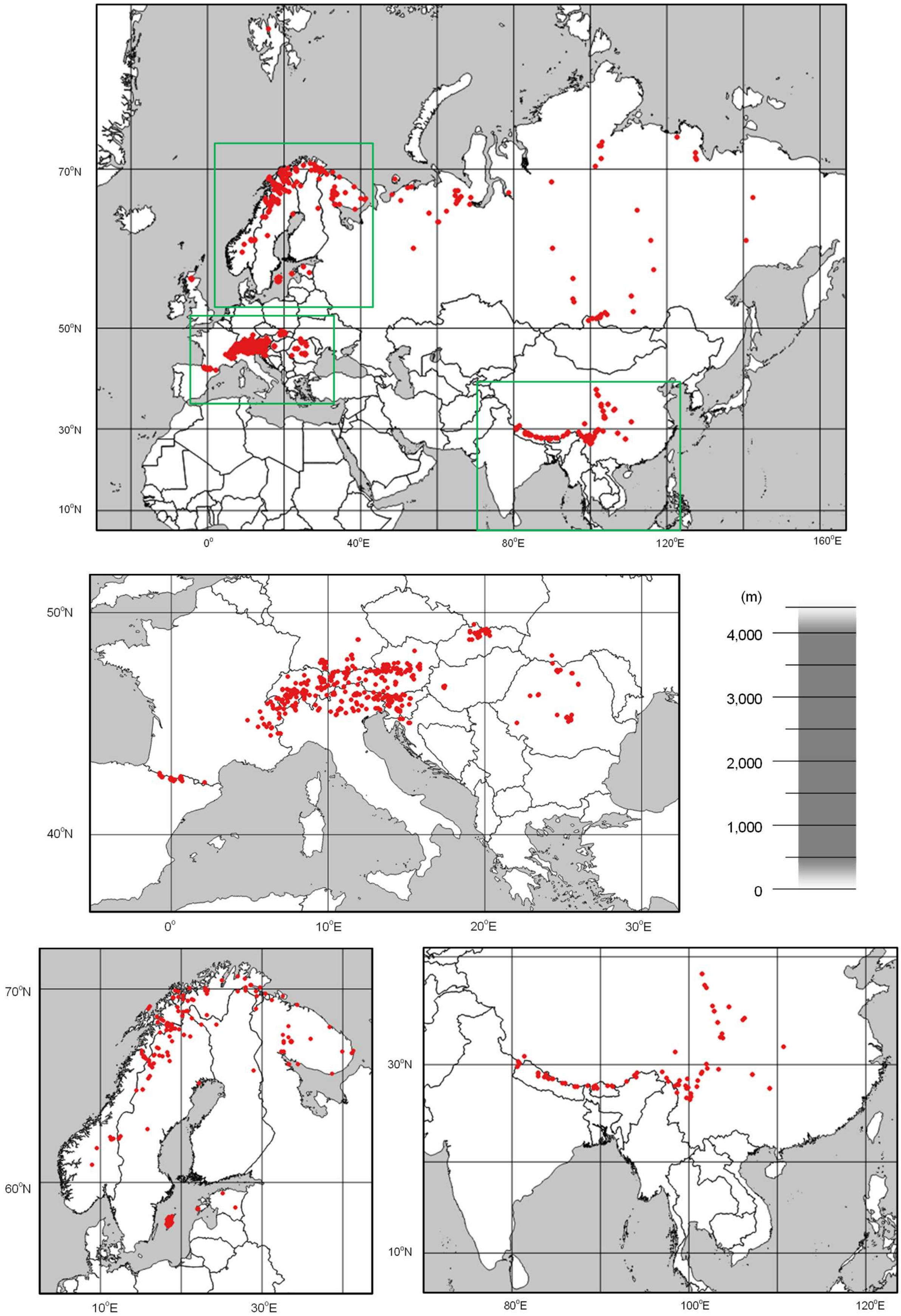
Plate 4.1. *Pinguicula alpina*



10 mm: 1, 2, 3, 6
10 mm: 4, 5
500 µm: 7

1. summer rosette in flower
2. hibernaculum
3. summer leaf
4. flower, front view
5. flower, lateral view
6. capsule (dried)
7. seed

P. alpina


70°N
50°N
30°N
10°N
0°
40°E
80°E
120°E
160°E
50°N
40°N
0°
10°E
20°E
30°E
(m)
4,000
3,000
2,000
1,000
0
70°N
60°N
10°E
30°E
30°N
10°N
80°E
100°E
120°E

Sect. *Andinae* (Casper) Shimai, comb. nov.

TYPE: *Pinguicula calyptrata* Kunth

SYNONYMS: Sect. *Pionophyllum* DC., Ser. *Andinae* Casper, Ser. *Antarcticae* Casper

2. ***Pinguicula antarctica*** Vahl, Enum. Pl. (1805) 192.

TYPE: *ad fretum Magellanicum* (the Strait of Magellan), *Commerson ex herb. Jussiaei s.n.* (holotype: P!, isotype: MPU, K-photo ex-MPU!).

SYNONYMS: *P. magellanica* Commerson ex Franchet, *P. obtusa* Herb. Banks ex Benjamin

DESCRIPTION: Perennial herb. Root filiform, elastic. Stem very short. Leaf monomorphic, 3-10, yellowish-green, oblong to ovate, margin involute, apex obtuse to rather acute, 10-25 mm long. 7-18 mm wide, Scape 1-2, sparsely glandulous, 25-200 mm long. Calyx bilabiate, upper lip 3-lobed, lobes oblong to ovate, 2-2.5 mm long, connate at base or to middle, lower lip 2-lobed, lobes slightly smaller than uppers. Flower white to faintly pale purple, dark purple veins at base of lobes, yellow trichomes at base of lower throat. Corolla bilabiate, ca. 10 mm across, zygomorphic, 8-10 mm long including spur, upper lip 2-lobed, lobes orbicular with emarginate tip, lower lip 3-lobed, lobes larger than uppers, obovate with emarginate tip, tube white to faintly pale purple with dark purple veins, cylindrical to conical, spur yellow, saccate to conical, 1-3 mm long. Capsule subglobose. Seed narrowly ellipsoid. $2n = 16$. (Plate 4.2).

PHENOLOGY: I, II, III, X, XII

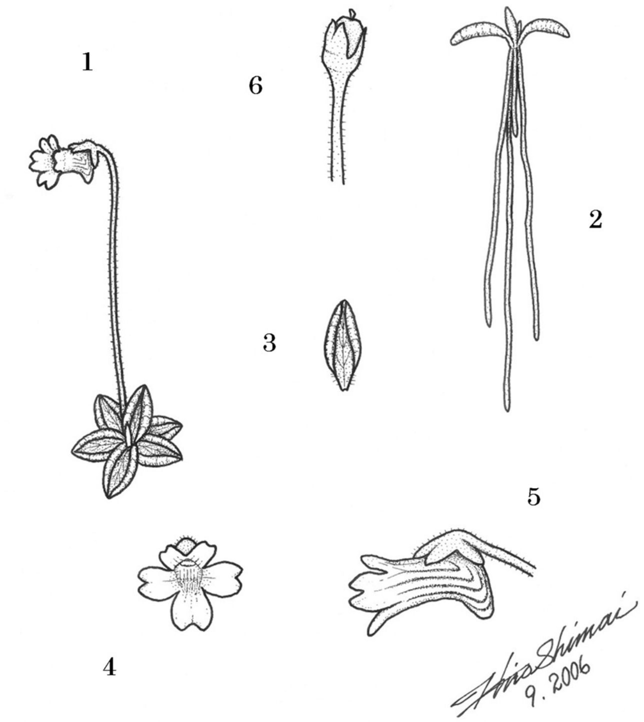
ETYMOLOGY: native of the Antarctic region

HABITAT: Sphagnum or wet peaty soil in open grasslands, bushes or sphagnum bogs. Often exposed to direct sunlight.

DISTRIBUTIONS: ARGENTINA (Nequén, Río Negro, Tierra del Fuego); CHILE (IX, XII). 0-2,050 m.

DISCUSSION: *Pinguicula antarctica* is found in the Patagonian regions of Argentina and Chile stretching down south to Tierra del Fuego. Casper (1966a) showed that Chiloe Island was the northernmost habitat for the species, but it occurs more north. It is morphologically very similar to *P. chilensis* and their distribution areas are more or less continuous and are partially overlapped each other causing taxonomical confusions. The morphology of vegetative parts in both species are very similar having monomorphic leaves and elastic root systems throughout the year without forming hibernacula. A main difference between the two is seen on the flowers. The corolla tube of *P. antarctica* has dark purple veins, while that of *P. chilensis* does not have. *P. antarctica* is more frequently seen in Southern Patagonia.

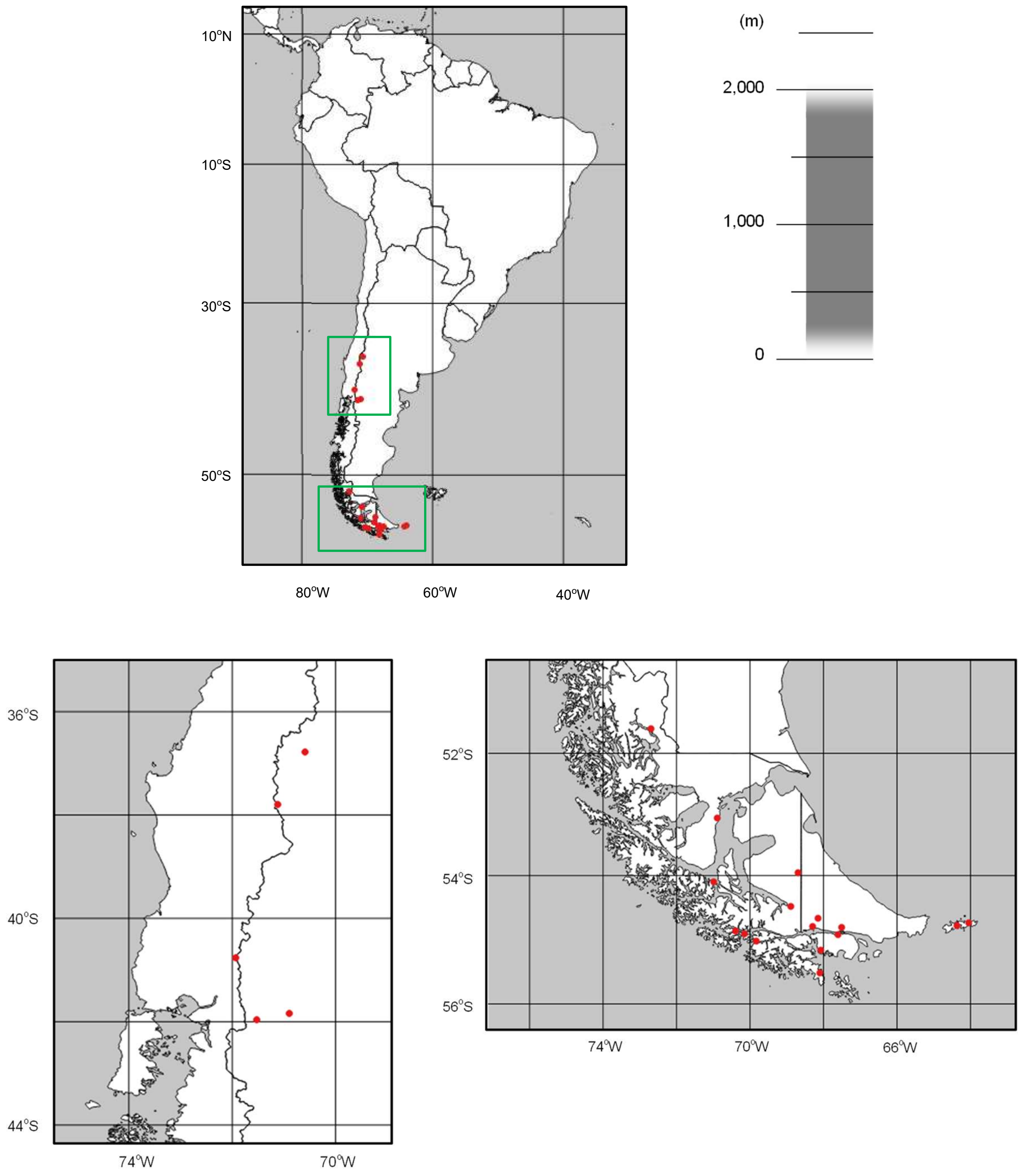
Plate 4.2. *Pinguicula antarctica*



10 mm: 1, 2, 3
5 mm: 4, 5, 6

1. habit with flower
2. habit with roots
3. leaf
4. flower, front view
5. flower, lateral view
6. capsule

P. antarctica



3. ***Pinguicula calyptrata*** Kunth, Nov. Gen. et Sp. 2 (1817) 226.

TYPE: Loxa, Regno Novo-Granat., *Humboldt & Bonpland 3319* (holotype: P!; isotype: P!).

SYNONYMS: *P. antarctica* Fernández-Pérez, *P. huilensis* Cuatrecasas

DESCRIPTION: Perennial herb. Root filiform, elastic. Stem very short. Leaf monomorphic, 5-10, maroon, sometimes yellowish-green, ovate to ovate-oblong, margin involute, apex obtuse to rather acute, 10-35 mm long, 7-20 mm wide. Runner formed underground, producing clonal plantlet at apex. Scape 1-4, densely glandulous, 15-180 mm long. Calyx bilabiate, upper lip 3-lobed, lobes ovate, 1.5-4 mm long, connate at base, lower lip 2-lobed, lobes triangular, smaller than uppers. Flower pale purple, purple at base of lips, yellow trichomes often forming two ridges at base of middle lobe. Corolla bilabiate, 10-15 mm across, zygomorphic, 10-15 mm long including spur, upper lip 2-lobed, lobes obovate, deeply notched to bifid at tip, lower lip 3-lobed, lobes larger than uppers, tube purple with darker veins, subcylindrical, yellow trichomes at base of lower throat, spur yellow, conical, 1-3.5 mm long. Capsule ovoid. Seed ellipsoid 450-600 X 150-240 µm. $2n = 16$. (Plate 4.3).

PHENOLOGY: I, II, III, IV, V, VI, VII, VIII, IX, X, XI, XII

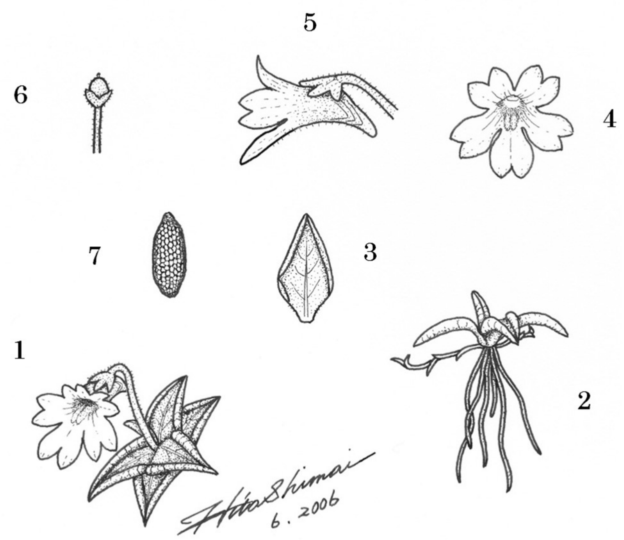
ETYMOLOGY: calyptrate (referring to the flower?)

HABITAT: Wet loamy, silty, or calcareous soil in slopes or on cliffs. Often exposed to direct sunlight.

DISTRIBUTION: COLOMBIA (Cauca); ECUADOR (Azuay, Carchi, Chimborazo, El Oro, Loja, Morona-Santiago, Napo, Pichincha, Sucumbíos, Tungurahua). 2,100-4,160 m.

DISCUSSION: *Pinguicula calyptrata* is found at the Andean regions of Colombia and Ecuador. The type locality mentioned as Loxa in the original description could be Loja, Ecuador. The species sometimes forms a large colony on wet steep slopes or vertical cliffs often covered by alga. It may be due to, at least partially, underground runners sprouting from a mother plant that produce a clonal plantlet at each apex. *P. calyptlata* is very similar to *P. involuta* distributed in Bolivia and Peru, but *P. calyptrata* has yellow trichomes at the base of lower lip while *P. involuta* does not. The tip of lobes is deeply emarginate in *P. calyptrata* while it is retuse to shallowly emarginate in *P. involuta*. *P. calyptrata* is locally abundant although it is not too frequently found.

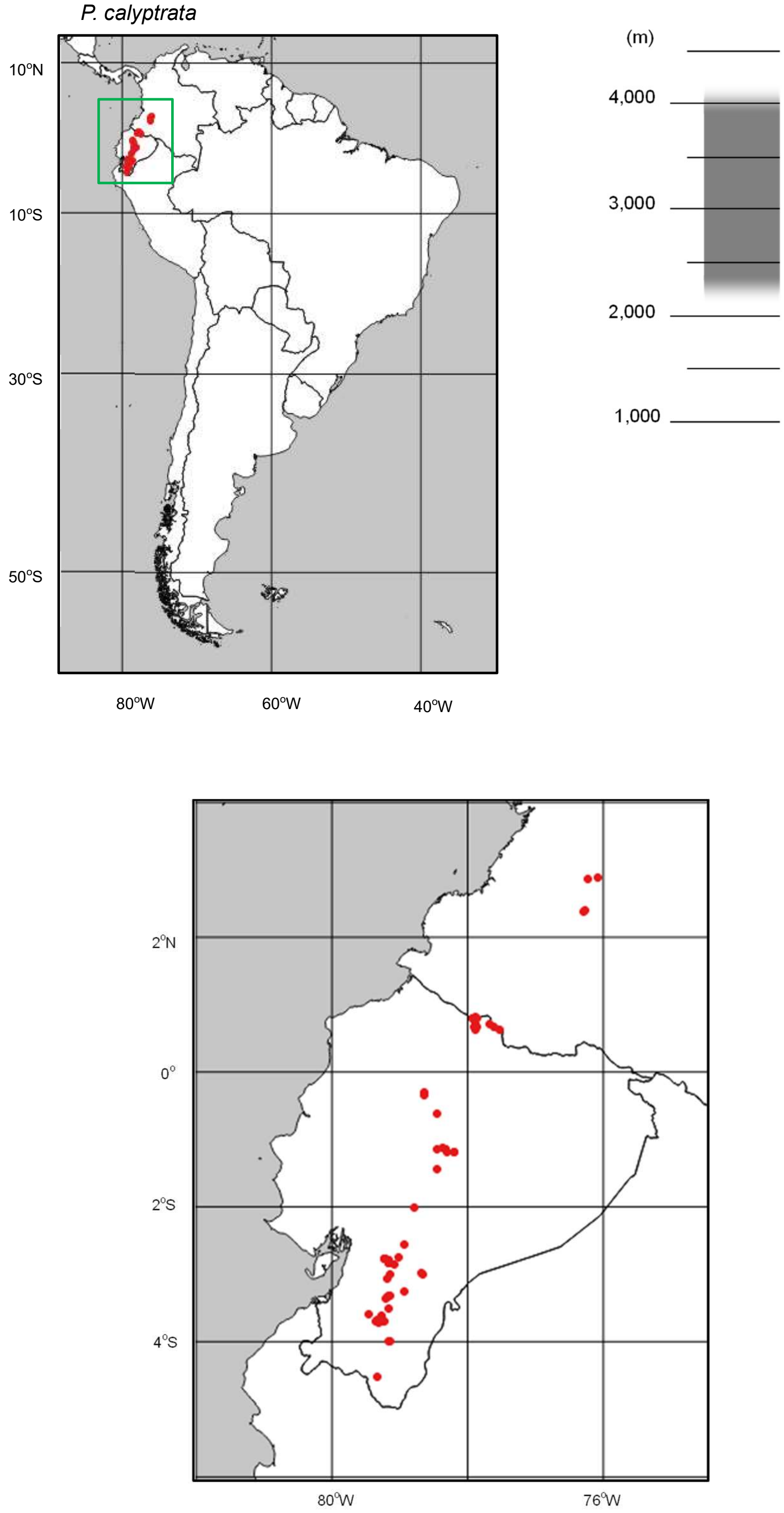
Plate 4.3. *Pinguicula calyptrata*



10 mm: 1, 2, 3, 6
10 mm: 4, 5
300 µm: 7

1. habit with flower
2. habit with roots and runners
3. leaf
4. flower, front view
5. flower, lateral view
6. capsule
7. seed

P. calyptrata



4. ***Pinguicula chilensis*** Clos, Hist. Fis. Pol. Chile, Bot. 4 (1849 [1848?]) 365.

TYPE: *Esta planta se cria en los pantanos de la provincial de Valdivia, en el Corral, cerca de Daglipulli* (This plant grows in wet places of the Province of Valdivia, Corral, near Daglipulli), January 1835, *Gay 169* (holotype: P; isotype: P!).

SYNONYMS: *P. antarctica* Donat, *P. antarctica* Thomsson

DESCRIPTION: Perennial herb. Root filiform, elastic. Stem very short. Leaf monomorphic, 3-8, yellowish-green, oblong to ovate, margin involute, apex obtuse to rather acute, 12-24 mm long, 8-11 mm wide. Scape 1-2, sparsely glandulous, 20-180 mm long. Calyx bilabiate, upper lip 3-lobed, lobes oblong-lanceolate, 1.5-3 mm long, lower lip 2-lobed, lobes slightly smaller than uppers. Flower pale purple, white at base of lips, yellow trichomes in lower throat. Corolla bilabiate, zygomorphic, 9-13 mm long including spur, 8-13 mm across, upper lip 2-lobed, lobes obovate, notched at tip, lower lip 3-lobed, lobes similar to uppers but larger, tube pale purple, cylindrical, spur yellow, conical, 2-3 mm long. Capsule ovoid. Seed narrowly ellipsoid, 700-930 X 190-250 µm. $2n = 16$. (Plate 4.4).

PHENOLOGY: I, II

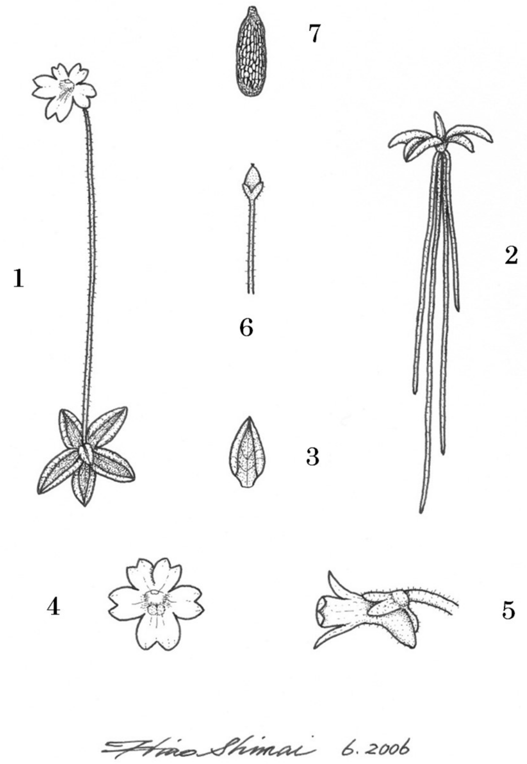
ETYMOLOGY: native of Chile

HABITAT: Wet fine sand or sphagnum in open grasslands or slopes. Often exposed to direct sunlight.

DISTRIBUTION: ARGENTINA (Neuquén, Río Negro); CHILE (IX, X, XIV). 700-2,500 m.

DISCUSSION: *Pinguicula chilensis* is distributed in the northern part of Patagonia, in Chile and Argentina. The vegetative parts of *P. chilensis* and *P. antarctica* are very similar and they can be hardly identifiable without flowers. Moreover, their distribution areas are partially overlapped each other in northern Patagonia. The differences between the two species are summarised in *P. antarctica* (species number 2). It seems that the population density at each microhabitat is relatively small and sparse.

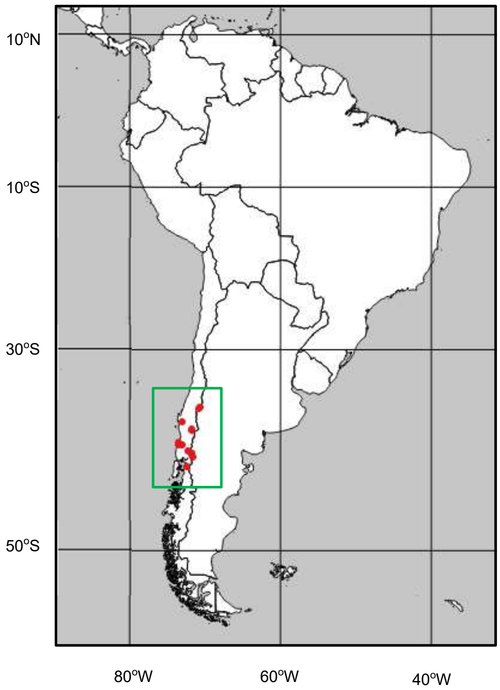
Plate 4.4. *Pinguicula chilensis*

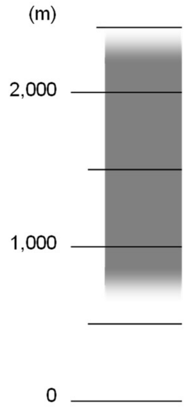


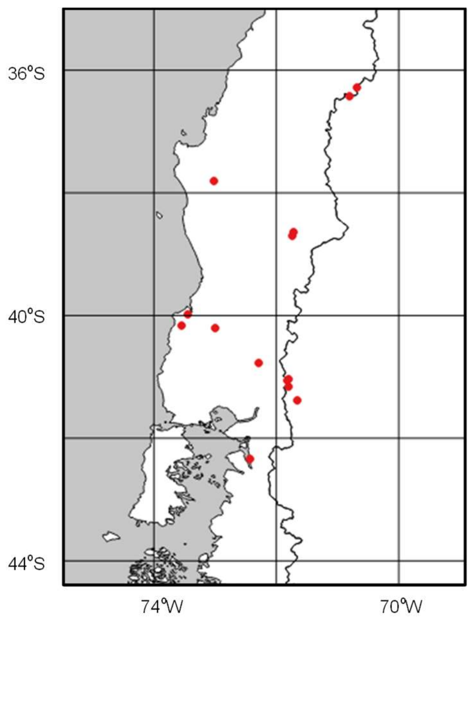
- 10 mm: 1, 2, 3, 6
- 10 mm: 4, 5
- 500 µm: 7

1. habit with flower
2. habit with root
3. leaf
4. flower, front view
5. flower, lateral view
6. capsule
7. seed

P. chilensis







5. ***Pinguicula involuta*** Ruíz et Pavón, Fl. Peruv. et Chil. 1 (1798) 20.

TYPE: PERU. *in altis frigidis et humidis Pillao, et Panamo Huassahuassi, inter Muscos* (in high cold and moist Pillao, and Panao Huassahuassi, among mosses) *Ruíz et Pavón*; *Pavón 93361* (type status unknown: A!, BM!, GH, K-photo ex-MPU!, MPU), ex herb *Pavón s.n.* (possible isotype: FI!).

SYNONYM: *P. macrostyla* Benjamin

DESCRIPTION: Perennial herb. Root filiform, elastic. Stem very short. Leaf monomorphic, 4-12, yellowish-green or maroon, ovate-oblong, margin involute, apex obtuse to rather acute, 8-30 mm long, 4-17 mm wide. Scape 1-4, densely glandulous, 35-100 mm long. Calyx bilabiate, upper lip 3-lobed, lobes oblong-ovate, 1-2 mm long, lower lip 2-lobed, lobes similar to uppers. Flower faintly pale purple to pale purple, base of lips slightly darker. Corolla bilabiate, 8-12 mm across, zygomorphic, 11-14 mm long including spur, upper lip 2-lobed, lobes subquadrate to subrectangular, tip shallowly emarginate to emarginate, lower lip 3-lobed, lobes obovate to subrectangular, tip shallowly notched, tube pale purple with darker veins, conical, spur pale yellow, subcylindrical, 2.5-4.5 mm long. Capsule subglobose. Seed ellipsoid. (Plate 4.5).

PHENOLOGY: I, III, V, VI, VII, VIII, IX, X, XI, XII

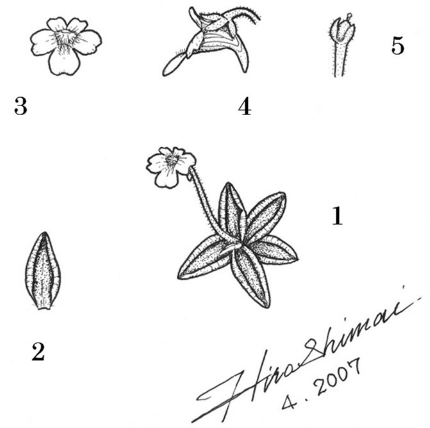
EPITHET: involute, rolled inward (referring to the leaf)

HABITAT: Wet calcareous sandstone in steep slopes or on cliffs. Tolerant to various light intensities.

DISTRIBUTION: BOLIVIA (Cochabamba, La Paz); PERU (Amazonas, Cuzco, Huánuco, Lambayeque, Pasco, Piura, San Martín). 2,542-4,267 m.

DISCUSSION: *Pinguicula involuta* is confined to the Andean regions of Bolivia and Peru. The species is morphologically very similar to *P. calyptrata*, distributed in Colombia and Ecuador. The differences between the two species are discussed in *P. calyptrata* (species number 3). As far as known, the distribution areas of the two species are not overlapped. *P. involuta* also produces runners forming a clonal plantlet at the apex as *P. calyptrata* does. The collection records of the *P. involuta* are much sparse and less frequent, possibly because of higher elevations with extremely limited means of access to the locality. Little information regarding the ecology and current status at the habitat for the species is available. A review will be needed for the populations in northern Peru.

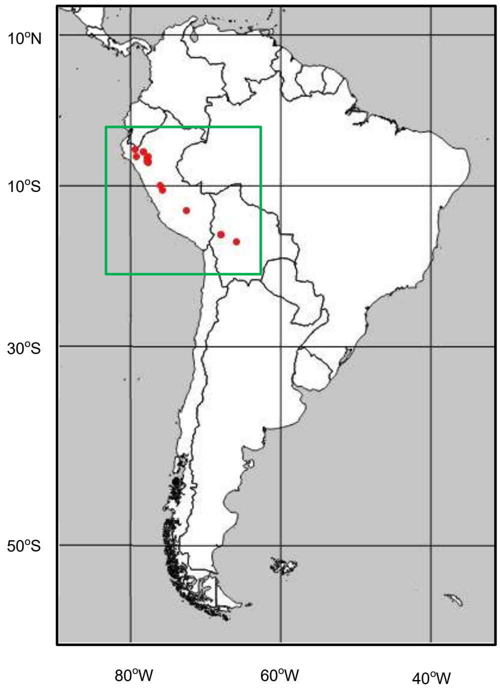
Plate 4.5. *Pinguicula involuta*

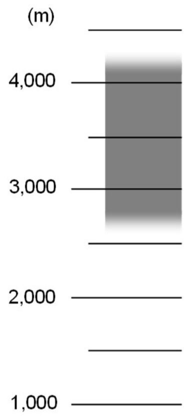


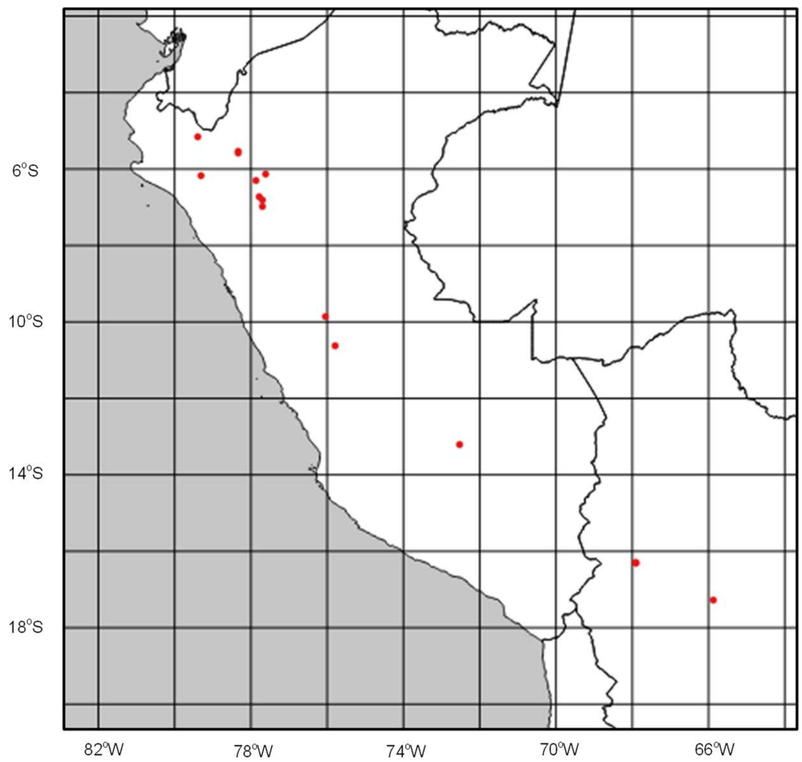
10 mm: 1, 2
10 mm: 3, 4, 5

1. habit with flower
2. leaf
3. flower, front view
4. flower, lateral view
5. capsule

P. involuta


10°N
10°S
30°S
50°S
80°W
60°W
40°W


(m)
4,000
3,000
2,000
1,000


6°S
10°S
14°S
18°S
82°W
78°W
74°W
70°W
66°W

6. ***Pinguicula jarmilae*** Halda et Malina, Acta Mus. Richnov., Sect. Nat. 14 (2007) 110.

TYPE: BOLIVIA. *department Chuquisaca: saxetum verrticalium humidum prope urbi Nuevo Mundo at 1750 m supra mare* (department of Chuquisaca: wet vertical rocks above Nuevo Mundo at altitude 1,750 m above sea level), 20 November 2007, *Halda 11972* (holotype: PR).

SYNONYM: *P. chuquisacensis* Beck, Fleischm. et Borsch

DESCRIPTION: Perennial herb. Root filiform, elastic. Stem very short. Leaf monomorphic, 4-15, yellowish-green, oblong-ovate, base narrowly cuneate, margin irregularly undulate and slightly revolute, apex obtuse, 20-110 mm long, 8-30 mm wide. Runner formed underground, producing clonal plantlet at apex. Scape 1-5, densely glandulous, 30-110 mm long. Calyx bilabiate, upper lip 3-lobed, lobes ovate, ca. 2 mm long, connate at base, lower lip 2-lobed, lobes smaller than uppers. Flower white to faintly pale lilac. Corolla bilabiate, 8-12 mm across, zygomorphic, 8-15 mm long including spur, upper lip 2-lobed, lobes obovate-oblong, tip notched to bifid, lower lip 3-lobed, lobes similar to uppers but larger, tube faintly pale yellowish-green with darker veins, cylindrical, spur yellowish-green, narrowly conical to conical, 1-3 mm long. Capsule subglobose. Seed narrowly ellipsoid, 480-580 X 110-200 µm. (Plate 4.6).

PHENOLOGY: VIII, XI

ETYMOLOGY: dedicated to Jarmila Haldova (wife of Josef J. Halda, one of the authors who described this species)

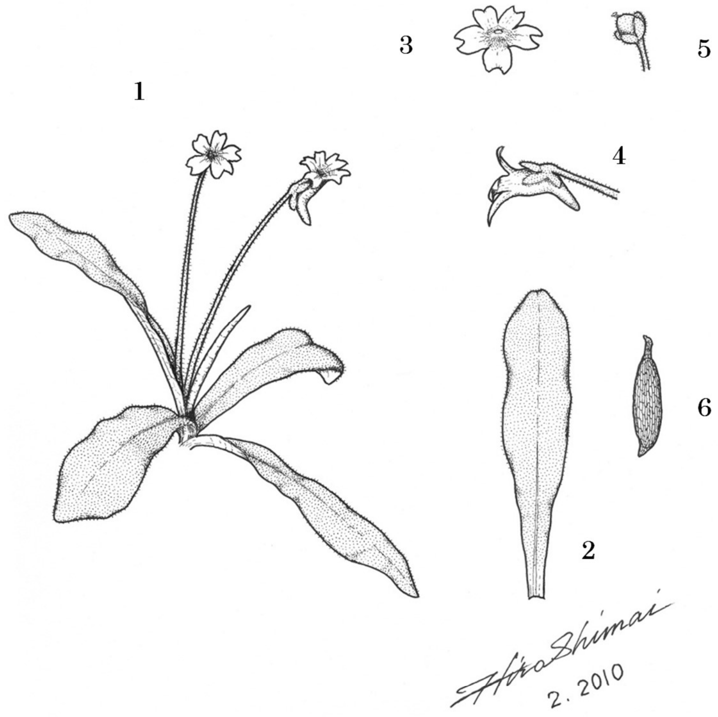
HABITAT: Seasonally wet sandstone cliffs at a roadside. Tolerant to low light intensity.

DISTRIBUTION: BOLIVIA. Chuquisaca, known only from Nuevo Mundo. 1,750-2,518 m.

DISCUSSION: *Pinguicula jarmilae* is known only from the Nuevo Mundo Valley (ca. 100 km east of Sucre) in the Department of Chuquisaca, Bolivia. Herbarium specimens have been collected repeatedly at the area since 1995. It is unclear all of them were collected at the same locality, but Beck et al. (2008) reported that the different altitudinal ranges (1,750-2,518 m) indicated on each herbarium label could be attributed to the accuracy of GPS data. It was described as *P. jarmilae* by Halda et al. (2007) but it was almost simultaneously described as *P. chuquisacensis* by Beck et al. (2008). Due to an earlier published date, *P. jarmilae* is adopted for a valid scientific name here. Close relationships between the species and *P. calyptrata*, and *P. involuta* have been suggested by Beck et al. (2008) but *P. jarmilae* characteristically has a whitish flower and longer leaves.

So far, it is known only in Nuevo Mundo. Urgent actions may be necessary for the conservation of the species.

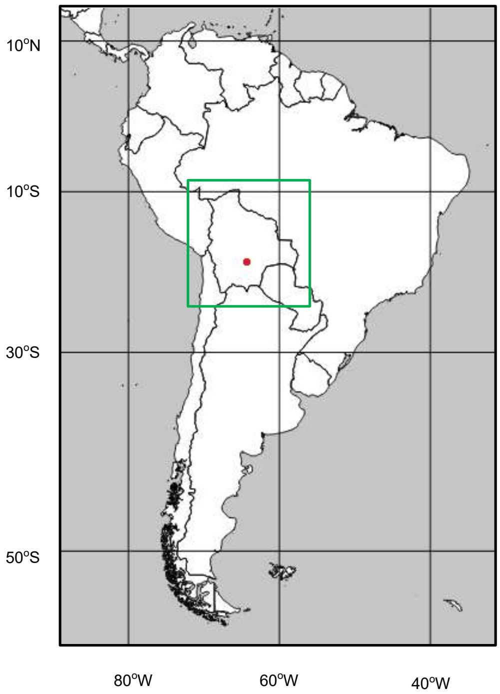
Plate 4.6. *Pinguicula jarmilae*

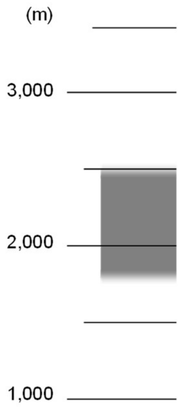


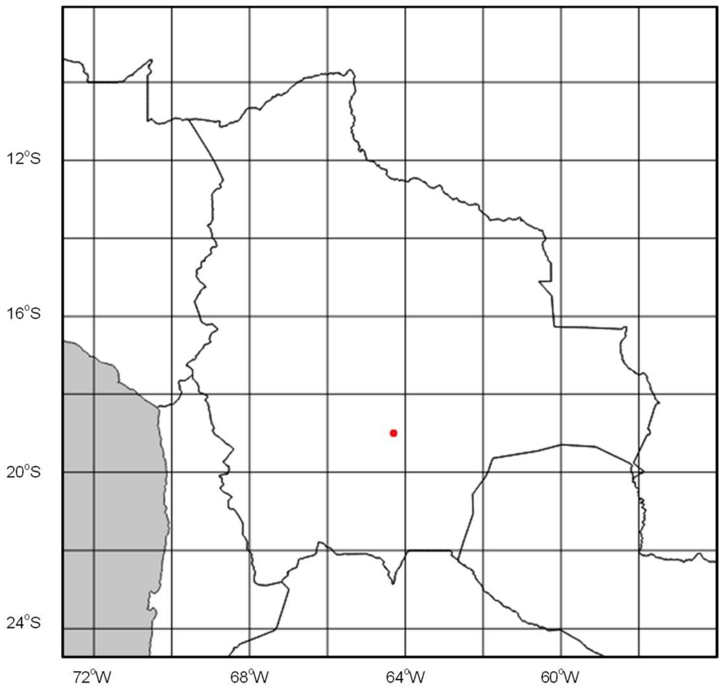
10 mm: 1, 2
10 mm: 3, 4, 5
0.3 mm: 6

1. habit with flower
2. leaf
3. flower, front view
4. flower, lateral view
5. capsule
6. seed

P. jarmilae


10°N
10°S
30°S
50°S
80°W
60°W
40°W


(m)
3,000
2,000
1,000


12°S
16°S
20°S
24°S
72°W
68°W
64°W
60°W

Sect. *Cardiophyllum* Casper (1962) Feddes. Repert. 66, 34.

TYPE: *Pinguicula hirtiflora* Tenore

SYNONYM: Sect. *Pionophyllum* DC.

7. ***Pinguicula crystallina*** Smith, Flora Graeca 1 (1806) 8.

TYPE: *in rivulis prope vicum Camandriae in insulâ Cypro* (stream near the village of Camandriae in the Island of Cyprus), 1787, *Bauer s.n.* (holotype: OXF!; isotype: BM?).

SYNONYM: *P. habilii* Yıldırım, Şenol et Pirhan

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf monomorphic, 6-9, yellowish-green, oblong-elliptic to ovate-elliptic, but occasionally linear-lanceolate, margin irregularly involute, apex obtuse, 20-100 mm long, 10-20 mm wide. Scape 1-6, densely glandulous, 35-180 mm long. Calyx bilabiate, upper lip 3-lobed, lobes broadly ligulate, 2-3 mm long, lower lip lobe not divided, broadly obovate, tip obtuse to emarginate. Flower often monstrous, pale purple, white at lower half of lips, or rarely entirely white, yellow trichomes in throat. Corolla bilabiate, 8-15 mm across, zygomorphic, 10-20 mm long including spur, upper lip 2-lobed, lobes suborbicular to ovate or triangular, lower lip 3-lobed, lobes larger than uppers, lateral lobes obliquely quadratus to cuneate, obovate or triangular, middle lobe wider than laterals, tip obtuse to truncate or shallowly emarginate, tube yellowish-green, conical, spur yellowish-green, cylindrical, 3-10 mm long, sometimes incurved. Capsule globose. Seed narrowly ellipsoid, 800-990 X 240-340 µm. $2n = 24, 28$. (Plate 4.7).

PHENOLOGY: IV, V, VI, VII, VIII, IX

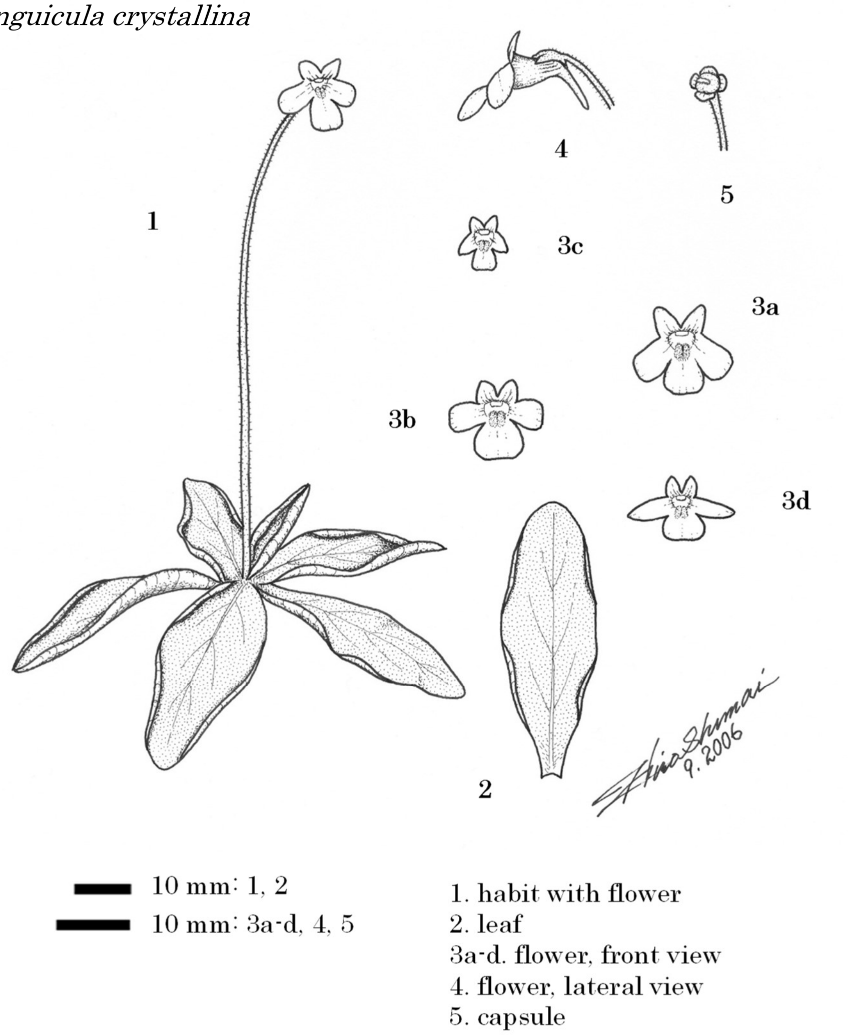
ETYMOLOGY: crystalline (referring to the shiny leaf)

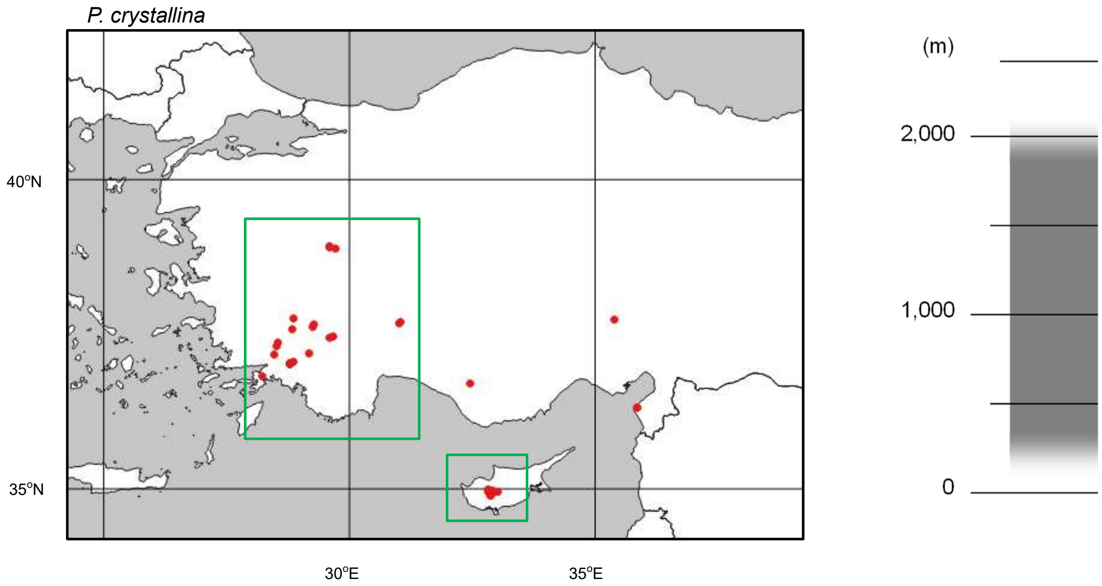
HABITAT: Wet calcareous sand, sandstone, or serpentine in slopes or on cliffs (often vertical or overhanging). Tolerant to various light intensities.

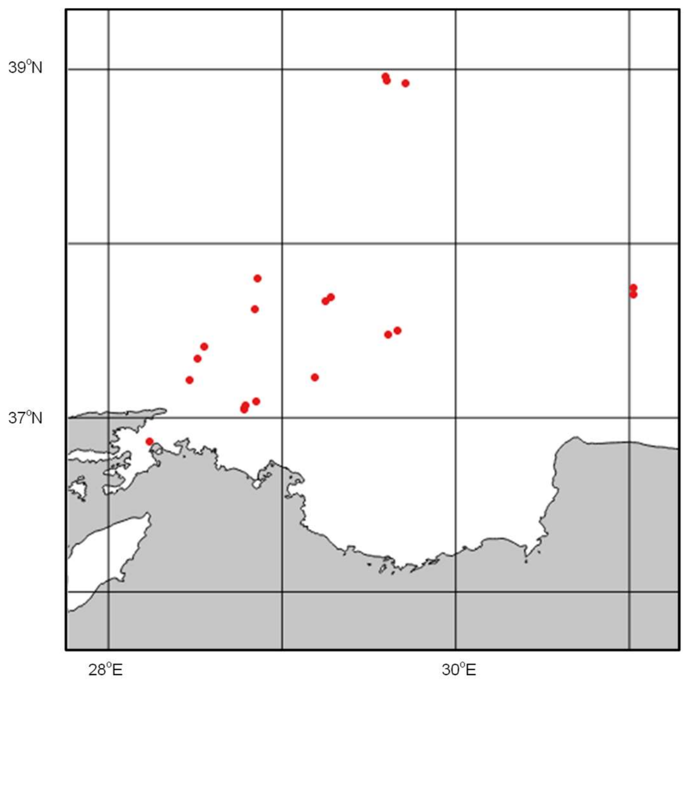
DISTRIBUTION: CYPRUS (Limassol, Nicosia); TURKEY (Adana, Antalya, Burdur, Denizli, Hatay, Isparta, Kütahya, Muğla, Uşak). 85-2,100 m.

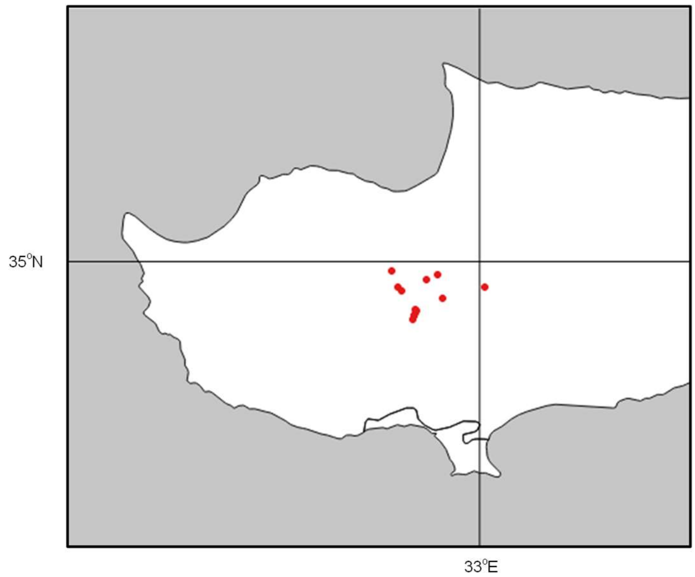
DISCUSSION: *Pinguicula crystallina* is distributed in Cyprus and Anatolia. The species is often considered to be endemic to the Tróodos Mountains in Cyprus, but it also occurs in Anatolia. It is morphologically very similar to *P. hirtiflora*, though the two species are geographically isolated from each other. Because of their morphological diversities, particularly shapes of corolla lobes, it is sometimes difficult to distinguish them. In general, the tip of the lower lip lobes in *P. crystallina* is rounded to truncate, or very shallowly emarginate, while that of *P. hirtiflora* is often emarginate. A clear difference between the two was seen in DNA sequences. Although the distribution of *P. crystallina* is very restricted, a number of plants often form large colonies on wet rock walls or open grasslands. The type locality "Camandriae (also spelled as Comandriae, Commandaria etc.)" in Cyprus was annotated possibly as "Kato Amiandos" (a village located at the eastern slope of the mountains) by Taylor (1985), but Comandriae is a region on the southern slope of the mountain.

Plate 4.7. *Pinguicula crystallina*




P. crystallina
40°N
35°N
30°E
35°E
(m)
2,000
1,000
0


39°N
37°N
28°E
30°E


35°N
33°E

8. ***Pinguicula hirtiflora*** Tenore, Fl. Nap. 3 (1811) 18.

TYPE: M.te della Cava de Castellammare, all'Acqua Santa, s.d., *Tenore* (lectotype: NAP!, designated by Peruzzi et al. 2004).

SYNONYMS: *P. albanica* Griseb., *P. crystallina* Smith subsp. *hirtiflora* (Tenore) Strid, *P. hirtiflora* Tenore subsp. *megaspilaea* Nyman, *P. hirtiflora* Tenore var. *decipiens* Bornmüller, *P. hirtiflora* Tenore var. *euboea* Beauverd et Topali, *P. hirtiflora* Tenore var. *gionae* Contandriopoulos et Quézel, *P. hirtiflora* Tenore var. *louisii* (Markgr.) Ernst, *P. hirtiflora* Tenore var. *megaspilaea* (Boiss. et Heldr.) Schindler, *P. hirtiflora* Tenore f. *pallida* Casper, *P. laeta* Pantocsek, *P. lavalvae* Innangi et Izzo, *P. louisii* Markg., *P. megaspilaea* Boiss. et Herder., *P. vulgaris* Petangna, *P. vulgaris* L. var. *hirtiflora* Cesati, Passerini et Gibelli

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf monomorphic, 6-9, yellowish-green, elliptic-oblong to obovate-oblong, margin slightly involute or revolute, apex obtuse, 20-80 (or up to 120) mm long, 10-35 mm wide. Scape 1-7, densely glandulous, 35-145 mm long. Calyx bilabiate, upper lip 3-lobed, lobes spatulate, ca. 2 mm long, lower lip 2-lobed, lobes smaller than uppers. Flower often monstrous, pale purple, white at lower half of lips, often with dark purple veins at base of upper lobes, yellow trichomes in throat.

Corolla bilabiate, 6-20 mm across, zygomorphic, 13-32 mm long including spur, upper lip 2-lobed, lobes ovate to oblong, tip obtuse to truncate or emarginate, lower lip 3-lobed, lobes larger than uppers, oblong-ovate to subquadrate or rather cuneate, tip truncate to retuse or emarginate, tube yellowish-green, conical, spur yellowish-green, cylindrical, 5-18 mm long. Capsule globose. Seed narrowly ellipsoid, 700-1,020 X 210-340 µm. 2*n* = 16, 24, 27, 28, 32, 48, 56. (Plate 4.8).

PHENOLOGY: III, IV, V, VI, VII, VIII, IX, X, XI

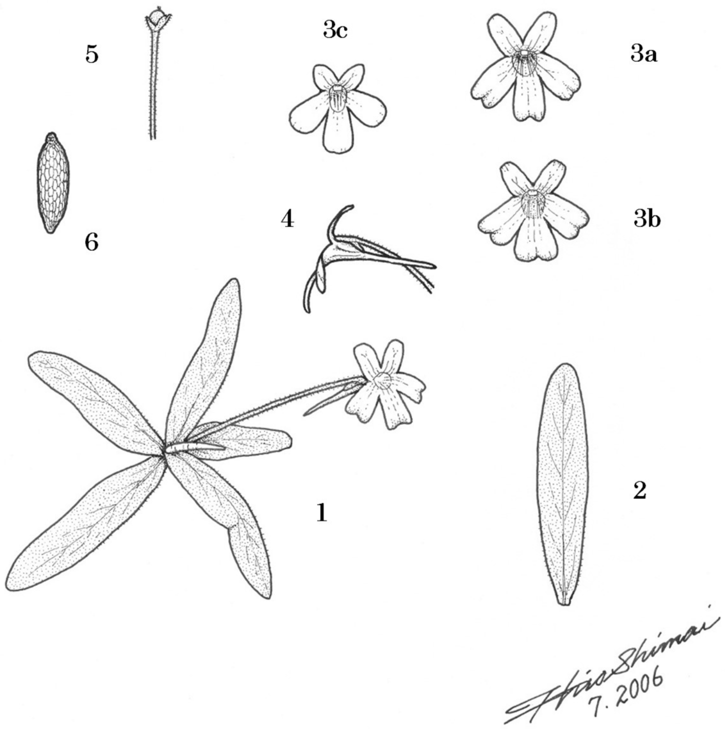
ETYMOLOGY: hairy-flowered

HABITAT: Wet calcareous sandstone or limestone in slopes or on cliffs (often vertical or overhanging). Tolerant to various light intensities.

DISTRIBUTION: ALBANIA (Berat, Dibër, Durrës, Elbasan, Korçë, Kukës, Shkodrës, Tiranë, Vlorë); BOSNIA AND HERZEGOVINA (Republika Srpska); FRANCE (Alpes-Maritimes); GREECE (Achaïa, Árta, Évia, Évritanía, Fokída, Grevená, Ioánina, Kardítsa, Korinthia, Messinia, Pieriá, Tríkala, Viotia); ITALY (Calabria, Campania); KOSOVO (Deçan, Gjakovë); MACEDONIA (Bitola). 0-2,341 m.

DISCUSSION: *Pinguicula hirtiflora* is widely distributed from France, Italy (the lectotype locality is located in the Region of Campania) to the former Yugoslavian countries and Greece. The species often bears abnormal flowers, e.g. having very small corolla lobes, a 1-lobed or 3-lobed upper lip, or two or more spurs. It is sometimes treated as a subspecies of *P. crystallina* (e.g. Strid and Tan 1991), but see *P. hirtiflora* (species number 8) for the differences between the two. Some intraspecific taxa have been recognised such as *P. hirtiflora* var. *louisii*, the former Yugoslavian populations sometimes having non-emarginate corolla lobes and a longer spur (Ernst 1961), *P. hirtiflora* var. *gionae*, Greek populations with longer leaves up to ca. 80 mm long (Contandriopoulos and Quézel 1974), *P. hirtiflora* var. *megaspilaea*, Peloponnesian populations having much longer leaves up to ca. 120 mm long (Boissier 1879), and *P. hiriflora* f. *pallida*, Albanian populations having white flowers (Casper 1962a, 1966a), but those have not been regarded in this work taking account for its morphological variability within each population or region although a further study is necessary for the group. *P. hirtiflora* often forms large colonies on wet limestone rocks or slopes at a microhabitat and locally abundant though the microhabitat often tends to be very small.

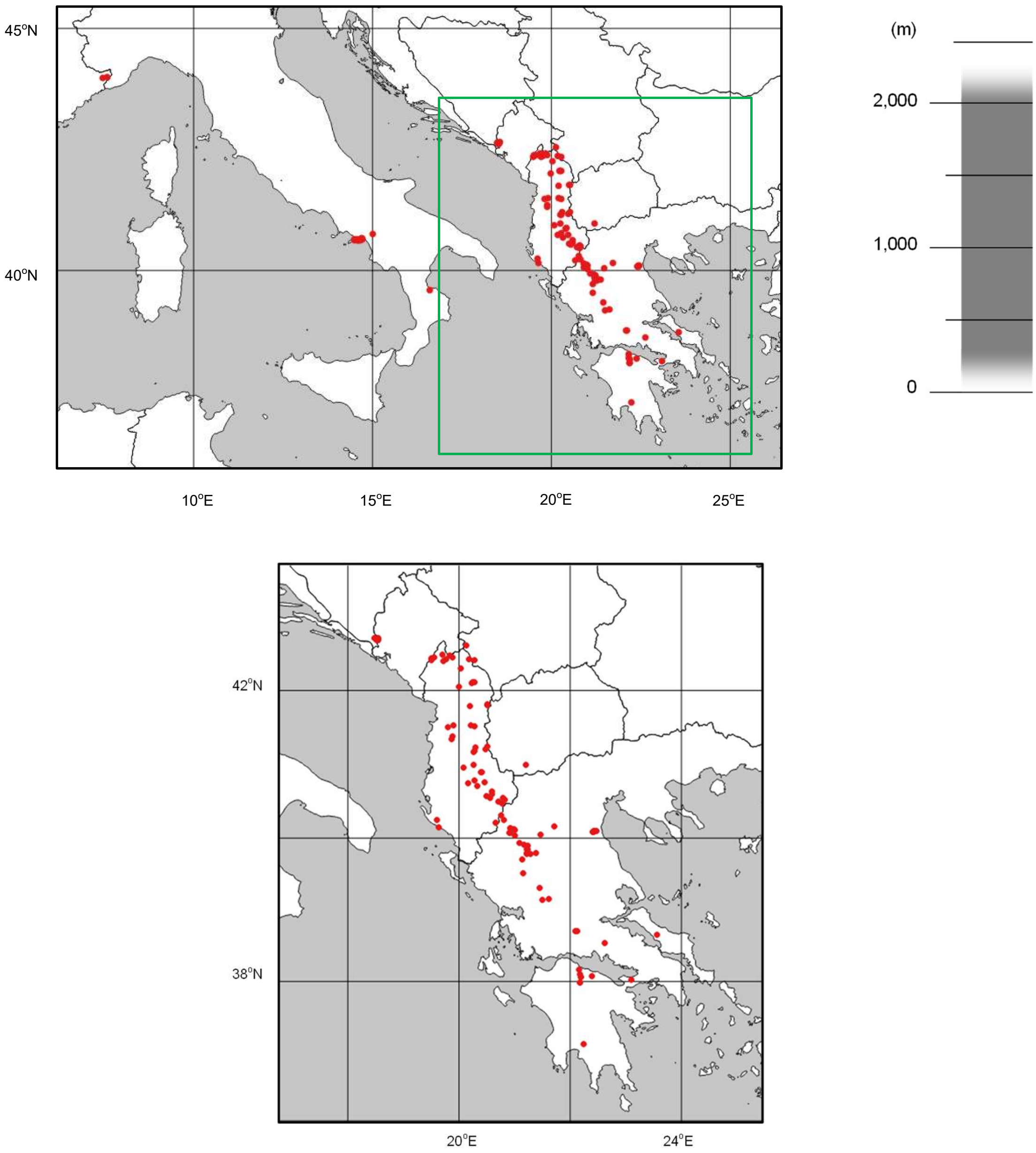
Plate 4.8. *Pinguicula hirtiflora*



10 mm: 1, 2
10 mm: 3a-c, 4, 5
500 µm: 6

1. habit with flower
2. leaf
3a-c. flower, front view
4. flower, lateral view
5. capsule
6. seed

P. hirtiflora



Sect. *Caribensis* Shimai, sect. nov.

TYPUS: *Pinguicula albida* Wright ex Griseb.

DESCRIPTO: Herba perennis. Radicibus filiformibus. Rhizoma nimis brevis. Terrestris, epipetrica vel epiphytica. Folia monomorpha, 1 ad numerosa, albido-viridis ad flavo-viridis vel purpurea, filiformis ad suborbiculata, usque ad 200 mm longa. Scapi 1-6, usque ad 230 mm longi, glandulis. Calyx bilabiatus, labium superum trilobum, lobis lanceolatis ad ovatis vel ellipticis, 2-3 mm longis, labium inferum bilobum, paulum minor. Corolla albida ad caerulea vel rubro-purpurea, bilabiata, usque ad 35 mm lata, usque ad 40 mm longa (calcare incluso), labium superum bilobum, lobis oblongis ad obovatis vel orbicularis, labium inferum trilobum, lobis diversus, tubus cylindricus ad conicus, calcar cylindricum ad subcylindricum, 2-7 mm longum.

DISTRIBUTIO: CUBA; CIV. SANTO DOMINGO

TYPE: *Pinguicula albida* Wright ex Griseb.

SYNONYMS: Sect. *Discoradix* Casper, Sect. *Pionophyllum* Ernst, Subsect. *Homophylliformis* Casper, Ser. *Albidae* Casper

DESCRIPTION: Perennial herb. Roots filiform. Stem very short. Terrestrial to lithophytic or epiphytic. Leaf monomorphic, 1 to numerous, whitish-green to yellowish-green or maroon, filiform to suborbicular, up to 200 mm long. Scape 1-6, up to 230 mm long glandulous. Calyx bilabiate, upper 3-lobed, lobes lanceolate to ovate or elliptic, 2-3 mm long, lower 2-lobed, lobes slightly smaller than upper. Flower white to dark blue or reddish-purple. Corolla bilabiate, up to 35 mm across, up to 40 mm long including spur, upper-lip 2-lobed, oblong to obovate or suborbicular, lower-lip 3-lobed, lobes diverse, tube cylindrical to conical, spur cylindrical to subcylindrical, 2-7 mm long.

DISTRIBUTION: CUBA; DOMINICAN REPUBLIC

9. ***Pinguicula albida*** Wright ex Griseb., Cat. Pl. Cub. (1866) 162.

TYPE: CUBA. Occ. *Grisebach 561*, (holotype: GOET!; isotypes *Wright 2885 ex Griseb. 561*: BM!, BP!, K (destroyed in March 1943 while on loan to Berlin), IEB-photo ex-NY!, LE!, MO!, NY!, US!, WU!).

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf monomorphic, 4-12, whitish-green, ovate to suborbicular, margin narrowly involute, apex obtuse, 10-45 mm long, 5-35 mm wide. Scape 1-4, sparsely glandulous, 50-200 mm long, often falling down and parallel to the ground.

Calyx bilabiate, upper lip 3-lobed, lobes ovate, ca. 2 mm long, connate to middle, lower lip 2-lobed, lobes oblong, connate at base. Flower white, yellow trichomes in throat. Corolla bilabiate, 6-8 mm across, subactinomorphic, 7-15 mm long including spur, upper lip 2-lobed, lobes obovate, lower lip 3-lobed, lobes only slightly larger than uppers, tube yellow with reddish veins, subcylindrical to conical, angled at below meddle, spur yellow, subcylindrical, 2-3 mm long. Capsule ovoid. Seed ellipsoid, 400-530 X 200-250 µm. $2n = 16$. (Plate 4.9).

PHENOLOGY: I, II, III, VI, VII, X, XI, XII

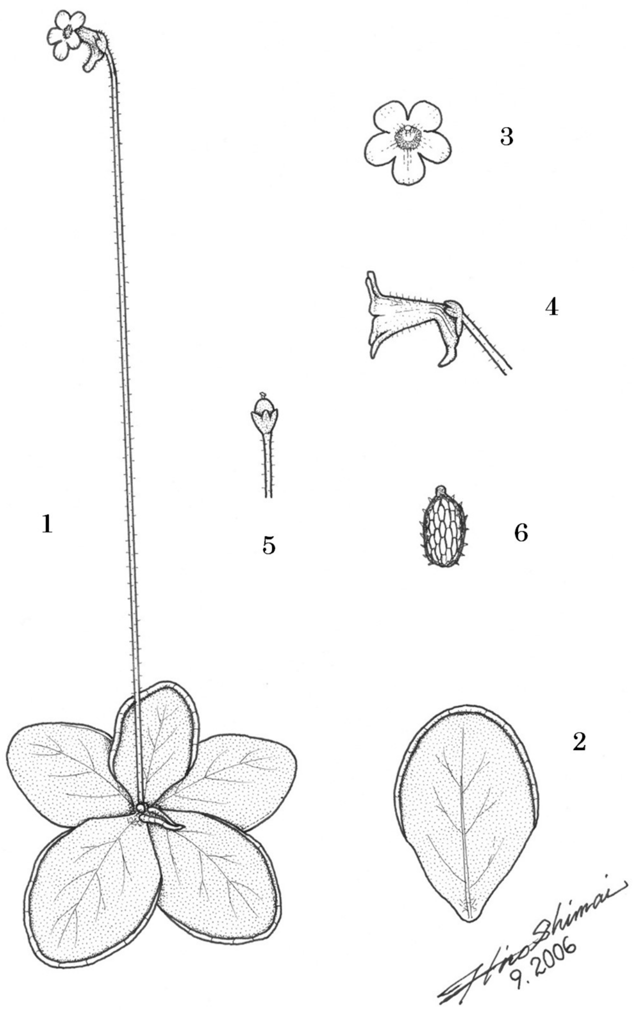
ETYMOLOGY: whitish (referring to the flower)

HABITAT: Somewhat wet sandy soil in bush or open palm forest margins. Low light intensity.

DISTRIBUTION: CUBA (Pinar del Río). 0-400 m.

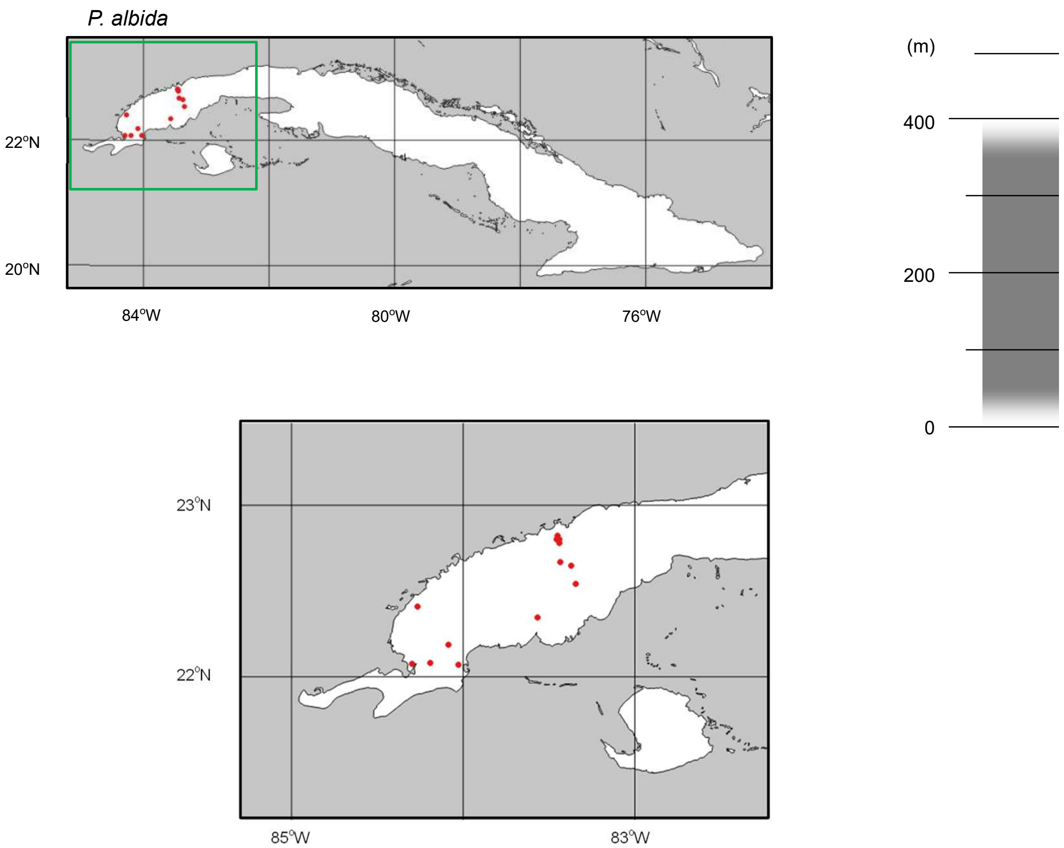
DISCUSSION: *Pinguicula albida* is endemic to the Province of Pinar del Río, Cuba. The species is often found under juvenile palm trees of *Acoelorraphe wrightii*, providing shade over the microhabitat of *P. albida*. A very thin, thread-like flower scape elongates up to 200 mm and often falls parallel to the ground. It seems that the number of plants in each microhabitat is relatively small and the population density is rather sparse. This plant is probably biannual, so that regular seed propagations at the habitat may be necessary although pollination seems to be not always successful. It is morphologically very similar to *P. jaraguana*, endemic to the Province of Holguín, Cuba, but their geographical distributions are apparently isolated from each other.

Plate 4.9. *Pinguicula albida*



10 mm: 1, 2
5 mm: 3, 4, 5
500 μm: 6

1. habit with flower
2. leaf
3. flower, front view
4. flower, lateral view
5. capsule
6. seed



P. albida
22ºN
20ºN
84ºW
80ºW
76ºW
(m)
400
200
0
23ºN
22ºN
85ºW
83ºW

10. ***Pinguicula benedicta*** Barnhart, Mem. Torrey Bot. Club 16 (1910) 110.

TYPE: CUBA. Oriente, trail, Camp La Barga to Camp San Benito, 23 February 1910, *Shafer 4025* (holotype?: A!).

SYNONYMS: *P. bissei* Casper, *P. caryophyllacea* Casper, *P. infundibuliformis* Casper, *P. lippoldii* Casper, *P. toldensis* Casper

DESCRIPTION: Variable species. Perennial herb. Root filiform, elastic. Stem very short. Leaf monomorphic, 3-8, yellowish-green or maroon, obovate to ovate, margin often slightly involute, apex obtuse to rather acute, 10-20 mm long, 8-13 mm wide. Scape 1, glabrous or densely glandulous, 50-140 mm long. Calyx bilabiate, upper lip 3-lobed, lobes ovate, ca. 2 mm long, lower lip 2-lobed, lobes slightly smaller than uppers. Flower reddish-purple to pink or sometimes white. Corolla bilabiate, 12-18 mm across, zygomorphic, 12-20 mm long including spur, upper lip 2-lobed, lobes oblong to obovate or suborbicular, lower lip 3-lobed, lobes larger then uppers, tip rounded to truncate, tube purple, cylindrical to conical, spur purple, cylindrical, pendulous to incurved, 4-6 mm long. Capsule globose. Seed ellipsoid, 490-550 X 250-280 µm. $2n = 18$. (Plate 4.10).

PHENOLOGY: I, II, III, VI, XI

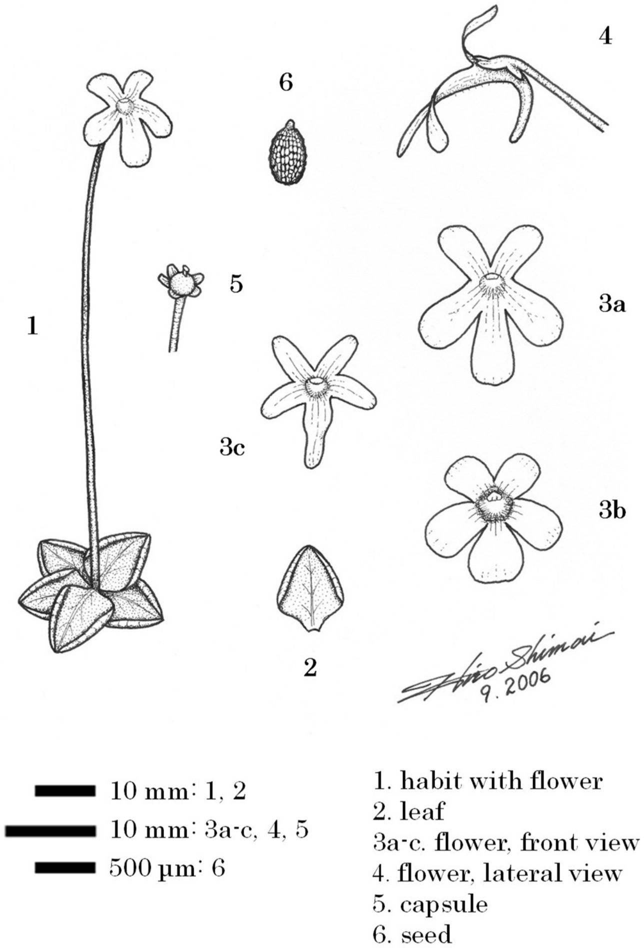
ETYMOLOGY: prized

HABITAT: Wet loamy or silty soil in slopes or serpentine cliffs along riversides. Tolerant to various light intensities.

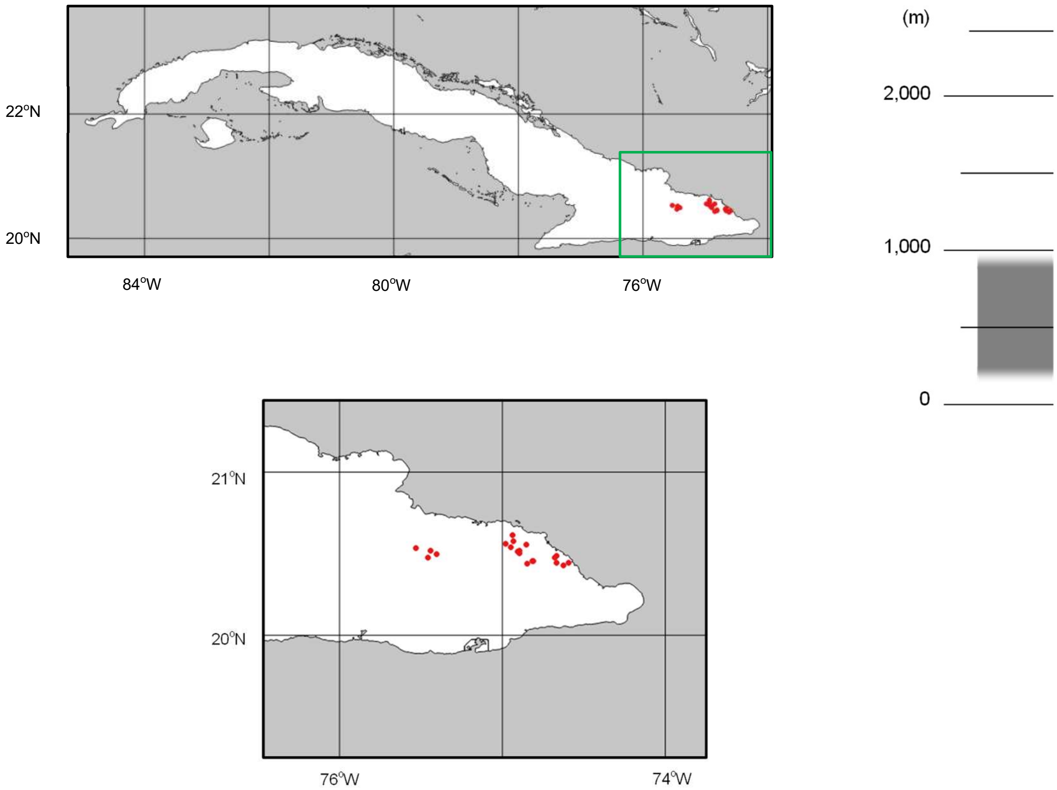
DISTRIBUTION: CUBA (Guantánamo, Holguín, Santiago de Cuba). 155-1,000 m.

DISCUSSION: *Pinguicula benedicta* is endemic to the Provinces of Holguín, Guantánamo, and Santiago de Cuba (the Province of Oriente has been split into 6 smaller provinces since 1976); the holotype locality is likely located in Alejandro de Humboldt National Park in the Province of Holguín today. This species is morphologically very variable. Different shapes of corolla lobes and corolla colours are seen even within the same microhabitat. Some recently described species from eastern Cuba, such as *P. infundibuliformis* (Casper 2003), *P. bissei* and *P. caryophyllacea* (Casper 2004), *P. lippoldii* and *P. toldensis* (Casper 2007) are likely synonymous with *P. benedicta*. Therefore, those are reasonably considered as conspecific and treated as such here. *P. benedicta* is easily distinguished from other Cuban species particularly by flower colour. The species is often found on wet slopes along rivers or streams but it seems that the number of plants at each locality is relatively small.

Plate 4.10. *Pinguicula benedicta*



P. benedicta



11. ***Pinguicula casabitoana*** Jiménez, Rhodora 62 (1960) 238.

TYPE: DOMINICAN REPUBLIC. Alto de Casabito, Province of La Vega, 1400 m, 17 July 1955, *Jiménez 3029* (holotype: unknown; isotypes: JE!).

SYNONYM: *P. cladophila* Ernst

DESCRIPTION: Epiphyte. Perennial herb. Root filiform, elastic. Stem very short. Leaf monomorphic, 15-40, yellowish-green, linear-lanceolate, margin strongly revolute, apex rather acute, 25-30 mm long, 3-4 mm wide. Scape 1 or more, densely glandulous, 25-50 mm long. Calyx bilabiate, upper lip 3-lobed, lobes lanceolate, ca. 3 mm long, connate to middle, lower lip 2-lobed, lobes broadly ovate, slightly smaller than uppers. Flower white, yellow trichomes in throat. Corolla bilabiate, 7-9 mm across, zygomorphic, 8-15 mm long including spur, upper lip 2-lobed, lobes suborbicular, lower lip 3-lobed, lobes suborbicular, larger than uppers, tube faintly pale yellow, shortly cylindrical, spur faintly pale yellow, subcylindrical to conical, 1-2 mm long. Capsule subglobose. Seed fusiform-ellipsoid. (Plate 4.11).

PHENOLOGY: V, XI

ETYMOLOGY: native of Alto de Casabito

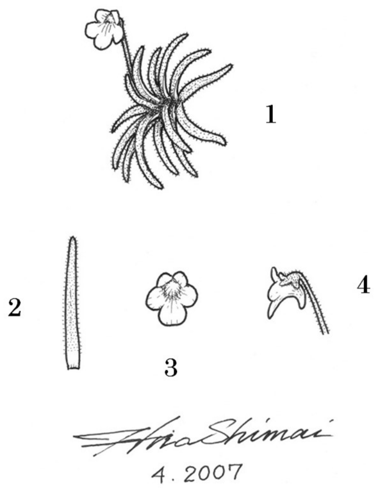
HABITAT: Epiphytic on dry twigs or stems of different trees growing in wet places.

Low light intensity.

DISTRIBUTION: DOMINICAN REPUBLEC (La Vega, Monseñor Nouel, Peravia, San Juan). 800-2,075 m.

DISCUSSION: *Pinguicula casabitoana* is endemic to mountain regions in the Dominican Republic. This species is an epiphyte growing directly on stems and twigs of shrubs or small trees, but the ecology is still poorly known. As Casper (1987) suggested, it is morphologically similar to Cuban *P. lignicola*, but *P. casabitoana* has much narrower leaves and smaller flowers than *P. lignicola*. Also, geographical distribution areas are isolated from each other. Some literatures (e.g. Casper 1966a, Ernst 1961) treat this species as *P. cladophila*, but it is synonymous with *P. casabitoana*. Current status of the species is poorly known, but it is likely that the species migrates from one to another within the same ecological area. The population number seems to be small and it has been only occasionally found.

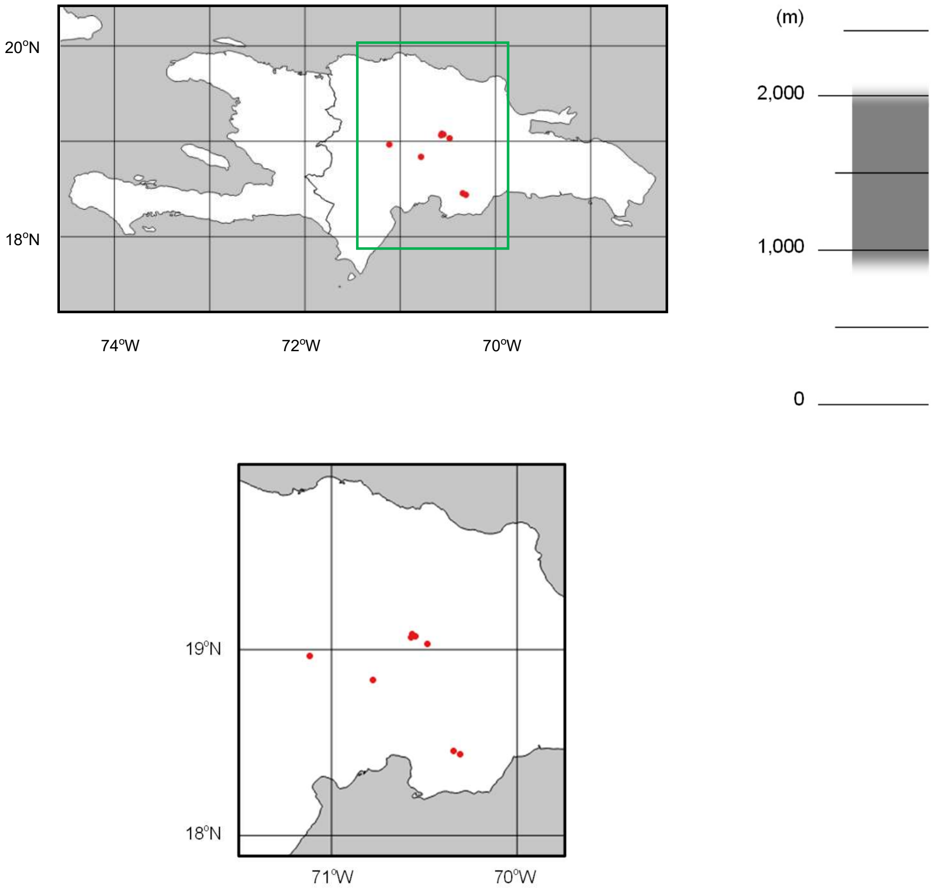
Plate 4.11. *Pinguicula casabitoana*



10 mm: 1, 2
10 mm: 3, 4

1. habit with flower
2. leaf
3. flower, front view
4. flower, lateral view

P. casabitoana



12. ***Pinguicula cubensis*** Urquiola et Casper, Willdenowia 33 (2003) 170.

TYPE: CUBA. *Pinar del Río, La Palma, Sierra de Cajálbana, ladera sur, salto de agua cerca de la cima* (Pinar del Río: La Palma, south-facing slope of the Sierra de Cajálbana, waterfall near the summit), 23 June 2001, *Stenzel & Márquez 1129* (holotype: JE!; isotypes: HAJB, HPPR).

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf monomorphic, 6-11, yellowish-green, subelect, linear-lanceolate to oblong-lanceolate, margin revolute, apex rather acute, 38-75 mm long, 2-11 mm wide. Scape 1-4, sparsely glandulous, 90-200 mm long. Calyx bilabiate, upper lip 3-lobed, lobes oblong to elliptic, ca. 2 mm long, lower lip 2-lobed, lobes smaller than uppers, connate at base or to near tips. Flower white, yellow trichomes in throat. Corolla bilabiate, 7-15 mm across, zygomorphic, 9-15 mm long including spur, upper lip 2-lobed, lobes oblong, lower lip 3-lobed, lobes similar to uppers but slightly larger, tube yellow with reddish veins, cylindrical, acutely angled at middle, spur yellow, saccate to shortly cylindrical, 2-3 mm long. Capsule ovoid to subglobose. Seed ellipsoid, 450-650 X 210-300 µm. (Plate 4.12).

PHENOLOGY: VI

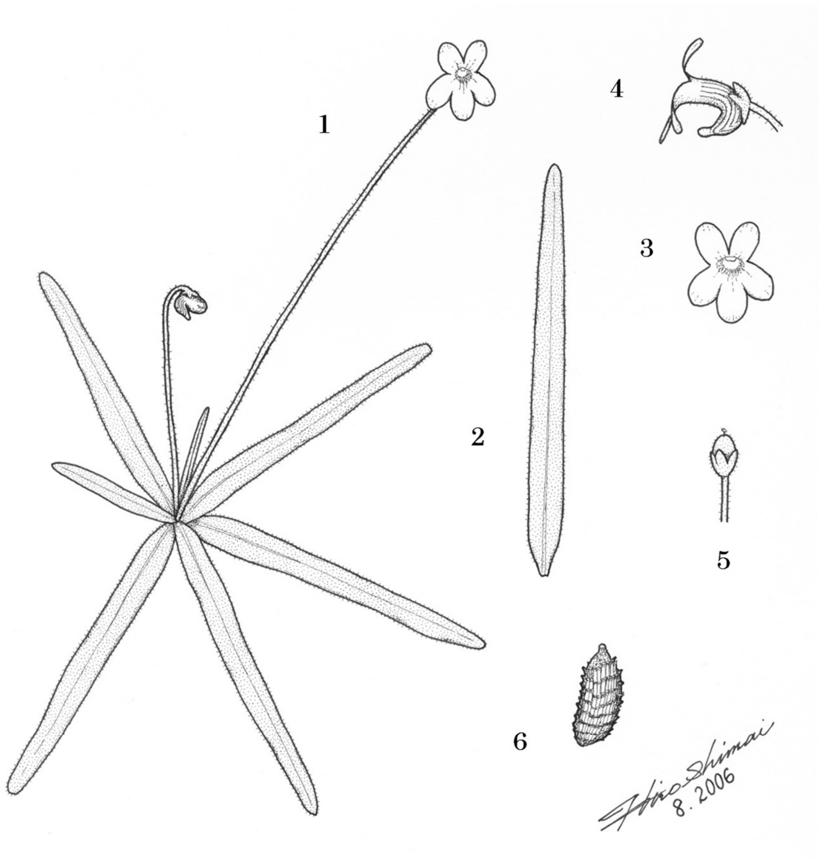
ETYMOLOGY: native of Cuba

HABITAT: Wet serpentine rock walls covered by algae. Exposed to direct sunlight.

DISTRIBUTION: CUBA (Pinar del Río). Known only from the type locality. 220 m.

DISCUSSION: *Pinguicula cubensis* is endemic to the Cajálbana Mountains in the Province of Pinar del Río, Cuba. It has been hitherto recorded only from wet serpentine rock walls covered by algae at an altitude of 220 m in the southern slope of the mountains. It is morphologically somewhat similar to *P. filifolia*, found in the coastal regions of Pinar del Río and Isla de la Juventud but *P. cubensis* has broader leaves than *P. filifolia*. Since the description by Casper and Urquiola (2003), no observation has been reported for the species. The number of population at the habitat is relatively small and the species certainly faces to extinction due to environmental stresses and/or climate changes.

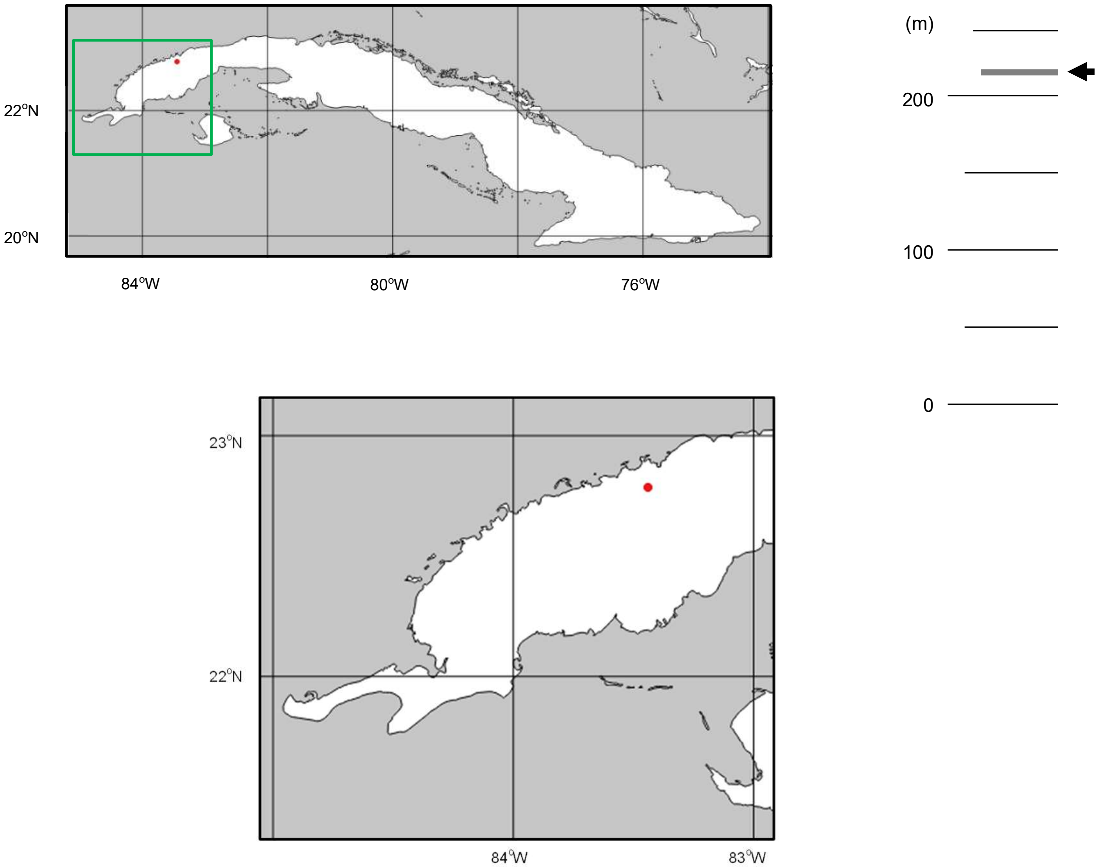
Plate 4.12. *Pinguicula cubensis*



10 mm: 1, 2
10 mm: 3, 4, 5
500 µm: 6

1. habit with flower
2. leaf
3. flower, front view
4. flower, lateral view
5. capsule
6. seed

P. cubensis



13. ***Pinguicula filifolia*** Wright ex Griseb., Cat. Pl. Cub. (1866) 162.

TYPE: CUBA. occ. *Grisebach 560* (holotype: GOET!; isotypes *Wright 2886 ex Griseb. 560*: BM!, IEB-photo ex-NY!, K (destroyed in March 1943 while on loan to Berlin), LE!, MO!, NY!, P!, US!.

SYNONYM: *P. filifolia* Wright ex Griseb. subsp. *alba* Dominguez, Panfet et Miranda

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short, often caespitose. Leaf monomorphic, 7-20, yellowish-green, elect, filiform, margin slightly revolute, apex acute, 60-200 mm long, up to 1 mm wide, base oblong to lanceolate. Scape 1-6, densely glandulous, 90-230 mm long. Calyx bilabiate, upper lip 3-lobed, lobes obovate-oblong to linear oblong, ca. 2 mm long, lower lip 2-lobed, lobes smaller than uppers. Flower white to faintly pale purple or pale yellow, yellow trichomes in throat. Corolla bilabiate, 6-12 mm across, subactinomorphic, 12-18 mm long including spur, upper lip 2-lobed, lobes oblong-obovate, lower lip 3-lobed, lobes similar to uppers, middle lobe only slightly larger than laterals, tube yellow with reddish veins, cylindrical, sometimes angled at middle, spur yellow, cylindrical, 3-5 mm long. Capsule subglobose. Seed unknown. $2n = 18$. (Plate 4.13).

PHENOLOGY: I, II, III, IV, VIII, X, XI, XII

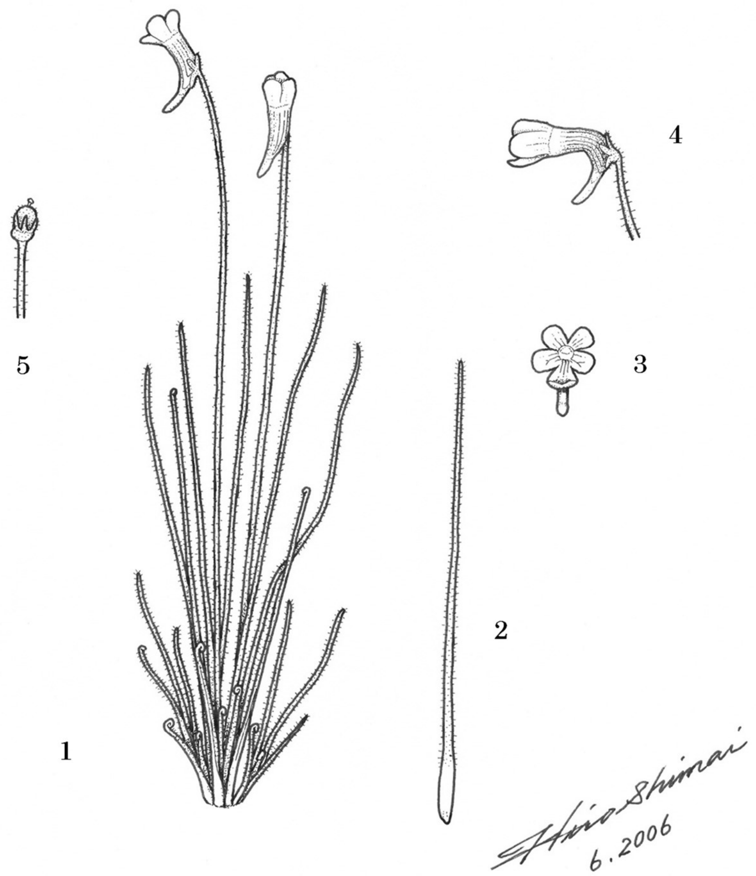
ETYMOLOGY: slender-leaved or having thread-like leaf

HABITAT: Wet fine sands in bare lands or pond margins. Exposed to direct sunlight.

DISTRIBUTION: CUBA (Isla de la Juventud, Pinar del Río). near sea level.

DISCUSSION: *Pinguicula filifolia* is an endemic species to the Province of Pinar del Río and the Isla de la Juventud (formerly called as Isla de Pinos), Cuba. Although the distribution area is restricted, a number of the plants often form large colonies in wet sandy soils near the coast. Also a single plant often produces many vegetative buds at the base to form a large clump. The plant may totally disappear during a drought season at the microhabitat, but the seed scattered onto the soil will germinate in the next wet season and regenerate the colony. Different flower colours such as white, faintly pale purple or pale yellow have been reported, but the thread-like leaf is apparently characteristic within the genus. The species is locally abundant.

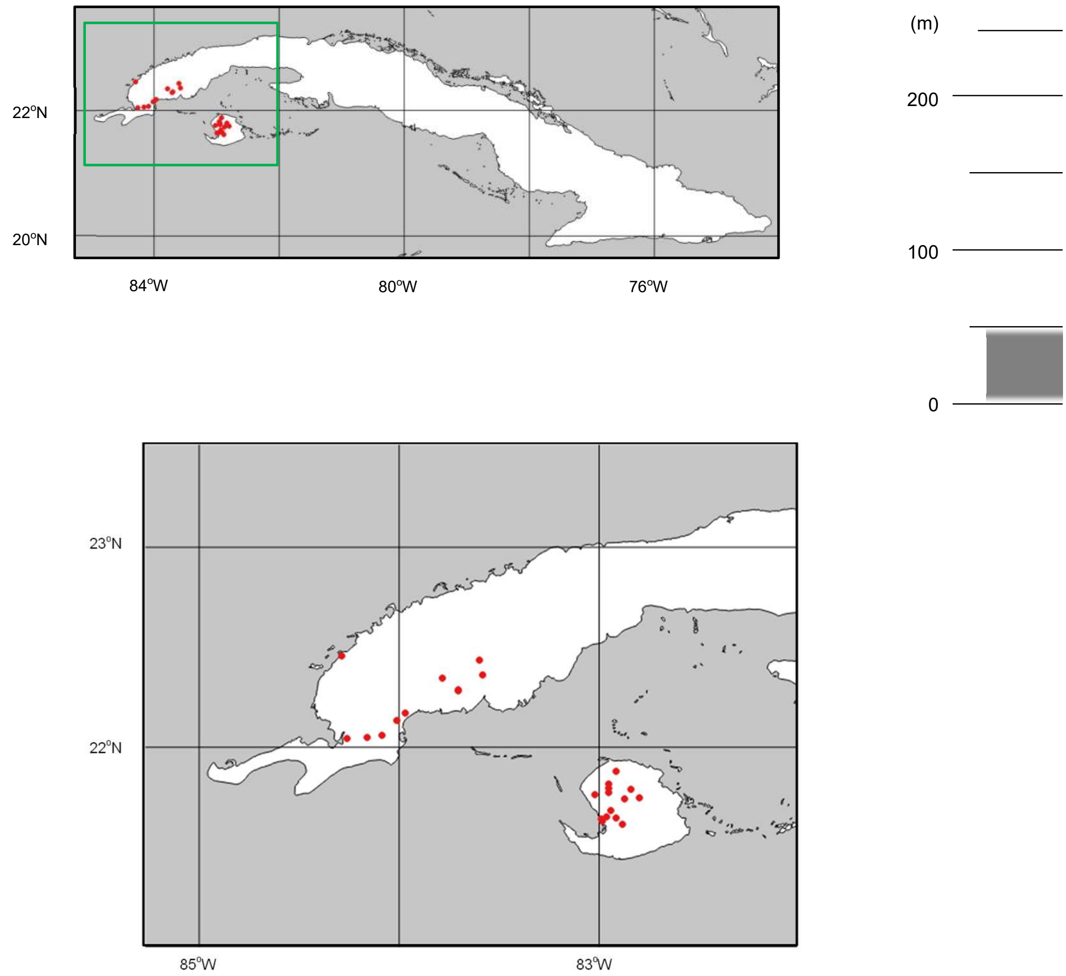
Plate 4.13. *Pinguicula filifolia*



10 mm: 1, 2
10 mm: 3, 4, 5

1. habit with flower
2. leaf
3. flower, front view
4. flower, lateral view
5. capsule

P. filifolia



14. ***Pinguicula jackii*** Barnhart

a. ***Pinguicula jackii*** Barnhart **var. *jackii*** Barnhart, Addisonia 15 (1930) 61.

TYPE: CUBA. on the face of perpendicular rock with north exposure, at above 2500 feet (ca. 760 m) altitude at Las Lagunas, Buenos Aires, province of Santa Clara, 5 December 1928, *Jack 6794* (holotype: US!).

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf monomorphic, 5-16, yellowish-green, obovate to suborbicular, base cuneate, margin narrowly involute, apex obtuse, 27-100 mm long, 18-50 mm wide, lower surface sparsely glandulous. Scape 1-6, densely glandulous, 40-120 mm long. Calyx bilabiate, upper lip 3-lobed, lobes elliptic, ca. 3 mm long, lower lip 2-lobed, lobes similar to uppers. Flower dark blue, fading gradually to pale blue. Corolla bilabiate, 20-35 mm across, zygomorphic, 25-40 mm long including spur, upper lip 2-lobed, lobes ovate to oblong-ovate, lower lip 3-lobed, lobes similar to uppers but slightly larger, middle lobe wider, tube pale blue with darker veins, conical, spur faintly pale blue, cylindrical 5-7 mm long. Capsule globose. Seed globose, 450-520 X 390-420 μm. (Plate 4.14).

PHENOLOGY: II, III, V, VII, VIII, XII

ETYMOLOGY: dedicated to John George Jack, at the Arnold Arboretum, who first collected this species

HABITAT: Calcareous sandstone cliffs (often vertical or overhanging). Low light intensity.

DISTRIBUTION: CUBA (Cienfuegos). 700-914 m.

DISCUSSION: *Pinguicula jackii* var. *jackii* is an extremely rare endemic species to Cuba. It was first collected by John G. Jack, of the Arnold Arboretum, in December 1928. The holotype locality of the Province of Santa Clara (or Las Villas) has been split into 3 smaller provinces since 1976 and it is located in the Province of Cienfuegos at present. It is morphologically similar, particularly vegetative parts, to *P. albida*, but can be distinguished by having a larger rosette, glands also on the lower surface of the leaves, and a much larger corolla. *P. jackii* var. *jackii* has characteristically dark blue flowers, rare in the genus, but the colour fades and the corolla diameter increases day by day after anthesis. Current localities known today are only a few with very limited population numbers at each microhabitat and those are highly restricted to south of the Pico de San Juan, in the far east of the Province of Cienfuegos It occurs on relatively dry (or seasonally wet?) lime-sandstone vertical walls in rather dark forests.

b. ***Pinguicula jackii*** Barnhart **var. *parviflora*** Ernst, Bot. Jahrb. 80 (1961) 168.

TYPE: CUBA. Santa Clara (neotype: S!, near El Naranjo, 900 m, 18 July 1958, *Webster et al. 205*, designated here).

SYNONYM: *Pinguicula lithophytica* Panfet-Valdés et Temple

DESCRIPTION: Leaf identical with that of *P. jackii* var. *jackii*. Flower white, sometimes faintly pale purple at tip of corolla lobes, yellow in throat. Corolla bilabiate, 18-20 mm across, zygomorphic, 10-18 mm long including spur, upper lip 2-lobed, lobes broadly obovate, lower lip 3-lobed, lobes similar to uppers but slightly larger, tube yellow with reddish veins, subcylindrical, spur yellow with reddish veins, cylindrical, 5-8 mm long.

PHENOLOGY: VII

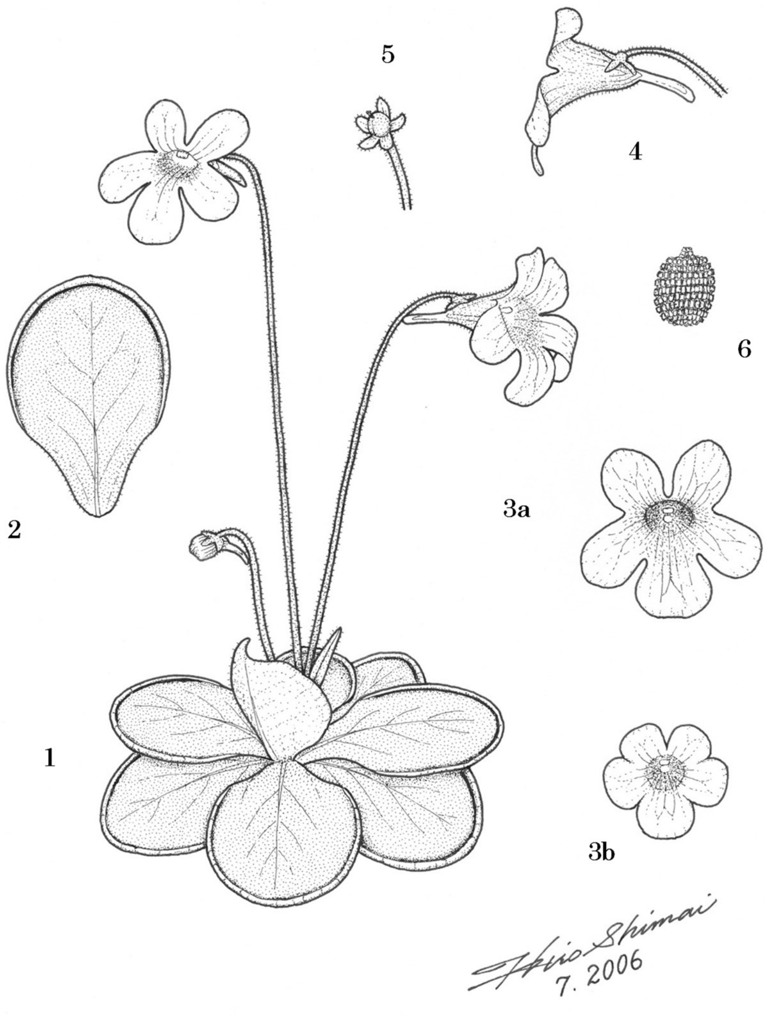
ETYMOLOGY: small-flowered

DISTRIBUTION: CUBA (Cienfuegos). 800-900 m.

DISCUSSION: *Pinguicula jackii* var. *parviflora* was described by Ernst (1961) as having a smaller corolla in comparison to *P. jackii* var. *jackii*. It also differs from *P. jackii* var. *jackii* as having thicker yellow spur and the colouration of corolla lobes which is nearly white or sometimes only faintly pale purple at the tip. Otherwise, the vegetative morphologies are identical between the two varieties.

P. lithophytica, described by Panfet-Valdés and Temple (2008) based on the material collected at Los Tornos, San Blas in the Province of Cienfuegos, is likely synonymous with *P. jackii* var. *parviflora*. The distribution area of this variety, restricted to the far eastern side of the Province of Cienfuegos, is exactly sympatric with that of *P. jackii* var. *jackii* although they may not occur together at the same microhabitat. Only a few localities have been known within a very small area and the number of plants at each habitat is extremely limited.

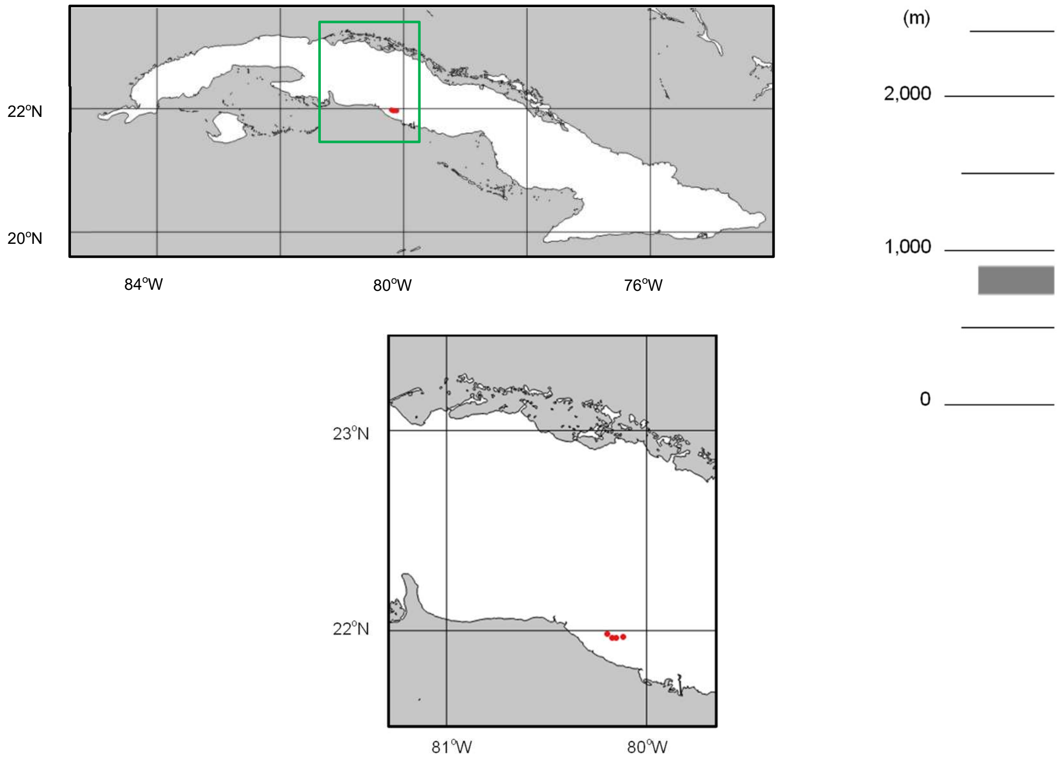
Plate 4.14. *Pinguicula jackii*



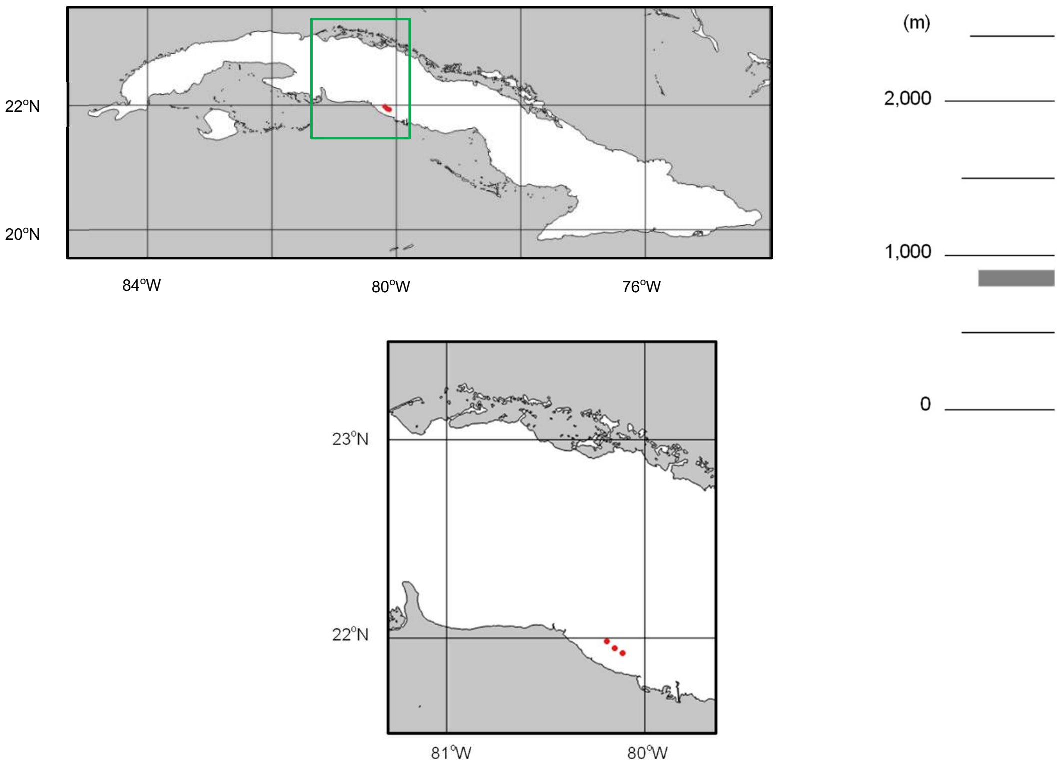
10 mm: 1, 2
10 mm: 3a-b, 4, 5
500 µm: 6

1. habit with flower
2. leaf
3a. flower, front view
3b. flower, front view (*P. jackii* var. *parviflora*)
4. flower, lateral view
5. capsule
6. seed

P. jackii var. *jackii*



P. jackii var. *parviflora*



15. ***Pinguicula jaraguana*** Casper, Haussknechtia 9 (2003) 141.

TYPE: CUBA. Prov. Holguín: Mun. Moa, Arroyo Jaragua, ~74º52' W ~20º25' N, 25 February 1979, *Bisse, Lepper, Köhler, Diaz, Gutierrez, Dietrich, Rändel, Schaarschmidt, Herrera & Miklos PFC-39913* (holotype: JE!; isotypes: B!, HAJB).

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf monomorphic, 6-12, whitish-green, obovate to spatulate, margin narrowly involute, apex obtuse, base cuneate, 20-40 mm long, 8-12 mm wide. Scape 1-4, sparsely glandulous, 70-150 mm long. Calyx bilabiate, upper lip 3-lobed, lobes oblong, 2-3 mm long, lower lip 2-lobed, lobes smaller than uppers. Flower white, yellow trichomes in throat. Corolla bilabiate, 6-10 mm across, subactinomorphic, up to 18 mm long including spur, upper lip 2-lobed, lobes oblong-ovate, lower lip 3-lobed, lobes only slightly larger than uppers, tube yellow with reddish veins, cylindrical, angled at base, spur yellow, cylindrical to saccate, 1-3 mm long. Capsule ovoid. Seed unknown. (Plate 4.15).

PHENOLOGY: II, III, IV

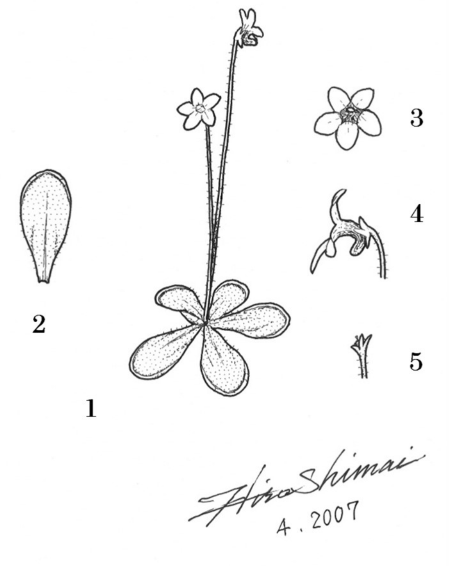
ETYMOLOGY: native of Arroyo Jaragua

HABITAT: Wet slopes in gorges along rivers and streams. Low light intensity.

DISTRIBUTION: CUBA (Holguín). Altitude range unknown.

DISCUSSION: *Pinguicula jaraguana* was described by Casper (2003) based on herbarium specimens collected at the Arroyo Jaragua in the Province of Holguín, Cuba, in February 1979 by a group of H. Bisse and colleagues. The distribution seems to be restricted to the riversides of the Arroyo Jaragua and the Río Jiguani within the province. This species is morphologically similar to *P. albida* and it used to be temporally known as the "Oriente population" of *P. albida*. Indeed, *P. jaraguana* and *P. albida* are morphologically similar; however, the distributions of the two are isolated from each other. The leaf shape of *P. jaraguana* is rather spatulate while that of *P. albida* is suborbicular. The material was not obtained for the phylogenic study here, but it could be biogeographically more closely related to *P. benedicta* rather than *P. albida*. The current status of the species at the habitat is unknown.

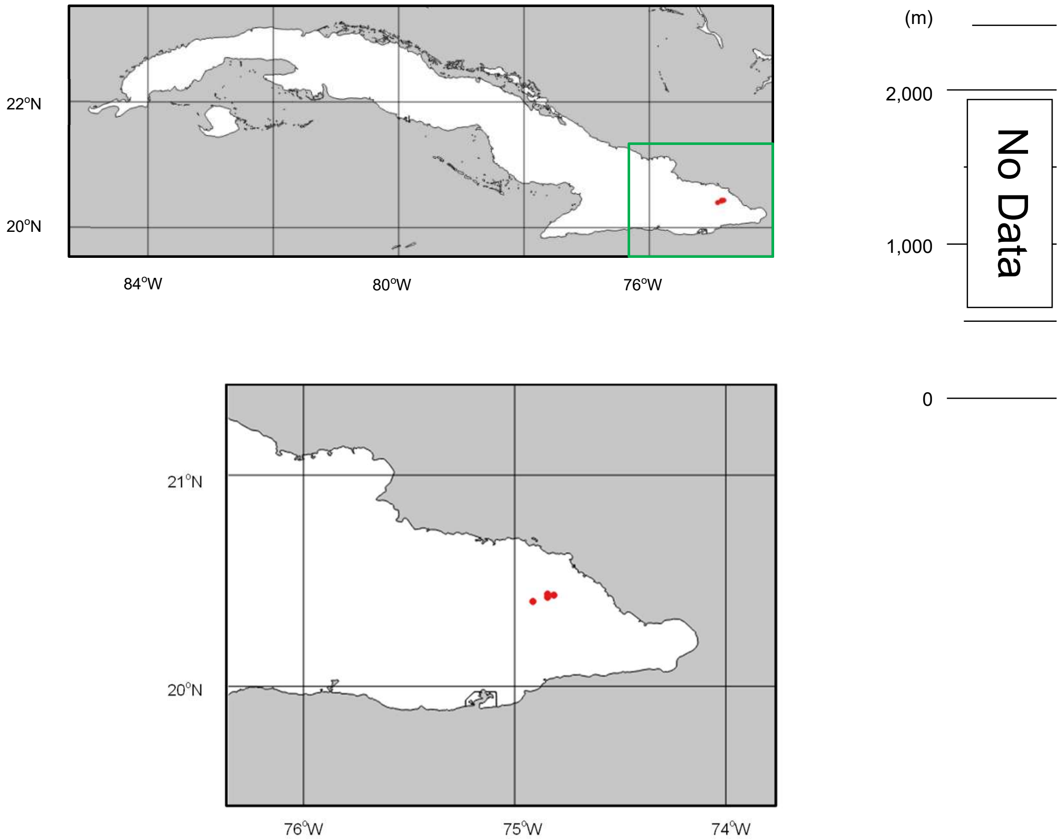
Plate 4.15. *Pinguicula jaraguana*



10 mm: 1, 2
10 mm: 3, 4, 5

1. habit with flower
2. leaf
3. flower, front view
4. flower, lateral view
5. capsule

P. jaraguana



16. ***Pinguicula lignicola*** Barnhart, Mem. Torrey Bot. Club 16 (1920) 110.

TYPE: Oriente: Vicinity of Camp San Benito, 23 February 1910, *Shafer 4031* (holotype?: A!; syntype: A!).

DESCRIPTION: Epiphyte. Perennial herb. Root filiform, elastic. Stem very short. Root producing clonal plantlet at tip. Leaf monomorphic, 10-20, yellowish-green, oblong-oblanceolate to oblong-spatulate, margin revolute, apex rather obtuse, 5-15 mm long, 1-3 mm wide. Scape 1-3, sparsely glandulous, 15-60 mm long. Calyx bilabiate, upper lip 3-lobed, lobes broadly ovate, ca. 2 mm long, lower lip 2-lobed, lobes smaller than uppers, connate to middle. Flower white, yellow trichomes in throat. Corolla bilabiate, 8-17 mm across, zygomorphic, 8-15 mm long including spur, upper lip 2-lobed, lobes obovate, lower lip 3-lobed, lobes similar to uppers but larger, tube yellow with reddish veins, conical, somewhat angled at middle, spur yellow, cylindrical, incurved to rather uncinate, 2-3 mm long. Capsule subglobose. Seed fusiform-ellipsoid. (Plate 4.16).

PHENOLOGY: I, II, III, IV, V, VI, XII

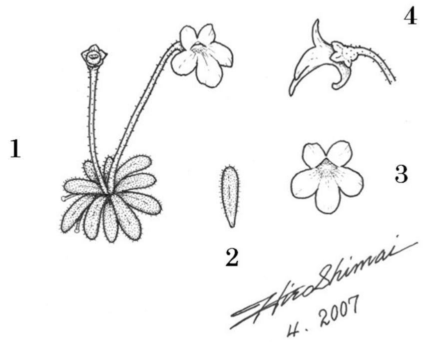
ETYMOLOGY: growing on trees

HABITAT: Epiphytic on branches or stems of *Podocarpus* or pine trees often along streams in forests. Low light intensity.

DISTRIBUTION: CUBA (Guantánamo, Holguín). 600-1,100 m.

DISCUSSION: *Pinguicula lignicola* is a very rare Cuban endemic species. The first specimen of the species was collected in December 1910 by John A. Shafer at San Benito in the Province of Oriente; the type locality is likely in the Alejandro de Humboldt National Park in the Province of Holguín at present. It is an epiphyte often occurring on twigs or stems of *Podocalpus* (*P. aristulatus* Parl., *P. ekmanii* Urb., *P. victorinianus* Carabis (Mill 2015)), pine trees or shrubs in wet serpentine areas. *P. lignicola* has a characteristic root system that the root apex anchors directly on the epidermal of the twigs or stems. *P. lignicola* is morphologically similar to *P. casabitoana*, endemic to the Dominican Republic, but *P. lignicola* has larger flowers and broader leaves. It seems that *P. lignicola* occasionally migrates one place to another within the same ecological area.

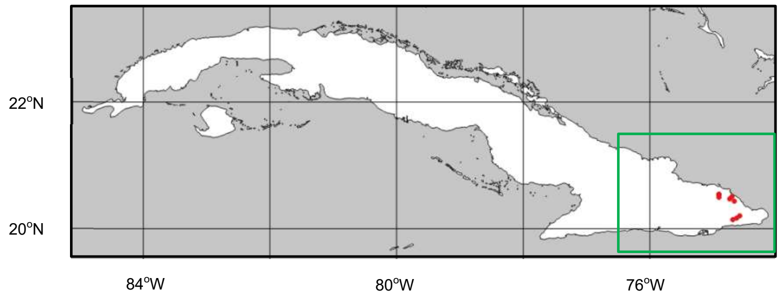
Plate 4.16. *Pinguicula lignicola*

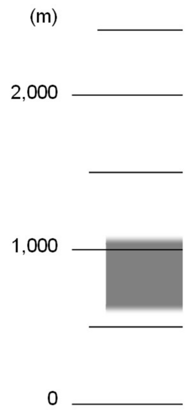


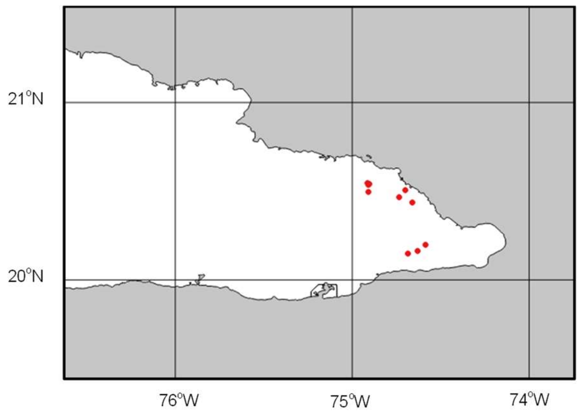
10 mm: 1, 2
10 mm: 3, 4

1. habit with flower and fruit
2. leaf
3. flower, front view
4. flower, lateral view

P. lignicola







Sect. *Elongatae* (Casper) Shimai, comb. nov.

TYPE: *Pinguicula elongata* Benjamin

SYNONYMS: Sect. *Pionophyllum* Ernst, Subsect. *Heterophylliformis* Casper, Ser. *Elongatae* Casper

17. ***Pinguicula elongata*** Benjamin, Linnaea 20 (1847) 318.

TYPE: COLOMBIA. Sierra Nevada de Santa Marta, *Purdie 1045* (holotype: K!; isotype: E!).

SYNONYM: *P. diversifolia* Cuatrecasas

DESCRIPTION: Perennial herb. Root filiform, elastic. Stem very short. Leaf dimorphic, summer leaf 3-12, yellowish-green or maroon, elect to subelect, linear-lanceolate, margin slightly revolute, apex acute, 70-180 mm long, 5-30 mm wide, winter leaf up to 15, ovate, acute, concave, small. Winter rosette ovoid with roots. Scape 1-6, densely glandulous, 90-240 mm long. Calyx bilabiate, upper lip 3-lobed, lobes triangular-lanceolate to oblong-lanceolate, 2-5 mm long, lower lip 2-lobed, lobes slightly smaller than uppers. Flower white to faintly pale purple, yellowish trichomes at base of lower lip. Corolla bilabiate, 15-23 mm across, zygomorphic, 12-23 mm long including spur, upper lip 2-lobed, lobes ovate to oblong-ovate, tip rather acute, lower lip 3-lobed, lobes similar to uppers but slightly larger, tube purple with darker veins, conical to subcylindrical, spur pale purple, saccate to conical, 2-4 mm long. Capsule globose. Seed ellipsoid, 800-1,250 X 270-340 μm. (Plate 4.17).

PHENOLOGY: IV, V, VI, VII, VIII, XI

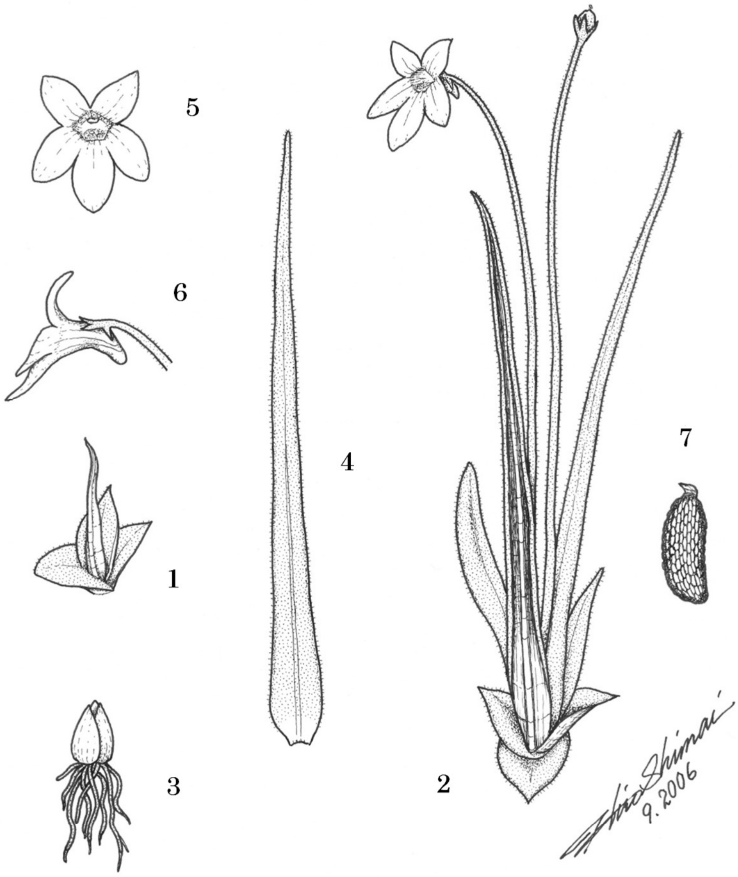
ETYMOLOGY: elongated (referring to the leaf)

HABITAT: Wet calcareous sand or gravelly soils in open slopes or grasslands. Exposed to direct sunlight.

DISTRIBUTION: COLOMBIA (Arauca, Bogotá, Boyacá, Cesar, Cundinamarca, La Guajira, Magdalena, Santander); VENEZUELA (Apre, Mérida). 2,400-4,100 m.

DISCUSSION: *Pinguicula elongata* is found only at higher altitudes of the Sierra Nevada de Santa Marta and the Andean regions in Colombia and Venezuela. The species morphologically differs from the other South American species as forming seasonally different shapes of leaves, linear-lanceolate summer leaves and winter leaves forming a winter rosette. The winter rosette of *P. elongata* differs from that of Mexican species since it consists of thin (in thickness) and incurved scale leaves with roots. It should be critically clarified whether it is a "winter rosette" or a "hibernaculum". Little information of the current status at the habitat is available, but it seems locally common.

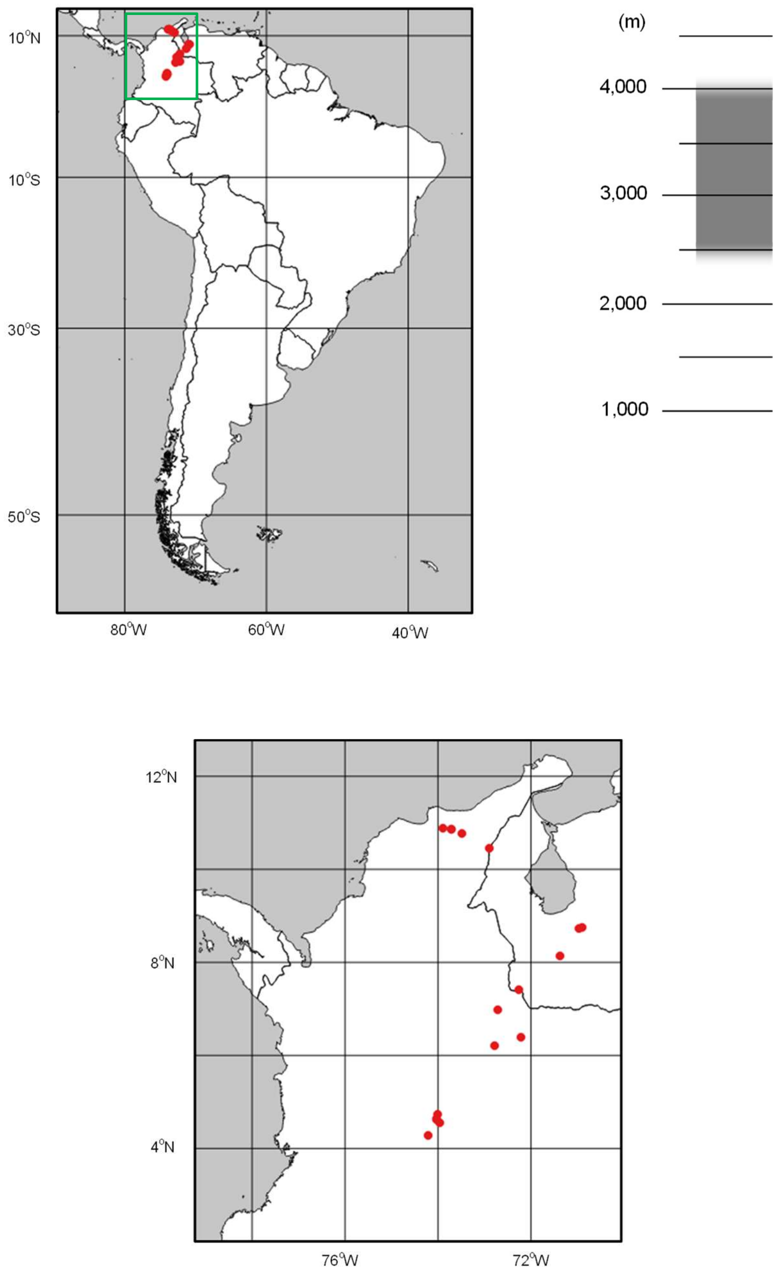
Plate 4.17. *Pinguicula elongata*



10 mm: 1, 2, 3, 4
10 mm: 5, 6
500 µm: 7

1. spring rosette
2. summer rosette with flower and fruit
3. winter rosette
4. summer leaf
5. flower, front view
6. flower, lateral view
7. seed

P. elongata



10°N
10°S
30°S
50°S
80°W
60°W
40°W
(m)
4,000
3,000
2,000
1,000
12°N
8°N
4°N
76°W
72°W

Sect. *Isoloba* Casper (1963) Bot. Jb. 82, 330.

TYPE: *Pinguicula pumila* Michx.

SYNONYMS: Subgen. *Isoloba* Barnhart, Sect. *Brandonia* DC., Sect. *Pionophyllum* DC., Subsect. *Agnatiformis* Casper, Subsect. *Primuliformis* Casper

18. ***Pinguicula caerulea*** Walter, Fl. Carol. (1788) 63.

TYPE: USA. (holotype: Herb. *Walter* destroyed; see Fernald and Schubert 1948. paratype: Fig. 3 in Plate 1113, as *Utricularia gibba*, Rhodora 50, Fernald and Schubert 1948!).

SYNONYMS: *Isoloba elatior* (Michx.) Raf., *P. australis* Chapman, *P. caerulea* Walter f. *leucantha* Schnell, *P. elatior* Michx.

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf monomorphic, 5-30, ovate to oblong, margin involute, apex rather acute, 15-65 mm long, 8-23 mm wide. Scape 1-7, densely glandulous, very hairy with non-glandular hairs at lower part, 100-330 mm long. Calyx bilabiate, upper lip 3-lobed, lobes ovate to oblong-lanceolate, 3-8 mm long, lower lip 2-lobed, lobes similar to uppers. Flower bluish-purple, veins darker. Corolla bilabiate, 20-30 mm across, subactinomorphic, 19-40 mm long including spur, upper lip 2-lobed, lobes obovate, notched at tip, lower lip 3-lobed, lobes similar to uppers but only slightly larger, terete process covered by white hairs projecting from lower throat, tube yellow with purple veins, conical, spur yellow, subcylindrical, 3-11 mm long. Capsule subglobose. Seed ellipsoid, 450-480 X 180-200 µm. $2n = 32$. (Plate 4.18).

PHENOLOGY: I, II, III, IV, V, VI, VII, IX

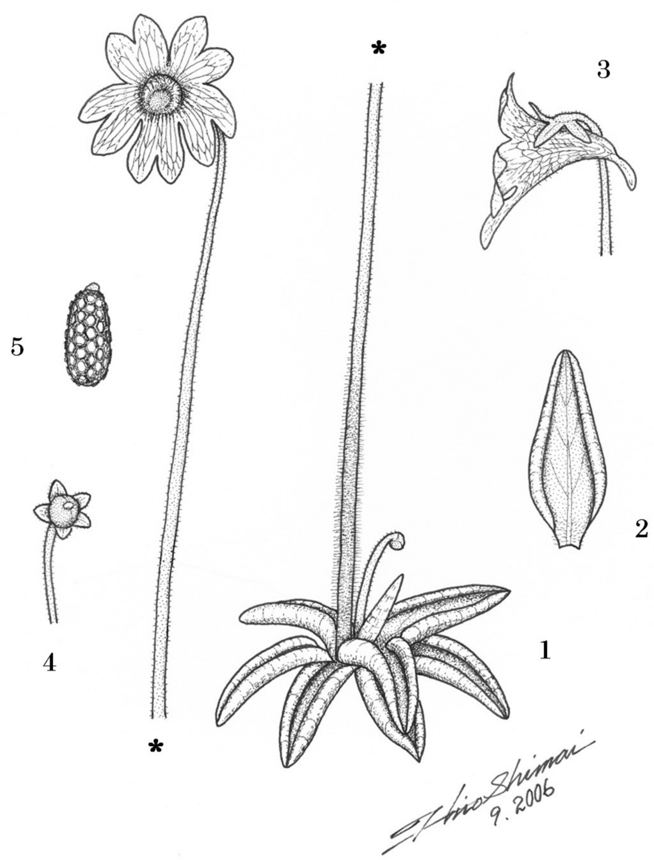
ETYMOLOGY: dark blue (referring to the flower)

HABITAT: Wet sandy or peaty soil in open grasslands, bushes, forest margins or roadsides. Often exposed to direct sunlight.

DISTRIBUTION: USA (Florida, Georgia, North Carolina, South Carolina). near sea level.

DISCUSSION: *Pinguicula caerulea* is widely distributed in lower altitudes of North Carolina to Florida, the southeastern United States. The distribution of the species is largely overlapped with that of *P. lutea*, and vegetative morphologies of those two species are almost identical. They can be easily identified only during a flowering season by their flower colours and the scape of *P. caerulea* is densely covered by non-glandular hairs. However, it is uncommon to find both species together at the same microhabitat, may suggesting different subtle environmental preferences. The flower colour of *P. caerulea* is basically bluish-purple with prominent darker veins, but occasionally dark purple without veins or entirely white flowers are found (Schnell 1980, 2002). *P. caerulea* is locally common at the habitat, particularly in the Florida Peninsula.

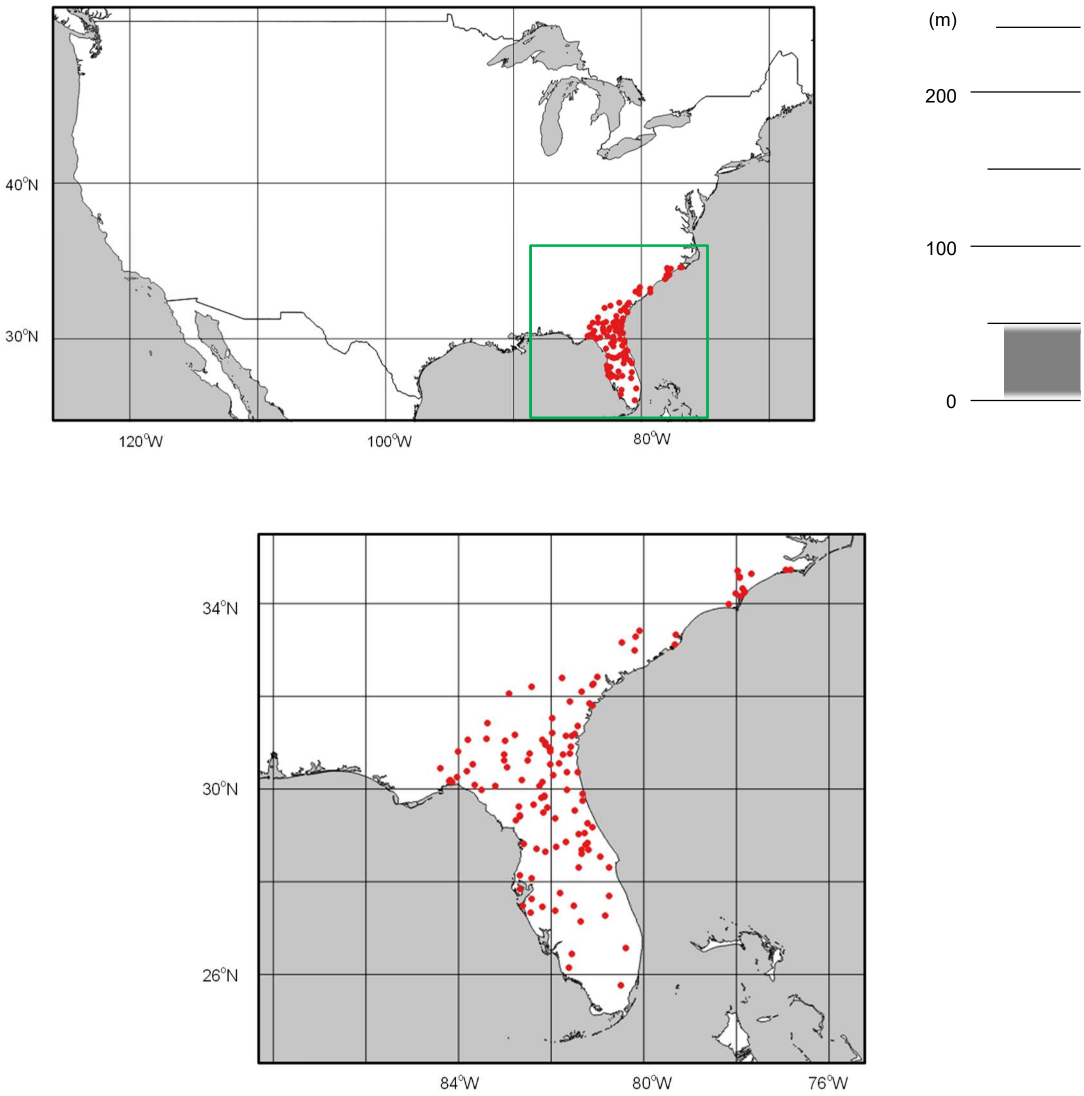
Plate 4.18. *Pinguicula caerulea*



10 mm: 1, 2, 3, 4
300 μm: 5

1. habit with flower
2. leaf
3. flower, lateral view
4. capsule
5. seed

P. caerulea



19. ***Pinguicula ionantha*** Godfrey, Am. Midl. Nat. 66 (1961) 405.

TYPE: USA. Florida: Franklin County, shallow water, depression in flatwoods, 11 miles (ca. 18 km) S of Sumatra, 26 March 1960, *Godfrey 59362* (holotype: GH!; isotypes: BVS!, CLF, FLAS!, JE!, MSC!, NY!, S!, UC, US!, USF!; paratypes: FLAS!, NCU!, UFS!).

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf monomorphic, 5-15, yellowish-green, oblong-ovate, margin slightly involute, apex obtuse to rather acute, 40-80 mm long, 20-25 mm wide. Scape 1-9, densely glandulous, 100-250 mm long. Calyx bilabiate, upper lip 3-lobed, lobes oblong, ca. 4 mm long, lower lip 2-lobed, lobes smaller than uppers, connate to middle. Flower white to faintly pale purple, dark purple in throat. Corolla bilabiate, 20-25 mm across, subactinomorphic, 12-23 mm long including spur, upper lip 2-lobed, lobes obovate, tip emarginate to notched, lower lip 3-lobed, lobes similar to uppers, terete process covered by yellow hairs projecting from lower throat, tube purple, with darker veins but usually not conspicuous, conical, spur yellow to rather orange, subcylindrical, 4-5 mm long, pendulous. Capsule globose, 500-610 X 240-270 µm. Seed pyriform to ovoid. $2n = 22$. (Plate 4.19).

PHENOLOGY: II, III, IV

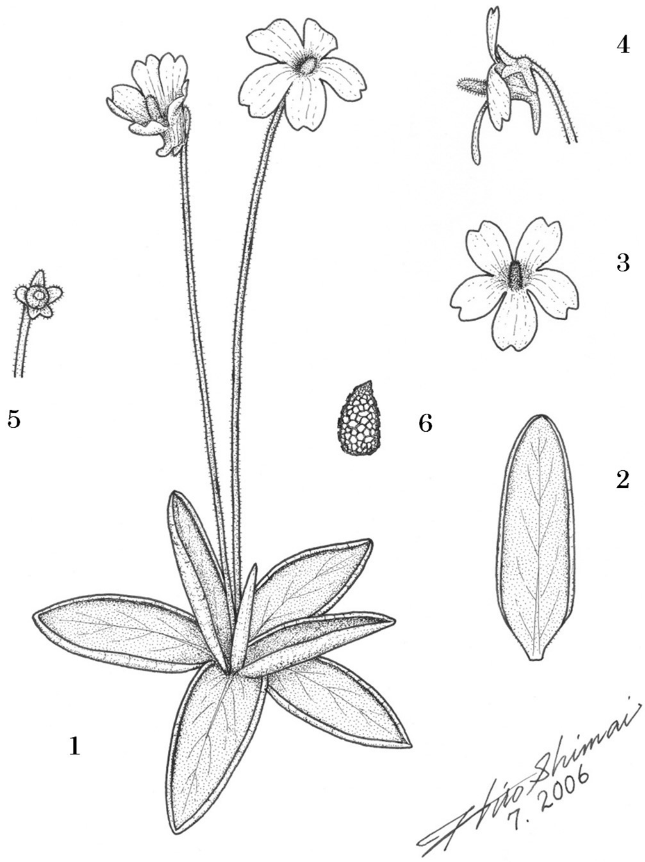
ETYMOLOGY: violet-flowered

HABITAT: Wet sandy or muddy soil in open grasslands, forest margins or roadsides. Exposed to direct sunlight.

DISTRIBUTION: USA (Florida). near sea level.

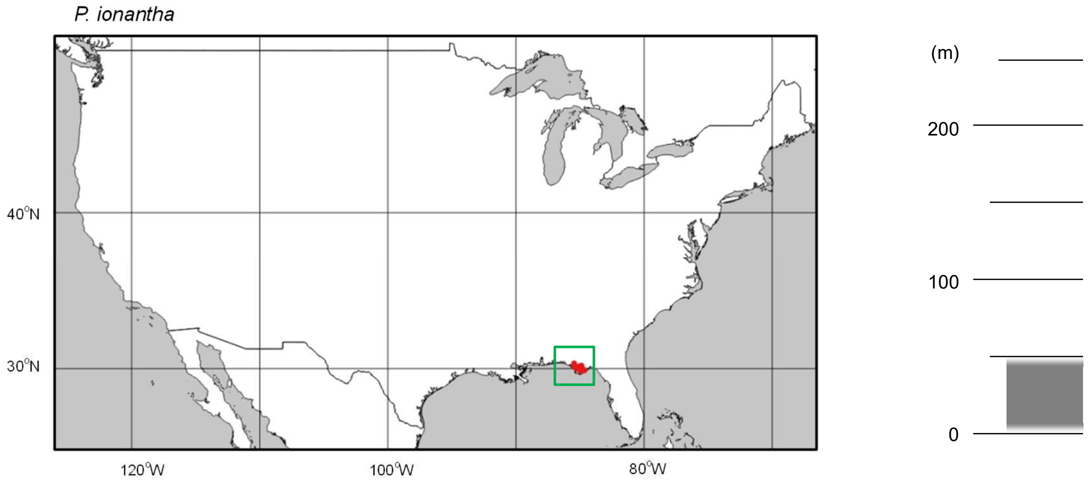
DISCUSSION: *Pinguicula ionantha* is endemic to very narrow areas of the Florida Panhandle region in the USA. An earlier specimen record was seen in 1937, but it was identified as *P. planifolia*. It was recognised by R. K. Godfrey and H. Larry Stripling in spring of 1960 at the Counties of Franklin and Liberty in Florida as an unknown taxon, and they immediately described it as a new species, i.e. *P. ionantha* (Godfrey and Stripling 1961). It is morphologically similar in some degree to *P. planifloia*, both of which are locally sympatric, but the tip of the corolla lobes in *P. ionantha* is not as deeply divided as that in *P. planifolia,* and the leaf is always yellowish-green while that of *P. planifolia* is often suffused with maroon. The distribution of the species is very restricted to only several counties in the Apalachicola region and the population density at each locality is relatively small.

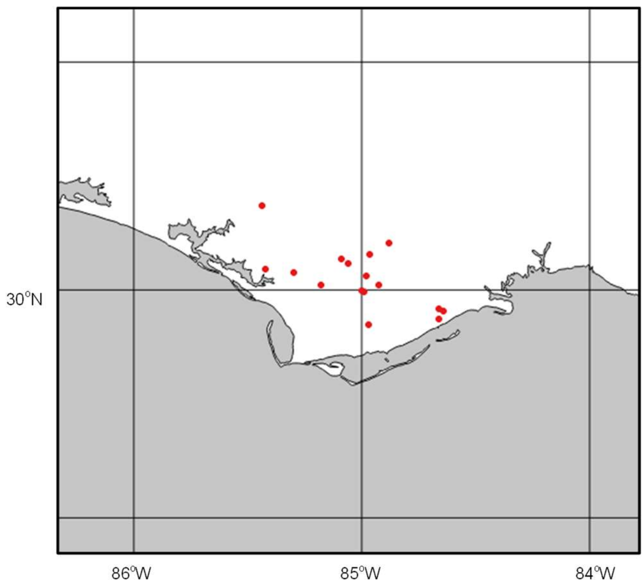
Plate 4.19. *Pinguicula ionantha*



10 mm: 1, 2, 3, 4, 5
500 μm: 6

1. habit with flower
2. leaf
3. flower, front view
4. flower, lateral view
5. capsule
6. seed


P. ionantha
40°N
30°N
120°W
100°W
80°W
(m)
200
100
0


30°N
86°W
85°W
84°W

20. ***Pinguicula lutea*** Walter, Fl. Carol. (1788) 63.

TYPE: USA. (holotype: Herb. *Walter* destroyed; see Fernald and Schubert 1948).

SYNONYMS: *Isoloba lutea* (Walter) Raf., *I. recurva* Raf., *P. campanulata* Lam., *P. edentula* Hook., *P. lutea* Walter var. *edentula* (Hook.) DC., *P. lutea* Walter var. *minor* DC., *P. lutea* Walter f. *alba* Folkerts et Freeman

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf monomorphic, 5-30, yellowish-green, ovate to oblong, margin strongly involute, apex rather acute, 15-85 mm long, 6-24 mm wide. Scape 1-6, densely glandulous, 60-440 mm long. Calyx bilabiate, upper lip 3-lobed, lobes oblong, ca. 6 mm long, lower lip 2-lobed, lobes similar to uppers. Flower yellow. Corolla bilabiate, 25-35 mm across, subactinomorphic, 19-42 mm long including spur, upper lip 2-lobed, lobes obovate, tip notched, lower lip 3-lobed, lobes similar to uppers but only slightly larger, terete process covered by yellow hairs projecting from lower throat, tube yellow with purple veins, conical, spur yellow, cylindrical, 5-10 mm long. Capsule subglobose. Seed pyriform to ovoid, 410-510 X 150-230 μm. $2n = 32$. (Plate 4.20)

PHENOLOGY: I, II, III, IV, V

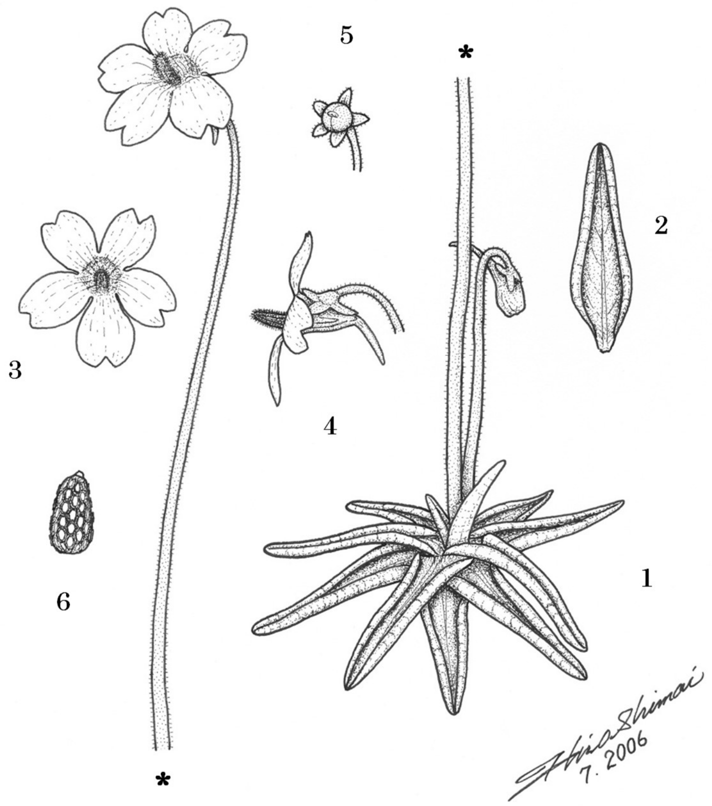
ETYMOLOGY: yellow (referring to the flower)

HABITAT: Fine sand in open grasslands, bushes, forest margins or roadsides. Often exposed to direct sunlight.

DISTRIBUTION: USA (Alabama, Florida, Georgia, Louisiana, Mississippi, North Carolina, South Carolina). 0-145 m.

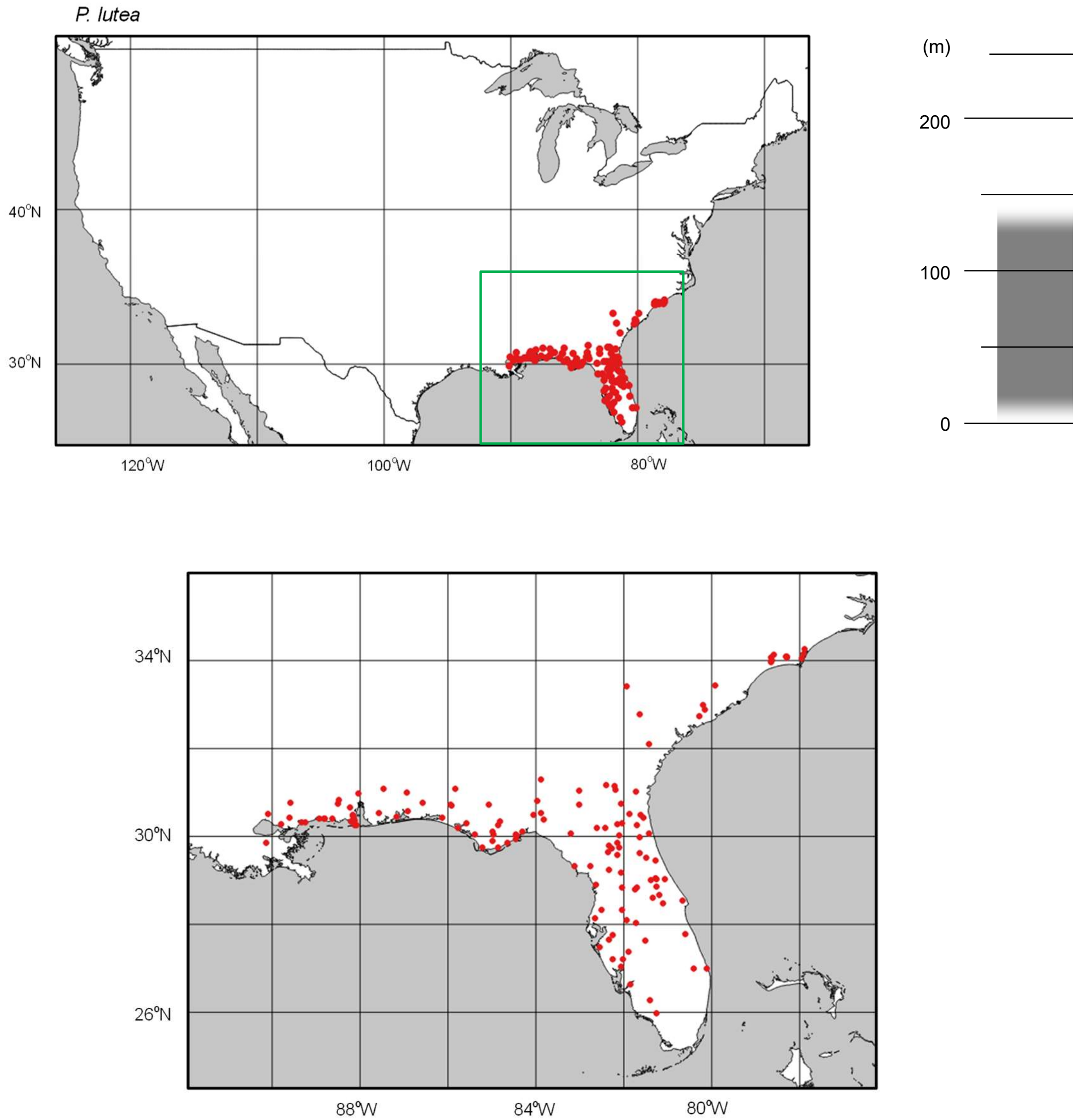
DISCUSSION: *Pinguicula lutea* is endemic to the lower altitudinal regions of the southeastern USA, North Carolina to Louisiana. The rosette of this species is morphologically identical with that of *P. caerulea* and the distributions of the two species are partially sympatric, particularly at the Atlantic Coastal Plains to the Florida Peninsula. However, they are normally not found together at the same microhabitats. *P. lutea* often prefers drier sandy soils at forest margins or in savannas. It has characteristically bright yellow flowers, the most important character to identify the species, but very rarely white or brownish-yellow flower strains have been reported (Folkerts and Freeman 1989, Schnell 2002). *P. lutea* is locally common, but their population density at each microhabitat is relatively sparse.

Plate 4.20. *Pinguicula lutea*



10 mm: 1, 2, 3, 4, 5
0.3 mm: 6

1. habit with flower
2. leaf
3. flower, front view
4. flower, lateral view
5. capsule
6. seed


P. lutea
40°N
30°N
120°W
100°W
80°W
(m)
200
100
0
34°N
30°N
26°N
88°W
84°W
80°W

21. ***Pinguicula planifolia*** Chapman, Fl. South. U.S. ed. 3 (1897) 303.

TYPE: shallow ponds, Apalachicola, Florida, 9 March 1896, *Chapman 4353a* (holotype?: ZT!, isotypes: PAD!, WU!).

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf monomorphic, 6-18, maroon or reddish-yellow, oblong to oblong-lanceolate or oblong-oblanceolate, margin slightly involute, apex obtuse to rather acute, 40-120 mm long, 10-28 mm wide. Scape 1-4, densely glandulous, 230-400 mm long. Calyx bilabiate, upper lip 3-lobed, lobes oblong-lanceolate, 4-5mm long, lower lip 2-lobed, lobes smaller than uppers, connate at base. Flower white to pale purple, purple at base of lips to throat. Corolla bilabiate, 25-30 mm across, subactinomorphic, 20-33 mm long including spur, upper lip 2-lobed, lobes oblong-oblanceolate to obovate-oblong, tip deeply notched or bifid, lower lip 3-lobed, lobes similar to uppers but only slightly larger, terete process covered by yellow hairs projecting from lower throat, tube reddish-purple with darker veins, cylindrical, spur yellow, cylindrical, 2-4 mm long. Capsule globose. Seed narrowly ellipsoid. $2n = 32$. (Plate 4.21).

PHENOLOGY: II, III, IV, VII, XI

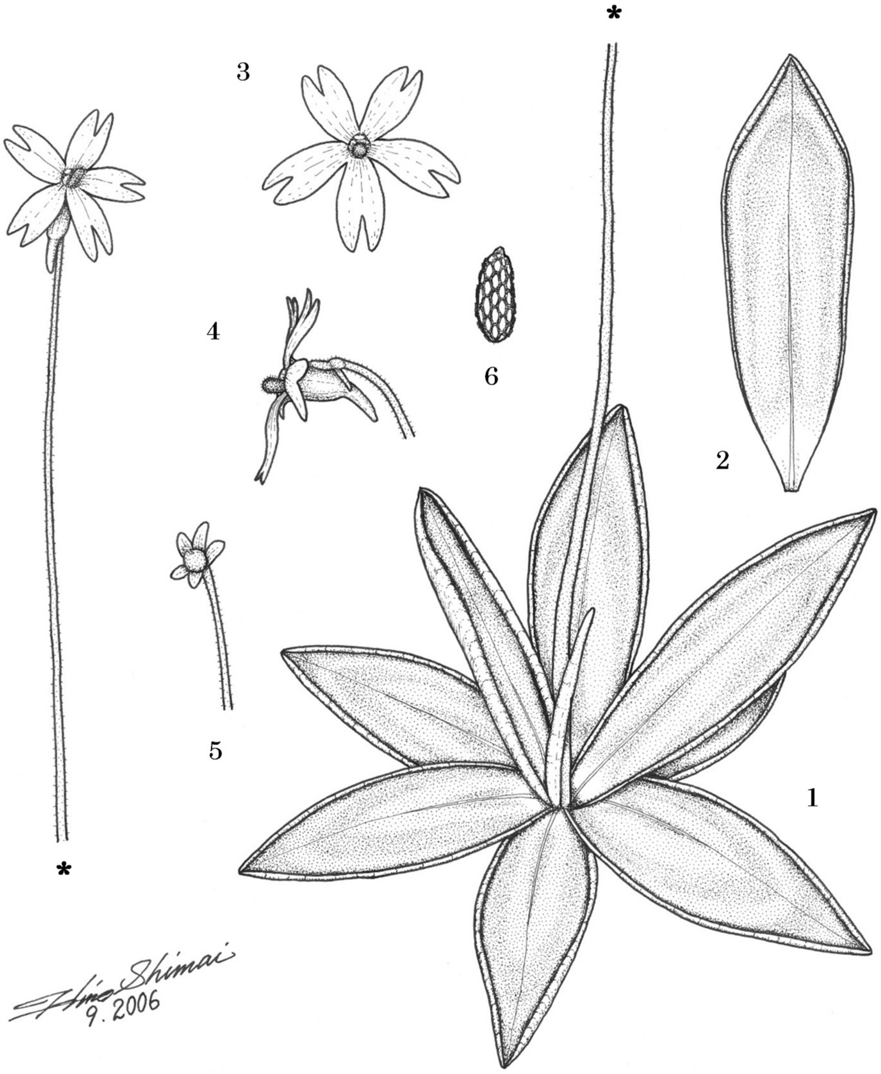
ETYMOLOGY: flat-leaved

HABITAT: Wet sandy or muddy soil in bogs or sometimes submerge in shallow water. Often exposed to direct sunlight.

DISTRIBUTION: USA (Alabama, Florida, Mississippi). 0-46 m.

DISCUSSION: *Pinguicula planifolia* is confined to relatively narrow areas along the Gulf of Mexico, from the Florida Panhandle to Louisiana. It can be more often found in very shallow pools or very damp bogs. The rosette is sometimes submerged partially or completely in water pools. It is morphologically similar and its distribution area is locally sympatric with *P. ionantha*, Differences between the two species are discussed in *P. ionantha* (species number 19). Although it seems locally abundant, the species has a risk of rapid decline of the population number at the habitat due to drought and/or other environmental stresses.

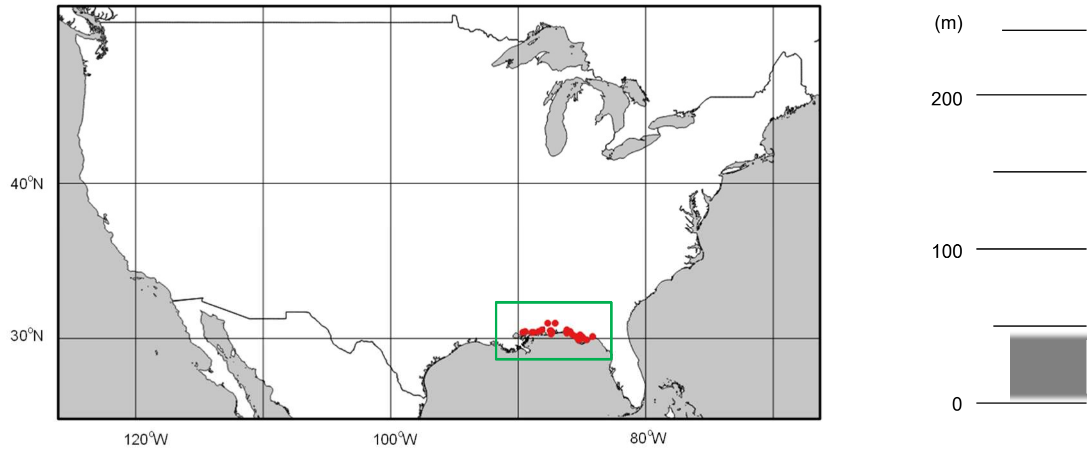
Plate 4.21. *Pinguicula planifolia*

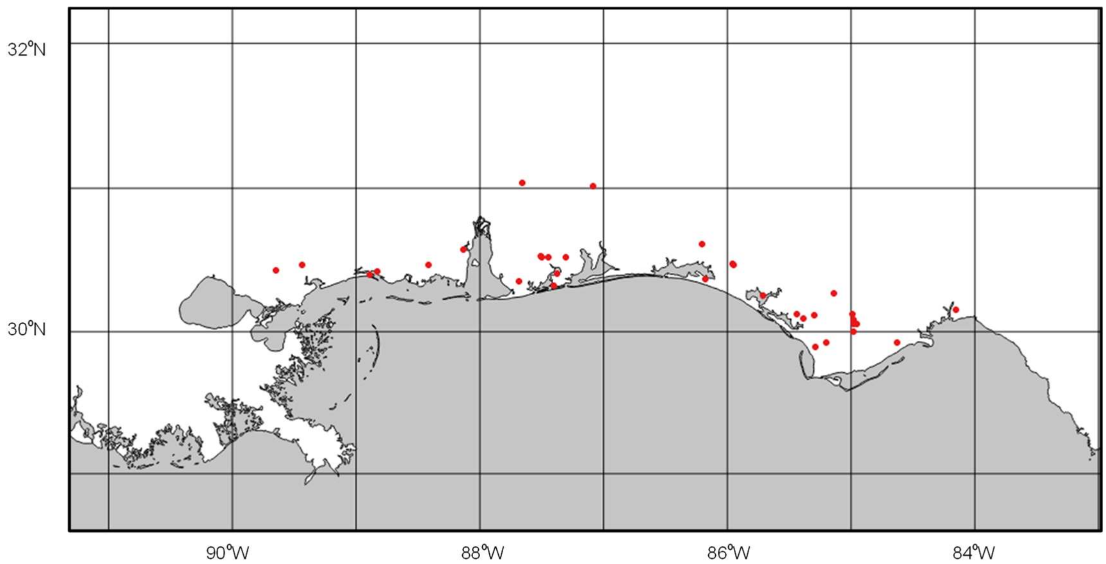


10 mm: 1, 2
10 mm: 3, 4, 5
300 µm: 6

1. habit with flower
2. leaf
3. flower, front view
4. flower, lateral view
5. capsule
6. seed

P. planifolia





22. ***Pinguicula primuliflora*** Wood et Godfrey, Rhodora 59 (1957) 219.

TYPE: USA. Florida: Walton Co., very abundant in shallow running water all over a springy, swampy woodland, intermixed with Sphagnum, at Cluster Springs, 4 March 1956, *Godfrey 54416* (holotype: GH!; isotypes: FLAS!, FSU, K!, MICH!, MO!, NY!, S!, UC, US!, USF!).

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf monomorphic, 8-16, yellowish-green, narrowly oblong, often concave, margin involute, apex obtuse to rather acute, 25-90 mm long, 5-25mm wide, often producing clonal plantlet near tip. Scape 1-6, densely glandulous, 80-280 mm long. Calyx bilabiate, upper lip 3-lobed, lobes oblong-lanceolate, 4-6 mm long, lower lip 2-lobed, lobes smaller than uppers, connate to middle. Flower pale pink to pale purple, white at lower half of lips, yellow in throat. Corolla bilabiate, 20-30 mm across, subactinomorphic, 15-26 mm long including spur, upper lip 2-lobed, lobes obovate to oblong-obovate, tip notched, lower lip 3-lobed, lobes similar to uppers but only slightly larger, terete process covered by yellow hairs projecting from lower throat, tube yellow with purple veins, subcylindrical, spur yellow, narrowly conical to subcylindrical, pendulous, 2-5 mm long. Capsule subglobose. Seed pyriform to ovoid, 390-550 X 200-320 µm. $2n = 22, 32$. (Plate

4.22).

PHENOLOGY: II, III, IV, V, VI

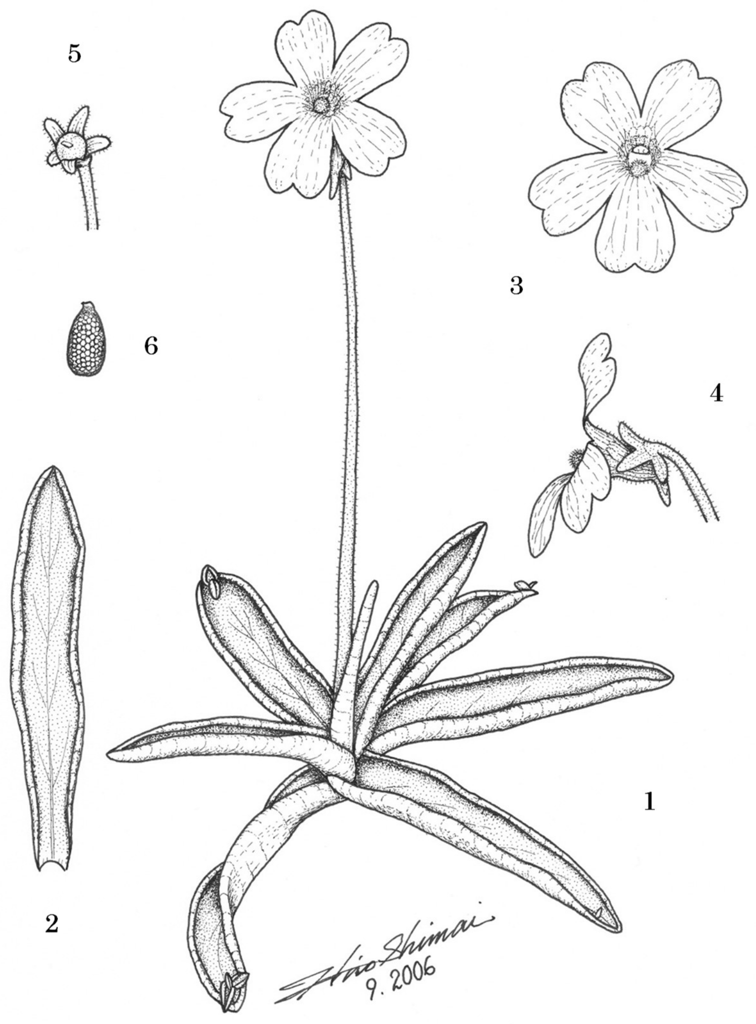
ETYMOLOGY: resembling the primrose flower

HABITAT: Very wet sandy or muddy soil in bogs or along streams. Often exposed to direct sunlight.

DISTRIBUTION: USA (Alabama, Florida, Georgia, Mississippi). near sea level.

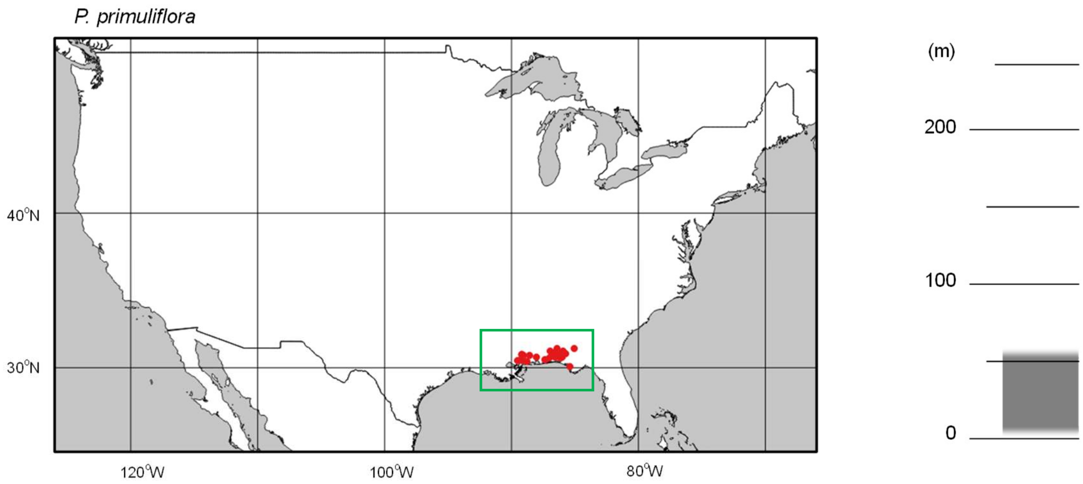
DISCUSSION: *Pinguicula primuliflora* has been recorded from the coastal regions of Alabama, Florida, Louisiana and Mississippi in the southeastern USA. Although *P. primuliflora* was described in 1957, specimens had been collected before then but were identified as *P. ionantha* or *P. pumila*. Because of its morphological characteristics, it may not be confused with other *Pinguicula* species at the habitat. *P. primuliflora* has much narrower and more concave leaves than the other species found in the regions and it often produces clonal plantlets near the tip of the leaves. It is found in very wet places such as peat bogs, muddy soils, slow-flowing stream banks or pool margins. As a result of the frequent asexual reproductions as well as seed reproductions, it often forms large colonies at the habitat. However, the distribution area seems to be shrinking in the recent years. In Japan, artificially naturalized populations that are normally removed from the site as an alien species have been reported from the Prefectures of Aichi, Okayama, and Shizuoka.

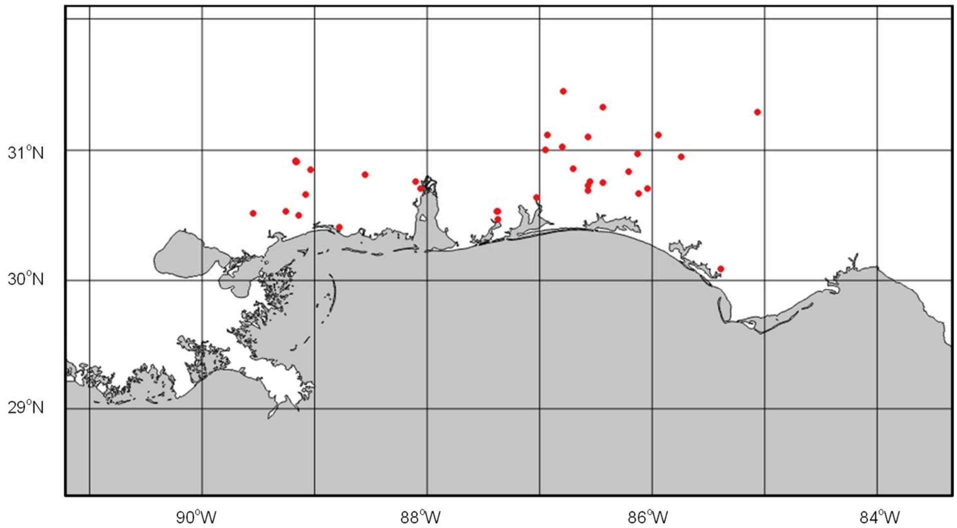
Plate 4.22. *Pinguicula primuliflora*



10 mm: 1, 2
10 mm: 3, 4, 5
500 µm: 6

1. habit with flower
2. leaf
3. flower, front view
4. flower, lateral view
5. capsule
6. seed


P. primuliflora
40°N
30°N
120°W
100°W
80°W
(m)
200
100
0


31°N
30°N
29°N
90°W
88°W
86°W
84°W

23. ***Pinguicula pumila*** Michx., Fl. Bor. Am. 1 (1803) 11.

TYPE: USA. *in humidis apricis Georgiae* (wet sunny place in Georgia), *Michaux s.n.* (holotype: P!).

SYNONYMS: *Isoloba pumila* (Michx.) Raf., *P. australis* Nutt., *P. floridensis* Chapman, *P. pumila* Michx. var. *buswellii* Moldenke, *P. pumila* Michx. f. *alba* Moldenke

DESCRIPTION: Biannual herb. Root filiform, fragile. Stem very short. Leaf monomorphic, 5-20, yellowish-green, sometimes with maroon veins, ovate, margin slightly to strongly involute, apex obtuse to rather acute, 7-26 mm long, 3-12 mm wide. Scape 1-12, densely glandulous, 35-180 mm long. Calyx bilabiate, upper lip 3-lobed, lobes ovate, 1.5-2.5 mm long, lower lip 2-lobed, lobes smaller than uppers connate at base. Flower white, pale lilac to purple, cream or yellow, yellow in throat. Corolla bilabiate, 8-15 mm across, subactinomorphic, 8-20 mm long including spur, upper lip 2-lobed, lobes obovate, tip notched, lower lip 3-lobed, lobes similar to uppers but only slightly larger, terete process covered by yellow hairs projecting from lower throat, tube pale yellow to yellow with dark orange veins, cylindrical, angled at middle, spur yellow to brown, cylindrical, pendulous, 2-7 mm long. Capsule globose. Seed pyriform to ovoid, 370-470 X 180-200 μm. $2n = 22$. (Plate 4.23).

PHENOLOGY: I, II, III, IV, V, VI, VII, X, XI, XII

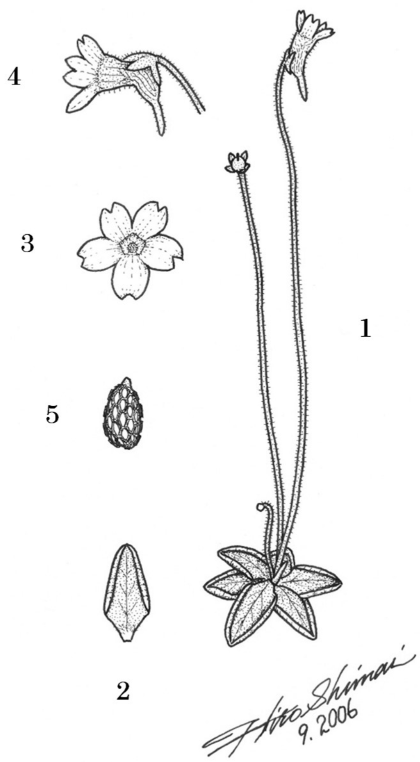
ETYMOLOGY: dwarf (referring to the plant)

HABITAT: Wet peaty or sandy soil (occasionally with coral fragments) in open grasslands, bushes, forest margins or roadsides. Tolerant to various light intensities.

DISTRIBUTION: BAHAMAS (Andros Isl., Grand Bahama Isl., Great Abaco Isl.); USA (Florida, Georgia, Louisiana, North Carolina, South Carolina, Texas). 0-100 m.

DISCUSSION: *Pinguicula pumila* has been widely recorded from North Carolina to Texas along the Coastal Plain and the Bahamas. The flower colour is basically pale purple, but it is also white, cream or yellow depending on strains. A few different flower colorus may sometimes be found within the same microhabitat. This is the smallest *Pinguicula* species (often ca. 30 mm across in rosette diameter) in the regions and may not be confused with other species at the habitat, particularly during the flowering season. The species often prefers wet to somewhat drier sandy soils in savannas, pine forest margins or along roadsides. In Big Pine Key in Florida, for example, it can be found in soils with coral fragments. *P. pumila* is often believed to be a biannual or short-lived perennial. In some areas, particularly in Florida, it is common but the population density at each habitat seems to be relatively sparse.

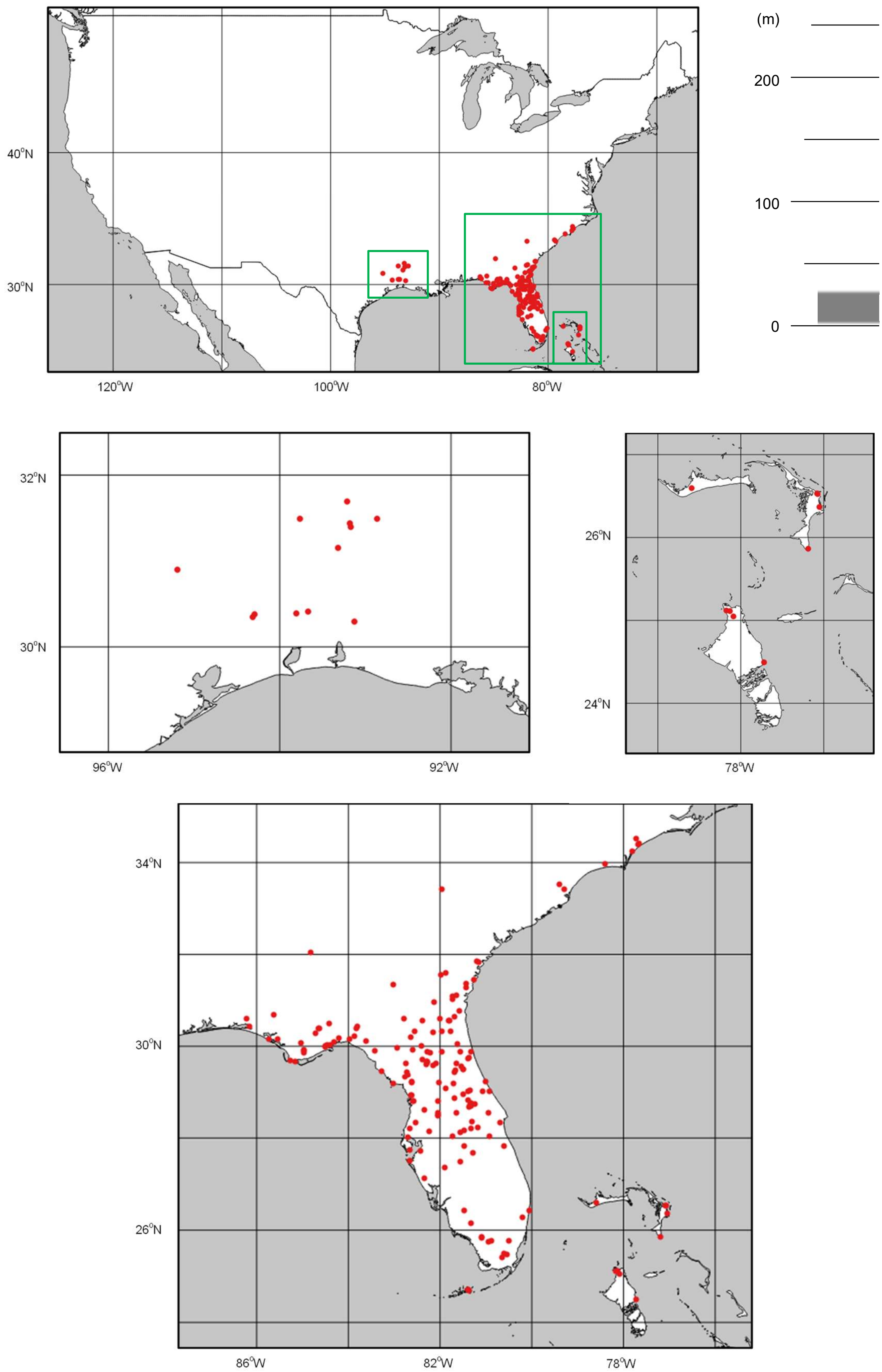
Plate 4.23. *Pinguicula pumila*



10 mm: 1, 2
10 mm: 3, 4
300 μm: 5

1. habit with flower and fruit
2. leaf
3. flower, front view
4. flower, lateral view
5. seed

P. pumila


(m)
200
100
0
40°N
30°N
120°W
100°W
80°W
32°N
30°N
96°W
92°W
26°N
24°N
78°W
34°N
30°N
26°N
86°W
82°W
78°W

Sect. *Membraniformis* Shimai, sect. nov.

TYPUS: *Pinguicula lilacina* Schlecht. et Cham.

DESCRIPTO: Annua vel biennis. Radicibus filiformibus, luxuriosus valde. Rhizoma nimis brevis. Terrestris. Folia monomorpha, 3-8, albido-viridis, late spatulata ad obovate vel suborbiculata, margine involuta, membranacea, usque ad 35 mm longa, Scapi 1-9, glandulis, usque ad 170 mm longi. Calyx bilabiatus, labium superum trilobum, lobis ± oblongis, usque ad 1.5 mm longis, labium inferum bilobum, lobis paulum parvus. Corolla albida ad albido-purpurea vel albido-lilacina, bilabiata, 3-13 mm lata, 3-17 mm longa (calcare incluso), labium superum bilobum, lobis ± oblongis cum margine integris, vel subquadratus cum apices serratus, labium inferum trilobum, lobis ± oblonga, labium inferum trilobum, lobis ± oblongis, in fauce inferum cum vel sine trapeziform convexum verruca, tubus cylindricus ad conicus, calcar cylindricum ad angustatum conicum, 1-4 mm longum.

DISTRIBUTIO: MEXICO ad PANAMA

TYPE: *Pinguicula lilacina* Schlecht. et Cham.

SYNONYM: Subsect. *Agnatiformis* Casper,

DESCRIPTION: Annual or biannual herbs. Root filiform, fragile. Stem very short.

Terrestrial, Leaf monomorphic, 3-8, whitish-green, broadly spatulate to obovate or suborbicular, margin involute, membranaceous, up to 35 mm long. Scape 1-9, glandulous, up to 170 mm long. Calyx bilabiate, upper 3-lobed, lobes ± oblong, up to 1.5 mm long, lower 2-lobed, lobes smaller than uppers. Flower white to faintly pale purple or pale lilac. Corolla bilabiate, 3-13 mm across, 3-17 mm long including spur, upper-lip 2-lobed, lobes ± oblong with entire margin or subquadrate with notched tip, lower-lip 3-lobed, lobes ± oblong, similar to uppers, entire margin, or notched tip, with or without trapeziform convex process in lower throat, tube cylindrical to conical, spur cylindrical to narrowly conical, 1-4 mm long.

DISTRIBUTION: MEXICO to PANAMA

24. ***Pinguicula crenatiloba*** DC., Prodr. Syst. Nat. 8 (1844) 30.

TYPE: in Calq. Dess. Fl. Mex. 2, Fig.1071-3. (lectotype?: in De Candolle 1874!).

SYNONYMS: *P. lilacina* Seemann, *P. nana* Mart. et Gal. ex Hemsley, *P. villosa* Sessé et Mociño

DESCRIPTION: Annual herb. Root filiform, fragile. Stem very short. Leaf monomorphic, 5-8, yellowish-green, ovate to obovate, margin involute, apex obtuse, base cuneate, 5-14 mm long, 3-7 mm wide. Scape 1-8, densely glandulous, 15-72 mm long. Calyx bilabiate, upper lip 3-lobed, lobes lanceolate, 1-2 mm long, connate to middle, lower lip 2-lobed, lobes similar to uppers. Flower somewhat translucent white. Corolla bilabiate, 3-5 mm across, zygomorphic, 3-7 mm long including spur, upper lip 2-lobed, lobes subquadrate to subrectangular, tip notched, lower lip 3-lobed, lateral lobes larger than uppers, middle lobe ovate, oblong or cuneate, tip notched or serrate, larger than laterals, tube yellowish-green, conical, spur translucent white, cylindrical, 1.5-2.5 mm long. Capsule globose. Seed narrowly ellipsoid, 270-370 X 120-180 µm. $2n = 16$. (Plate 4.24).

PHENOLOGY: VIII, IX, X, XI, XII

ETYMOLOGY: crenate-lobed (referring the flower)

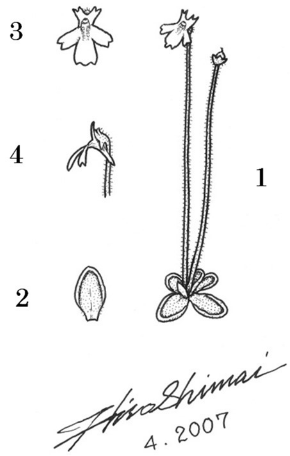
HABITAT: Wet or relatively dry mossy clay soil on slopes in forests or forest margins. Low light intensity.

DISTRIBUTION: COSTA RICA (San José); EL SALVADOR (Chalatenango, Santa Ana); GUATEMALA (Chiquimula, Santa Rosa?); HONDURAS (Comayagua, El Paraíso, Francisco Morazán, Ocotepeque, Olancho); MEXICO (Chiapas, Guerrero, Jalisco, México, Michoacán, Nayarit, Oaxaca, Sinaloa, Sonora);

PANAMA (Chiriquí, Coclé, Ngöbe Buglé, Panamá, Veraguas). 350-2,680 m.

DISCUSSION: *Pinguicula crenatiloba* is widely but sparsely distributed in Mexico and Central America. It is hard to be recognised in the field due to one of the smallest species in the genus. *P. crenatiloba* is sometimes confused with *P. clivorum* or *P. lilacina* (Standley and Steyermark 1944, Zamudio 1997b), but the rosette size of *P. crenatiloba* is much smaller than that of the two. *P. crenatiloba* characteristically has very tiny translucent white flowers with crenate-tipped lip lobes. It was described by De Candolle (1844) but little observations have been made for the species. According to Zamdio (per. com.), the species behaving as an annual in Pátzcuaro (ca. 2,200 m alt.) in the State of Michoacán, Mexico, needs to produce seeds by winter. It is assumed that the distribution area could be wider than that presented here. Inconsistent molecular analysis data result confusions on its taxonomic position. For the time being, it is placed in this section concerning the very thin leaf without forming a winter rosette and distributions, but further taxonomic studies are required.

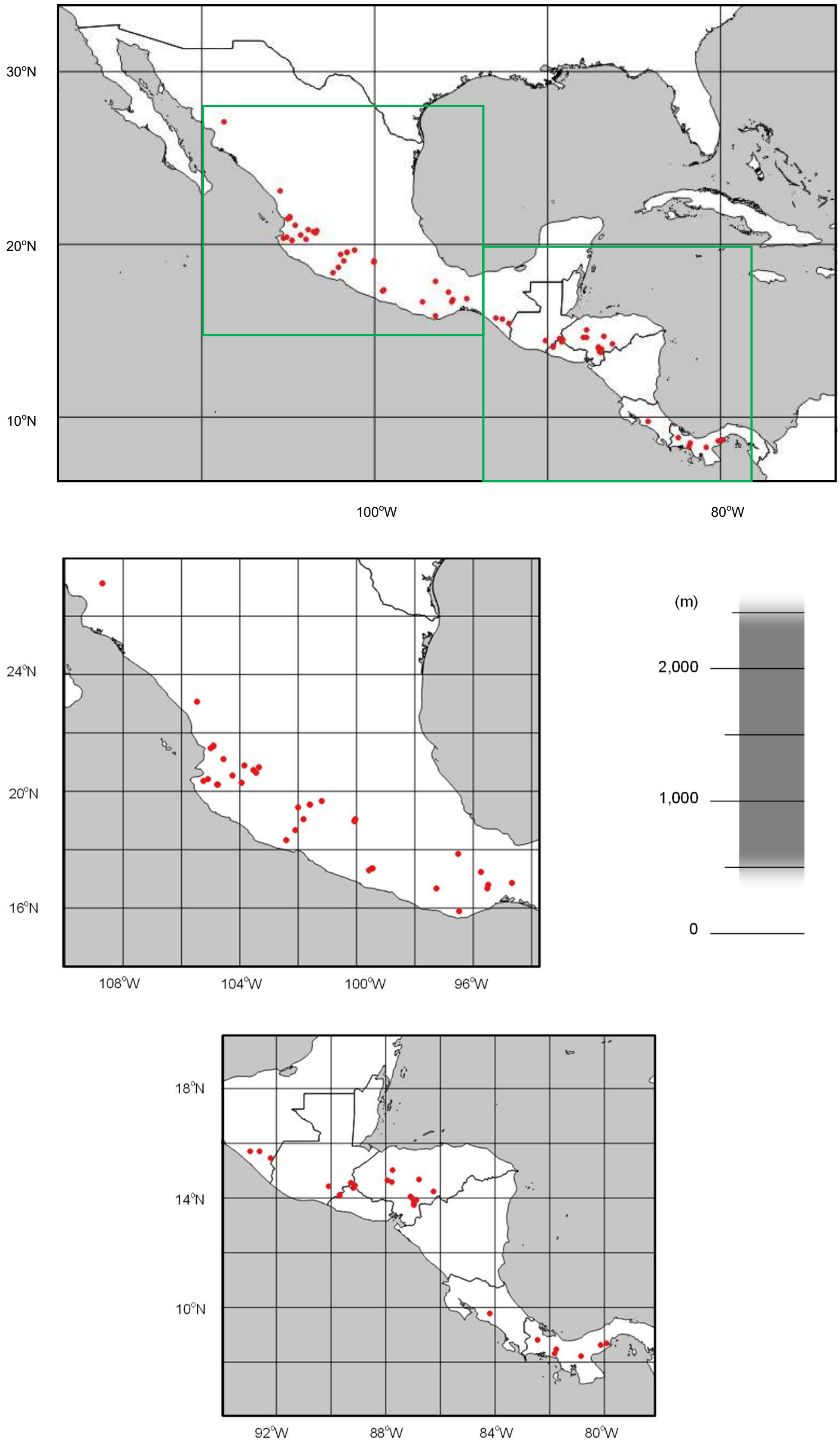
Plate 4.24. *Pinguicula crenatiloba*



10 mm: 1, 2
5 mm: 3, 4

1. habit with flower and fruit
2. leaf
3. flower, front view
4. flower, lateral view

P. crenatiloba



25. ***Pinguicula lilacina*** Schlecht. et Cham., Linnaea 5 (1830) 94.

TYPE: MEXICO. *in umbrosis prope Jalapam* (under shade near Jalapam), October 1828, *Schiede & Deppe 113* (holotype?: HAL!; isotypes: BM?, LE?, WU!).

SYNONYMS: *P. obtusiloba* DC., *P. scopulorum* Brandegee

DESCRIPTION: Biannual herb. Root filiform, fragile. Stem very short. Leaf monomorphic, 4-8, whitish-green, obovate to suborbicular, margin narrowly involute, apex obtuse, 15-35 mm long, 9-17 mm wide. Scape 1-9, densely glandulous, 35-170 mm long. Calyx bilabiate, upper lip 3-lobed, lobes oblong, ca. 1.5 mm long, connate at base, lower lip 2-lobed, lobes smaller than uppers. Flower faintly pale purple to pale lilac. Corolla bilabiate, 10-13 mm across, subactinomorphic, 8-17 mm long including spur, upper lip 2-lobed, lobes broadly obovate to suborbicular, lower lip 3-lobed, lobes similar to uppers, trapeziform convex process in lower throat, tube yellow with dark purple veins, narrowly conical to subcylindrical, spur yellow to brown, cylindrical to narrowly conical, 2-4 mm long. Capsule globose. Seed ellipsoid, 550-650 X 190-230 µm. $2n = 16$. (Plate 4.25).

PHENOLOGY: I, II, III, IV, VII, VIII, IX, X, XI, XII

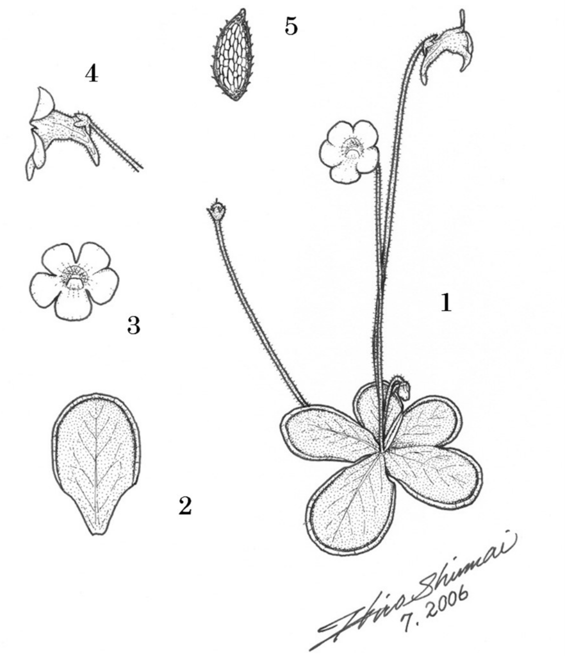
ETYMOLOGY: lilac (referring to the flower)

HABITAT: Sandy soils in wet grasslands. Tolerant to low light intensity.

DISTRIBUTION: GUATEMALA (Alta Verapaz, Baja Verapaz, Huehuetenango); HONDURAS (Isla de La Bahía); MEXICO (Chiapas, Jalisco, Nayarit, Oaxaca, Puebla, Querétaro, San Luis Potosí, Sinaloa, Tamaulipas, Veracruz). 0-2,400 m.

DISCUSSION: *Pinguicula lilacina* is widely distributed in Mexico to Guatemala, and Isla de La Bahía, Honduras. The holotype locality mentioned as Jalapam probably Jalapa in the State of Veracruz, Mexico. This species never form a winter rosette and very likely short-lived, possibly biannual. Therefore, continuous seed propagations at the habitat are necessary. It is morphologically very similar to *P. sharpii*, but *P. lilacina* has larger white to pale lilac flowers. Although the geographical distribution range is wider, it is very sparsely found in those countries. *P. lilacina* was described in an early time by Schlechtendal and Chamisso (1830), but little ecological observation has been made since then.

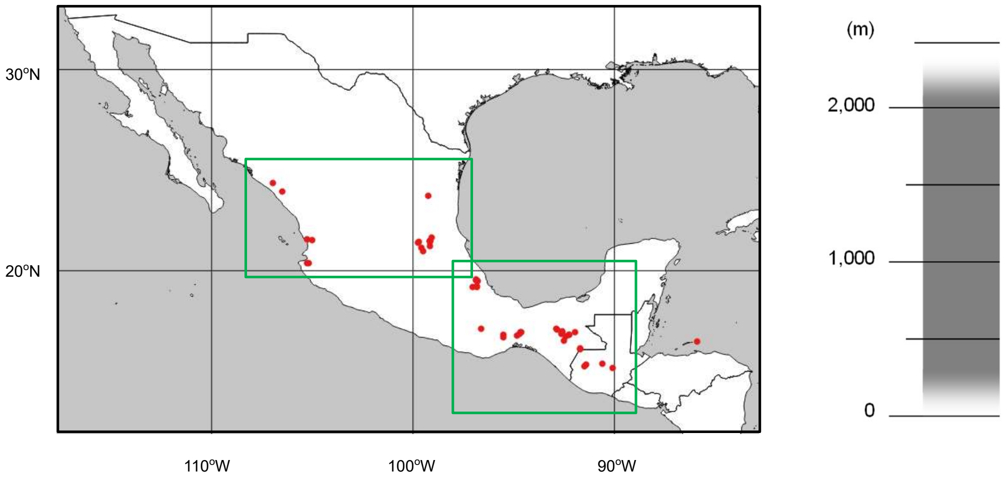
Plate 4.25. *Pinguicula lilacina*

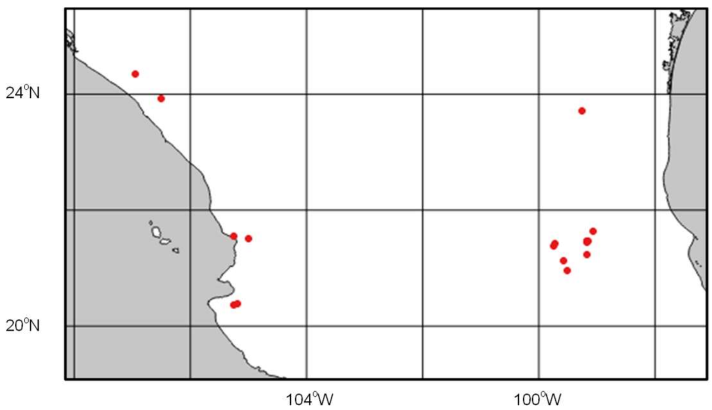


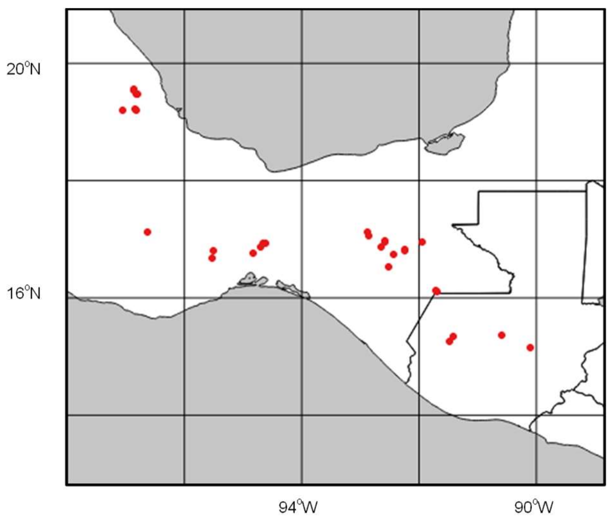
10 mm: 1, 2
10 mm: 3, 4
500 µm: 5

1. habit with flower and fruit
2. leaf
3. flower, front view
4. flower, lateral view
5. seed

P.lilacina


30ºN
20ºN
110ºW
100ºW
90ºW
(m)
2,000
1,000
0


24ºN
20ºN
104ºW
100ºW


20ºN
16ºN
94ºW
90ºW

26. ***Pinguicula sharpii*** Casper et Kondo, Brittonia 29 (1977) 112.

TYPE: MEXICO. Chiapas: on a moist and shaded bank along a road at Yerba Buena near Pueblo Nuevo, leg. A. J. Sharp, 18 December 1972 (holotype: Herb. Kondo collection no. 1668, Nagoya).

DESCRIPTION: Biannual herb. Root filiform, fragile. Stem very short. Leaf monomorphic, 4-8, whitish-green, obovate to suborbicular, margin narrowly involute, apex obtuse, base cuneate, 14-30 mm long, 10-20 mm wide. Scape 1-5, densely glandulous, 30-120 mm long. Calyx bilabiate, upper lip 3-lobed, lobes oblong, ca. 1 mm long, lower lip 2-lobed, lobes connate at base, smaller than uppers, connate at base. Flower white. Corolla bilabiate, 5-8 mm across, subactinomorphic, up to 9 mm long including spur, upper lip 2-lobed, lobes broadly obtuse, tip obtuse rather truncate, lower lip 3-lobed, lobes similar to uppers but only slightly larger, trapeziform convex process in lower throat, tube pale yellow with purple veins, cylindrical, spur yellow, cylindrical, pendulous, 1-3 mm long. Capsule ovoid. Seed ellipsoid, 550-700 X 180-240 µm. $2n = 16$. (Plate 4.26).

PHENOLOGY: no data

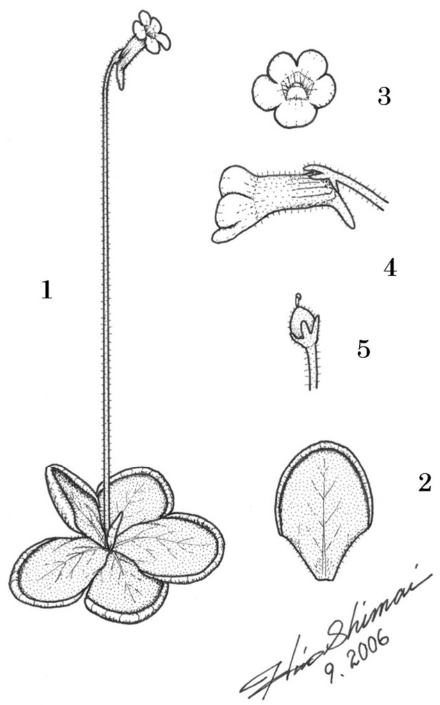
ETYMOLOGY: dedicated to A. J. Sharp, at the University of Tennessee, who first collected this species

HABITAT: Wet banks along roadsides. Low light intensity.

DISTRIBUTION: MEXICO (Chiapas). Known only from the type locality. Altitude range unknown.

DISCUSSION: *Pinguicula sharpii* has been recorded only once from Yerbabuena, near Pueblo Nuevo Solistahuacán in the State of Chiapas, Mexico. It was initially collected as a new *Pinguicula* taxon by A. J. Sharp in December 1972, and was sent to Tokuyoshi Kondo (also known as Masahiro Kondo, Katsuhiko Kondo's father), who later propagated and distributed it to many horticulturalists. To prevent possible future taxonomic confusions, Casper and Kondo (1977) described it as *P. sharpii*. It is morphologically very similar to *P. lilacina*, but comparing the two, *P. sharpii* has much smaller white flowers. A critical study will be needed for those two species if those are conspecific. It does not form any winter rosettes and presumably behaves as biannual at the habitat. The altitude around the type locality detected on a map could be approximately 1,750 m. K. Kondo's private herbarium collections have been transferred to TNS, but this type specimen is not included.

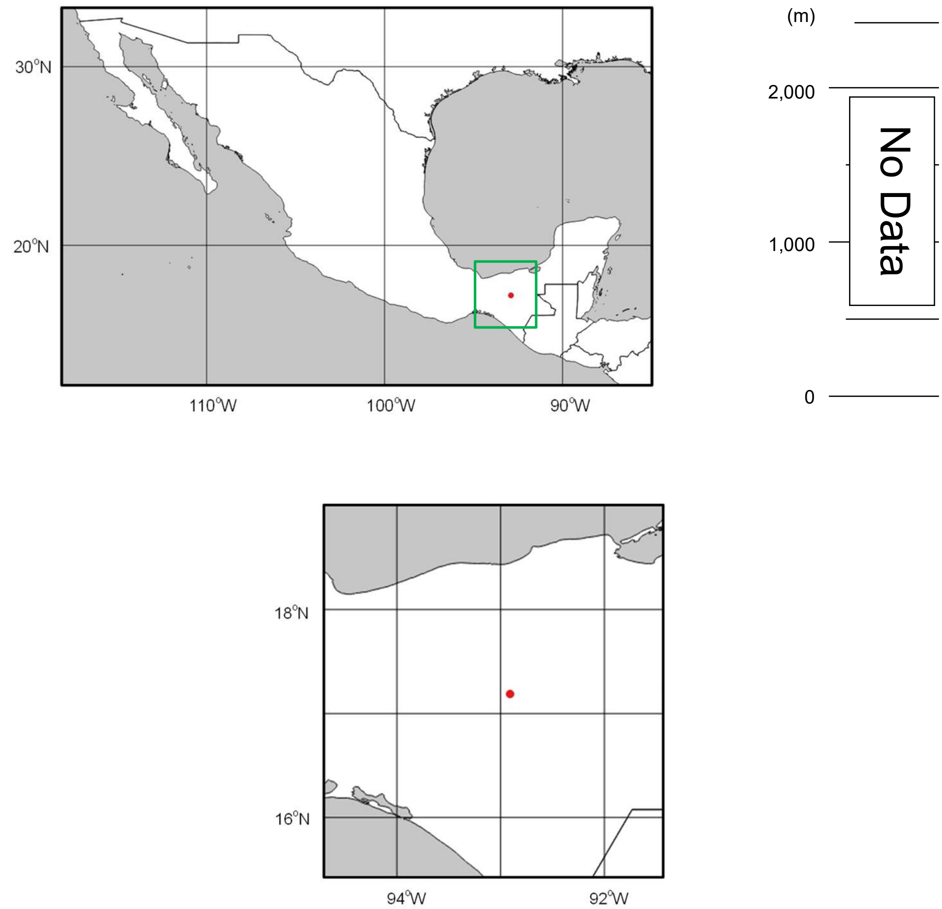
Plate 4.26. *Pinguicula sharpii*



10 mm: 1, 2
5 mm: 3, 4, 5

1. habit with flower
2. leaf
3. flower, front view
4. flower, lateral view
5. capsule

P. sharpii



27. ***Pinguicula takakii*** Zamudio et Rzedowski, Phytologia 60 (1986) 260.

TYPE: MEXICO. *San Luis Potosí, Municipio de Villa Juárez, Minas de Guascamá, 2 km al S.E. de Buenavista, ladera yesosa con Hechtia sp., Agave striata, Dasylirion longissimum y Dodonaea viscosa, alt. 1400m* (San Luis Potosí, Municipality of Villa Juárez, Minas de Guascamá, 2 km SE of Buenavista, gypsum hillsides with *Hechtia* sp., *Agave striata*, *Dasylirion longissimum* and *Dodonaea viscosa*, alt. 1,400m), 18 December 1980, *Zamudio 3789* (holotype: ENCB; isotypes: IEB!, MICH!, XAL; paratype: IEB!).

DESCRIPTION: Biannual herb. Root filiform, fragile. Stem very short. Leaf monomorphic, 3-8, whitish-green, broadly spatulate to obovate, margin involute, apex obtuse, base cuneate, 5-16 mm long, 4-12 mm wide. Scape 1-5, densely glandulous, 25-50 mm long. Calyx bilabiate, upper lip 3-lobed, lobes oblong-triangular, 0.8-1.4 mm long, lower lip 2-lobed, lobes smaller than uppers. Flower pale purple. Corolla bilabiate, 5-10 mm across, subactinomorphic, 6-14mm long including spur, upper lip 2-lobed, lobes obovate to subquadrate, lower lip 3-lobed, lobes similar to uppers, trapeziform convex process in lower throat, tube white to faintly pale purple with purple veins, conical, spur yellow, cylindrical, 2-3.5 mm long. Capsule subglobose. Seed ellipsoid. (Plate 4.27).

PHENOLOGY: XI, XII

ETYMOLOGY: dedicated to Francisco Takaki, who first collected this species

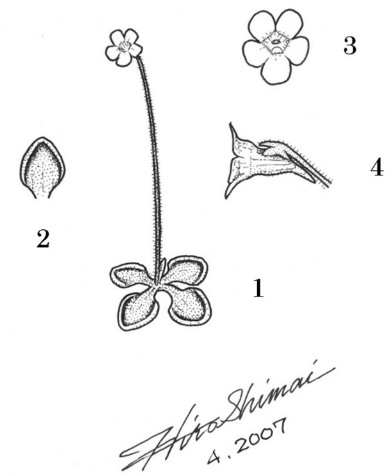
HABITAT: Gypsum hillsides with bushes. Low light intensity.

NATURAL HYBRID: X *P. gypsicola*

DISTRIBUTION: MEXICO (San Luis Potosí). A few localities have been recorded near the type locality. 1,260-1,420 m.

DISCUSSION: *Pinguicula takakii* is endemic to the Municipality of Villa Juárez in the State of San Luis Potosí, Mexico. The type locality Minas de Guascamá could be identical with Minas de Guaxcamá. It has a very close affinity to *P. lilacina* and *P. sharpii*, but can be distinguished by having narrower leaves and more involute leaf margins. The species seems to be short-lived, possibly biannual, without forming any winter rosette so that regular seed propagations at the habitat are necessary to maintain the populations. *P. gypsicola* occurs within the same area, but can be easily distinguished by the plant sizes and leaf shapes. A natural hybrid between the two has been recorded. It is very likely that the geographical distribution range of *P. takakii* is very narrowly restricted to the area. The population at the habitat could be small.

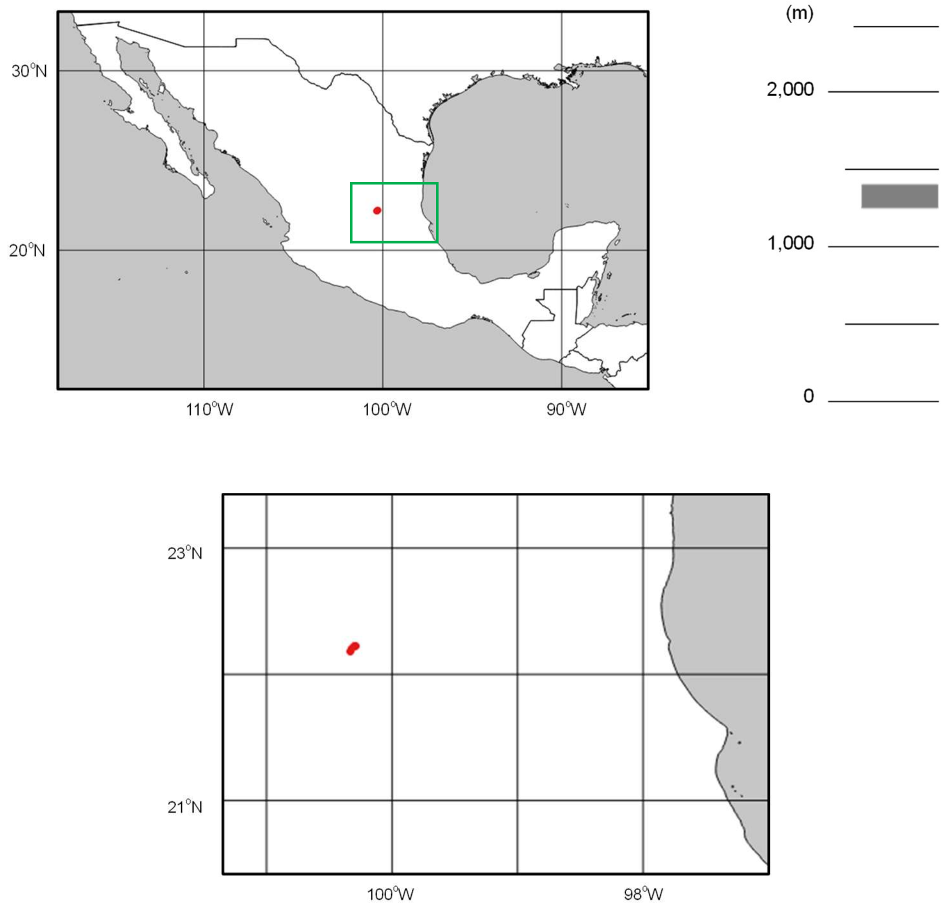
Plate 4.27. *Pinguicula takakii*



10 mm: 1, 2
5 mm: 3, 4

1. habit with flower
2. leaf
3. flower, front view
4. flower, lateral view

P. takakii



Sect. *Mesoamericana* Shimai, sect. nov.

TYPUS: *Pinguicula moranensis* Kunth

DESCRIPTO: Herba perennis. Radicibus filiformibus, luxuriosus valde. Rhizoma nimis brevis. Terrestris, epipetrica ad epiphytica. Folia plerumque dimorpha, folia aestivalia flavo-viridis ad purpurea, filiformis ad orbicularis, folia hiemalia numerosa, brevis, succulent. Rosula hiemis globosa ad lenticulata vel acetabuliformis. Scapi plerumque glandulis. Calyx bilabiatus, labium superum trilobum, labium inferum bilobum. Corolla albida ad rubro-purpurea vel coeruleo-violacea, bilabiata, labium superum lobi variae, bilobum, labium inferum trilobum, lobi variae, tubus conicus ad cylindricus, calcar cylindricum ad subcylindricum.

DISTRIBUTIO: EL SALVADOR; GUATEMALA; HONDURAS; MEXICO

TYPE: *Pinguicula moranensis* Kunth

SYNONYMS: Subgen. *Orcheosanthus* Barnhart, Subgen *Temnoceras* Barnhart, Sect. *Crassifolia* Speta et Fuchs, Sect. *Heterophyllum* Casper, Sect. *Longitubus* Zamudio et Rzedowski, Sect. *Microphyllum* Luhrs et Lampard, Sect. *Orcheosanthus* DC., Sect. *Orchidioides* Luhrs, Sect. *Pionophyllum* DC., Sect.

Temnoceras Ernst, Ser. *Agnatae* Casper

DESCRIPTION: Perennial herbs. Root filiform, fragile. Stem very short. Terrestrial to lithophytic or epiphytic. Leaf often dimorphic, summer leaf yellowish-green or maroon, filiform to orbicular, winter leaf numerous, small, thick. Winter rosette globose to lenticular or acetabuliform. Scape often glandulous. Calyx bilabiate, upper 3-lobed, lower 2-lobed. Flower white to reddish-purple or bluish-purple. Corolla bilabiate, upper lip 2-lobed, lobes variable, lower lip 3-lobed, lobes variable, tube conical to cylindrical, spur ± cylindrical to subcylindrical.

DISTRIBUTION: EL SALVADOR; GUATEMALA; HONDURAS; MEXICO

28. ***Pinguicula acuminata*** Bentham, Pl. Hartweg (1839) 71.

TYPE: MEXICO. *in umbrosis prope Chico* (under the shade near Chico), *Hartweg s.n.* (holotype: K; destroyed in March 1943 while on loan to Berlin).

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf dimorphic, summer leaf 2-5, yellowish-green or maroon, ovate, margin narrowly involute, apex obtuse to rather acute, base sometimes cordate, 20-90 mm long, 15-85 mm wide, petiole 12-80 mm long, abruptly continuing from lamina, winter leaf 18-36, obovate to lanceolate, thick, apex acuminate, 6-19 mm long, 3-9 mm wide. Winter rosette subglobose. Scape 2-7, glandulous only upper part and calyx, 75-175 mm long. Calyx bilabiate, upper lip 3-lobed, lobes oblong-lanceolate, 2.6-3 mm long, lower lip 2-lobed, lobes smaller than uppers. Flower white to faintly pale purple, yellowish-green in throat, yellowish trichomes at base of lips to throat. Corolla bilabiate, 15-20 mm across, subactinomorphic, 17-22 mm long including spur, upper lip 2-lobed, lobes oblong to obovate or subcuneate, lower lip 3-lobed, lobes similar to uppers but only slightly larger, tube yellowish-green, subcylindrical, angled at middle, spur yellowish-green, subcylindrical, sometimes incurved, 3-5 mm long. Capsule unknown. Seed unknown. $2n = 22$. (Plate 4.28).

PHENOLOGY: II, III, IV, V, IX. Scape arising mainly from winter rosette but also from spring or summer rosette.

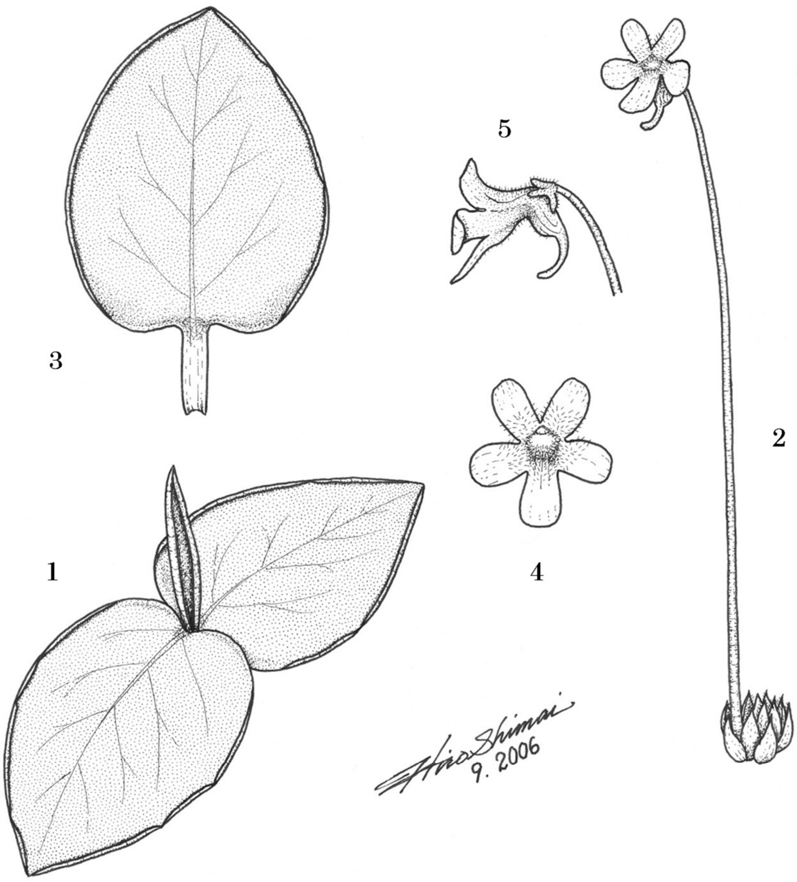
ETYMOLOGY: acuminate or sharp-pointed (referring to the winter leaf)

HABITAT: Loamy soil between rocks in misty forests. Low light intensity.

DISTRIBUTION: MEXICO (Distrito Federal, Hidalgo, México, Michoacán, Querétaro, Tlaxcala). 2,073-3,020 m.

DISCUSSION: *Pinguicula acuminata* was described with a very brief Latin diagnosis by Bentham (1839) based on the materials collected at El Chico in the State of Hidalgo, It is often thought that this species was confined to the El Chico region; however, it is more widely distributed in Central Mexico. It was thought to be a lost species since little available information. Luhrs (in International *Pinguicula* Study Group Newsletter, No. 4. (1994)) reported rediscovery of the species at El Chico in May 1989 and additionally several other localities in October 1991 with more detailed morphological and ecological observations. The shape of summer leaves between *P. acuminata* and *P. crassifolia*, both of which are found in El Chico, is very similar. Differences between the two are particularly seen in the flower colour, which is white in *P. acuminata* and vivid reddish-purple in *P. crassifolia*, and the former has more conspicuous leaf petioles. Also, the scape of *P. acuminata* is often glandulous only upper part while that of *P. crassifolia* is densely covered by non-glandular hairs throughout.

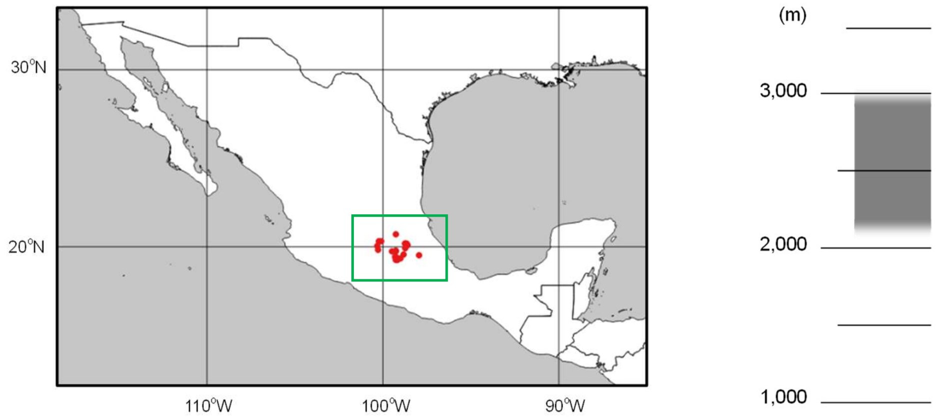
Plate 4.28. *Pinguicula acuminata*

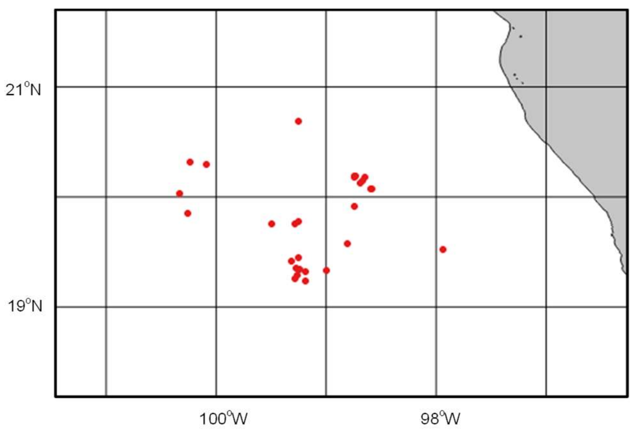


10 mm: 1, 2, 3
5 mm: 4, 5

1. summer rosette
2. winter rosette with flower
3. summer leaf
4. flower, front view
5. flower, lateral view

P. acuminata





29. ***Pinguicula agnata*** Casper, Feddes Repert. 67 (1963) 14.

TYPE: MEXICO. State of Hidalgo, Distr. Zimapán, Lower portion of nearly sheer calcareous north facing cliff on dry rocky slopes of Barranca de Tolimán somewhat above the mines on road from Zimapán to Mina Loma del Toro and Balcones, alt. ca. 5000' (ca. 1,520 m), 8 August 1948, *Moore & Wood 4395* (holotype: BH!; isotypes: A, BM!, MEXU!, U).

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf dimorphic, summer leaf 5-12, yellowish-green or maroon, subelect, thick, spatulate to oblanceolate or obovate, margin sometimes slightly revolute, apex obtuse, 35-70 mm long, 10-30 mm wide, winter leaf 15-20, spatulate to oblong-obovate, thick, apex obtuse, 10-30 mm long, 5-15 mm wide. Winter rosette acetabuliform. Scape 1-3, densely glandulous, 50-120 mm long. Calyx bilabiate, upper lip 3-lobed, lobes broadly ovate, 2.5-4 mm long, connate at base, lower lip 2-lobed, lobes smaller than uppers. Flower white to pale purple, darker at tip, with purple spots at base of lobes, yellow in throat. Corolla bilabiate, 10-25 mm across, subactinomorphic, 18-22 mm long including spur, upper lip 2-lobed, lobes obovate-oblong, lower lip 3-lobed, lobes slightly larger than uppers, tube yellowish-green to pale purple, cylindrical, spur yellowish-green, subcylindrical, up to 5 mm long. Capsule subglobose, 640-800 X 190-300 µm. Seed narrowly ellipsoid. $2n = 22$. (Plate 4.29).

PHENOLOGY: I, II, III, VI, VII, VIII, IX, X, XI, XII. Scape arising mainly from summer rosette but also from spring or winter rosette.

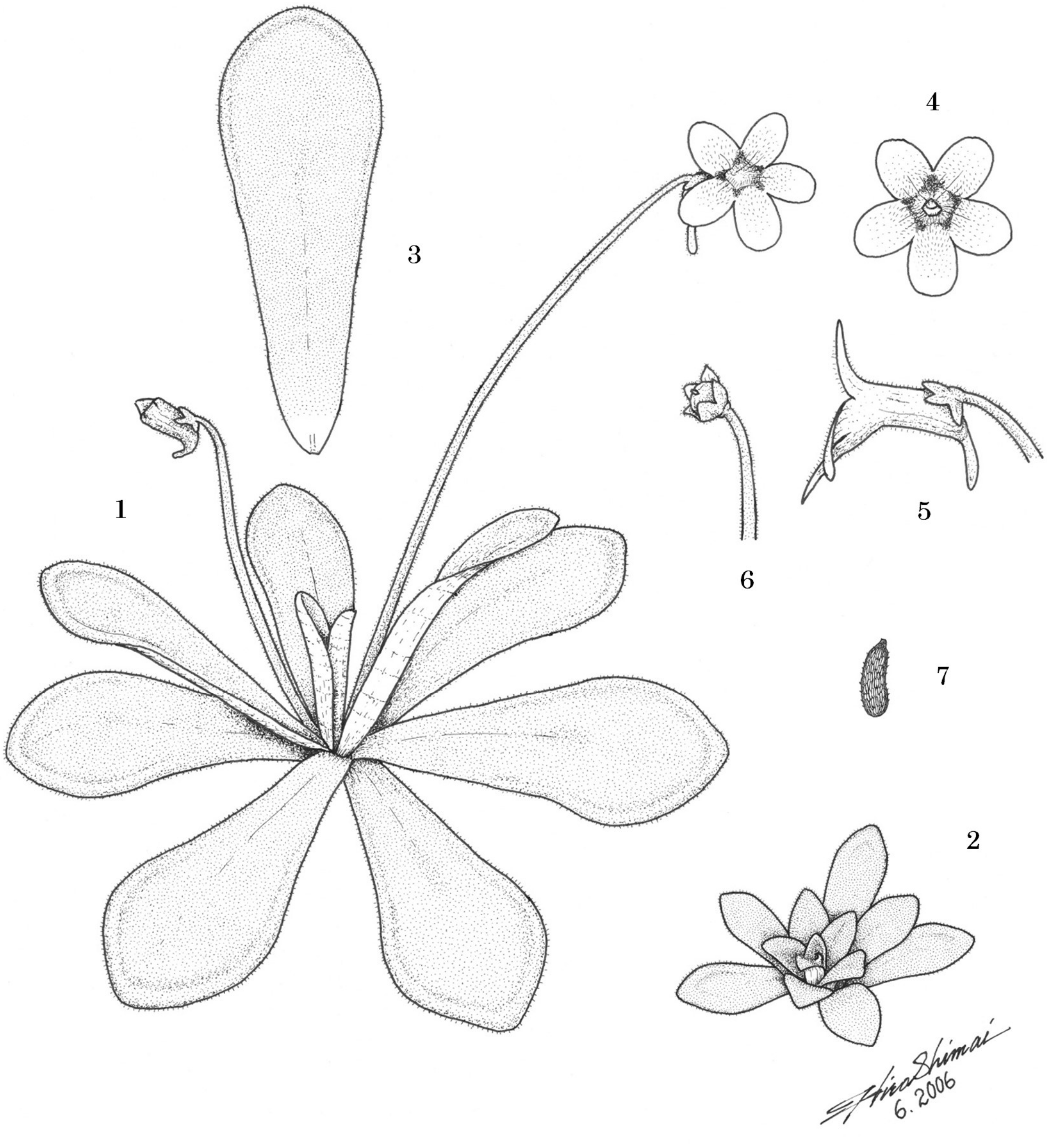
ETYMOLOGY: born after (having confusions of its taxonomic status)

HABITAT: Vertical calcareous rocks or cliffs. Tolerant to various light intensities.

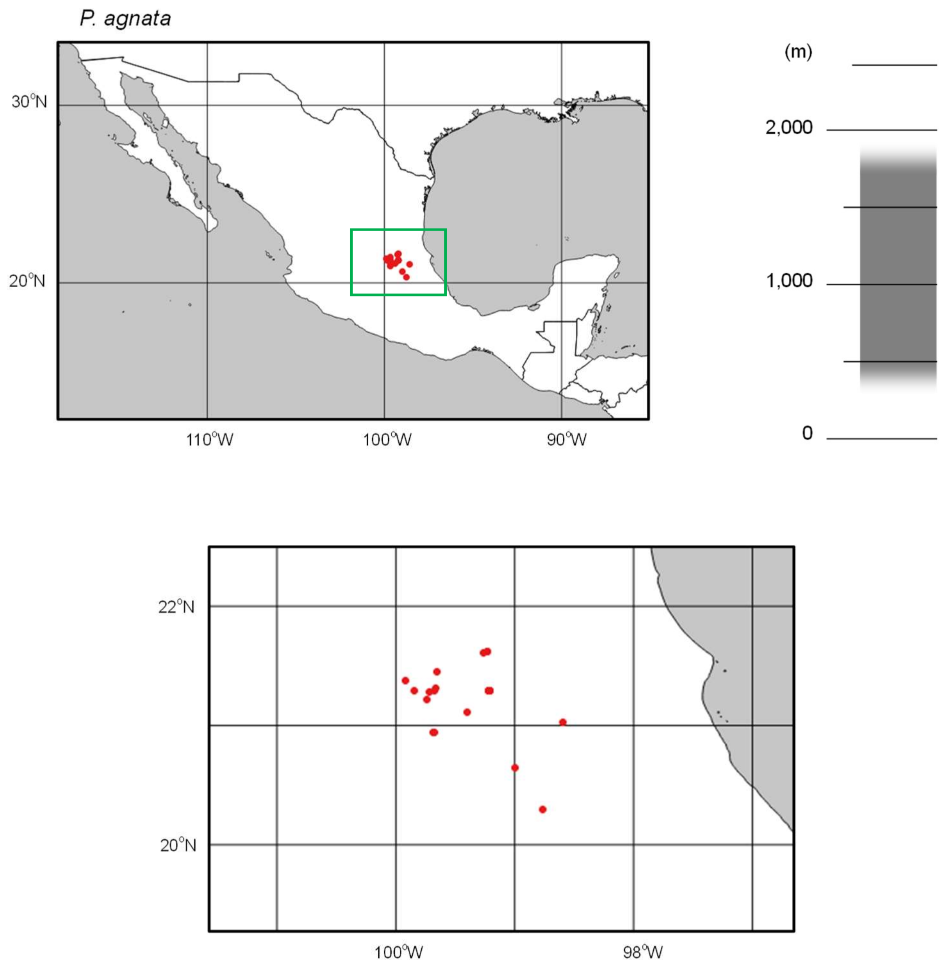
DISTRIBUTION: MEXICO (Guanajuato, Hidalgo, Querétaro). 330-1,959 m.

DISCUSSION: *Pinguicula agnata* was first collected by Moore and Wood in August 1948, near Zimapán in the State of Hidalgo, Mexico and the herbarium specimen was labeled as *P. crenatiloba*. Casper (1963) recognised that it was not *P. crenatiloba* and he described as a *P. agnata*. The plant size of *P. agnata* is much larger than that of *P. crenatiloba* without confusions between the two. *P. agnata* is morphologically somewhat similar to *P. gigantea* and *P. ibarrae*, but *P. agnata* has narrower leaves than the others. Taylor and Cheek (1983) reported that a number of plants grew on vertical cliffs in the Tolimán Canyon, Hidalgo, implying that it is locally abundant.

Plate 4.29. *Pinguicula agnata*



▬ 10 mm: 1, 2, 3	1. summer rosette with flower
▬ 10 mm: 4, 5, 6	2. winter rosette
▬ 500 µm : 7	3. summer leaf
	4. flower, front view
	5. flower, lateral view
	6. capsule
	7. seed


P. agnata
30°N
20°N
110°W
100°W
90°W
(m)
2,000
1,000
0
22°N
20°N
100°W
98°W

30. ***Pinguicula calderoniae*** Zamudio, Bol. Soc. Bot. Mex. 68 (2001) 85.

TYPE: MEXICO. *Querétaro, Municipio de Landa, extreme norte del Llano Chiquito* (Querétaro, Municipality of Landa, far north of Llano Chiquito, alt. 2,060 m), 13 June 2000, *Zamudio, Ocampo & Reznicek 11421* (holotype: IEB!; isotypes; IEB!, TEX!).

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf dimorphic, summer leaf 3-8, yellowish-green or maroon, subelect to parabolic, arcuate or pendulous, narrowly linear-lanceolate, margin revolute, apex acute, 60-260 mm long, 3-8.5 mm wide, winter leaf 6-30, elliptic, obovate to ovate, apex acute to acuminate, thick, 3-10 mm long, 1.5-4 mm wide. Winter rosette lenticular. Scape 1-3, densely glandulous, 60-150 mm long. Calyx bilabiate, upper lip 3-lobed, lobes lanceolate 2-3.5 mm long, lower lip 2-lobed, lobes smaller than uppers. Flower reddish-purple. Corolla bilabiate, 15-20 mm across, zygomorphic, 20-35 mm long including spur, upper lip 2-lobed, lobes oblong, lower lip 3-lobed, lobes similar to uppers but larger, middle lobe sometimes rather truncate at tip, tube faintly pale purple, narrowly conical to subcylindrical, spur reddish-purple, cylindrical but gradually tapering from tube to apex, 7-16 mm long. Capsule subglobose. Seed fusiform. $2n = 22$. (Plate

4.30).

PHENOLOGY: VI. Scape arising from late winter rosette or early summer rosette.

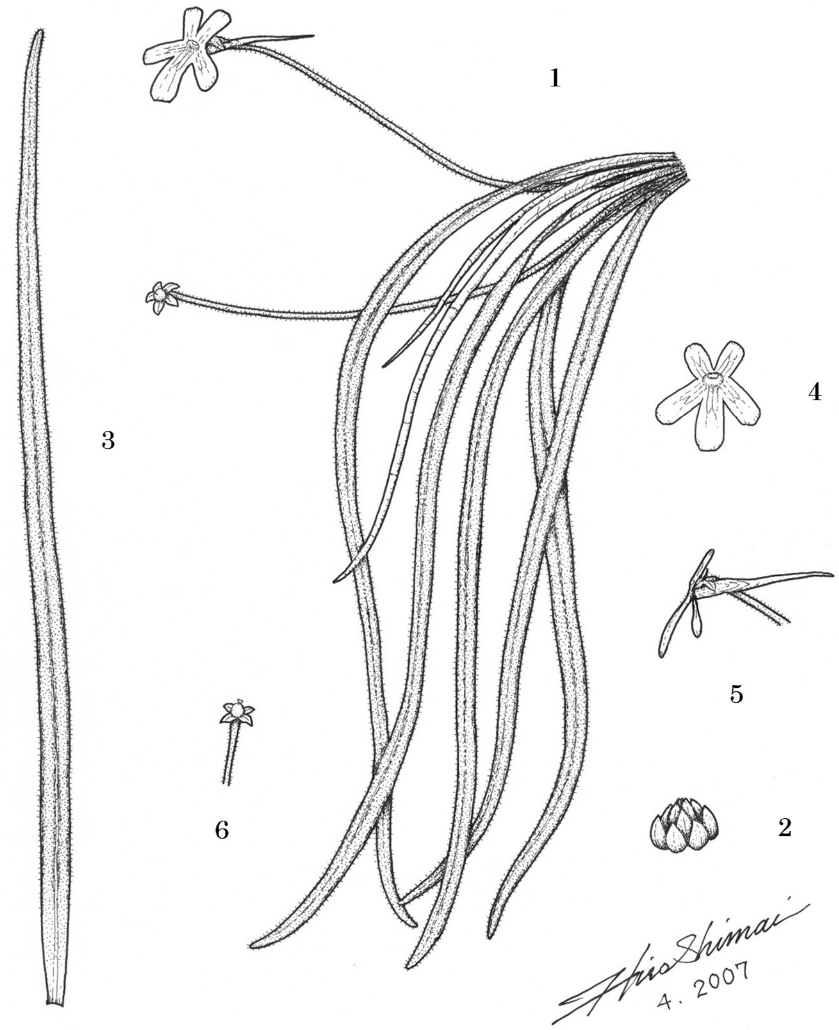
ETYMOLOGY: dedicated to Graciela Calderón de Rzedowski (Instituto de Ecología Centro Regional del Bajío), who has contributed to the Mexican flora

HABITAT: Calcium carbonate on vertical rocks or crevices of calcareous rocks in a higher humidity forest. Tolerant to low light intensity.

DISTRIBUTION: MEXICO (Querétaro, San Luis Potosí). 2,060-2,200 m.

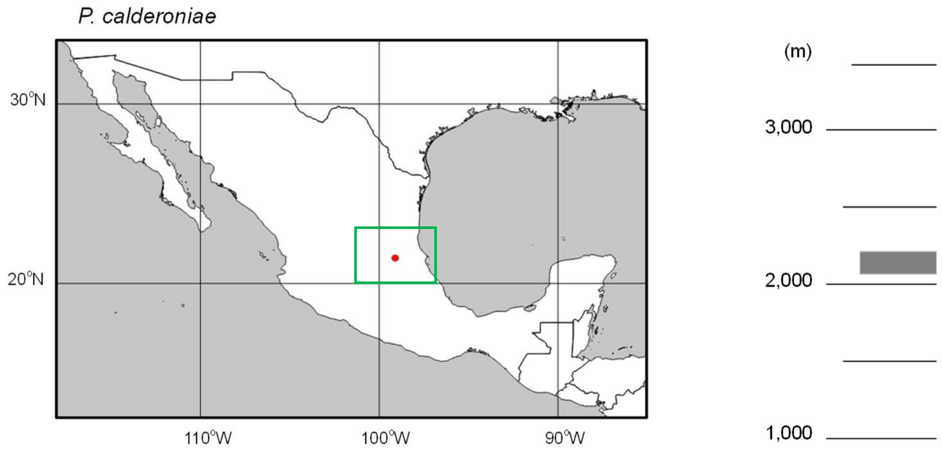
DISCUSSION: *Pinguicula calderoniae* is confined to calcareous rocks in forests near the Sierra Madre Oriental, on the state border of San Luis Potosí and Querétaro, Mexico (Zamudio 2001a, 2005). The summer leaf or *P. calderoniae* is somewhat similar to that of *P. gypsicola*, also occurring in the State of San Luis Potosí, but the former has broader and longer leaves than the latter. Similarly, *P. heterophylla* and *P. medusina* also have narrower leaves, but the distribution of *P. calderoniae* is geographically isolated from the two species. *P. calderoniae* shares the same microhabitat with *P. martinezii* at the Municipality of Landa de Matamoros in the State of Querétaro. The distribution of *P. calderoniae* seems to be restricted to a very narrow area.

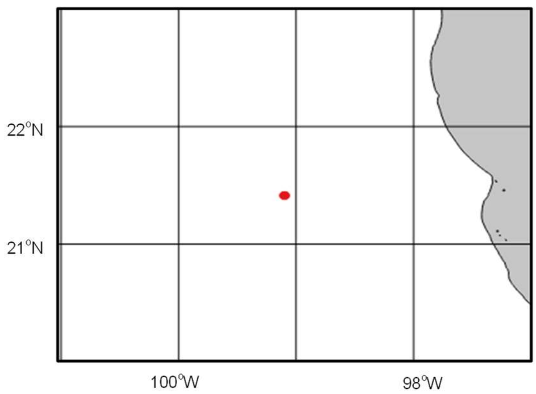
Plate 4.30. *Pinguicula calderoniae*



10 mm: 1, 2, 3, 6
10 mm: 4, 5

1. summer rosette with flower and fruit
2. winter rosette
3. summer leaf
4. flower, front view
5. flower, lateral view
6. capsule


P. calderoniae
30°N
20°N
110°W
100°W
90°W
(m)
3,000
2,000
1,000


22°N
21°N
100°W
98°W

31. ***Pinguicula clivorum*** Standley et Steyermark, Publ. Field Mus. Nat. Hist., Bot. Ser. 23 (1944) 179.

TYPE: GUATEMALA. Dept. Huehuetenango, on high bluffs in upper reaches of a barranco above San Juan Ixcoy, Sierra de los Cuchumatanes, alt. 2,400 m, 4 August 1942, *Steyermark 50061* (holotype: F!, K-photo ex-F!; isotype: DS).

SYNONYM: *P. barbata* Zamudio et Rzedowski

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf monomorphic, 11-17, yellowish-green, ovate to suborbicular, base cuneate, margin narrowly involute, apex obtuse, 18-46 mm long, 17-35 mm wide. Scape 1-8, densely glandulous, 30-100 mm long. Calyx bilabiate, upper lip 3-lobed, lobes oblong-lanceolate, 2.5-3.0 mm long, lower lip 2-lobed, lobes smaller than uppers. Flower faintly pale purple to pale purple, yellow spot at base of middle lobe. Corolla bilabiate, 8-9 mm across, zygomorphic, 12-18 mm long including spur, upper lip 2-lobed, lobes elliptic to oblong, lower lip 3-lobed, lobes obovate to oblong, often overlapping, middle lobe rather suborbicular, larger than laterals, connate to middle, tube pale purple, conical, spur yellowish-green, cylindrical, 3.8-6 mm long. Capsule subglobose. Seed ellipsoid to ovoid. (Plate 4.31).

PHENOLOGY: I, IV, VIII

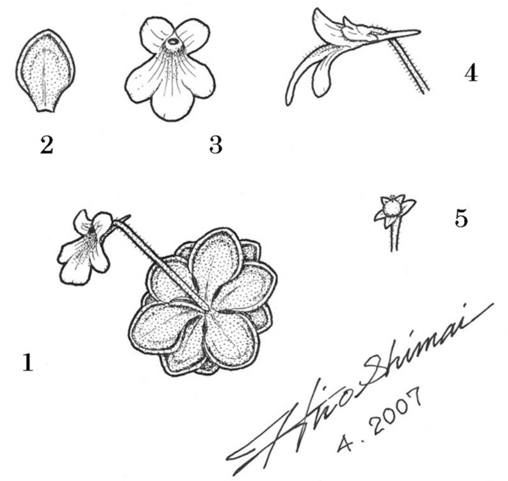
ETYMOLOGY: gently sloped, hilly

HABITAT: Wet calcareous rocks in steep slopes or on vertical cliffs in pine forests. Low light intensity.

DISTRIBUTION: GUATEMALA (Huehuetenango); MEXICO (Chiapas). 2,400-2,900 m.

DISCUSSION: *Pinguicula clivorum* was described by Standley and Steyermark (1944) based on the material collected in the Department of Huehuetenango, Guatemala. Casper (1966a) treated this taxon as "nomen dubium" in his monograph. Afterwards, Zamudio and Rzedowski (1986) described *P. barbata* based on a material collected in the State of Chiapas, Mexico; however, Zamudio (1997b) recognised that it was identical with *P. clivorum*. This species occurs in mountain regions of both Mexico and Guatemala, but it seems very rare and only a single locality has been known from each country, so far. It does not form any winter rosettes. Although the species is temporary placed in this section, its phylogenetic relationships to other species remain unknown.

Plate 4.31. *Pinguicula clivorum*

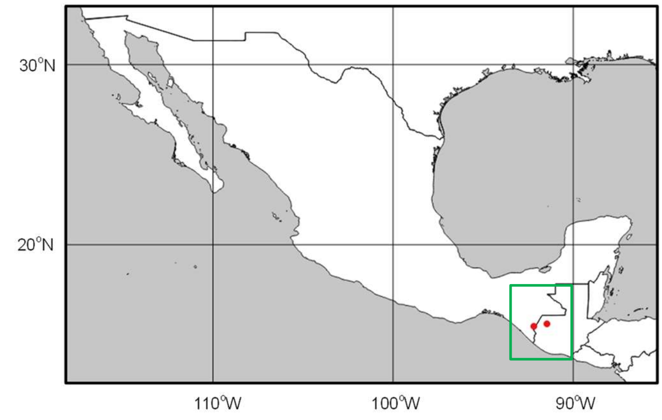


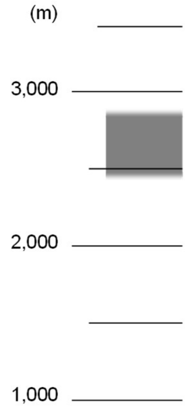
10 mm: 1, 2

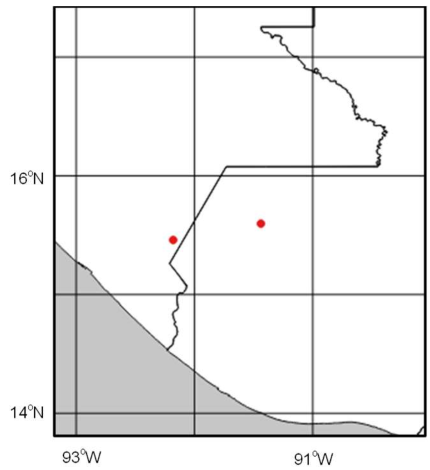
5 mm: 3, 4, 5

1. habit with flower
2. leaf
3. flower, front view
4. flower, lateral view
5. capsule

P. clivorum







32. ***Pinguicula colimensis*** McVaugh et Mickel, Brittonia 15 (1963) 138.

TYPE: MEXICO. Colima: mountain summit near the pass, 10-11 miles (ca. 16-18 km) south-southwest of Colima, sunny slopes, on gypsum, elevation ca. 500 m, 18 July 1957, *McVaugh 15534* (holotype: MICH!).

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf dimorphic, summer leaf 6-10, yellowish-green, obovate-spatulate to rhombate, slightly concave, margin slightly revolute, apex obtuse to rather acute, hairy at base, 45-120 mm long, 20-65 mm wide, winter leaf 25-135, spatulate, hairy at margin, thick, apex obtuse, 5-20 mm long, 2-5 mm wide. Winter rosette subglobose. Scape 1-4, densely glandulous, 30-190 mm long. Calyx bilabiate, upper lip 3-lobed, lobes oblong-lanceolate, ca. 3 mm long, lower lip 2-lobed, lobes similar to uppers. Flower pinkish-purple, white at base of lower lip, yellow in throat. Corolla bilabiate, 20-35 mm across, zygomorphic, 35-50 mm long including spur, upper lip 2-lobed, lobes suborbicular, tip sometimes slightly mucronate, lower lip 3-lobed, lobes similar to uppers but larger, often overlapping, tube very short, conical, spur faintly pale pink, cylindrical, 20-40 mm long. Capsule subglobose. Seed fusiform-ellipsoid, 600-950 X 190-210 µm. $2n = 22$. (Plate 4.32).

PHENOLOGY: VI, XII. Scape arising from late winter rosette or early summer rosette.

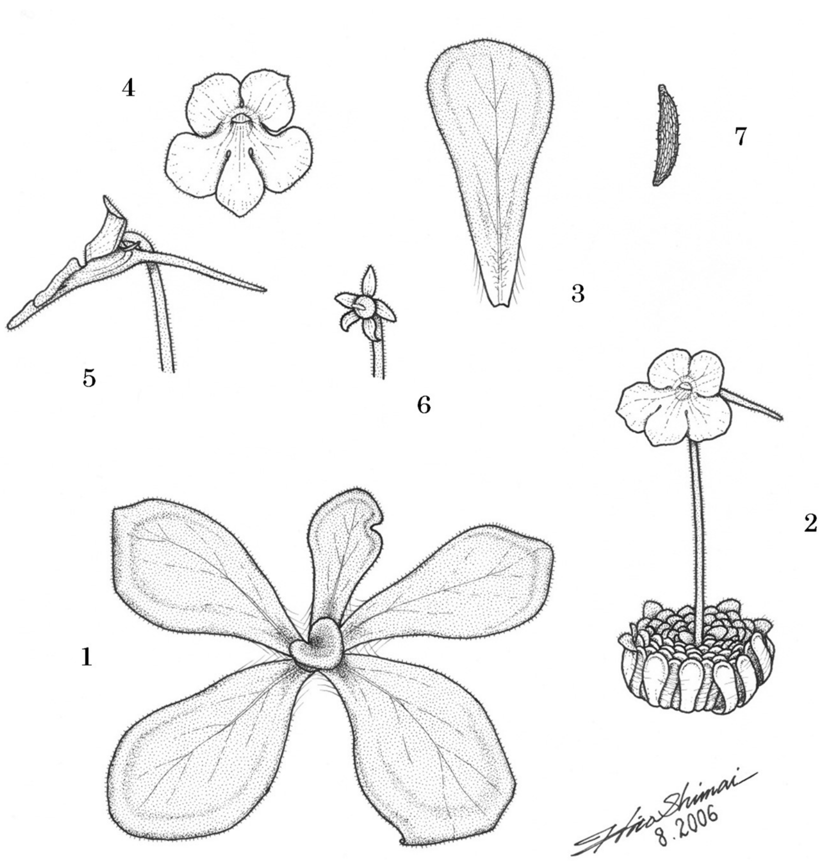
ETYMOLOGY: native of Colima

HABITAT: Wet calcareous sand or limestone on cliffs. Low light intensity.

DISTRIBUTION: MEXICO (Colima). 240-500 m.

DISCUSSION: *Pinguicula colimensis* is endemic to the State of Colima, Mexico. Some herbarium records from the States of Guerrero and Michoacán have been documented by a few taxonomists (e.g. Casper 1966a, 1966b, McVaugh and Mickel 1963), but Zamudio (2001b) stated that other species were misidentified as *P. colimensis*. Also, Kondo (1969) reported that the chromosome number of *P. colimensis* from Oaxaca was $2n = 44$, but the species does not occur in Oaxaca whereas the material examined was highly likely *P. hemiepiphytica* (Zamudio 2001b). Historically, *P. colimensis* has been often confused with other morphologically similar species. It has somewhat smaller pinkish-purple flower, spatulate to rhombate leaves with slightly revolute margin and long hairs at the base, different from other similar species.

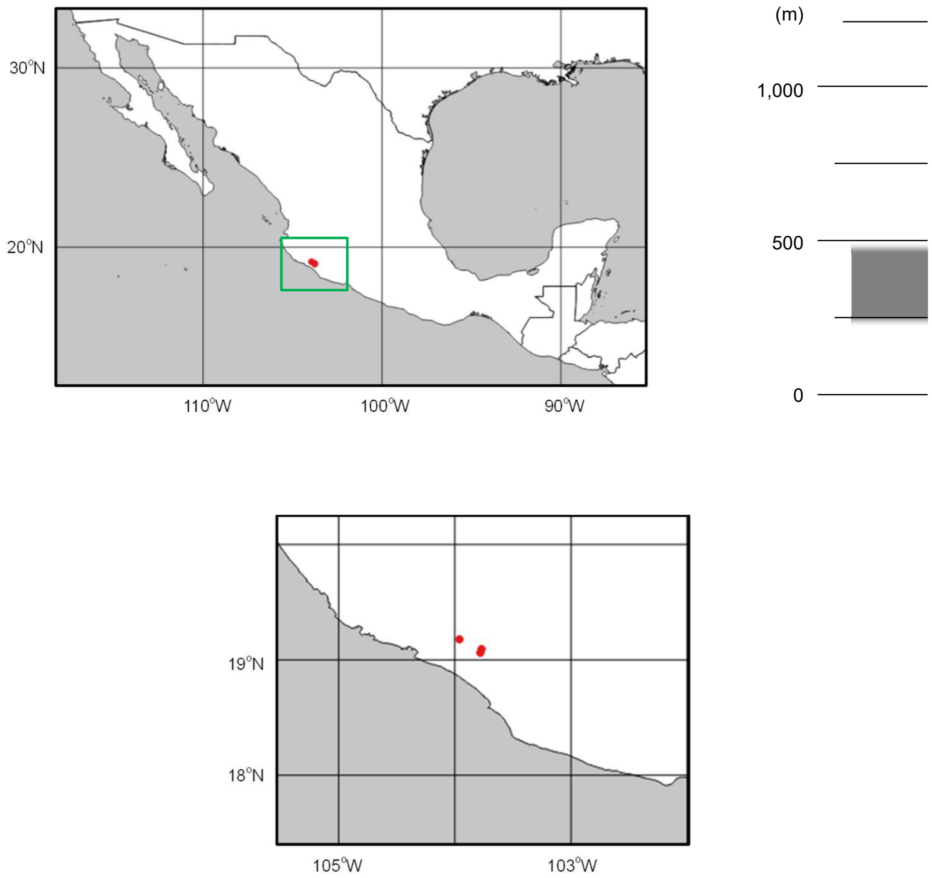
Plate 4.32. *Pinguicula colimensis*



10 mm: 1, 2, 3
10 mm: 4, 5, 6
500 μm: 7

1. summer rosette
2. winter rosette with flower
3. summer leaf
4. flower, front view
5. flower, lateral view
6. capsule (immature)
7. seed

P. colimensis



33. ***Pinguicula conzattii*** Zamudio et van Marm, Acta Bot. Mex. 62 (2003) 16.

TYPE: MEXICO. *Oaxaca, municipio de Santo Tomás Ocotepec, alrededores de la Cueva de la Hoya, ca. 10 km al NE de Santiago Nuyoó* (Oaxaca, Municipality of Santo Tomás Ocotepec, around the Cueva de la Hoya, ca. 10 km northeast of Santiago Nuyoó, alt. 2,400 m), 20 November 1998, *Zamudio & Ocampo 10933* (holotype: IEB!; isotypes: IEB!, MEXU!).

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf dimorphic, summer leaf 4-6, yellowish-green or maroon, broadly-ovate to suborbicular, margin narrowly involute, apex rather obtuse, 28-50 mm long, 25-48 mm wide, hairy at base, petiole 10-20 mm long, hairy at margin, winter leaf many, spatulate to obovate, thick, apex obtuse, 3.5-10 mm long, 1.5-4 mm wide. Winter rosette subglobose. Scape 1-6, densely glandulous, glands conspicuously long, 70-170 mm long. Calyx bilabiate, upper lip 3-lobed, lobes triangular-elliptic to lanceolate, 2-3 mm long, lower lip 2-lobed, lobes smaller than uppers, connate at base. Flower white to faintly pale purple, slightly darker at outer margin. Corolla bilabiate, 20-25 mm across, subactinomorphic, 18-30 mm long including spur, upper lip 2-lobed, lobes obovate to suborbicular, tip obtuse to truncate, lower lip 3-lobed, lobes similar to uppers but slightly larger, tube faintly pale purple, cylindrical, somewhat angled at below middle, spur yellowish-green, subcylindrical, pendulous, 3-6 mm long. Capsule subglobose. Seed fusiform. (Plate 4.33).

PHENOLOGY: XI, XII. Scape arising from late summer rosette or early winter rosette.

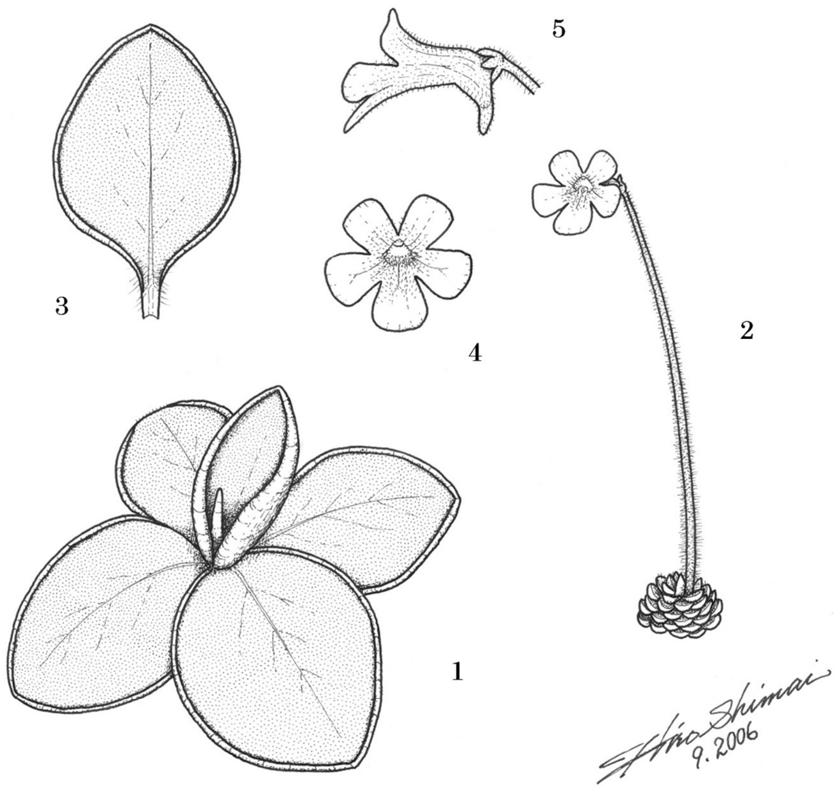
ETYMOLOGY: dedicated to an Italian botanist, Don Cassiano Conzatti (1862-1951), who studied the flora of Oaxaca

HABITAT: Mossy calcareous rock walls in mountain forest. Low light intensity.

DISTRIBUTION: MEXICO (Oaxaca). 2,400-2,715 m.

DISCUSSION: *Pinguicula conzattii* has been known only from two localities in the State of Oaxaca, Mexico. This plant was initially collected between Santo Tomás Ocotepec and Santiago Nuyoó by a German theologian, Alfred B. Lau in September 1987, and the plant was propagated and grown as *P.* sp. "Santiago Nuyoo Pass" among European horticulturalists before officially described (Zamudio and van Marm 2003). *P. conzattii* is morphologically confusing with *P. mirandae*, also occurring in Oaxaca, but *P. conzattii* has smaller winter leaves and a winter rosette without forming runners. Little ecological information and current status at the habitat are available for the species.

Plate 4.33. *Pinguicula conzattii*

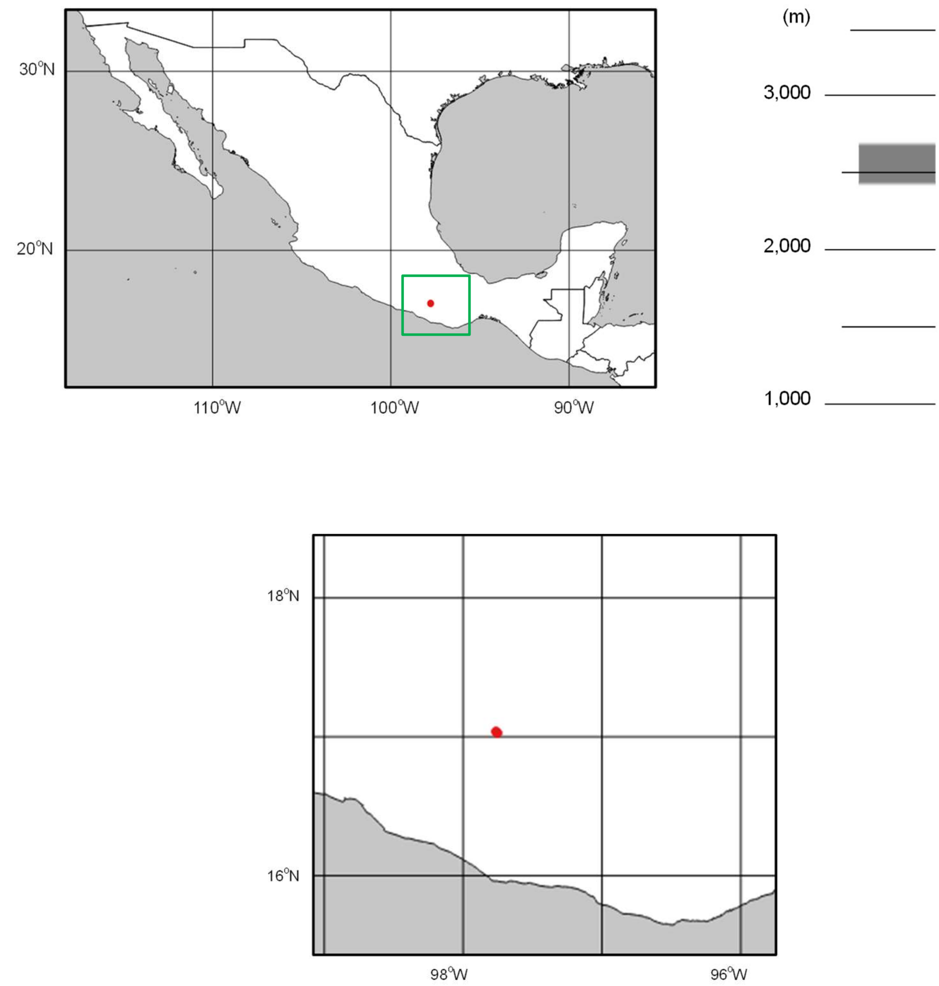


10 mm: 1, 2, 3

10 mm: 4, 5

1. summer rosette
2. winter rosette with flower
3. summer leaf
4. flower, front view
5. flower, lateral view

P. conzattii



34. ***Pinguicula crassifolia*** Zamudio, Acta. Bot. Mex. 3 (1988) 21.

TYPE: MEXICO. *Hidalgo, municipio de El Chico, Las Ventanas, en zona contigua al bosque de Abies, alt. 3000 m* (Hidalgo, Municipality of El Chico, Las Ventanas, adjacent to the forest zone of *Abies*, alt. 3,000 m), 11 April 1976, *Medina 1316* (holotype: ENCB as *P. macrophylla*; isotypes: IEB!, MEXU!).

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf dimorphic, summer leaf 5-7, yellowish-green or maroon, elliptic-ovate, margin narrowly involute, apex obtuse, 37-110 mm long, 16-60 mm wide, hairy at base, petiole up to 45 mm long, winter leaf 20-60, ovate to oblanceolate, apex rather acute, thick, 3-11 mm long, 1.5-6 mm wide. Winter rosette subglobose. Scape 1-4, very hairy, 47-85 mm long. Calyx bilabiate, upper lip 3-lobed, lobes triangular-lanceolate, 1.5-3.5 mm long, connate at base, lower lip 2-lobed, lobes similar to uppers but usually slightly smaller. Flower reddish-purple, slightly paler at base of lips. Corolla bilabiate, 20-30 mm across, zygomorphic, 23-50 mm long including spur, upper lip 2-lobed, lobes cuneate to obovate-oblong, lower lip 3-lobed, lobes similar to uppers but slightly larger, tube pale reddish-purple with darker veins, narrowly conical, spur pale reddish-purple, vaguely extending from tube, cylindrical, 8-25 mm long. Capsule globose. Seed fusiform.

$2n = 22$. (Plate 4.34).

PHENOLOGY: I, II, III, IV, V. Scape arising from winter rosette.

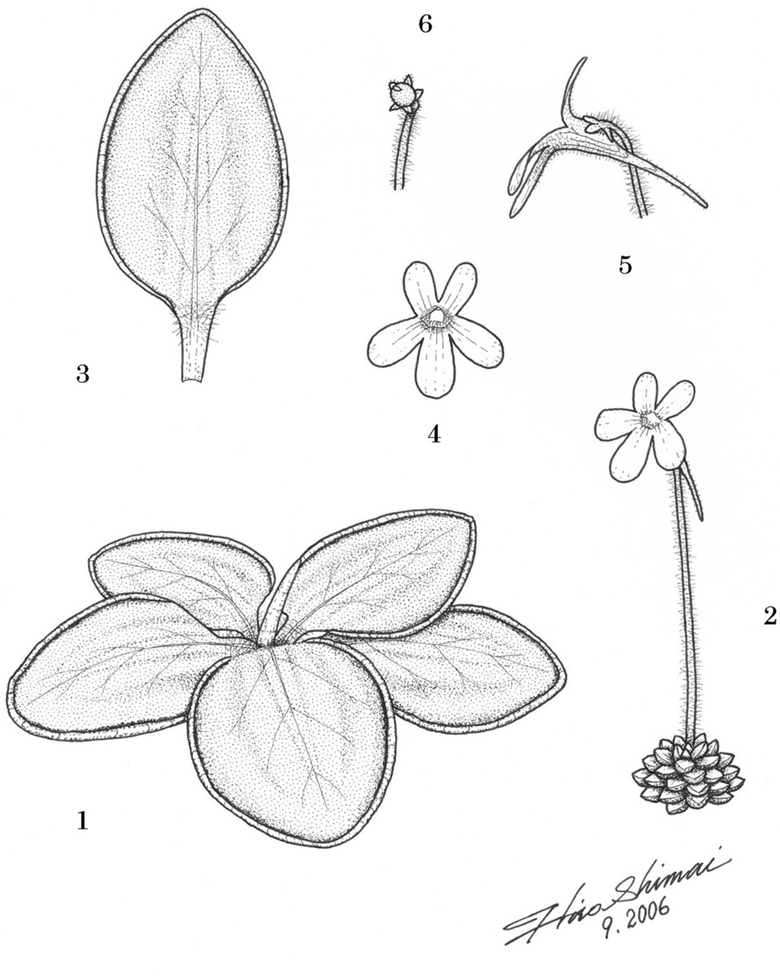
ETYMOLOGY: thick-leaved (referring to winter leaves)

HABITAT: Mossy calcareous sand stone cliffs in forest. Tolerant to low light intensity.

DISTRIBUTION: MEXICO (Hidalgo). A few localities have been recorded around the type locality. 2,800-3,000 m.

DISCUSSION: *Pinguicula crassifolia* is endemic to the El Chico region in the State of Hidalgo, Mexico. It was originally identified and vouchered as *P. macrophylla*, not distributed in the state, by Miguel Medina in 1976. Afterwards, it was determined as a different taxon and described as *P. crassifolia* by Zamudio (1988). Without flowers, *P. crassifolia* is morphologically very similar to *P. acuminata*, also found in El Chico. The differences between the two are discussed in *P. acuminata* (species number 29). *P. moranensis* is also sympatric in El Chico but *P. crassifolia* has more reddish flowers. The distribution area is highly restricted to a small area and the population number at the habitat seems to be small.

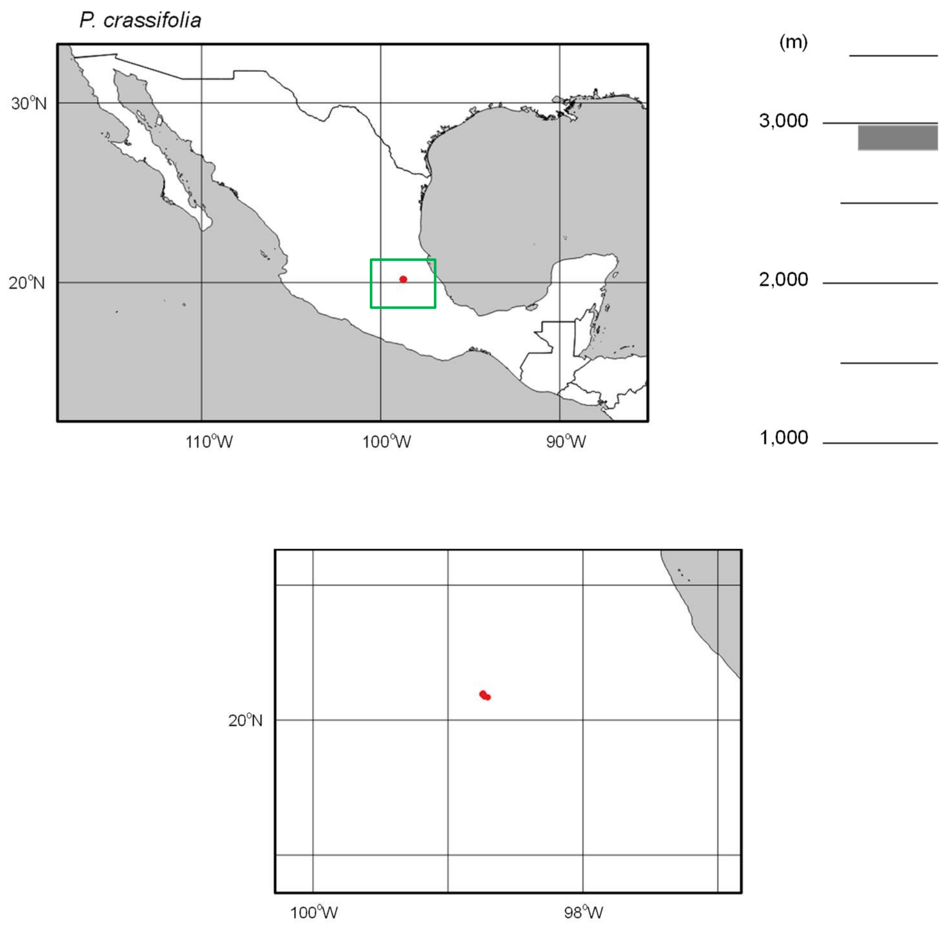
Plate 4.34. *Pinguicula crassifolia*



10 mm: 1, 2, 3

10 mm: 4, 5, 6

1. summer rosette
2. winter rosette with flower
3. summer leaf
4. flower, front view
5. flower, lateral view
6. capsule


P. crassifolia
30°N
20°N
110°W
100°W
90°W
(m)
3,000
2,000
1,000
20°N
100°W
98°W

35. ***Pinguicula cyclosecta*** Casper, Feddes Repert. Spec. Nov. 67 (1963) 11.

TYPE: MEXICO. Sierra Madre Oriental, Dulces Nombres, Nuevo León, and just east of border into Tamaulipas, 24°N., 99,5°-100,5°W., in limestone crevices on cliffs near El Caracol, 3 mi. (ca. 5 km) ne. Dulces Nombres, 17 June 1948, *Meyer & Rogers 2538* (holotype: MO!; paratype: BM!).

SYNONYM: *P. lateciliata* McVaugh et Mickel

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf dimorphic, summer leaf 6-12, pale green, outer margin sometimes maroon, obovate, apical margin narrowly involute, apex obtuse, cuneate at base, 15-35 mm long, 5-25 mm wide, winter leaf 35-80, ovate-spatulate, tip slightly involute, thick, apex obtuse, 5-10 mm long, 2-5mm wide. Winter rosette acetabuliform. Scape 1-5, densely glandulous, 30-120 mm long. Calyx bilabiate, upper lip 3-lobed, lobes oblong-lanceolate, ca. 2 mm long, lower lip 2-lobed, lobes slightly smaller than uppers. Flower glossy, bluish-purple to purple, white at base of lower lips. Corolla bilabiate, 20-25 mm across, zygomorphic, 25-35 mm long including spur, upper lip 2-lobed, lobes suborbicular, lower lip 3-lobed, often overlapping, lobes similar to uppers but slightly larger, tube very short, broadly conical, spur pale purple, cylindrical, 15-30 mm long. Capsule subglobose. Seed fusiform-elliptic, 600-900 X 150-180 µm. $2n = 22$. (Plate 4.35).

PHENOLOGY: II, IV, V, VI, VII, VIII, X. Scape arising from spring or summer rosette.

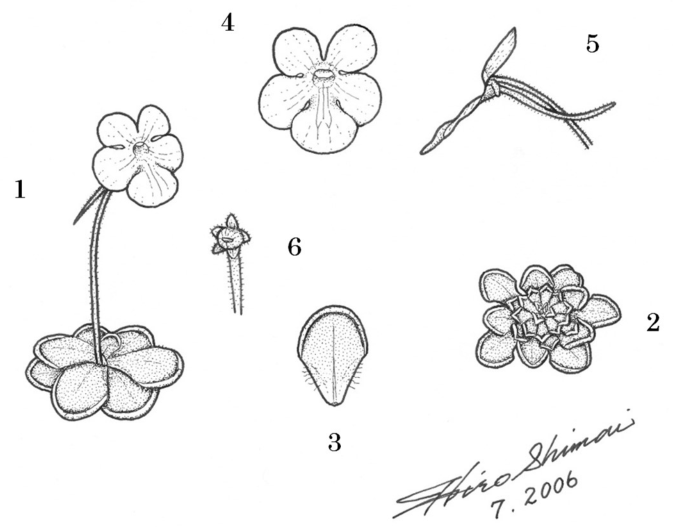
ETYMOLOGY: having rounded segments (referring to the flower)

HABITAT: Crevices on limestone cliffs. Tolerant to low light intensity.

DISTRIBUTION: MEXICO (Nuevo León, Tamaulipas). 340-2,195 m.

DISCUSSION: *Pinguicula cyclosecta* was initially collected and vouchered as *P. lilacina* by F. G. Meyer and D. J. Rogers in 1948. Simultaneously, Casper (1963) and McVaugh and Mickel (1963) described as *P. cyclosecta* and *P. lateciliata*, respectively based on the same herbarium specimen deposited at the Missouri Botanical Garden. It is somewhat ambiguous which name is given to a priority, but it seems that Casper (1963) published slightly earlier than McVaugh and Mickel (1963) and *P. cyclosecta* has been generally accepted; therefore, *P. cyclosecta* is adopted here. *P. cyclosecta* having rounded corolla lobes and glossy purple flower colour may not be confused with other species occurring in the same region. According to Zamudio (2001b), the species is very rare and is restricted to small geographical areas in the Sierra Madre Oriental.

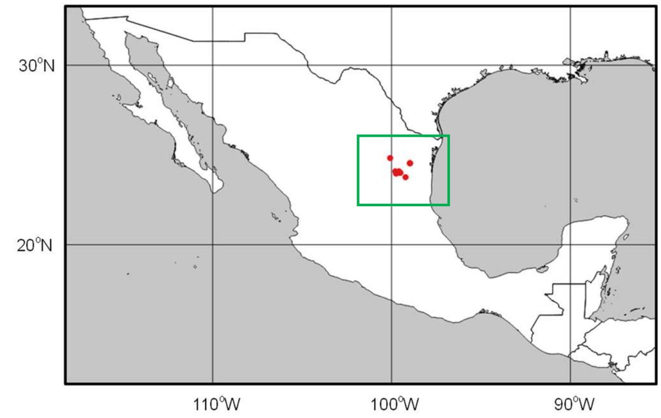
Plate 4.35. *Pinguicula cyclosecta*

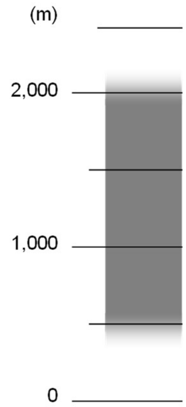


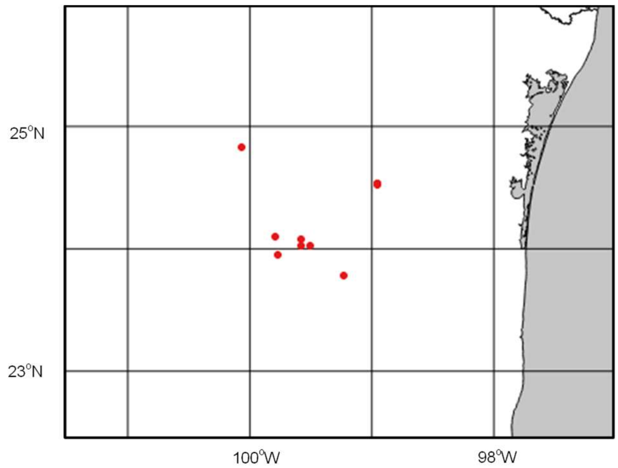
10 mm: 1, 2, 3
10 mm: 3, 4, 5, 6

1. summer rosette with flower
2. winter rosette
3. summer leaf
4. flower, front view
5. flower, lateral view
6. capsule

P. cyclosecta







36. ***Pinguicula debbertiana*** Speta et Fuchs, Linz. Biol. Beitr. 24 (1992) 375.

TYPE: MEXICO. *San Luis Potosí, an der Kreuzung Huizache* (San Luis Potosí, at the intersection of Huizache), March-April 1989, *Debbert*, cult. Botanical Garden of Munich, 5 May 1991 (holotype: Herb. Speta; isotype: M).

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf dimorphic, summer leaf 24-30, yellowish-green or maroon, obovate to obovate-oblong, thick, apical margin sometimes narrowly involute, apex obtuse, 6-13 mm long, 3-8 mm wide, winter leaf many (sometimes more than 100), obovate to spatulate, thick, apex obtuse, ca. 8 mm long, ca. 5 mm wide. Winter rosette lenticular. Scape 2-3, glabrous, 30-70 mm long. Calyx bilabiate, upper lip 3-lobed, lobes oblanceolate ca. 2 mm long, lower lip 2-lobed, lobes smaller than uppers, connate at base. Flower bluish-purple to purple, darker veins at base of lips, white in throat, yellow trichomes forming 2 prominent ridges at base of middle lobe. Corolla bilabiate, 12-16 mm across, zygomorphic, 20-25 mm long including spur, upper lip 2-lobed, lobes subquadratus to obovate, tip truncate, lower lip 3-lobed, lobes similar to uppers but slightly longer and narrower, middle lobe rather cuneate, tube very short, cylindrical, dorsally compressed, spur yellowish-green with purple veins, subcylindrical, 5-8 mm long. Capsule globose. Seed unknown. $2n = 22$. (Plate 4.36).

PHENOLOGY: III. Scape arising from winter rosette.

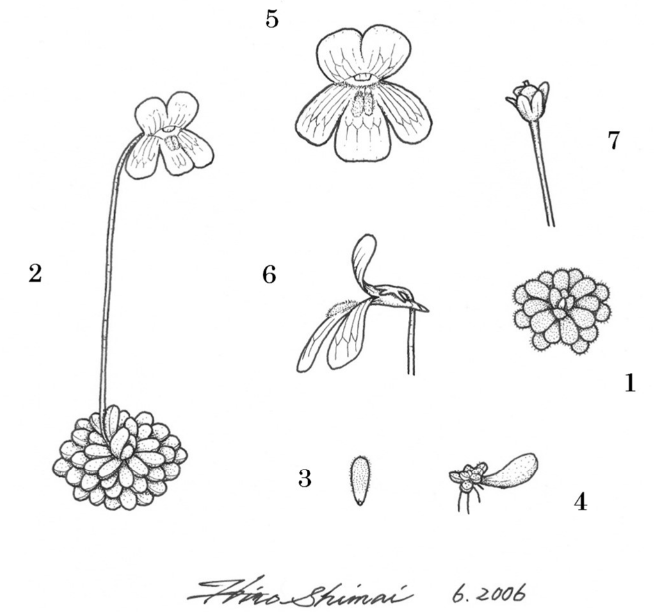
ETYMOLOGY: dedicated to Paul Debbert, at the University of Munich, who first collected the species

HABITAT: Unknown

DISTRIBUTION: MEXICO (San Luis Potosí). 1,800 m.

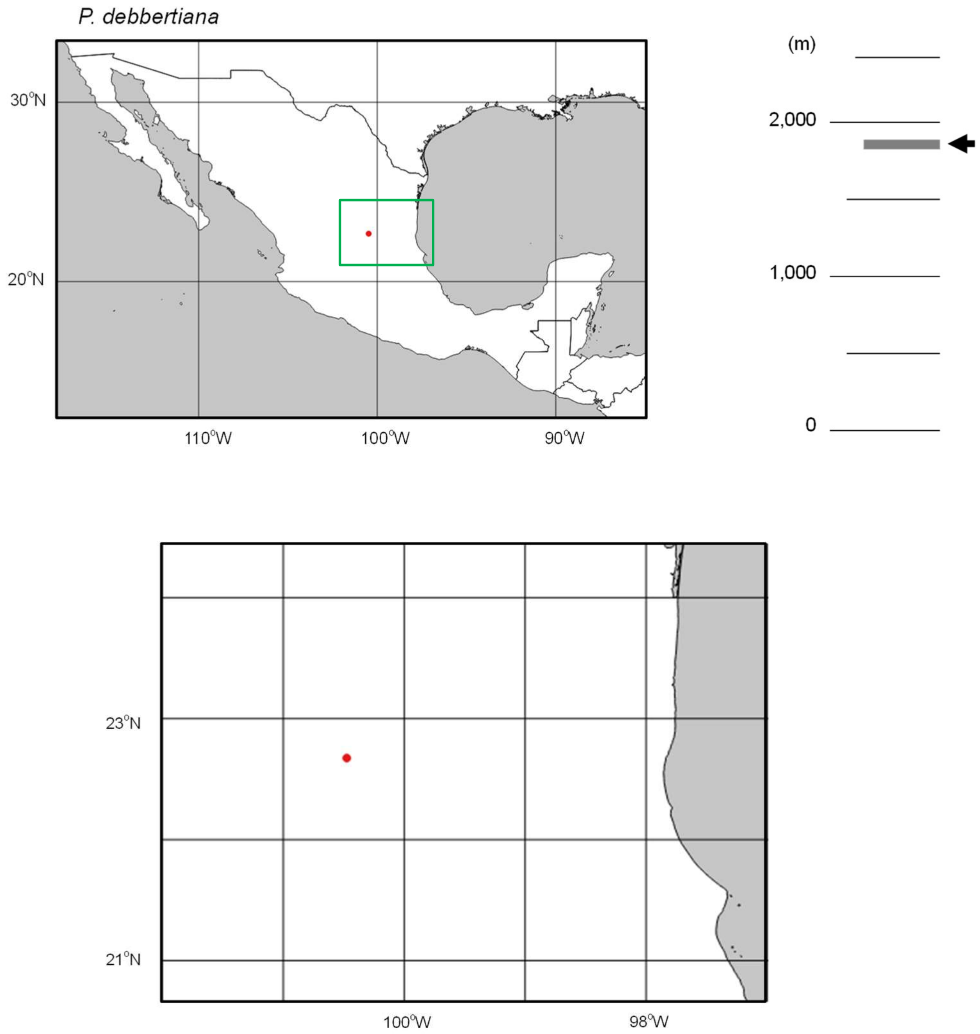
DISCUSSION: *Pinguicula debbertiana* was originally collected at El Huizache in the State of San Luis Potosí by a German botanist, Paul Debbert during his botanical expedition to Mexico in 1989. Afterwards, the species was described based on the cultivated materials at the Botanical Garden of Munich. The holotype specimen is a Franz Speta's personal collection. It has been hitherto recorded only from the type locality. The rosette of the species is morphologically very similar to that of a few other species, e.g. *P. esseriana* and *P. ehlersiae*, occurring in the same region, but the corolla having deeply bilabiate lips, a dorsally compressed tube, and two ridges of yellow-trichomes at the base of lower lip are apparently characteristic. The ecology and current status at the habitat is unknown.

Plate 4.36. *Pinguicula debbertiana*



10 mm: 1, 2, 3, 4
10 mm: 5, 6
5 mm: 7

1. summer rosette
2. winter rosette with flower
3. summer leaf
4. winter leaf producing plantlet
5. flower, front view
6. flower, lateral view
7. capsule


P. debbertiana
30°N
20°N
110°W
100°W
90°W
(m)
2,000
1,000
0
23°N
21°N
100°W
98°W

37. ***Pinguicula ehlersiae*** Speta et Fuchs, Stapfia 10 (1982) 114.

TYPE: MEXICO. San Luis Potosí, Guadalcázar (100,6°/2,5°), March 1979, *Ehlers*, cult. BGL, 12 January 1981, BGL (holotype: Herb. Speta).

SYNONYMS: *P. esseriana* Kirchner var. *ehlersiae* (Speta et Fuchs) Zamudio, *P. hintoniorum* Turner

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf dimorphic, summer leaf 17-35, grayish-green or maroon, obovate to spatulate, thick, apical margin narrowly involute, apex obtuse, base cuneate, 7-25 mm long, 5-13 mm wide, winter leaf up to 60, obovate to spatulate, thick, apex obtuse, 3-10 mm long, 2-4 mm wide. Winter rosette subglobose. Scape 1-2, densely glandulous, 50-165 mm long. Calyx bilabiate, upper lip 3-lobed, lobes lanceolate ca. 3 mm long, lower lip 2-lobed, lobes smaller than uppers, connate at base. Flower pink to reddish-purple, white at base of lower lip. Corolla bilabiate, 18-28 mm across, zygomorphic, 25-30 mm long including spur, upper lip 2-lobed, lobes obovate-cuneate, tip rather truncate, lower lip 3-lobed, lobes similar to uppers but slightly larger, lateral lobes oblique, tube very short, shortly cylindrical, spur faintly pale purple with darker veins, pendulous, cylindrical, sometimes thicker near tip, 18-23 mm long. Capsule subglobose, 650-900 X

210-300 µm. Seed narrowly ellipsoid. $2n = 22, 32, 44$. (Plate 4.37).

PHENOLOGY: II, III, IV. Scape arising from winter rosette.

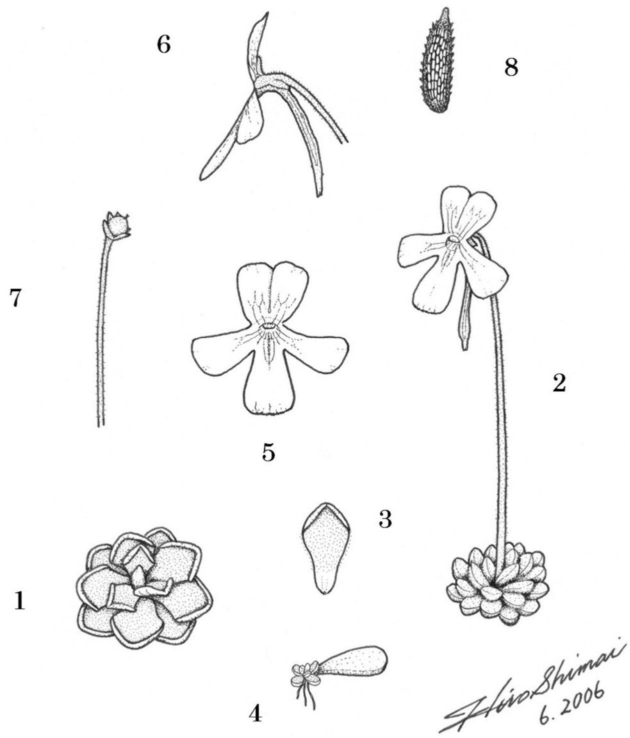
ETYMOLOGY: dedicated to Renate Ehlers, who first collected this species

HABITAT: Gypsum rocks. Tolerant to various light intensities.

DISTRIBUTION: MEXICO (Nuevo León, San Luis Potosí). 1,210-2,000 m.

DISCUSSION: *Pinguicula ehlersiae*, spelled as *P. ehlersae* in the original description, was originally collected at Guadalcázar in the State of San Luis Potosí, Mexico by Renate Ehlers and was described by Speta and Fuchs (1982) based on the materials cultivated at the Botanical Garden of Linz, Austria. The type specimens are likely Franz Speta's personal collections. According to Luhrs (1995a), *P. hintoniorum* described by Turner (1994) was identical with *P. ehlersiae*. Zamudio (2001b) treated as *P. esseriana* var. *ehlersiae*, but Zamudio (per. com.) recently thinks that *P. esseriana* is a hybrid between *P. debbertiana* and *P. ehlersiae*. *P. ehlersiae*, often having a shorter corolla tube, wider lobes of lower lip, and without a yellow spot at the base of middle lobe of the lower lip, differs from *P. esseriana*. *P. ehlersiae* has been found in the States of Nuevo León and San Luis Potosí.

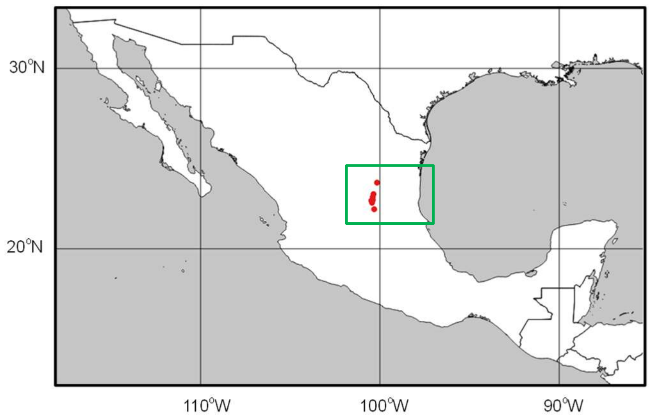
Plate 4.37. *Pinguicula ehlersiae*

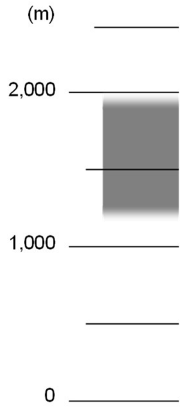


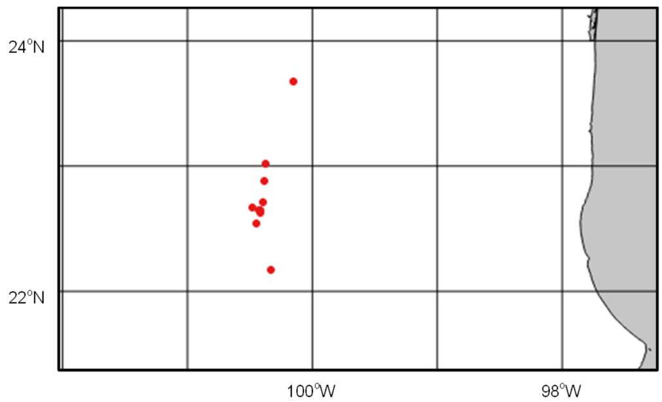
10 mm: 1, 2, 3, 4
10 mm: 5, 6, 7
500 μm: 8

1. summer rosette
2. winter rosette with flower
3. summer leaf
4. winter leaf producing plantlet
5. flower, front view
6. flower, lateral view
7. capsule
8. seed

P. ehlersiae







38. ***Pinguicula elizabethiae*** Zamudio, Acta Bot. Mex. 47 (1999) 16.

TYPE: MEXICO. *Hidalgo, arroyo Tolimán, municipio de Zimapán* (Hidalgo, Arroyo Tolimán, Municipality of Zimapán, alt. 1,000 m), *Zamudio & Pérez 10029* (holotype: IEB!; isotypes: IEB!, MEXU!).

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf dimorphic, summer leaf 5-12, yellowish-green, obovate to suborbicular or broadly spatulate, margin flat to only slightly involute, sometimes gently undulate, apex obtuse, base cuneate and hairy, 35-72 mm long, 10-53 mm wide, winter leaf 45-125, spatulate to oblong-spatulate, thick, apex obtuse to rather acute, 5-17 mm long, 2-4 mm wide. Winter rosette subglobose. Scape 1-5, densely glandulous, 30-60 mm long. Calyx bilabiate, upper lip 3-lobed, lobes lanceolate to oblong, 1.5-3.5 mm long, lower lip 2-lobed, lobes smaller than uppers. Flower dark pink to pinkish-purple, white at base of lower lip, yellow trichomes in throat. Corolla bilabiate, 18-25 mm across, zygomorphic, 36-46 mm long including spur, upper lip 2-lobed, lobes suborbicular to broadly obovate, lower lip 3-lobed, lobes larger than uppers, often overlapping, tube yellowish-green, very short, conical, spur pale reddish-purple, cylindrical, 15-28 mm long. Capsule subglobose. Seed fusiform-ellipsoid, 750-900 X 160-210 µm.

$2n = 22$. (Plate 4.38).

PHENOLOGY: VIII, IX, X. Scape arising from summer rosette.

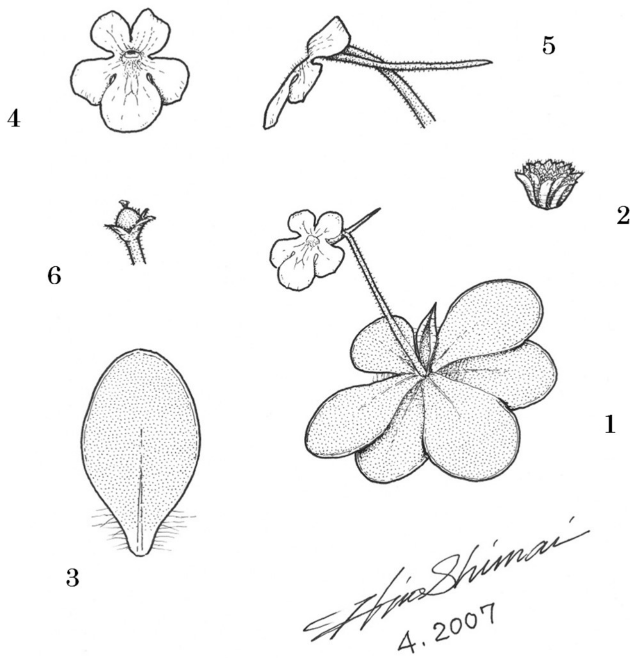
ETYMOLOGY: dedicated to Elizabeth Argüelles, who collected plants in Querétaro for many years

HABITAT: Mossy rocks in steep slopes or on vertical cliffs. Low light intensity.

DISTRIBUTION: MEXICO (Hidalgo, Querétaro). 1,000-1,595 m.

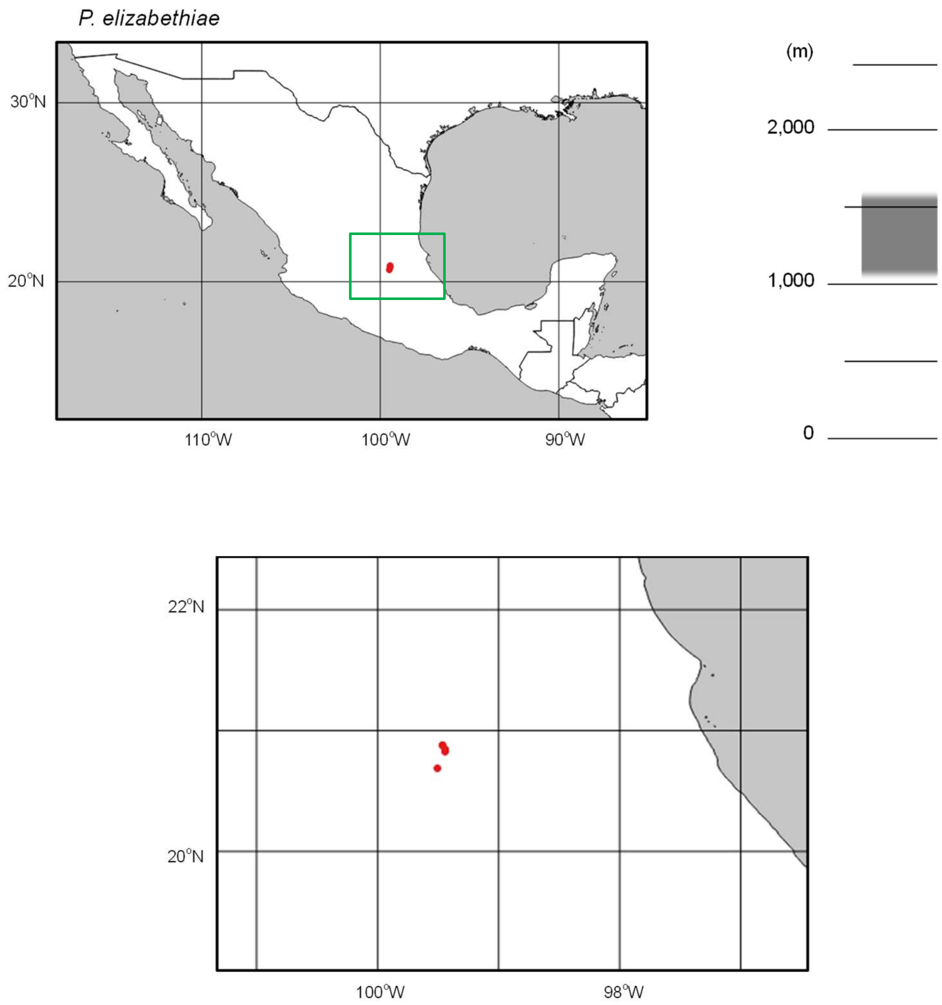
DISCUSSION: *Pinguicula elizabethiae* is recorded only from the Canyons of Río Moctezuma and Arroyo Tolimán in the States of Hidalgo and Querétaro, Mexico. According to Zamudio (1999a), the species was initially collected by Ricardo Z. Ortega in 1990 during prospective studies to assess the environmental impact prior to a construction of hydroelectric dams above the Río Moctezuma Canyon. *P. elizabethiae* is morphologically similar to *P. colimensis*, but the former has smaller and more rounded summer leaves than the latter, and their distribution areas are geographically isolated from each other. *P. elizabethiae* is locally sympatric with *P. agnata* or *P. moctezumae*, but it can be morphologically identifiable. The habitat is highly restricted to small areas within the states.

Plate 4.38. *Pinguicula elizabethiae*



10 mm: 1, 2, 3
10 mm: 4, 5, 6

1. summer rosette with flower
2. winter rosette
3. summer leaf
4. flower, front view
5. flower, lateral view
6. capsule


P. elizabethiae
30°N
20°N
110°W
100°W
90°W
(m)
2,000
1,000
0
22°N
20°N
100°W
98°W

39. ***Pinguicula emarginata*** Zamudio et Rzedowski, Phytologia 60 (1986) 258.

TYPE: MEXICO. *Veracruz, Municipio de Atzalán, Tatzayanala, orilla del río, sobre peñas, alt. 1400 m* (Veracruz, Municipality of Atzalán, Tatzayanala, river sides, on rocks, alt. 1,400 m), 10 January 1970, *Ventura 347* (holotype: ENCB; isotypes: IEB!, MEXU!, MICH!, XAL).

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf monomorphic, 5-16, yellowish-green or maroon, obovate, margin narrowly involute, apex obtuse, base rather cuneate, 10-50 mm long, 5-25 mm wide. Scape 1-7, densely glandulous, 40-120 mm long. Calyx bilabiate, upper lip 3-lobed, lobes oblong to oblong-lanceolate, 1.5-2 mm long, lower lip 2-lobed, lobes smaller than uppers, connate at base. Flower white to pale purple, with purple veins, yellow at base of lower throat. Corolla bilabiate, 8-18 mm across, zygomorphic, 8-16.5 mm long including spur, upper lip 2-lobed, lobes oblong to subquadrate, tip notched to irregularly serrate, lower lip 3-lobed, lobes larger than uppers, obovate to cuneate, tip notched to emarginate or irregularly serrate, tube very short, broadly conical, spur yellowish-green, cylindrical, 4-7 mm long. Capsule subglobose. Seed narrowly ellipsoid, 650-830 X 200-250 μm. $2n$ = 22. (Plate 4.39).

PHENOLOGY: I, III, V, VI

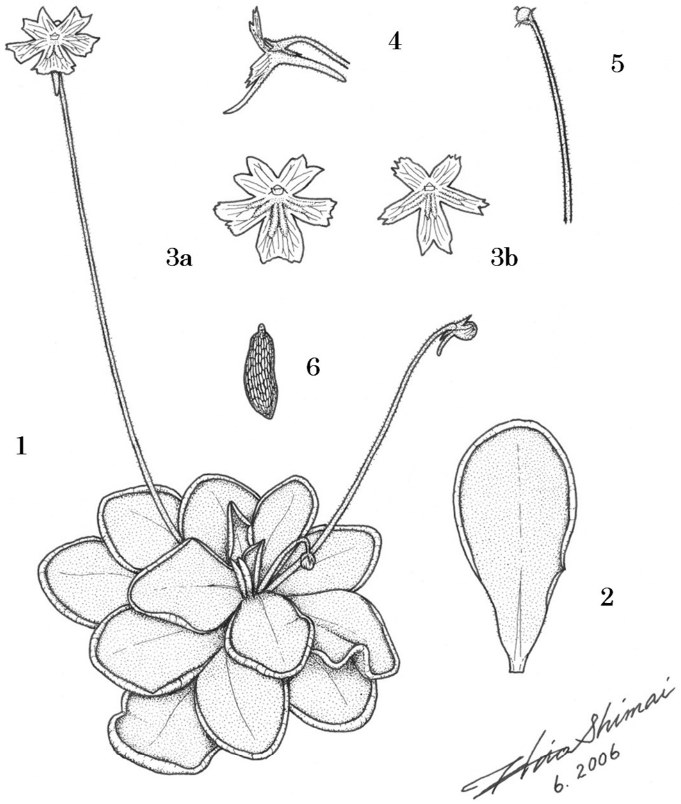
ETYMOLOGY: emarginated or shallowly notched (referring to the flower)

HABITAT: Very wet sandstone cliffs on streamside in forests. Tolerant to low light intensity.

DISTRIBUTION: MEXICO (Puebla, Veracruz). 830-1,550 m.

DISCUSSION: *Pinguicula emarginata* is endemic to the States of Puebla and Veracruz, Mexico. The tip of corolla lobes is irregularly emarginate and lips have purple veins. The shape of corolla lobes and colour strength of veins vary among strains, but those are apparently characteristics for the species. Therefore, *P. emarginata* may not be confused with other species particularly it is in flower. The species basically does not form winter rosettes but it may very rarely form a winter rosette in a drought season. Although the distribution area is highly restricted, the population number and density at the habitat is relatively large.

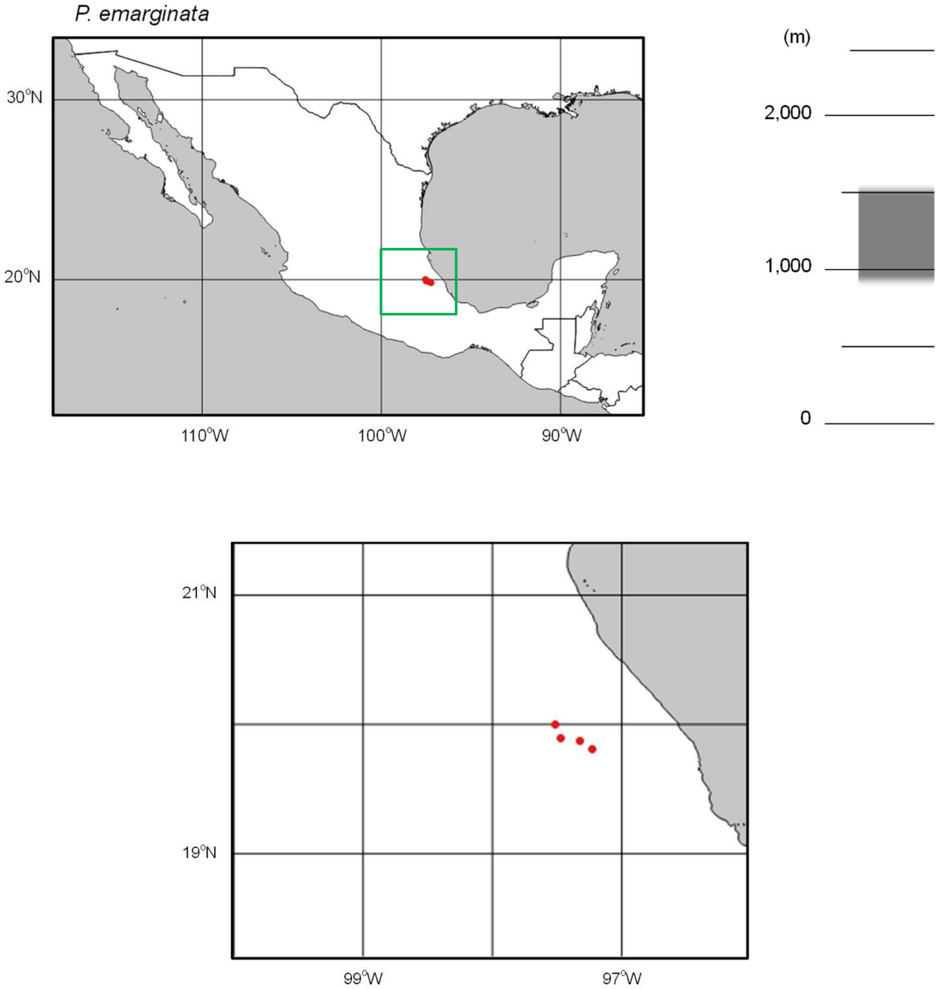
Plate 4.39. *Pinguicula emarginata*



10 mm: 1, 2, 5
10 mm: 3a-b, 4
500 µm: 6

1. habit with flower
2. leaf
3a-b. flower, front view
4. flower, lateral view
5. capsule
6. seed

P. emarginata



40. ***Pinguicula esseriana*** Kirchner, Willdenowia 11 (1981) 317.

TYPE: MEXICO. *im Hochland von San Luis Potosí bei El Huizache* (in the highland of San Luis Potosí, at El Huizache), 1977, *Köhres s.n.* (holotype: BOCH; isotypes: B!, FRP).

SYNONYM: *P. jaumavensis* Debbert

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf dimorphic, summer leaf 10-35, pale green, sometimes suffused with maroon, thick, obovate, apical margin involute, apex obtuse, 7-25 mm long, 5-13 mm wide, winter leaf 15-70, obovate, thick, apex obtuse to rather acute, 5-20 mm long, 2-5.5 mm wide. Winter rosette subglobose. Scape 1-6, sparsely glandulous, 50-165 mm long. Calyx bilabiate, upper lip 3-lobed, lobes oblong-obovate, 2-3 mm long, lower lip 2-lobed, lobes smaller than uppers, connate to middle. Flower pale pinkish-purple, paler at base of lips, yellow spot at base of middle lobe. Corolla bilabiate, 17-25 mm across, zygomorphic, 25-30 mm long including spur, upper lip 2-lobed, lobes obovate-cuneate to oblong-cuneate, tip obtuse to truncate, lower lip 3-lobed, lobes similar to uppers but slightly larger, lateral lobes oblique, tube yellowish-green, conical to subcylindrical, spur yellowish-green with purple veins, cylindrical, pendulous, 10-30 mm long.

Capsule subglobose. Seed narrowly ellipsoid, 590-770 X 110-200 µm. $2n = 32$. (Plate 4.40).

PHENOLOGY: I, II, III, IV, IX. Scape arising from winter rosette.

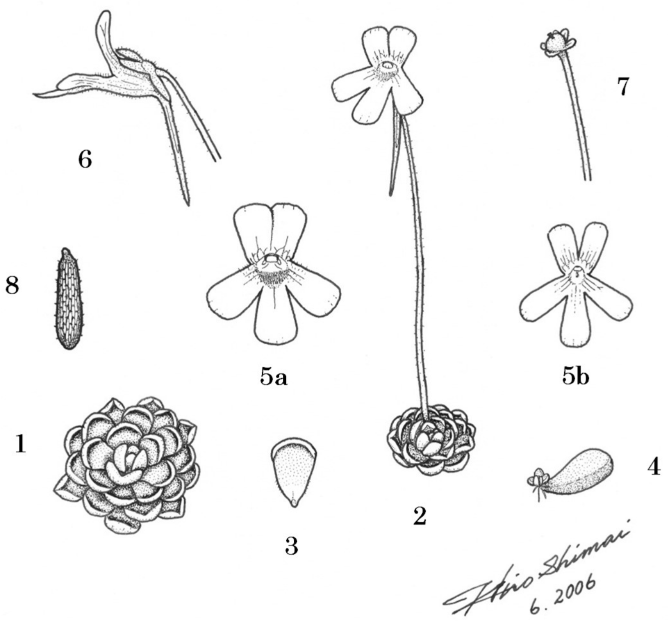
ETYMOLOGY: dedicated to Prof. Karl Esser, the director at the Botanical Garden of Ruhr-University Bochum

HABITAT: Crevices on calcareous rocks. Tolerant to low light intensity.

DISTRIBUTION: MEXICO (Hidalgo, Nuevo León, Querétaro, San Luis Potosí, Tamaulipas). 152-2,420 m.

DISCUSSION: *Pinguicula esseriana* was initially discovered at El Huizache in the State of San Luis Potosí, Mexico as an unidentified *Pinguicula* taxon by Gerhard Köhres, a cactus collector, during his field trip to Mexico in 1977. A single material was sent to the Botanical Garden of the Ruhr-University Bochum, and was described as *P. esseriana* (Kirchner 1981). *P. jaumavensis*, described by Debbert (1991) based on the materials from the State of Tamaulipas, is synonymous with *P. esseriana*. It is sometimes confused with *P. ehlersiae* since some populations show intermediate floral morphologies between the two, which are locally sympatric. Zamudio (per. com.) thinks that *P. esseriana* could be a hybrid between *P. debbertiana* and *P. ehlersiae* in accordance to his field observations. Compared with *P. ehlersiae*, in general, *P. esseriana* has a longer corolla tube and a yellow spot at the base of lower lip.

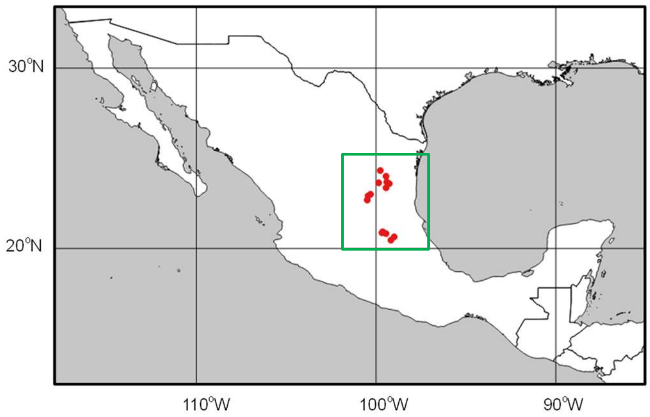
Plate 4.40. *Pinguicula esseriana*

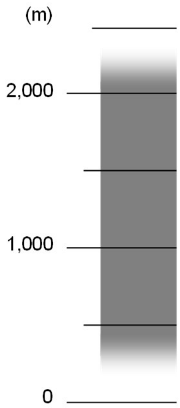


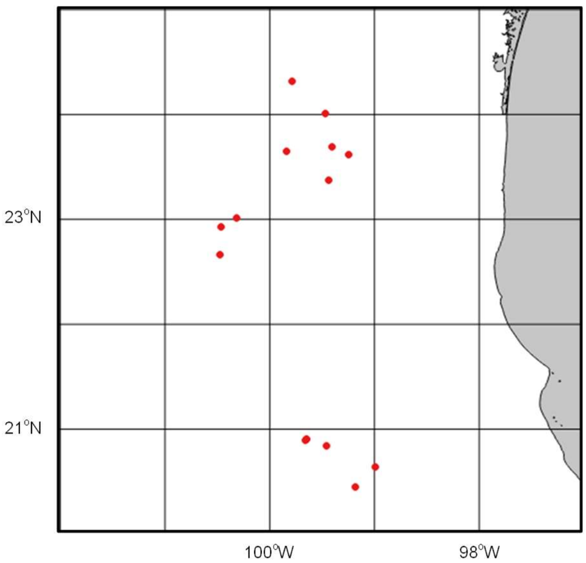
10 mm: 1, 2, 3
10 mm: 4, 5a-b, 6, 7
500 µm: 8

1. summer rosette
2. winter rosette with flower
3. summer leaf
4. winter leaf producing plantlet
5a-b. flower, front view
6. flower, lateral view
7. capsule
8. seed

P. esseriana







41. ***Pinguicula gigantea*** Luhrs, Phytologia 79 (1995) 389.

TYPE: MEXICO. Oaxaca, steep slopes near San Bartolomé Ayautla, 500-800 m, coll. A. Lau s.n., 1987, from cult. Plants, August-September 1995, *Luhrs 9505* (holotype: TEX!; isotype: L).

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf inconspicuously dimorphic, summer leaf 10-13, yellowish-green, or sometimes maroon, subelect, obovate to oblong-obovate, margin sometimes only slightly revolute and undulate, apex obtuse, 60-165 mm long, 40-80 mm wide, lower surface sparsely glandulous, winter leaf 6-9, similar to summer leaf but smaller, 30-60 mm long, 24-38 mm wide. Winter rosette similar to summer rosette but slightly smaller with fewer leaves. Scape 1-5, densely glandulous, 100-185 mm long. Calyx bilabiate, upper lip 3-lobed, lobes ovate, 3-4 mm long, connate to middle, lower lip 2-lobed, lobes slightly smaller than uppers. Flower pale purple to faintly pale purple, sometimes slightly darker at base of lips, yellowish-green or yellow in throat. Corolla bilabiate, 18-30 mm across, subactinomorphic, 28-33 mm long including spur, upper lip 2-lobed, lobes subquadratus to oblong-cuneate or elliptic, tip truncate, lower lip 3-lobed, lobes similar to uppers, tube yellowish-green, cylindrical, spur yellowish-green, subcylindrical to clavate, 5-8 mm long. Capsule subglobose. Seed narrowly ellipsoid, 650-800 X 210-260 µm. $2n = 22$. (Plate 4.41).

PHENOLOGY: XI

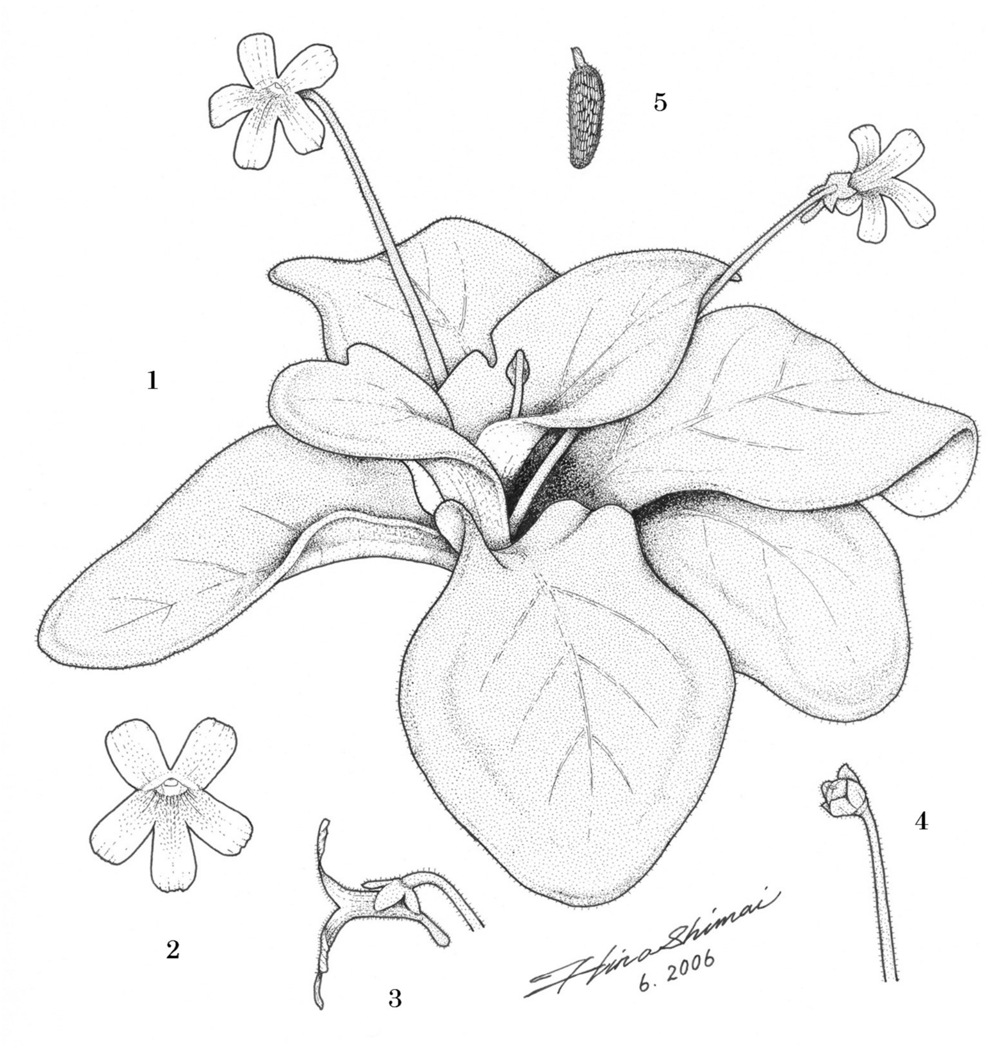
ETYMOLOGY: gigantic or very large (referring to the plant)

HABITAT: Calcareous rocks in steep slopes or on vertical cliffs. Low light intensity.

DISTRIBUTION: MEXICO (Oaxaca). Known only from the type locality. 500-900 m.

DISCUSSION: *Pinguicula gigantea* was initially collected near San Bartolomé Ayautla in the State of Oaxaca, Mexico by a German theologian, Alfred B. Lau in 1987. The species is hitherto known only from the type locality. The plants had been propagated and had been cultivated among horticulturalists as "*P.* sp. Ayautla" nom. nud. before Luhrs (1995b) officially described as *P. gigantea*, based on one of the cultivated materials. It is morphologically similar to a few other species (e.g. *P. agnata, P. ibarrae,* or *P. martinezii*); however, *P. gigantea* forms a much larger summer rosette and has glands sparsely on the lower surface of the leaf. *P. gigantea* forms a slightly smaller rosette than a summer rosette. The function of winter leaf is the same as that of summer leaf while other morphologically similar species (*P. agnata, P. ibarrae,* or *P. martinezii*) forming winter rosettes have functionally different leaves in summer and in winter.

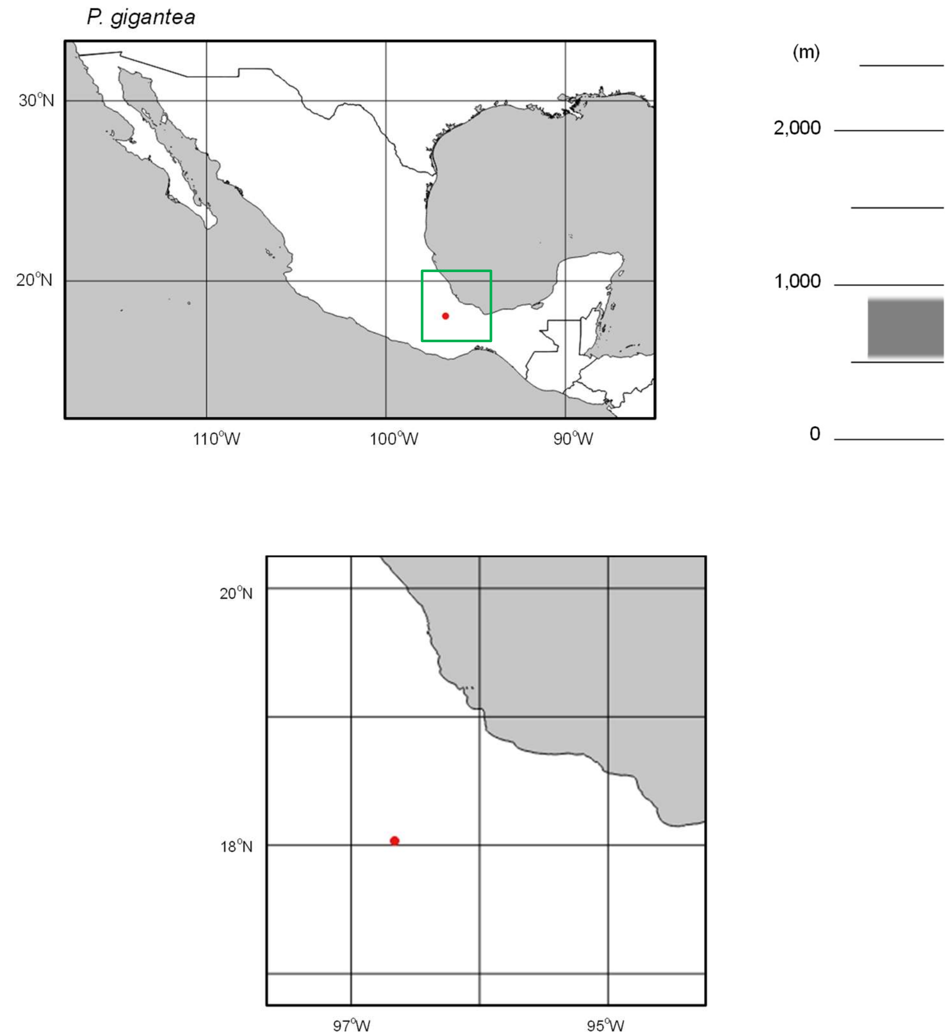
Plate 4.41. *Pinguicula gigantea*



10 mm: 1
10 mm: 2, 3, 4
300 µm: 5

1. habit with flower
2. flower, front view
3. flower, lateral view
4. capsule
5. seed

summer leaf (see Plate 4.90)


P. gigantea
30°N
20°N
110°W
100°W
90°W
(m)
2,000
1,000
0
20°N
18°N
97°W
95°W

42. ***Pinguicula gracilis*** Zamudio (1988), Acta Bot. Mex. 3 (1988) 25.

TYPE: MEXICO. *Nuevo León, municipio de Monterrey, ladera norte del Cerro de las Mitras, sobre rocas calizas en taludes muy escarpados, en bosque de encinos alt. 1450 m* (Nuevo León, Municipality of Monterrey, northern slope of Cerro de las Mitras, on limestone rocks in very steep slope in an oak forest, alt. 1,450 m), 19 February 1987, *Zamudio & González 5184* (holotype: IEB!; isotypes: CHAPA, ENCB, MEXU!, MICH!, TEX!, XAL).

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf dimorphic, summer leaf 5-20, yellowish-green, outer margin sometimes maroon, obovate, apical margin involute, apex obtuse to rather acute, 8-16 mm long, 4-10 mm wide, winter leaf 10-35, spatulate to oblanceolate, thick, apex obtuse, 3-12 mm long, 1.5-4 mm wide. Winter rosette lenticular. Scape 1-4, glabrous, 18-57 mm long. Calyx bilabiate, upper lip 3-lobed, lobes elliptic to oblong 1.3-3 mm long, lower lip 2-lobed, lobes smaller than uppers, slightly connate at base. Flower white with thin purple veins at base of lips, yellow spot at base of middle lobe, only faintly pale purple in throat. Corolla bilabiate, 7-16 mm across, zygomorphic, 10-19 mm long including spur, upper lip 2-lobed, lobes oblong, lower lip 3-lobed, lobes larger than uppers, lateral lobe obovate-oblong, middle lobe obovate-spatulate, tip shallowly emarginate, much wider than laterals, tube white, very short, conical, spur yellowish-green, cylindrical, 3-6.5 mm long. Capsule subglobose. Seed narrowly ellipsoid. $2n = 22$. (Plate 4.42).

PHENOLOGY: I, II, IV. Scape arising from winter rosette.

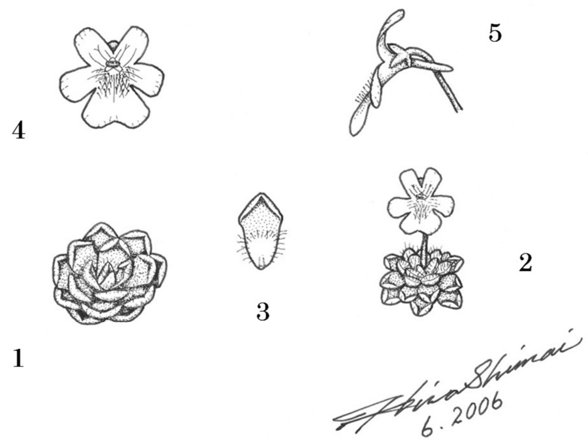
ETYMOLOGY: slender

HABITAT: Limestone rocks on vertical cliffs in an oak forest. Low light intensity.

DISTRIBUTION: MEXICO (Coahuila, Nuevo León, Tamaulipas). 1,450-2,120 m.

DISCUSSION: *Pinguicula gracilis* was initially collected near Monterrey in the State of Nuevo León, Mexico by E. Ramirez-Alvarez in February 1980 as a possible close relative of *P. pumila*, not found in Mexico. S. Zamudio and S. González made an additional specimen collection in 1987 at the same locality and in the following year, Zamudio (1988) described it as *P. gracilis*. This species is morphologically similar to *P. immaculata* or *P. nivalis*, also found in the State of Nuevo León and having white flowers. However *P. gracilis* has very fine purple veins in the lower half of corolla lips and the throat is only faintly pale purple while *P. immaculata* and *P. nivalis* have pure white flowers with yellowish-green at the base of lower lip. Zamudio (1988) thought that the species might be annual in the original description, but it is no doubt perennial forming a winter rosette.

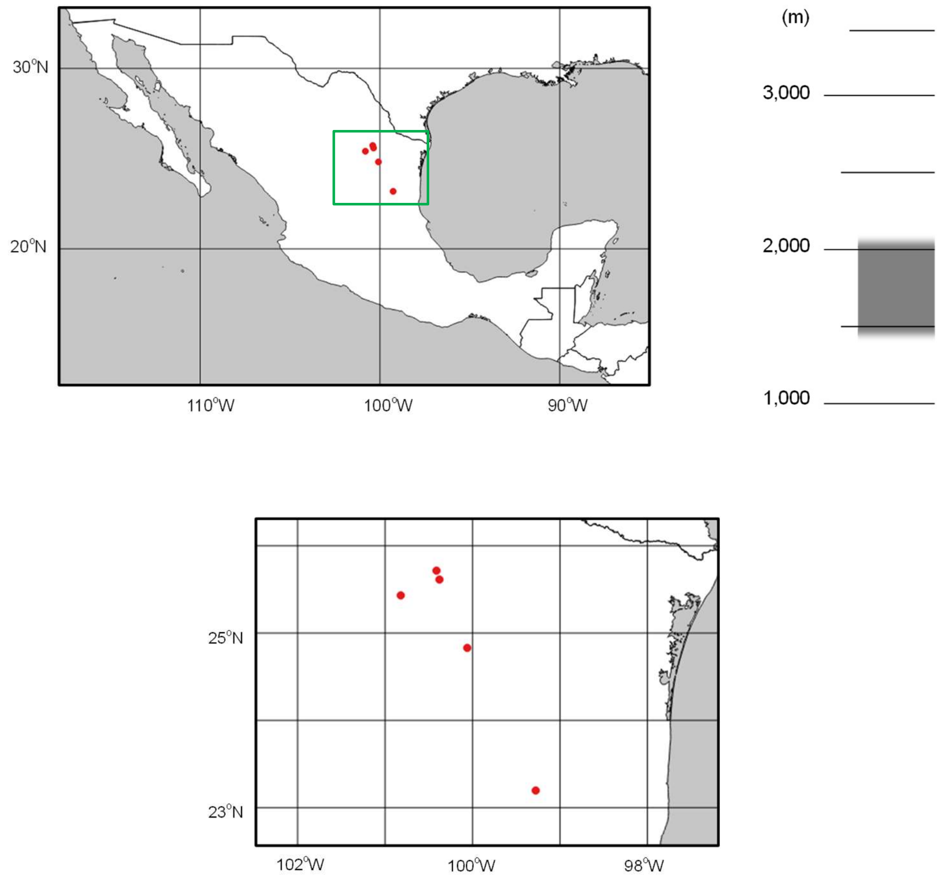
Plate 4.42. *Pinguicula gracilis*



10 mm: 1, 2, 3
10 mm: 4, 5

1. summer rosette
2. winter rosette with flower
3. summer leaf
4. flower, front view
5. flower, lateral view

P. gracilis



43. ***Pinguicula greenwoodii*** Cheek, Kew Bull. 49 (1994) 813.

TYPE: MEXICO. Oaxaca, Iacatepec (Zacatepec) road, 19 April 1987, *Greenwood G-1377* (holotype: K!; isotypes: K!).

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf monomorphic, 5-8, yellowish-green, ovate to obovate, margin narrowly involute, apex obtuse, base cuneate, 30-50 mm long, 17-30 mm wide. Scape 1-3, densely glandulous, 85-140 mm long. Calyx bilabiate, upper lip 3-lobed, lobes ovate, 4-5 mm long, slightly connate at base, lower lip 2-lobed, lobes smaller than uppers, connate at base. Flower faintly pale purple, with dark green veins at lower half of lips. Corolla bilabiate, 8-12 mm across, zygomorphic, 2.3-2.5 mm long including spur, lips rather connate at base, upper lip 2-lobed, lobes broadly suborbicular, connate at base, lower lip 3-lobed, lobes oblong, middle lobe larger than laterals, tube white with dark green veins, narrowly conical to subcylindrical, dorsally compressed, spur white with dark green veins, cylindrical, 9-11 mm long. Capsule globose. Seed narrowly ellipsoid. (Plate 4.43).

PHENOLOGY: IV

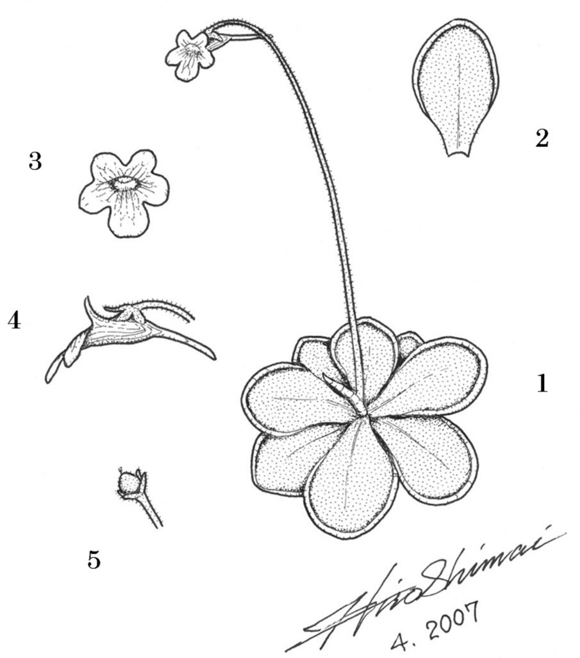
ETYMOLOGY: dedicated to Edward Greenwood, who first collected this species

HABITAT: Wet limestone cliffs in a forest. Low light intensity.

DISTRIBUTION: MEXICO (Oaxaca). Known only from the type locality. 1,550 m.

DISCUSSION: *Pinguicula greenwoodii* has been recorded only once at the type locality in the State of Oaxaca. In the original description by Cheek (1994), the exact holotype locality was omitted though a few keywords such as “Iacatepec (Zacatepec) road”, “1550 m alt.” and “about 30 km from the sea” were mentioned. It is assumed that this species does not form a winter rosette and may not be confused with other species at the habitat particularly when it is in flower, having somewhat connate lips at the base with dark green veins at the base of lips to the throat. It was unable to obtain the material for the phylogenetic analysis in this study, but *P. greenwoodii* has been temporally placed into this section. A further examination may verify its phylogenetic relationship and then it may need to modify the treatment.

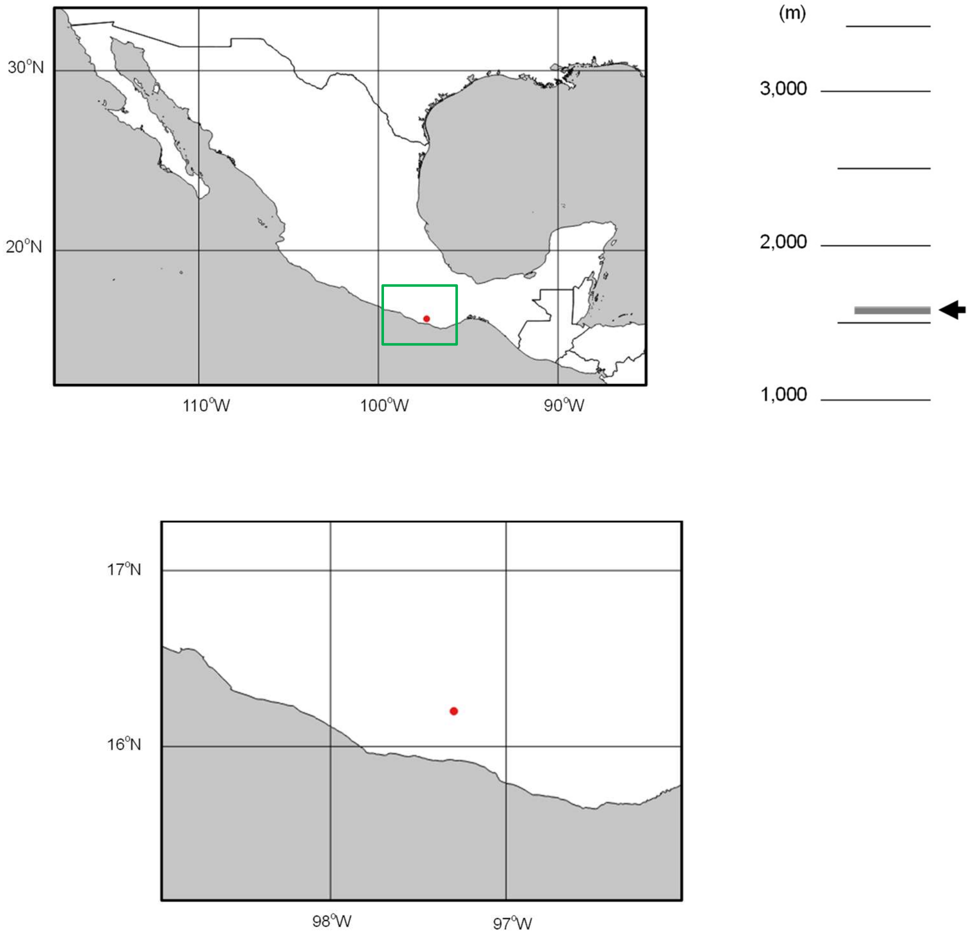
Plate 4.43. *Pinguicula greenwoodii*



10 mm: 1, 2
10 mm: 3, 4, 5

1. habit with flower
2. leaf
3. flower, front view
4. flower, lateral view
5. capsule

P. greenwoodii



44. ***Pinguicula gypsicola*** Brandegee, Univ. Calif. Pub. Bot. 4 (1911) 190.

TYPE: MEXICO. San Luis Potosí, collected on wet gypsum rocks at Minas de San Rafael, November 1910, *Purpus 4886* (holotype?: MEXU-photo ex-UC!, UC!; isotypes: BM!, E!, MEXU!, MO!, US; possible type: P!).

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf dimorphic, summer leaf 10-30, yellowish-green or maroon, subelect, linear-lanceolate, margin slightly revolute, apex rather acute, 30-130 mm long, 4-10 mm wide, winter leaf 100-170, oblong-cuneate to spatulate, apex rather acute, 4-20 mm long, 1-3.5 mm wide. Winter rosette lenticular to acetabuliform. Scape 1-5, densely glandulous, 60-170 mm long. Calyx bilabiate, upper lip 3-lobed, lobes broadly triangular-ovate, ca. 3 mm long, lower lip 2-lobed, lobes smaller than uppers. Flower reddish-purple to purple, often darker or with darker veins at base of lips, white spot or stripe at base of middle lobe. Corolla bilabiate, 13-20 mm across, zygomorphic, 30-50 mm long including spur, upper lip 2-lobed, lobes cuneate-oblong to oblong-obovate, tip rather truncate, lower lip 3-lobed, lobes similar to uppers but slightly larger, tube pale purple, very short, conical, spur faintly pale purple with darker veins, cylindrical, pendulous, 15-30 mm long. Capsule subglobose. Seed ellipsoid, 550-680 X 160-200 μm. $2n = 22$.

(Plate 4.44).

PHENOLOGY: III, VI, VII, IX, XI. Scape arising from summer rosette.

ETYMOLOGY: growing on gypsum

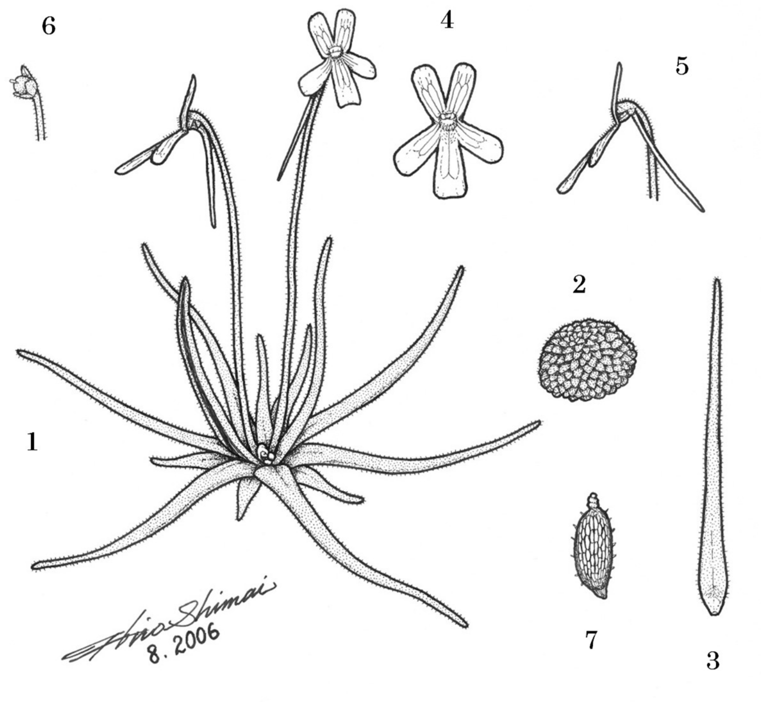
HABITAT: Relatively dry gypsum rock walls. Tolerant to low light intensity.

NATURAL HYBRID: X *P. takakii*

DISTRIBUTION: MEXICO (San Luis Potosí). A few localities have been recorded near the type locality. 1,200-1,400 m.

DISCUSSION: *Pinguicula gypsicola* was initially collected by Carl (Karl) A. Purpus in November, 1910 at Minas de San Rafael in the State of San Luis Potosí, Mexico. The specimens have been collected several times, but the distribution seems to be restricted around the type locality in the Municipality of Villa Juárez. *P. gypsicola*, having linear-lanceolate leaves, is one of the most characteristic species in the region and may not be confused with the other species at the habitat. It is morphologically similar to *P. moctezumae*, endemic to the Moctezuma Canyon in the States of Hidalgo and Querétaro, but *P. gypsicola* has much smaller reddish-purple or purple flowers. In Villa Juárez, *P. ehlersiae* and *P. takakii* are also seen, but they are morphologically different from *P. gypsicola*. The current status of the species at the habitat is poorly known.

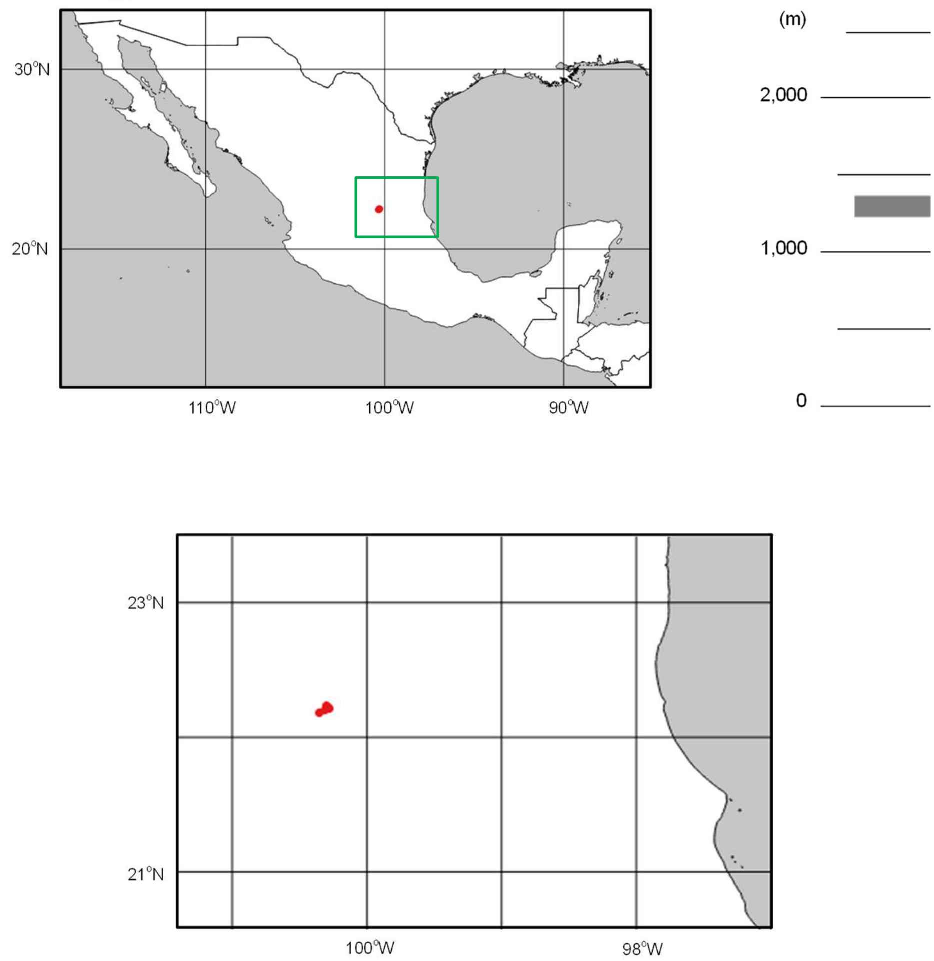
Plate 4.44. *Pinguicula gypsicola*



10 mm: 1, 2, 3
10 mm: 4, 5, 6
300 μm: 7

1. summer rosette with flower
2. winter rosette
3. summer leaf
4. flower, front view
5. flower, lateral view
6. capsule
7. seed

P. gypsicola



45. ***Pinguicula hemiepiphytica*** Zamudio et Rzedowski, Acta Bot. Mex. 14 (1991) 24.

TYPE: MEXICO. *Oaxaca, 58 km al N de Ixtlán, por la carretera a Valle Nacional, sobre taludes, entre colonias de musgos, bosque mesófilo de montaña, alt. 2200 m* (Oaxaca, 58 km north of Ixtlán, the road to Valle Nacional, among mosses in slopes, mountain forests, alt. 2,200 m), 12 October 1987, *Zamudio 5630* (holotype: IEB!; isotypes: CHAPA, ENCB, IEB!, MEXU!, MICH!, TEX!; paratype: MEXU!).

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf dimorphic, summer leaf 4-12, yellowish-green or maroon, elliptic to suborbicular, margin narrowly involute, apex obtuse, 20-70 mm long, 12-55 mm wide, winter leaf 30-50, spatulate to oblanceolate, thick, apex obtuse to rather acute, 10-20 mm long, 1-6 mm wide. Winter rosette lenticular. Scape 1-3, densely glandulous, 50-130 mm long. Calyx bilabiate, upper lip 3-lobed, lobes oblong, 3-6 mm long, lower lip 2-lobed, lobes similar to uppers, connate at base. Flower pink to pinkish-purple, white stripes at base of lower lip. Corolla bilabiate, 35-50 mm across, zygomorphic, 35-80 mm long including spur, upper lip 2-lobed, lobes quadrate-oblong, tip obtuse to truncate or slightly serrate, lower lip 3-lobed, lobes slightly larger than uppers, obovate-cuneate, tip truncate to slightly emarginate in middle lobe, tube pale reddish-purple with purple veins, shortly conical to subcylindrical, spur whitish-green to pale reddish-purple with purple veins, vaguely extending from tube, cylindrical, 12-50 mm long. Capsule subglobose. Seed fusiform-ellipsoid, 800-990 X 150-220 µm. $2n = 22$. (Plate 4.45).

PHENOLOGY: III, IV, V, VI, VII, VIII, IX, XI. Scape arising from summer rosette.

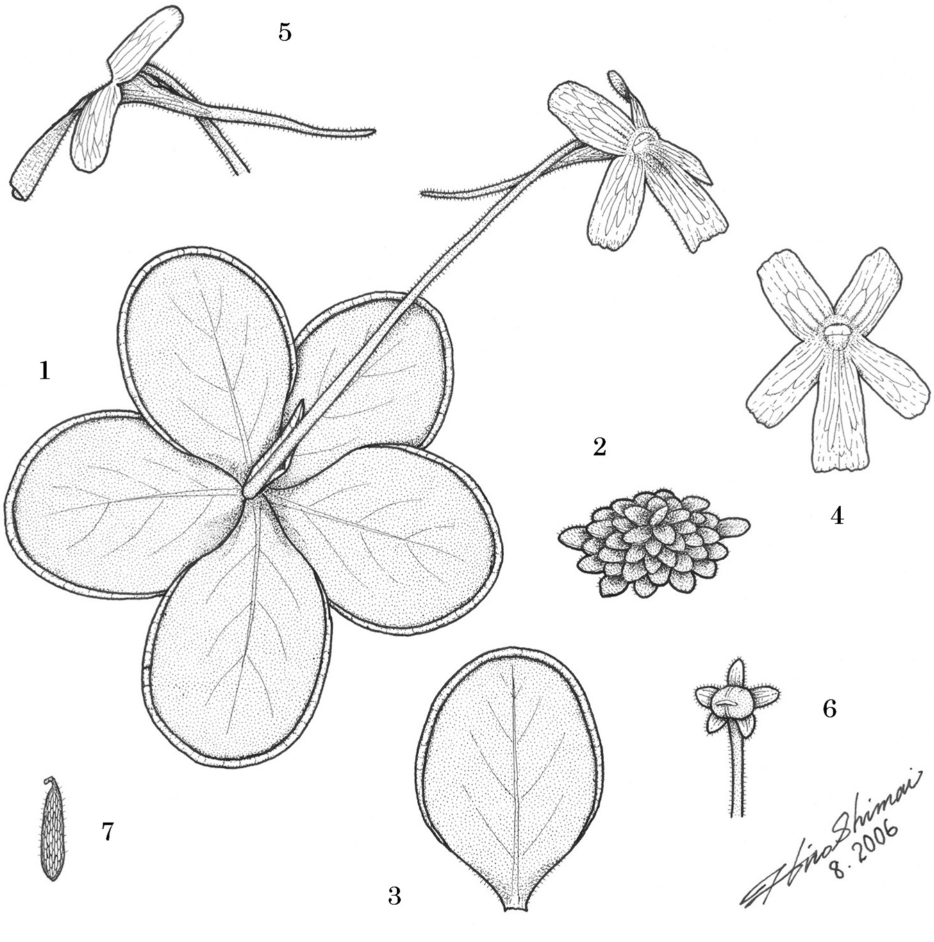
ETYMOLOGY: semi-epiphytic

HABITAT: Epiphytic on mossy tree trunks or mossy rock walls in mountain forests. Tolerant to low light intensities.

DISTRIBUTION: MEXICO (Oaxaca). 1,500-2,900 m.

DISCUSSION: *Pinguicula hemiepiphytica* is endemic to the State of Oaxaca, Mexico. Despite a number of specimen records, the distribution of the species seems to be mostly restricted to the northern slopes of the Sierra de Juárez, between Ixtlán and Valle Nacional in the state. Many collectors addressed that the species was often found on mossy tree trunks as an epiphyte, but it does also occur on mossy rocks or slopes (Zamudio and Rzedowski 1991). It is morphologically similar to a few other species, such as *P. laueana* or *P. moranensis*. *P. hemiepiphytica* has pink or pinkish-purple flowers with a white spot or stripe at the base of lower lip while *P. laueana* has red to reddish-orange or pinkish-red flowers often without a white spot at the base of the lower lip. The flower bud of *P. hemiepiphytica* arises from the summer rosette while that of *P. laueana* arises from the winter rosette. Moreover, their distributions are isolated from each other. In comparison to *P. moranensis*, *P. hemiepiphytica* has a much thicker and longer corolla tube gradually tapering to a spur while *P. moranensis* has a very short and conical one continuing to a distinctive spur. It seems *P. hemiepiphytica* is locally common though restricted to the small area.

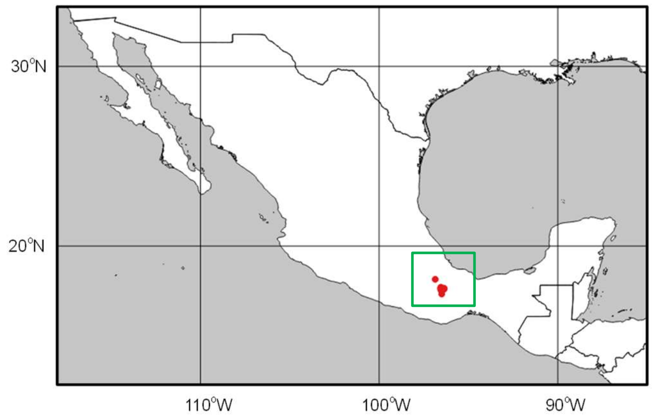
Plate 4.45. *Pinguicula hemiepiphytica*

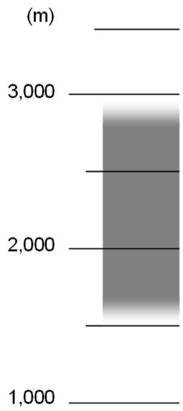


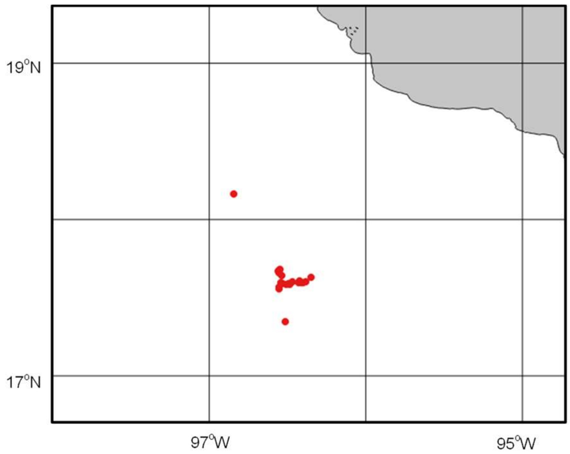
10 mm: 1, 2, 3, 4, 5
10 mm: 6
500 µm: 7

1. summer rosette in flower
2. winter rosette
3. summer leaf
4. flower, front view
5. flower, lateral view
6. capsule
7. seed

P. hemiepiphytica







46. ***Pinguicula heterophylla*** Bentham, Pl. Hartweg (1839) 70.

TYPE: Tuquila, 1840, *Hartweg 510* (holotype: K!; isotypes: BM!, E!, FI!, L, LD!, LE!, OXF!, P!).

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf dimorphic, summer leaf 5-20, yellowish-green or sometimes maroon, elect to arcuate, very narrowly linear-lanceolate to filiform, margin slightly revolute, apex acute, 100-250 mm long, 1-3 mm wide, base oblong-elliptic, winter leaf many, linear-lanceolate, apex acute, 10-25 mm long, 1-3 mm wide. Winter rosette globose. Scape 1-4, densely glandulous, 60-230 mm long. Calyx bilabiate, upper lip 3-lobed, lobes triangular-lanceolate, ca. 3 mm long, lower lip 2-lobed, lobes smaller than uppers. Flower white to faintly pale lilac, yellow trichomes at base of lower lip. Corolla bilabiate, 18-25 mm across, zygomorphic, 20-24 mm long including spur, upper lobes 2-lobed, lobes obovate-oblong, lower lip 3-lobed, lobes similar to uppers but slightly larger, tube white to pale green or pale purple, narrowly conical to subcylindrical, spur yellowish-green, cylindrical 4-5 mm long. Capsule globose-ovoid. Seed narrowly ellipsoid, 600-800 X 180-230 µm. $2n = 22$. (Plate 4.46).

PHENOLOGY: II, IV, V, VI, VII, VIII, IX. Scape arising from spring rosette or summer rosette.

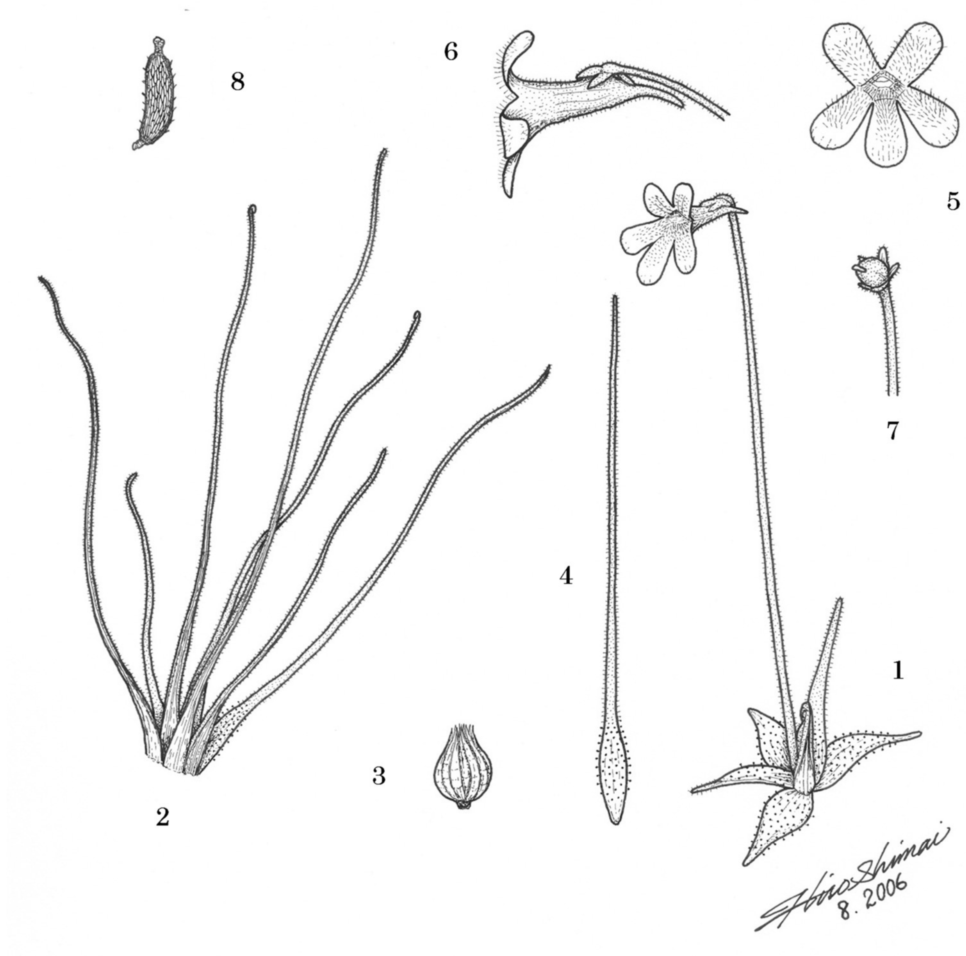
ETYMOLOGY: having different shapes of leaves

HABITAT: Calcareous rock walls. Low light intensity.

DISTRIBUTION: MEXICO (Guerrero, México, Michoacán, Morelos, Oaxaca). 1,208-3,068 m.

DISCUSSION: *Pinguicula heterophylla* has been recorded at least from five states in Mexico although the holotype locality "Tuquila" is not clearly known which state belongs to (or Juquila Mixes, Oaxaca?). It has very narrow thread-like leaves as well as *P. medusina* does. The two species are morphologically very similar, but *P. heterophylla* never produce a clonal plantlet at the tip of summer leaf whereas *P. medusina* frequently does. Both species occur in the State of Oaxaca, but it may not be at the same microhabitat. The shape of the winter rosette is globose resembling an onion bulb which morphologically differs from most of the other species in Mexico. Just before extending summer leaves, it has much shorter spring leaves and the scape arises during this phase (i.e. spring rosette) between the end of April and May at the habitat. It seems that *P. heterophylla* is locally common.

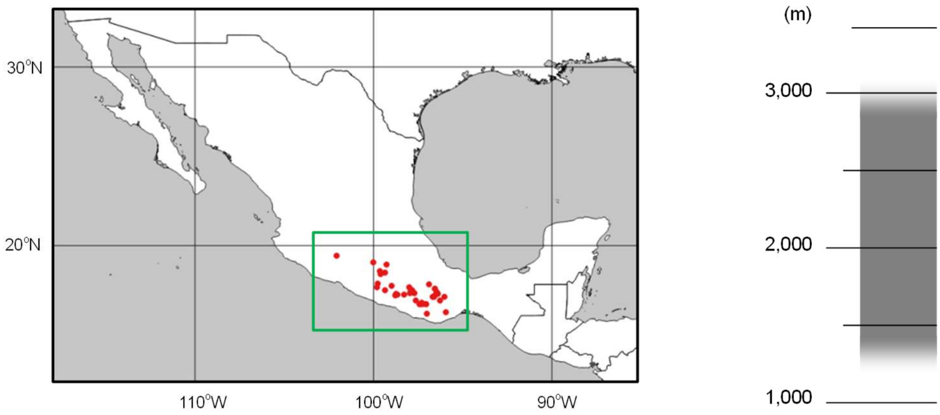
Plate 4.46. *Pinguicula heterophylla*

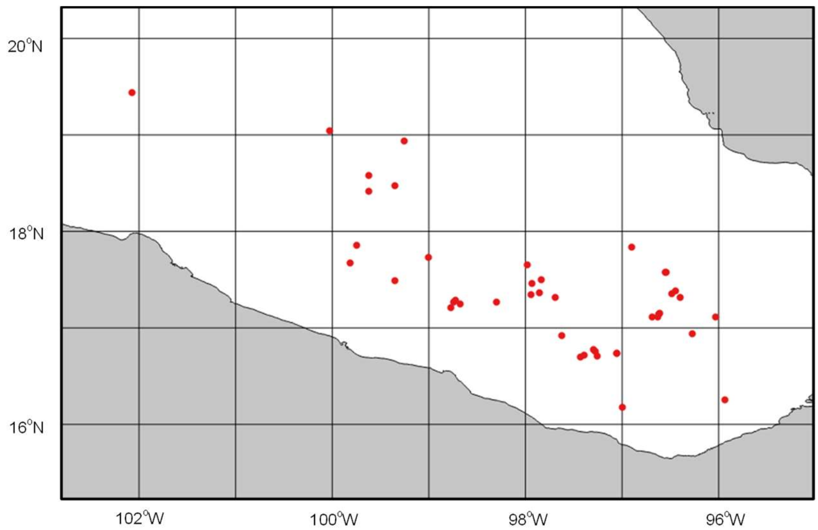


10 mm: 1, 2, 3, 4
10 mm: 5, 6, 7
300 µm: 8

1. spring rosette with flower
2. summer rosette
3. winter rosette
4. summer leaf
5. flower, front view
6. flower, lateral view
7. capsule
8. seed

P. heterophylla





47. ***Pinguicula ibarrae*** Zamudio, Acta Bot. Mex. 70 (2005), 70.

TYPE: MEXICO. *Hidalgo, municipio de Tlanchinol, ca. 11 km al N de Tlanchinol, por la carretera a Huejutla* (Hidalgo, Municipality of Tlanchinol, ca. 11 km north of Tlanchinol, road to Huejutla, alt. 1,100 m), 18 November 2001, *Zamudio, Ibarra & Zamudio 11814* (holotype: IEB!; isotypes: IEB!, MEXU!, TEX!).

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf dimorphic, summer leaf 8-20, yellowish-green, sometimes suffuse with maroon, obovate to ligulate, rather thick, margin narrowly involute, apex obtuse, base rather cuneate, 35-95 mm long, 15-45 mm wide, winter leaf 11-20, elliptic-obovate to spatulate, thick, apex obtuse, 12-25 mm long, 7-13 mm wide. Winter rosette acetabuliform. Scape 5-12, densely glandulous, 60-150 mm long. Calyx bilabiate, upper lip 3-lobed, lobes triangular to broadly elliptic, 3.5-6 mm long, connate at base, lower lip 2-lobed, lobes smaller than uppers, connate to middle. Flower white to faintly pale purple, yellow in throat, sometimes faintly pale lilac at margin of lobes, with reddish-purple spots at base of lobes. Corolla bilabiate, 25-35 mm across, subactinomorphic, 24-35 mm long including spur, upper lip 2-lobed, lobes obovate-oblong, tip obtuse to truncate, lower lip 3-lobed, lobes similar to uppers but only slightly larger, tube yellowish-green, cylindrical, spur yellowish-green, cylindrical, 4.5-8 mm long. Capsule subglobose. Seed narrowly ellipsoid, 800-1,050 X 190-250 µm. $2n = 22$. (Plate 4.47).

PHENOLOGY: III, XI. Scape arising from winter rosette, early summer rosette, or late summer rosette.

ETYMOLOGY: dedicated to Adolfo Ibarra Vázquez, who first collected and cultivated this species

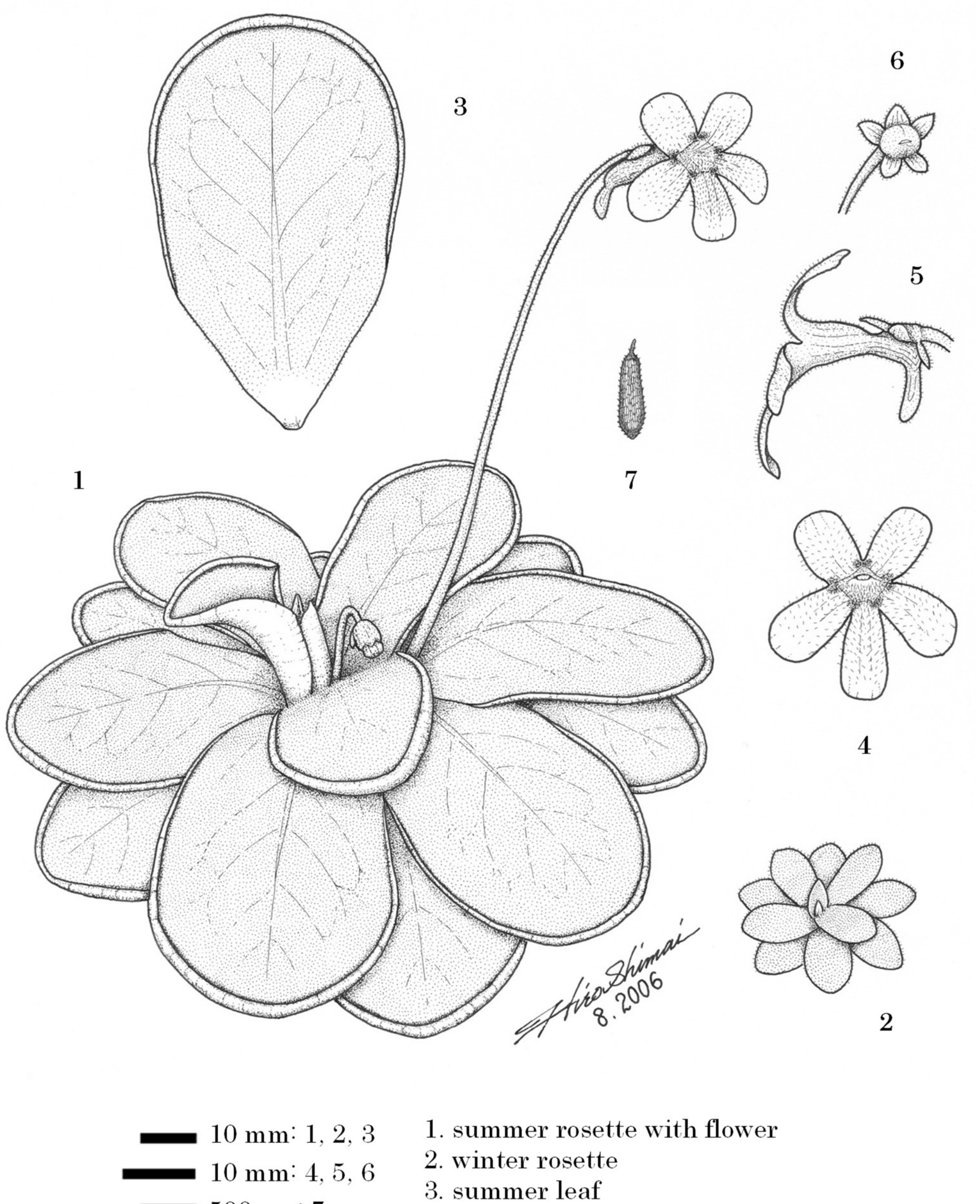
HABITAT: Rocks in steep slopes or on vertical cliffs in forests. Low light intensity.

DISTRIBUTION: MEXICO (Hidalgo, Querétaro). A few localities have been recorded around the type locality. 900-1,120 m.

DISCUSSION: *Pinguicula ibarrae* occurs in the States of Hidalgo and Querétaro, Mexico. It is normally regarded that its first collection and cultivation was made by a Mexican horticulturalist, Adolfo Ibarra Vázquez. The type locality is located at the Municipality of Tlanchinol in the State of Hidalgo, Mexico, but an earlier collection was made by T. B. Croat and D. P. Hannon in February 1987 at 18-23 miles (29-37 km) south of Huejutla (Zamudio 2005). This species is morphologically similar to a few other species, e.g. *P. agnata* or *P. gigantea*. In comparison to those, *P. ibarrae* has much broader summer leaves than *P. agnata*, and has flatter, thinner (in thickness) and softer texture summer leaves than *P.*

gigantea.

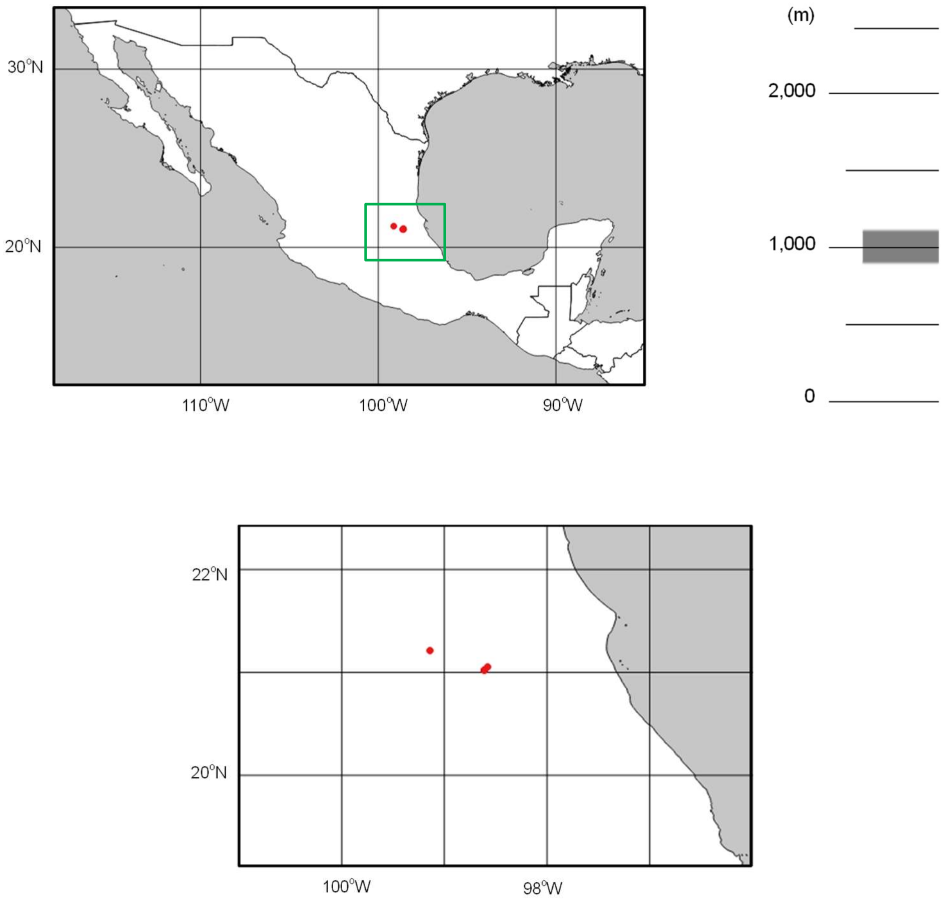
Plate 4.47. *Pinguicula ibarrae*



10 mm: 1, 2, 3
10 mm: 4, 5, 6
500 µm: 7

1. summer rosette with flower
2. winter rosette
3. summer leaf
4. flower, front view
5. flower, lateral view
6. capsule
7. seed

P. ibarrae



48. ***Pinguicula immaculata*** Zamudio et Lux, Acta Bot. Mex. 20 (1992) 40.

TYPE: MEXICO. *Nuevo León, municipio de Galeana, km 10 de la brecha entre Rayones y Galeana, cañada en laderas yesosas con matrral submontano de Mortonia greggii, Gochnatia hypoleuca, Agave sp. and Hechtia sp., alt. 1300 m* (Nuevo León, Municipality of Galeana, 10 km from the gap between Rayones and Galeana, limestone cliffs in the canyon with shrubs of *Mortonia greggii*, *Gochnatia hypoleuca*, *Agave* sp. and *Hechtia* sp., alt. 1,300 m), 26 February 1991, *Zamudio & Cols 6225* (holotype: IEB!; isotypes: CHAPA, ENCB, IEB!, MEXU!, MICH!, TEX!).

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf dimorphic, summer leaf 6-8, yellowish-green, outer margin sometimes maroon, elliptic to oblong, apical margin narrowly involute, apex obtuse to rather acute, hairy at base, 4-9 mm long, 3-5 mm wide, winter leaf 10-15, oblong, very hairy at margin, apex obtuse to rather acute, 4-8.5 mm long, 1-3 mm wide. Winter rosette subglobose, very hairy. Scape 1-3, glabrous, 15-60 mm long. Calyx bilabiate, upper lip 3-lobed, lobes triangular, 1-2 mm long, lower lip 2-lobed, lobes smaller than uppers. Flower white, yellowish-green at base of lower lip. Corolla bilabiate, 7-10 mm across, zygomorphic, 10-20 mm long including spur, upper lip 2-lobed, very small, oblong-ovate, lower lip 3-lobed, lobes larger than uppers, lateral lobes obliquely oblong-ovate, middle lobe obovate, shallowly emarginate at tip, much wider than laterals, tube purple, very short, conical, spur pale yellow, subcylindrical to conical, pendulous, 3.5-9 mm long. Capsule globose. Seed narrowly ellipsoid. (Plate 4.48).

PHENOLOGY: I, II, III. Scape arising from winter rosette.

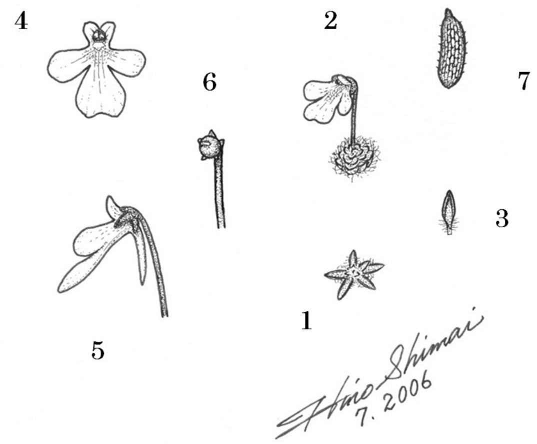
ETYMOLOGY: non-maculate (referring to the flower, compared with the flower of *P. gracilis*)

HABITAT: Dry gypsum rock walls. Tolerant to various light intensities.

DISTRIBUTION: MEXICO (Nuevo León). A few localities have been recorded around the type locality. 1,260-2,180 m.

DISCUSSION: *Pinguicula immaculata* is endemic to the State of Nuevo León, Mexico. In February 1990, A. Lux and J. Verduzco took photographs and specimens of two unidentified tiny *Pinguicula* taxa growing on gypsum walls at the Reyones region in the state, as a result, one was *P. rotundiflora* and the other was a new taxon, i.e. *P. immaculata* (Zamudio and Lux 1992). *P. immaculata*, morphologically similar to *P. gracilis* or *P. nivalis*, has much smaller upper lip lobes and narrower summer leaves than the two. Its specific epithet “non-maculate” referring to the pure white flower colouration was given to the species in comparison to the flower of *P. gracilis*, with very fine purple veins at the lower half of the lips (per. com., Zamudio). It is relatively sparse at the microhabitat.

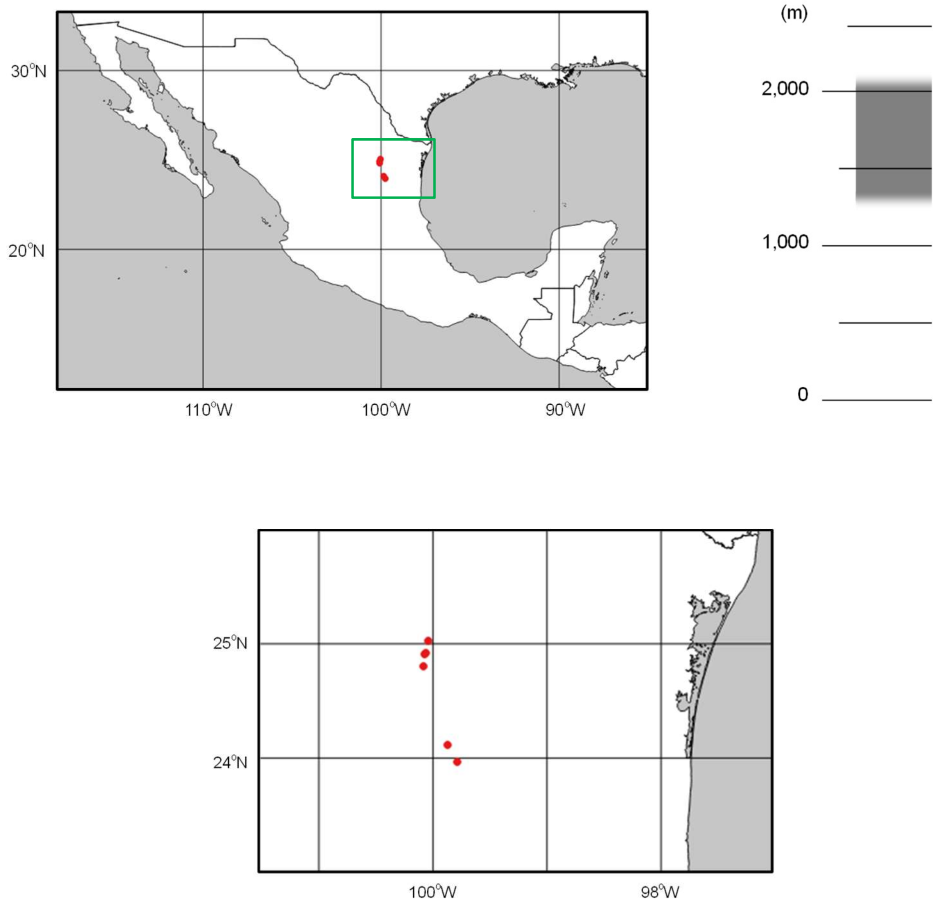
Plate 4.48. *Pinguicula immaculata*



10 mm: 1, 2, 3
10 mm: 4, 5, 6
300 µm: 7

1. summer rosette
2. winter rosette with flower
3. summer leaf
4. flower, front view
5. flower, lateral view
6. capsule
7. seed

P. immaculata



49. ***Pinguicula kondoi*** Casper, Feddes Repert. 85 (1974) 1.

TYPE: MEXICO. Tamaulipas, about 71 km from Tampico junction to Ciudad Victoria, February 1971, *Osada 1029* (holotype: NCU!; syntype: NCU!).

SYNONYM: *P. reticulata* Schlauer

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf dimorphic, summer leaf 10-15, yellowish-green to reddish-yellow or maroon, rather thick, obovate, apical margin narrowly involute, apex obtuse, base cuneate, 10-18 mm long, 10-15 mm wide, winter leaf 20-30, obovate, thick, somewhat hairy at margins and base, apical margin slightly involute, apex obtuse, base cuneate, 8-13 mm long, 7-9 mm wide. Winter rosette subglobose. Scape 1-3, densely glandulous, 20-90 mm long. Calyx bilabiate, upper lip 3-lobed, lobes oblong-lanceolate, ca. 2 mm long, connate at base, lower lip 2-lobed, lobes smaller than uppers. Flower white to faintly pale purple, with prominent purple veins, yellow in throat, yellow trichomes at base of lower lip. Corolla bilabiate, 8-12 mm across, subactinomorphic, 17-18 mm long including spur, upper lip 2-lobed, lobes broadly suborbicular, lower lip 3-lobed, lobes similar to uppers, tube pale yellow with dark reddish-purple veins, cylindrical, spur yellow to purple, subcylindrical, incurved, 4-5 mm long. Capsule subglobose. Seed unknown. $2n = 22$. (Plate 4.49).

PHENOLOGY: III, IV, V. Scape arising from summer rosette.

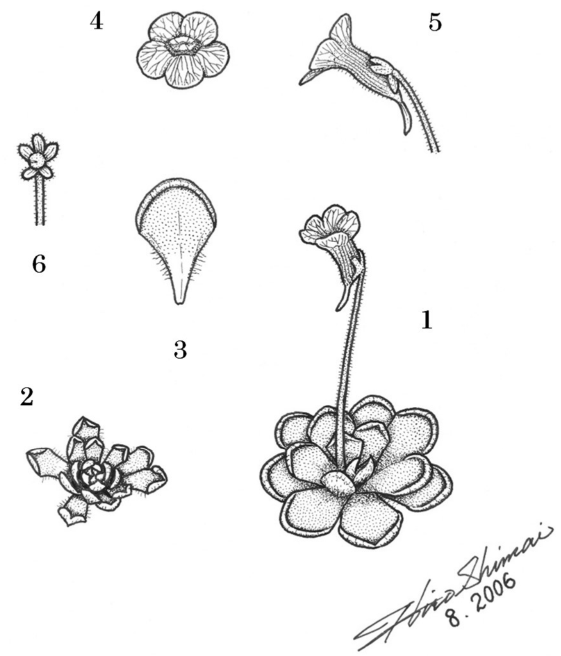
ETYMOLOGY: dedicated to Katsuhiko Kondo, who sent the material to S. J. Casper from S. Osada's collection

HABITAT: Dry gypsum hillsides. Tolerant to various light intensities.

DISTRIBUTION: MEXICO (Nuevo León, San Luis Potosí, Tamaulipas). 1,210-2,800 m.

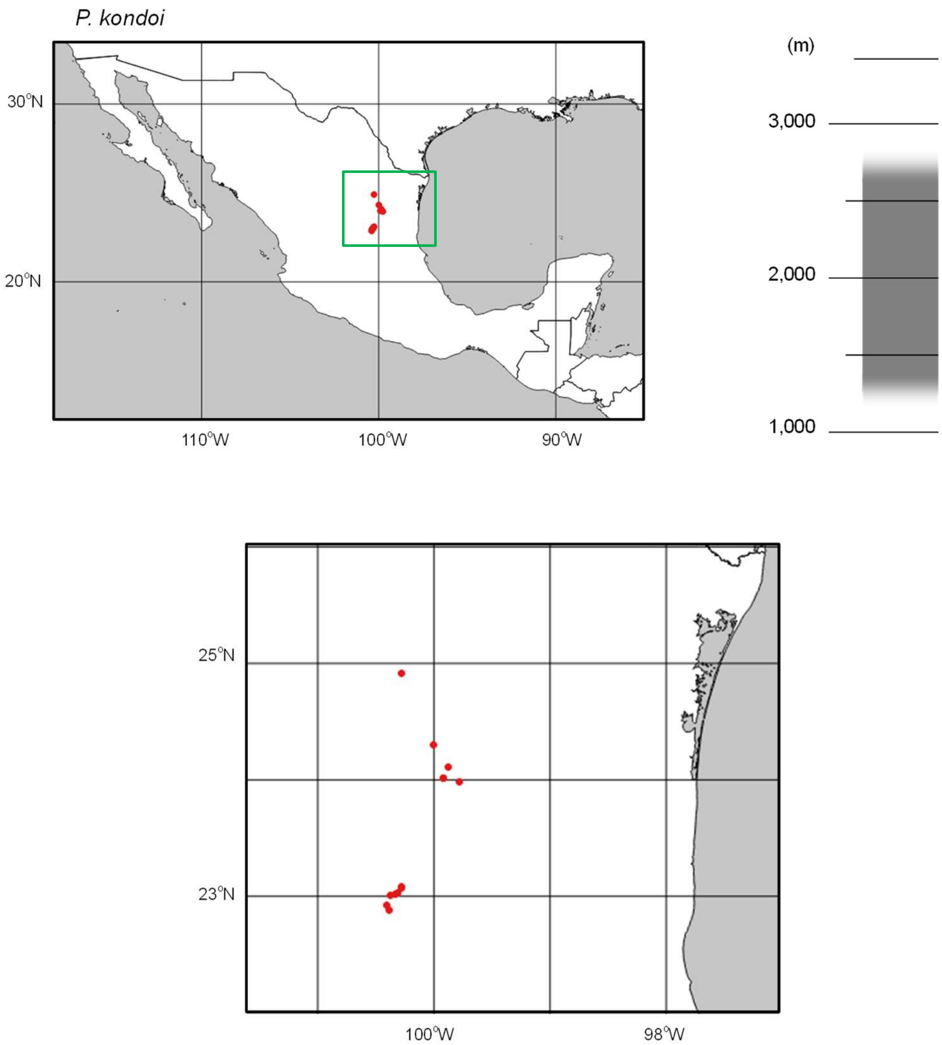
DISCUSSION: *Pinguicula kondoi* is distributed in the States of Nuevo León, San Luis Potosí, and Tamaulipas in Mexico. It was first collected in the State of Tamaulipas (exact locality unknown) by Seiichi Osada in February 1971. S. Osada requested identification of the taxon to Katsuhiko Kondo, who later sent the material to S. Jost Casper. The taxon was described as *P. kondoi* by Casper (1974). Afterwards, Schlauer (1991) described *P. reticulata* based on the material collected at Tula in the State of San Luis Potosí (Tamaulipas?) by G. Köhres in 1977. After examining herbarium specimens of both taxa, Luhrs (1995a) concluded that *P. reticulata* was synonymous with *P. kondoi* both having the same features. This species often has prominent reddish-purple veins entirely on corolla lobes that may not be confused with other species at the habitat. Some populations may have very pale reddish-purple veins. Little information regarding the habitat is available.

Plate 4.49. *Pinguicula kondoi*



10 mm: 1, 2, 3
10 mm: 4, 5, 6

1. summer rosette with flower
2. winter rosette
3. summer leaf
4. flower, front view
5. flower, lateral view
6. capsule (immature)


P. kondoi
30°N
20°N
110°W
100°W
90°W
(m)
3,000
2,000
1,000
25°N
23°N
100°W
98°W

50. ***Pinguicula laueana*** Speta et Fuchs, Phyton (Austria) 29 (1989) 94.

TYPE: MEXICO. Oaxaca, Sierra Mixe, leg. A. Lau 009, cult. Bot. Gad. Linz, 9 April 1987 & 30 October 1987 (holotype: Herb. Speta; isotype: LI?).

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf dimorphic, summer leaf 15-20, yellowish-green or maroon, elliptic-oblong to suborbicular, or obovate, margin sometimes narrowly involute, apex obtuse to rather acute, 25-50 mm long, 20-30 mm wide, winter leaf 30-50, obovate, thick, apex rather acute, 5-20 mm long, 0.5-0.8 mm wide. Winter rosette lenticular. Scape 2-4, densely glandulous, 80-200 mm long. Calyx bilabiate, upper lip 3-lobed, lobes oblong-ovate, ca. 5 mm long, lower lip 2-lobed, lobes slightly smaller than uppers, connate to middle or near tips. Flower red, sometimes reddish-orange or reddish-pink. Corolla bilabiate, 28-38 mm across, zygomorphic, 50-60 mm long including spur, upper lip 2-lobed, oblong to quadrate-oblong, tip rather truncate, lower lip 3-lobed, lobes similar to uppers but slightly larger, often overlapping at base, middle lobe rather truncate at tip, tube white to pale pink with reddish veins, conical to subcylindrical, spur white to pale pink with reddish veins, vaguely extending from tube, cylindrical, 30-45 mm long. Capsule globose. Seed narrowly ellipsoid, 850-1,150 X 190-240 µm. $2n$

= 22. (Plate 4.50).

PHENOLOGY: IV. Scape arising from late winter rosette or summer rosette.

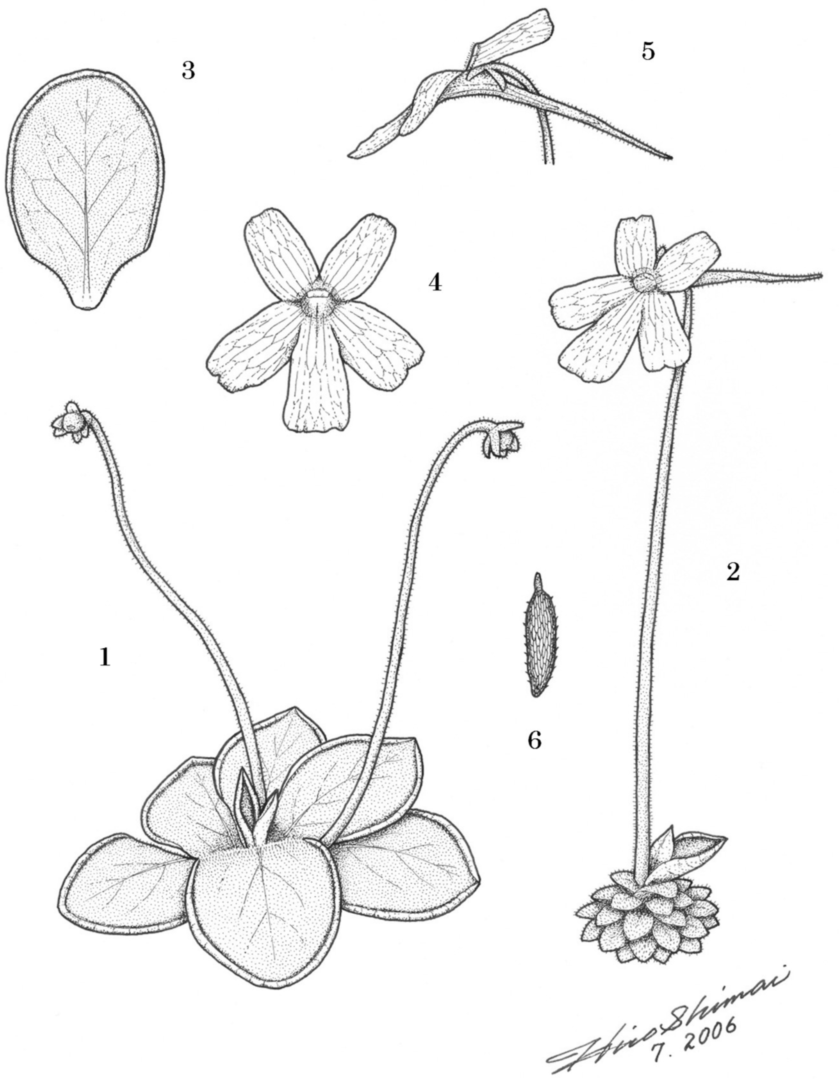
ETYMOLOGY: dedicated to a German theologian, Alfred B. Lau, who first collected this species and many other Mexican plant species at the field.

HABITAT: Mossy rock walls in forests. Low light intensity.

DISTRIBUTION: MEXICO (Oaxaca). 1,600-3,600 m.

DISCUSSION: *Pinguicula laueana* is endemic to the State of Oaxaca, Mexico. It was initially collected by a German theologian, Alfred B. Lau as an unidentified taxon at the Sierra Mixe. Speta and Fuchs (1989) described as *P. laueana* based on the cultivated materials. The holotype specimen is Franz Speta's personal collection (isotype not seen in LI). The species is morphologically very similar to *P. hemiepiphytica* and Zamudio and Rzedowski (1991) suggested that the two were likely conspecific. The distribution areas of the two are not overlapped each other; therefore, those are treated as different species here. The difference between the two is discussed in species number 45, *P. hemiepiphytica*.

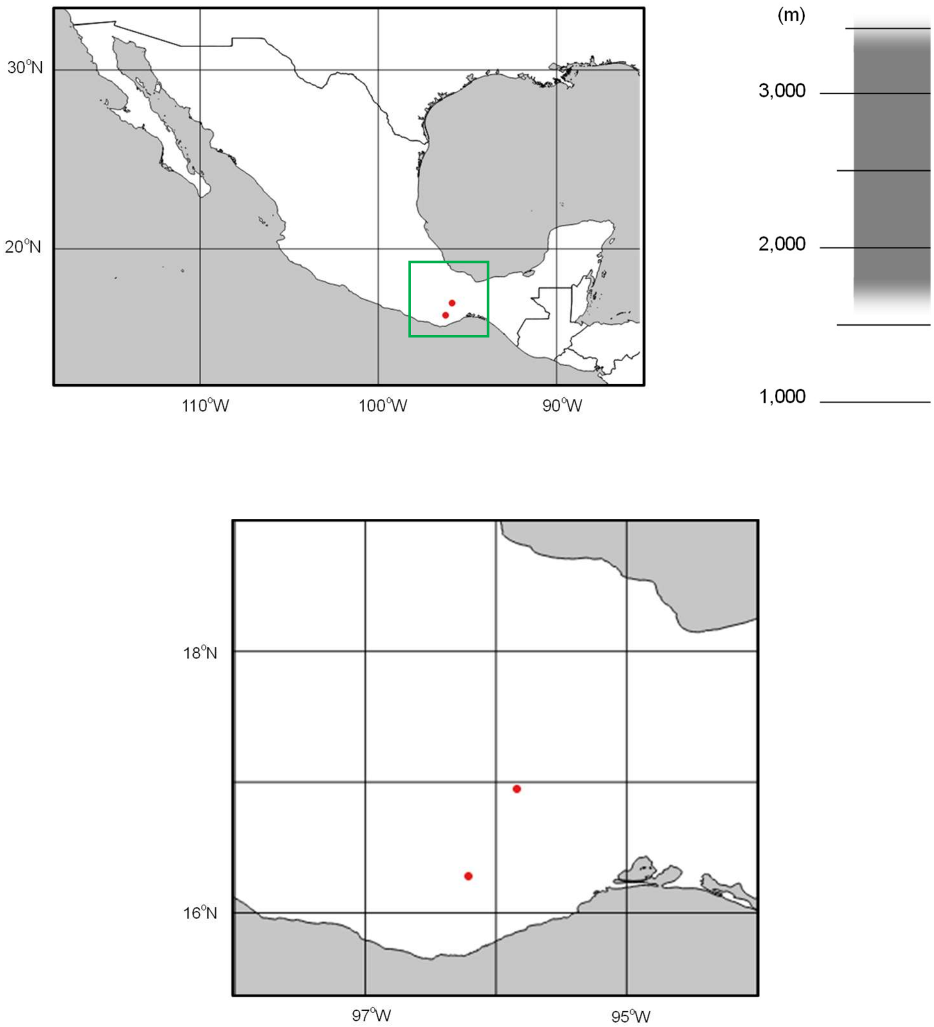
Plate 4.50. *Pinguicula laueana*



10 mm: 1, 2, 3
10 mm: 4, 5
500 μm: 6

1. rosette with fruit
2. winter rosette with flower
3. summer leaf
4. flower, front view
5. flower, lateral view
6. seed

P. laueana



51. ***Pinguicula laxifolia*** Luhrs, Phytologia 79 (1995) 116.

TYPE: MEXICO. Tamaulipas, Distr. Gómez Farías, Rancho del Cielo, between La Perra and Agua Linda, 31 March 1969, *Richardson 1211* (holotype: TEX!).

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf dimorphic, summer leaf 4-12, yellowish-green, sometimes with maroon suffusion, subelect or arcuate, elliptic to oblanceolate or somewhat spatulate, convex, apex obtuse, base narrowly cuneate, margin often revolute but sometimes narrowly involute, 32-68 mm long, 4-12 mm wide, winter leaf up to 17, obovate-spatulate, apex obtuse, base rather cuneate, 10-17 mm long, 1.5-5 mm wide. Winter rosette subglobose. Scape 1-3, densely glandulous, 60-93 mm long. Calyx bilabiate, upper lip 3-lobed, lobes oblong, ca. 2 mm long, lower lip 2-lobed, lobes slightly smaller than uppers. Flower pinkish-purple, paler at base of lips. Corolla bilabiate, 18-22 mm across, zygomorphic, 30-39 mm long including spur, upper lip 2-lobed, lobes oblong-obovate, lower lip 3-lobed, lobes obovate-orbicular, middle lobe larger then laterals, tube yellowish-green, conical to subcylindrical, spur yellowish-green, cylindrical, 10-17 mm long. Capsule subglobose. Seed unknown. (Plate 4.51).

PHENOLOGY: III, IV. Scape arising from early summer rosette.

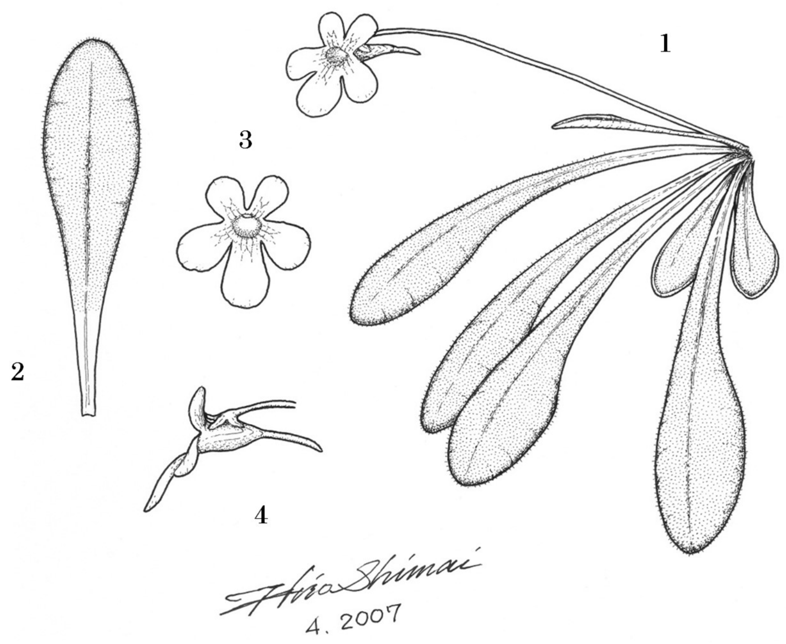
ETYMOLOGY: loosely-leaved

HABITAT: Calcareous rock walls in forest. Low light intensity.

DISTRIBUTION: MEXICO (Tamaulipas). Restricted to the type locality area. 1,890-2,040 m.

DISCUSSION: *Pinguicula laxifolia* is known only from the State of Tamaulipas, Mexico. It was originally collected by Alfred Richardson in March 1969 and deposited at the herbarium in the University of Texas at Austin as an unidentified taxon. Luhrs (1995a) described it as a new species, i.e. *P. laxifolia* based on the herbarium specimens. The summer leaf is oblanceolate to spatulate and the upper surface is often convex, but detailed morphological observations, particularly from the live materials, are still extremely limited. According to Zamudio (per. com.), the flower colour is darker than that mentioned in the original description as pinkish-purple. The distribution of this little known species is highly restricted to a very small area in the Municipality of Gómez Farías in the state. Details of its ecology and current status at the habitat are poorly known.

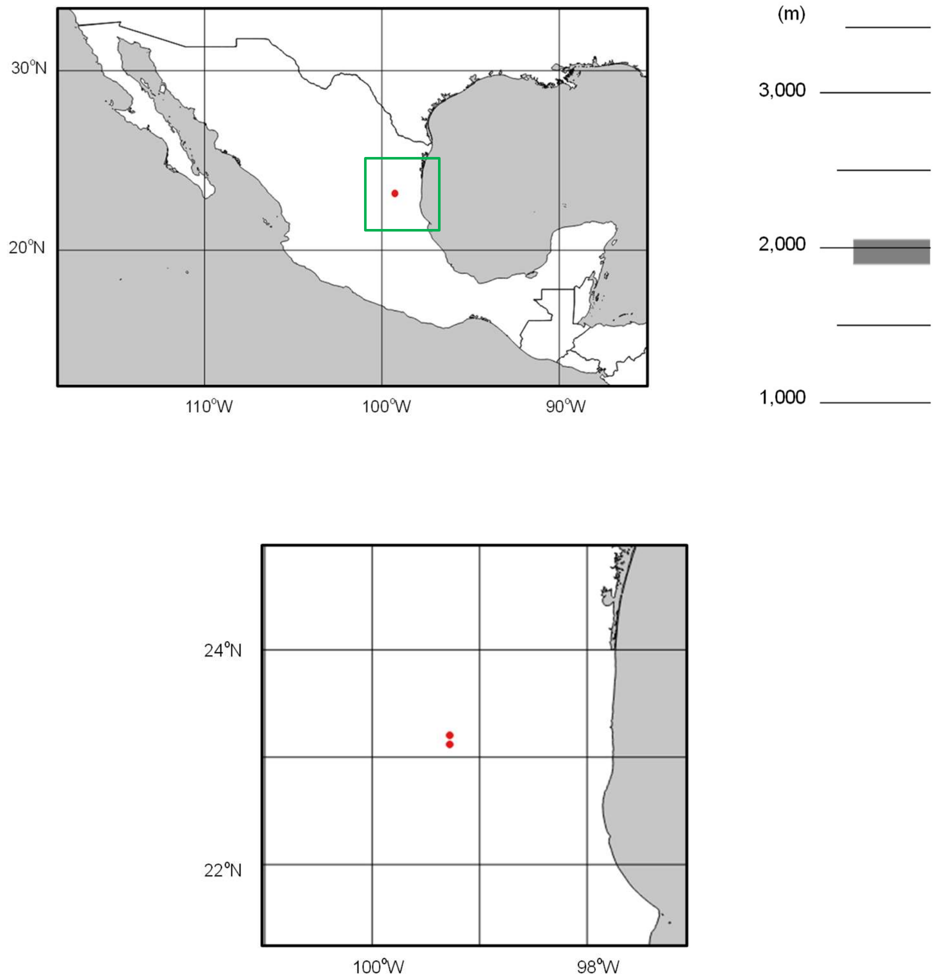
Plate 4.51. *Pinguicula laxifolia*



10 mm: 1, 2
10 mm: 3, 4

1. summer rosette with flower
2. summer leaf
3. flower, front view
4. flower, lateral view

P. laxifolia



52. ***Pinguicula macrophylla*** Kunth, Nov. Gen. et Spec. 2 (1817) 226.

TYPE: MEXICO. *crescit in Novae Hispaniae collibus inter urbem Guanaxuato et pagum Santa Rosa* (Guanajuato, hills between Guanajuato City and Santa Rosa), *Humboldot & Bonpland* (holotype: P!; isotype: P!).

SYNONYMS: *P. barkeriana* Sprague, *P. caudata* Hemsley

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf dimorphic, summer leaf 2-6, yellowish-green or maroon, ovate-elliptic to suborbicular, margin narrowly involute, apex obtuse, base often cordate, 28-135 mm long, 25-125 mm wide, petiole 12-60 mm long, winter leaf 30-45, ovate, elliptic to oblong-lanceolate, apex acute to acuminate, thick, 6-25 mm long, 3-9 mm wide. Winter rosette subglobose. Scape 1-7, densely glandulous, 75-300 mm long. Calyx bilabiate, upper lip 3-lobed, lobes oblong-lanceolate, ca. 4 mm long, lower lip 2-lobed, lobes smaller than uppers. Flower bluish-purple, often darker at base of lips, white spot or stripe at base of middle lobe. Corolla bilabiate, 20-35 mm across, zygomorphic, 35-55 mm long including spur, upper lip 2-lobed, lobes broadly oblong, reflexed at base, lower lip 3-lobed, lobes larger than uppers, obovate to obovate-oblong, lateral lobes oblique and reflexed or twisted, tube bluish-purple, very short, conical to somewhat saccate, spur pale purple, cylindrical, 17-33 mm long. Capsule subglobose, 900-1,100 X 150-210 μm. Seed fusiform-ellipsoid. $2n = 22$. (Plate 4.52).

PHENOLOGY: VI, VII, VIII, IX, X. Scape arising from spring rosette or summer rosette.

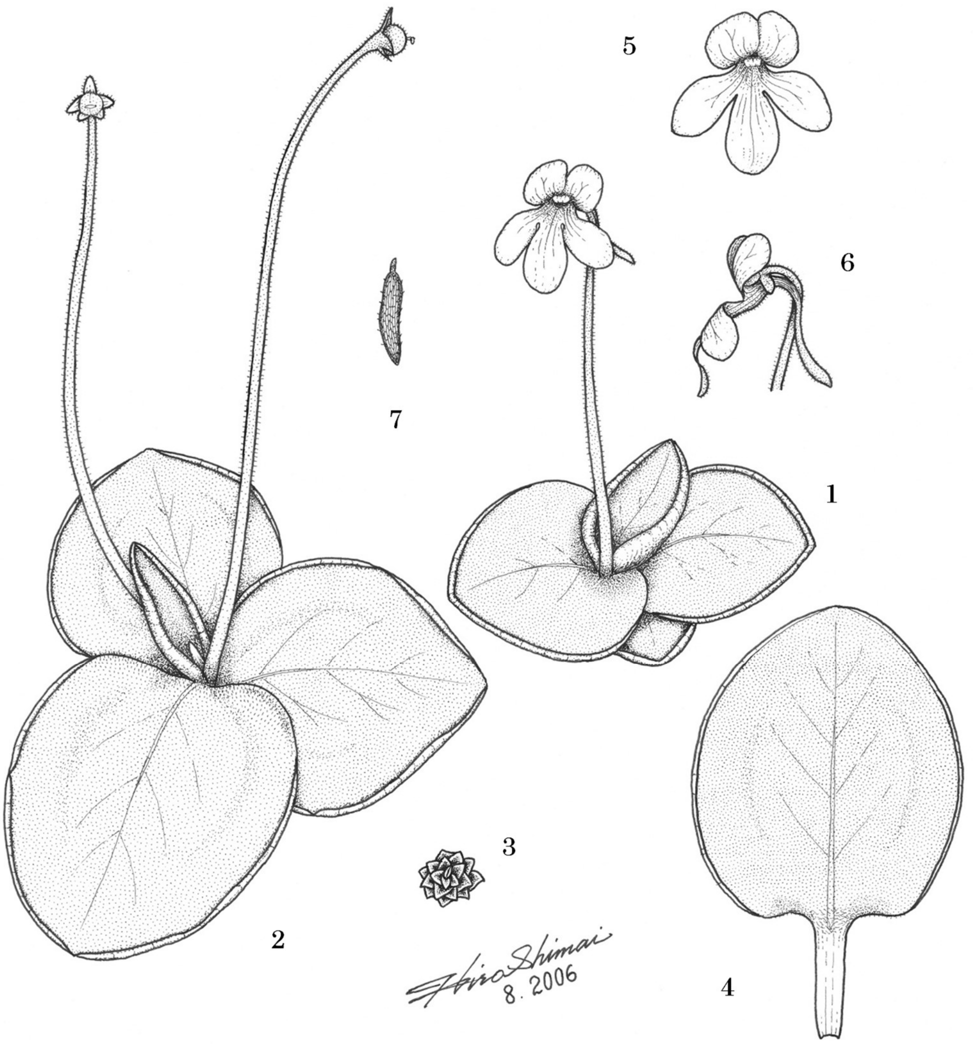
ETYMOLOGY: large-leaved

HABITAT: Mossy limestone cliffs in oak forests. Tolerant to low light intensity.

DISTRIBUTION: MEXICO (Guanajuato, Querétaro, San Luis Potosí). 1,250-2,580 m.

DISCUSSION: *Pinguicula macrophylla* is native to the States of Guanajuato, Querétaro, and San Luis Potosí, Mexico. The distribution map published by McVaugh and Mickel (1963) mistakenly included *P. moranensis* and *P. oblongiloba*, having a much wider distribution area, and overlaying the actual distribution area of *P. macrophylla*. In fact, *P. macrophylla* is morphologically similar to a few other species (e.g. *P. moranensis*, *P. oblongiloba*, or *P. orchidioides*), but it has a distinctive petiole abruptly contracted at the base of summer leaf lamina, and the lobes of upper lip often sharply recurved. The petiole is, however, not always visible unless digging out the plant as it may be buried in soils. *P. acuminata* also has a morphologically similar summer leaf with a long petiole, but the flower colour differs between the two. Amongst species above, *P. moranensis* could occur with *P. macrophylla* in the same regions. *P. macrophylla* is locally common.

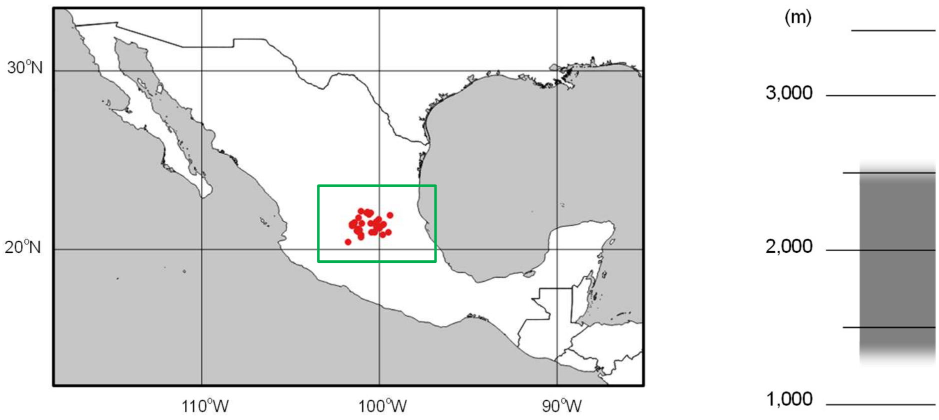
Plate 4.52. *Pinguicula macrophylla*

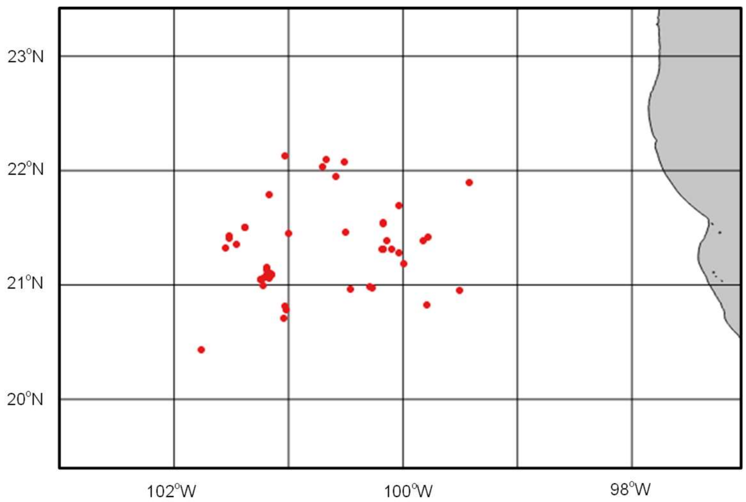


10 mm: 1, 2, 3, 4
10 mm: 5, 6
500 µm: 7

1. spring rosette with flower
2. summer rosette with fruit
3. winter rosette
4. summer leaf
5. flower, front view
6. flower, lateral view
7. seed

P. macrophylla





53. ***Pinguicula martinezii*** Zamudio, Acta Bot. Mex. 70 (2005) 76.

TYPE: MEXICO. *Querétaro, municipio de Landa de Matamoros, Llano Chiquito* (Querétaro, Municipality of Landa de Matamoros, Llano Chiquito, alt. 1,980 m), 17 February 1989, *Zamudio & Carranza 7150* (holotype: IEB!; isotypes: IEB!, MEXU!, TEX!).

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf dimorphic, summer leaf 6-14, yellowish-green or maroon, subelect, oblong-spatulate to oblong-oblanceolate, margin revolute, apex obtuse, 50-100 mm long, 13-25 mm wide, winter leaf 16-38, spatulate to oblong-spatulate, thick, apex obtuse, 8-40 mm long, 3.5-15 mm wide. Winter rosette lenticular. Scape 1-4, densely glandulous, 60-115 mm long. Calyx bilabiate, upper lip 3-lobed, lobes triangular to oblong, 2-4 mm long, connate to middle, lower lip 2-lobed, lobes smaller than uppers, connate at base. Flower white, pale purple at margin of lobes, often with reddish-purple spots at base of lobes, yellowish-green trichomes in throat. Corolla bilabiate, 16-20 mm across, subactinomorphic, 13-30 mm long including spur, upper lip 2-lobed, lobes oblong to broadly obovate, lower lip 3-lobed, lobes similar to uppers but sometimes narrower or smaller, tube pale yellowish-green, cylindrical, spur bright green, cylindrical, 2.5-5 mm long. Capsule subglobose. Seed ellipsoid, 790-840 X 190-240 μm.

PHENOLOGY: II, IV, IX, X. Scape arising mostly from winter rosette but sometimes also from summer rosette. (Plate 4.53).

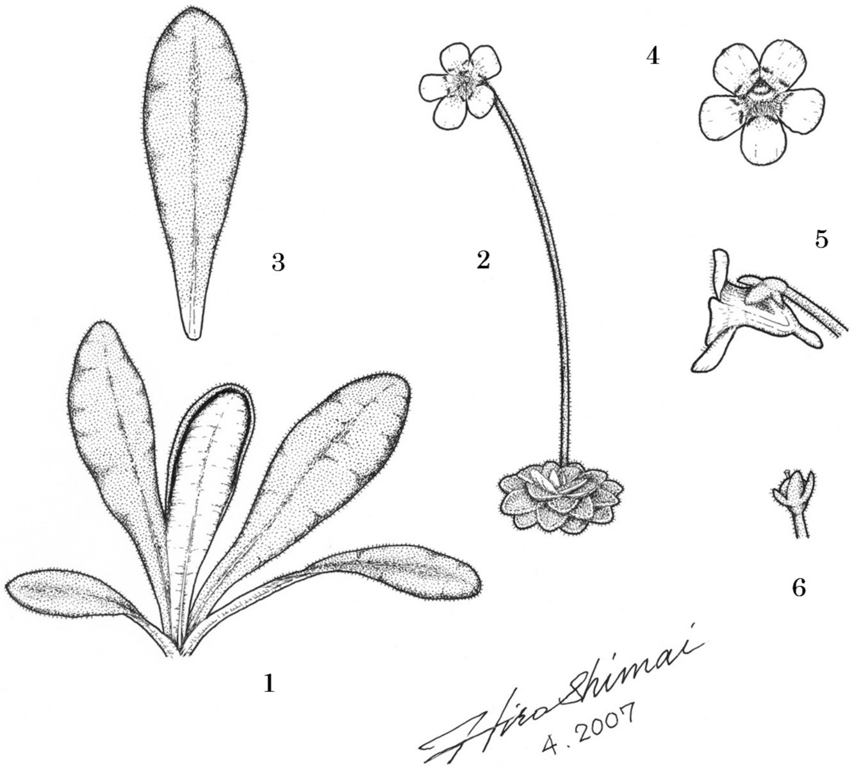
ETYMOLOGY: dedicated to Maximino Martínez (1888-1964), who studied Mexican plants

HABITAT: Calcareous rocks in steep slopes or on vertical cliffs in forests. Low light intensity.

DISTRIBUTION: MEXICO (Querétaro). A few localities have been recorded near the type locality. 1,980-2,840 m.

DISCUSSION: *Pinguicula martinezii* has been found only in the Municipality of Landa de Matamoros in the State of Querétaro, Mexico. Although *P. martinezii* was described in 2005, earlier specimens had been collected many times. Zamudio (2005) suggested a morphologically close relationship to *P. agnata*. Also the floral morphology is similar to that of *P. ibarrae*. The summer leaf of *P. martinezii* is spatulate with often convex upper surface, distinguishable from the two. *P. martinezii* shares the same microhabitat with *P. calderoniae*. Little information on at the habitat is available, but it seems the number of population is small.

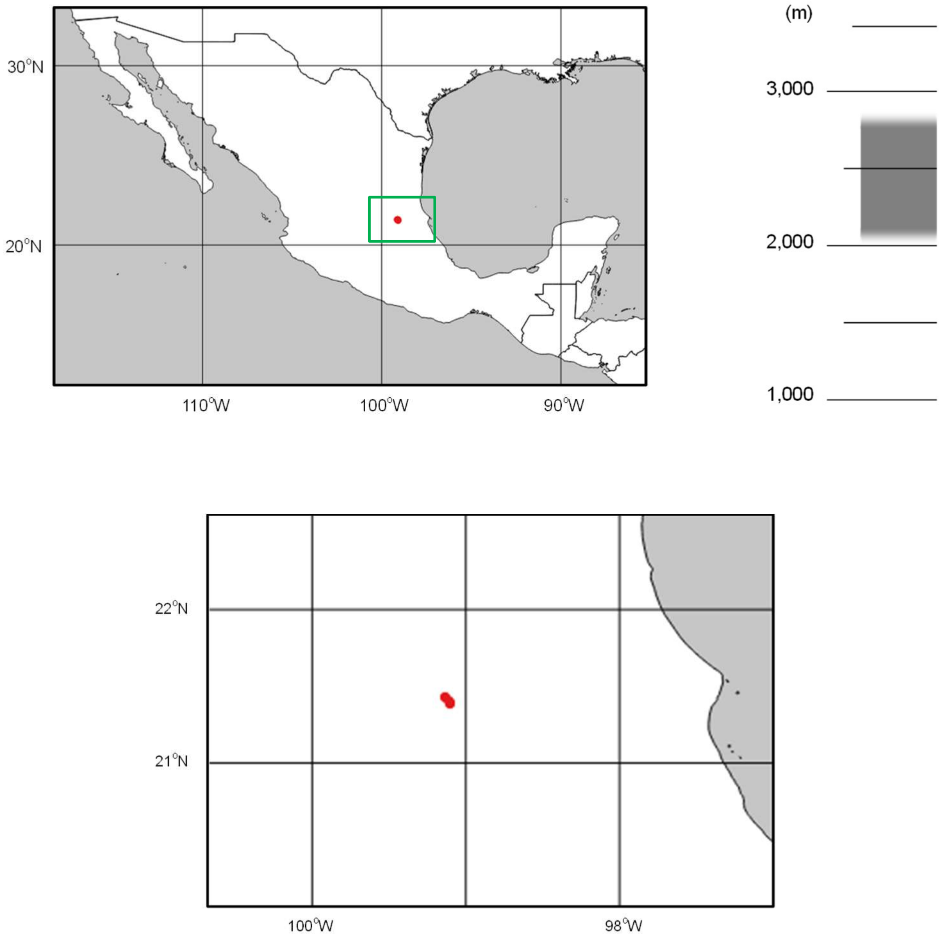
Plate 4.53. *Pinguicula martinezii*



10 mm: 1, 2, 3
10 mm: 4, 5, 6

1. summer rosette
2. winter rosette with flower
3. summer leaf
4. flower, front view
5. flower, lateral view
6. capsule

P. martinezii



54. ***Pinguicula medusina*** Zamudio et Studnička, Acta Bot. Mex. 53 (2000) 68.

TYPE: MEXICO. *Oaxaca, municipio de Juxtlahuaca, Laguna Encantada, ca. 3 km al N de Santiago Juxtlahuaca* (Oaxaca, Municipality of Juxtlahuaca, Laguna Encantada, ca. 3 km north of Santiago Juxtlahuaca, alt. 1,650-1,700 m), 27 May 1999, *Zamudio & Ocampo 11050* (holotype: IEB!; isotypes: IEB!, TEX!).

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf dimorphic, summer leaf 6-12, bright green or maroon, subelect to arcuate, very narrowly linear-lanceolate to filiform, margin slightly revolute, apex acute, base wider, 70-190 mm long, 0.5-8 mm wide, producing clonal plantlet at tip, winter leaf 70-90, linear-lanceolate, apex acute to acuminate, 8-23 mm long, 1.5-3.5 mm wide. Winter rosette globose. Scape 1-3, densely glandulous, 40-140 mm long. Calyx bilabiate, upper lip 3-lobed, lobes narrowly triangular, 1-2 mm long, lower lip 2-lobed, lobes slightly smaller than uppers, connate at base. Flower white, sometimes faintly pale lilac at margin of lobes, purple at base of lips. Corolla bilabiate, 15-23 mm across, zygomorphic, 16-23 mm long including spur, upper lip 2-lobed, lobes oblong to obovate-oblong, lower lip 3-lobed, lobes similar to uppers but slightly larger, tube purple with darker veins, cylindrical, spur yellowish-green, cylindrical, 3-5 mm long. Capsule subglobose. Seed fusiform. 2*n*

= 22. (Plate 4.54).

PHENOLOGY: V, VI, VIII. Scape arising from spring rosette or summer rosette.

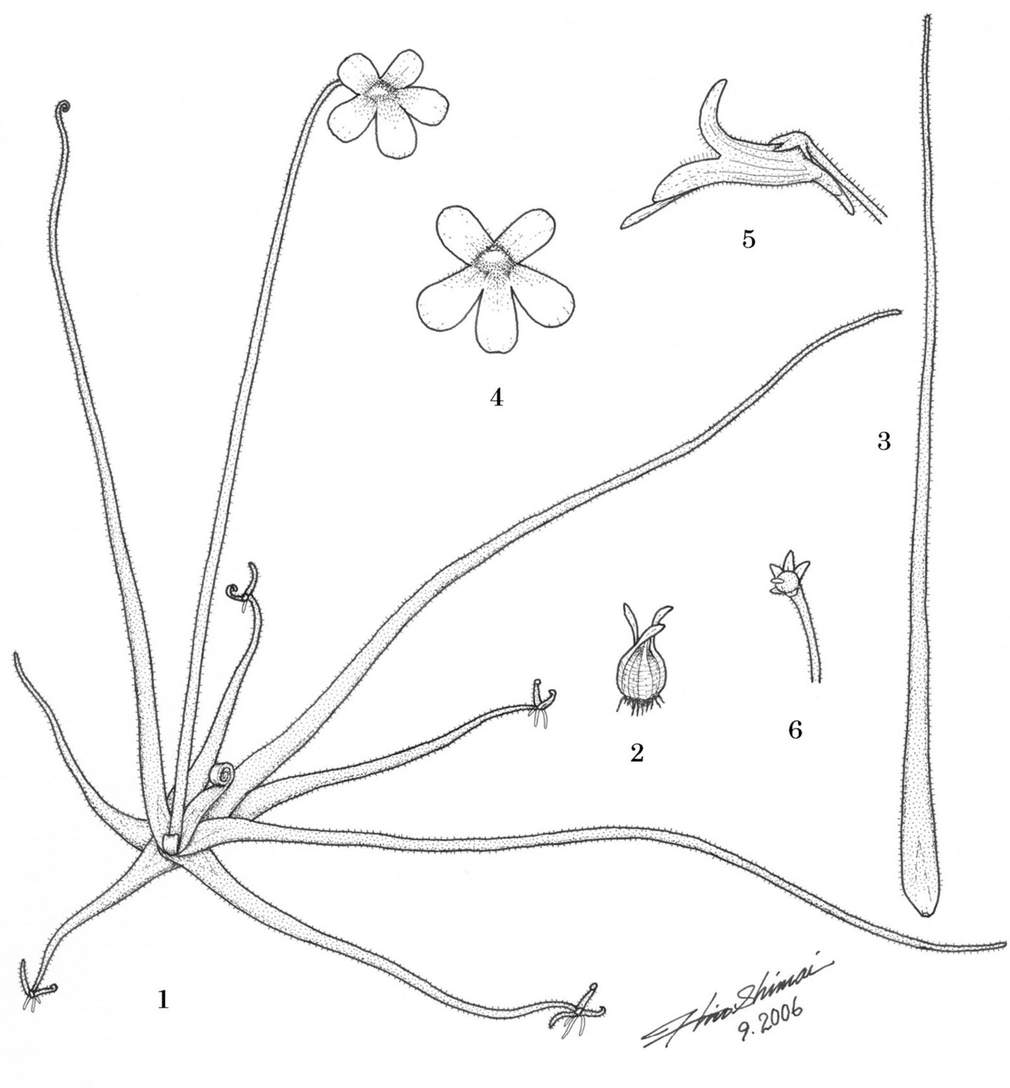
ETYMOLOGY: resembling Medusa, one of the Gorgon sisters, in the Greek myths

HABITAT: Gypsum hills or slopes in tropical forests with higher air humidity. Tolerant to low light intensity.

DISTRIBUTION: MEXICO (Oaxaca). 1,600-2,500 m.

DISCUSSION: *Pinguicula medusina* has been recorded only from the State of Oaxaca, Mexico. This plant had been widely cultivated under the name of *P. heterophylla* "alfredae" nom. nudu. among horticulturalists before officially described by Zamudio and Studnička (2000). *P. medusina* is morphologically very similar to *P. heterophylla*, but the former produces a clonal plantlet at the apex of the summer leaf while the latter never does so. More detailed morphological and ecological differences between the two have been compared by Zamudio and Studnička (2000). The restricted distribution area may encounter decline of the population number by different causes at the habitat.

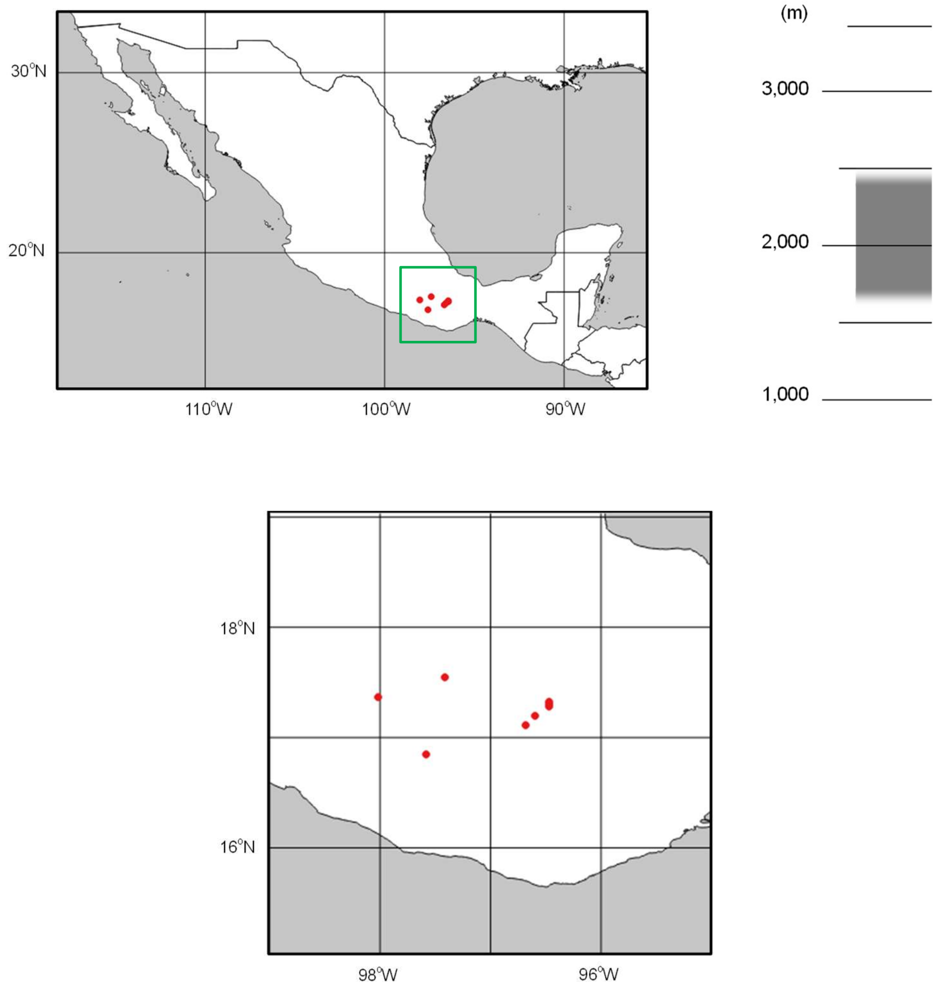
Plate 4.54. *Pinguicula medusina*



10 mm: 1, 2, 3
10 mm: 4, 5, 6

1. summer rosette with flower
2. winter rosette
3. summer leaf
4. flower, front view
5. flower, lateral view
6. capsule

P. medusina



55. ***Pinguicula mesophytica*** Zamudio, Acta Bot. Mex. 40 (1997) 65.

TYPE: EL SALVADOR. *departamento de Santa Ana, Montecristo* (Department of Santa Ana: Montecristo, alt. 2,300 m), 23 May 1963, *Molina & Molina 12601* (holotype: F!; isotypes: EAP!, NY!, TEX!).

DESCRIPTION: Epiphyte. Perennial herb. Root filiform, fragile. Stem very short. Leaf dimorphic, summer leaf 4-12, bright green, oblong to obovate or suborbicular, margin narrowly involute, apex obtuse, 12-42 mm long, 10-25 mm wide, petiole 6-18 mm long, winter leaf 14-16, obovate to spatulate, thick, apex obtuse, 5-15 mm long, 2-4.5 mm wide. Winter rosette lenticular. Scape 1-8, densely glandulous, 40-100 mm long. Calyx bilabiate, upper lip 3-lobed, lobes oblong-lanceolate, 2-3 mm long, lower lip 2-lobed, lobes smaller than uppers, slightly connate at base. Flower reddish-purple, white at base of lower lip. Corolla bilabiate, 20-40 mm across, zygomorphic, 25-40 mm long including spur, upper lip 2-lobed, lobes suborbicular, lower lip 3-lobed, lobes oblong to oblong-obovate, middle lobe slightly larger than laterals, tube pale purple, conical, very short, spur pale yellowish-green, cylindrical, 15-20 mm long. Capsule ellipsoid. Seed fusiform-ellipsoid, 800-1,110 X 230-280 µm. (Plate 4.55).

PHENOLOGY: III, IV, V, VI, VII. Scape arising from summer rosette.

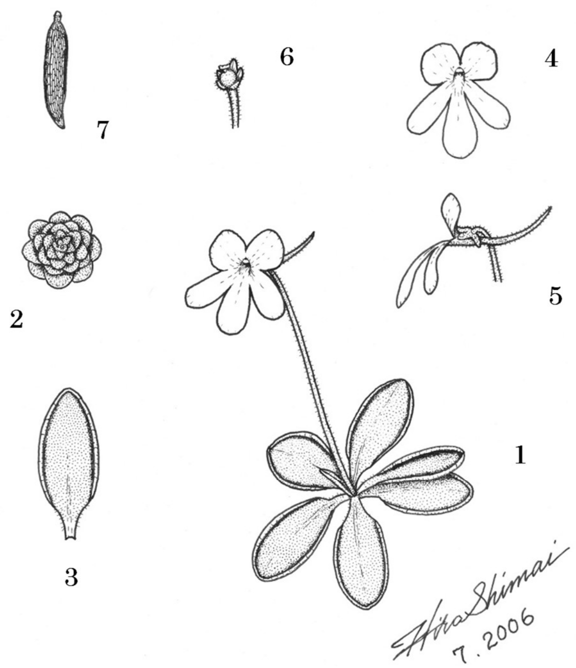
ETYMOLOGY: mesophytic and Mesoamerica (per. com., Zamudio)

HABITAT: Epiphytic on tree trunks exposed to breeze in forests at middle of mountains. Tolerant to low light intensity.

DISTRIBUTION: EL SALVADOR (Santa Ana); GUATEMALA (Chimaltenango, Huehuetenango, Sololá); HONDURAS (Intibucá, Lempira, Ocotepeque, Santa Bárbara); MEXICO (Chiapas). 1,380-3,100 m.

DISCUSSION: *Pinguicula mesophytica* is distributed in the State of Chiapas, Mexico and Central America (El Salvador, Guatemala, and Honduras). This used to be confused with *P. moranensis*, but was divided by Zamudio (1997a) as *P. mesophytica*, as having a different corolla in shape and size, a more distinctive petiole at the base of the summer leaf lamina, and an epiphytic or lithophytic habit. The lobes of upper lip are more rounded than those of *P. moranensis* and the size of summer rosette is mostly smaller than that of *P. moranensis*. The species often directly grows on mossy tree trunks or wet rocks (Zamudio 1997a). The exact distributional boundary of *P. mesophytica* is not clearly known since the habitat is restricted to cloud mountain forests.

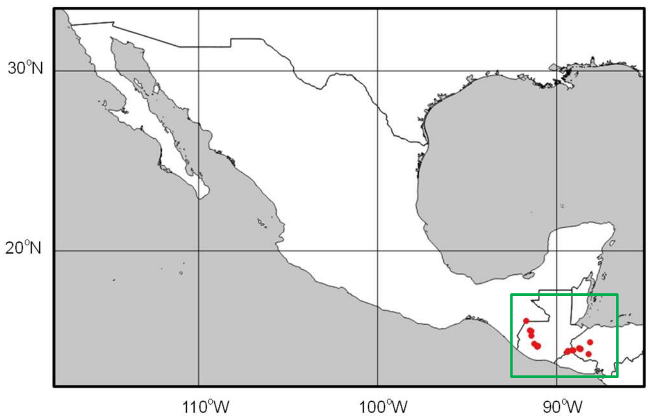
Plate 4.55. *Pinguicula mesophytica*

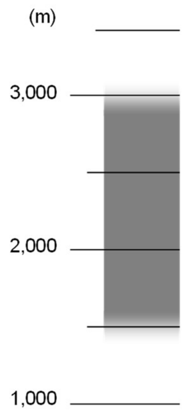


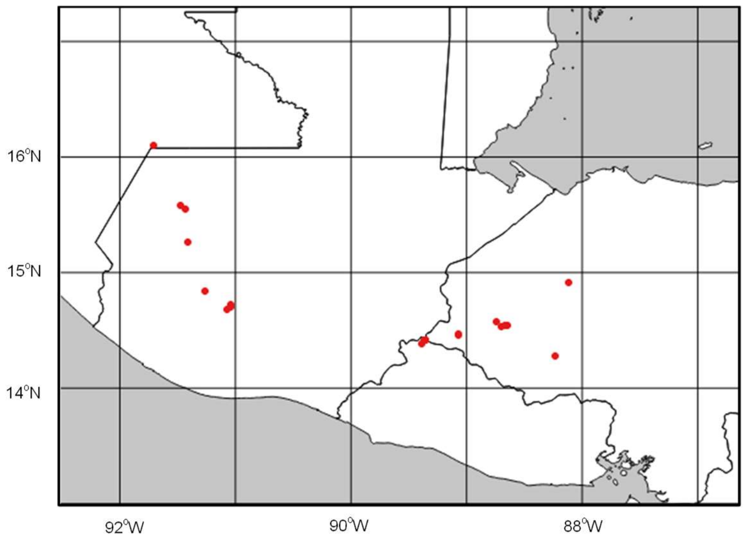
10 mm: 1, 2, 3
10 mm: 4, 5, 6
500 µm: 7

1. summer rosette with flower
2. winter rosette
3. summer leaf
4. flower, front view
5. flower, lateral view
6. capsule
7. seed

P. mesophytica







56. ***Pinguicula mirandae*** Zamudio et Salinas, Acta Bot. Mex. 37 (1996) 40.

TYPE: MEXICO. *Oaxaca, Distrito de Teotitlán, Municipio de Santa María Ixcatlán, Río Seco a Río Santiago 17°53' latitud norte, 87°07' longitud oeste. Selva baja caducifolia, en lugares sombreados* (Oaxaca, District of Teotitlán, Municipality of Santa María Ixcatlán, Río Seco to Río Santiago, 17°53'N 87°07'W. low deciduous forest, on rocks in shady places, alt. 1,250 m), 14 December 1991, *Salinas, Martínez-Correa & Martínez-Serrano 6733* (holotype: MEXU!; isotype: MEXU!; paratype: IEB!).

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf dimorphic, summer leaf 4-10, bright green, outer margin sometimes maroon, obovate to ligulate or suborbicular, apical margin narrowly involute, apex obtuse, base rather cuneate, 20-40 mm long, 15-30 mm wide, winter leaf 30-60, spatulate to oblong-spatulate, thick, apex acute, 7-26 mm long, 2.5-6 mm wide. Winter rosette lenticular or acetabuliform. Runner formed underground, producing clonal plantlet at apex. Calyx bilabiate, upper lip 3-lobed, lobes oblong, 2-2.5 mm long, lower lip 2-lobed, lobes smaller than uppers, connate at base. Scape 1-5, densely glandulous, 50-100 mm long. Flower white or faintly pale lilac. Corolla bilabiate, 10-17 mm across, subactinomorphic, 9-17 mm long including spur, upper lip 2-lobed, lobes broadly obovate, tip obtuse to truncate, lower lip 3-lobed, lobes similar to uppers, lateral lobes rather oblique, tube white to yellow or purple with darker purple veins, conical to subcylindrical, angled at middle, spur pale yellow to yellowish-green, narrowly conical to subcylindrical, 2-4 mm long. Capsule globose. Seed unknown. (Plate 4.56).

PHENOLOGY: XII. Scape arising from winter rosette.

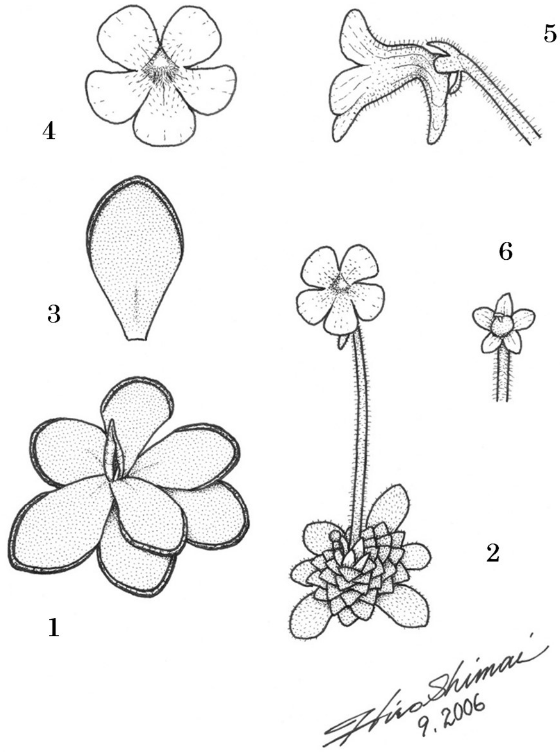
ETYMOLOGY: dedicated to Faustino Miranda, who studied the flora of the Tehuacán-Cuicatlán region

HABITAT: Steep rocks along rivers in tropical deciduous forests. Tolerant to low light intensity.

DISTRIBUTION: MEXICO (Oaxaca). 1,250-1,880 m.

DISCUSSION: *Pinguicula mirandae* is endemic to the State of Oaxaca, Mexico. The longitude at the type locality mentioned in the original description by Zamudio and Salinas (1996) may be 97°07'W. It is morphologically similar to *P. conzattii*, also endemic to the State of Oaxaca, but the differences are seen in the shapes of their winter rosette, and degrees of corolla tube angle. Although the two species are found in the same state, distribution areas are isolated from each other. According to Zamudio and Salinas (1996), *P. mirandae* forms runners producing a clonal plantlet at the apex which elongates up to 30 mm long. Little information for the ecology and current status at the habitat is available.

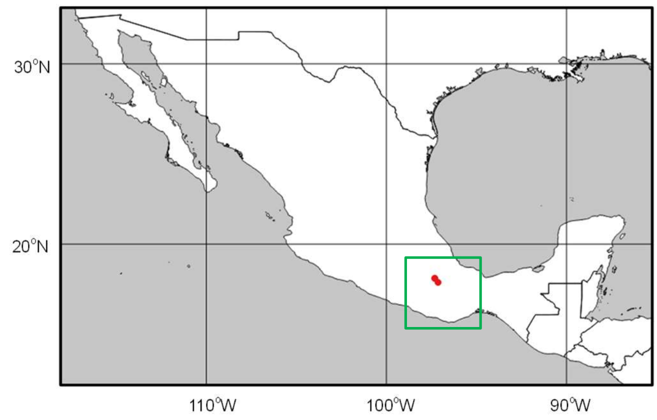
Plate 4.56. *Pinguicula mirandae*

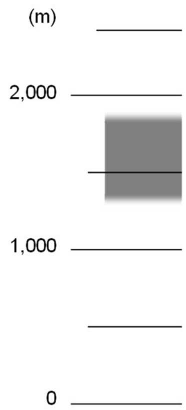


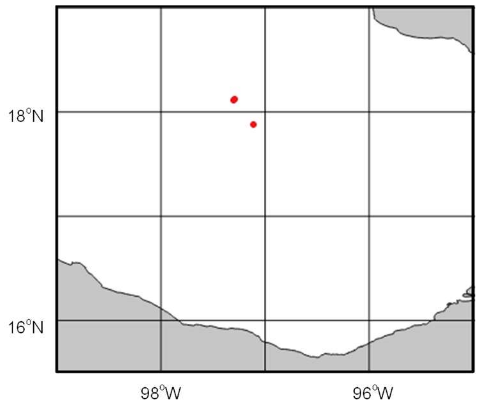
10 mm: 1, 2, 3
10 mm: 4, 5, 6

1. summer rosette
2. winter rosette with flower
3. summer leaf
4. flower, front view
5. flower, lateral view
6. capsule (immature)

P. mirandae







57. ***Pinguicula moctezumae*** Zamudio et Ortega, Acta Bot. Mex. 28 (1994) 58.

TYPE: MEXICO. *Querétaro, municipio de Cadereyta, Cañón del Río Moctezuma, ca. 6 km al S de Los Moras, Casa de Máquinas, alt. 1050 m* (Querétaro, Municipality of Cadereyta, Río Moctezuma Canyon, ca. 6 km south of Las Moras, Powerhouse, alt. 1,050 m), 3 March 1994, *Pérez-Calix 2904* (holotype: IEB!; isotypes: IEB!, MEXU!, MICH!, TEX!; paratype: IEB!).

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf dimorphic, summer leaf 8-20, yellowish-green, elect to subelect, linear-lanceolate, margin slightly revolute, apex rather acute, 50-130 mm long, 3-8 mm wide, winter leaf 20-30, elliptic to oblong-elliptic, thick, apex acute, 5-30 mm long, 3-7 mm wide. Winter rosette subglobose, but sometimes not formed. Scape 1-5, densely glandulous, 60-140 mm long. Calyx bilabiate, upper lip 3-lobed, lobes oblong-lanceolate, 2-4.5 mm long, lower lip 2-lobed, lobes smaller than uppers. Flower dark pink to pinkish-purple, white at base of lower lip, yellow in throat. Corolla bilabiate, 28-40 mm across, zygomorphic, 35-65 mm long including spur, upper lip 2-lobed, lobes orbicular, lower lip 3-lobed, lobes longer and narrower than uppers, oblong-obovate, lateral lobes rather oblique, tube pale pink, very short, shortly conical, spur white, cylindrical, 25-38 mm long. Capsule ellipsoid to subglobose. Seed fusiform-ellipsoid, 1,100-1,260 X 190-230 µm. $2n = 22$. (Plate 4.57).

PHENOLOGY: I, III, IV

ETYMOLOGY: native of Río Moctezuma

HABITAT: Calcium carbonate along streamside or on walls without water, or on calcareous rocks. Various light intensities.

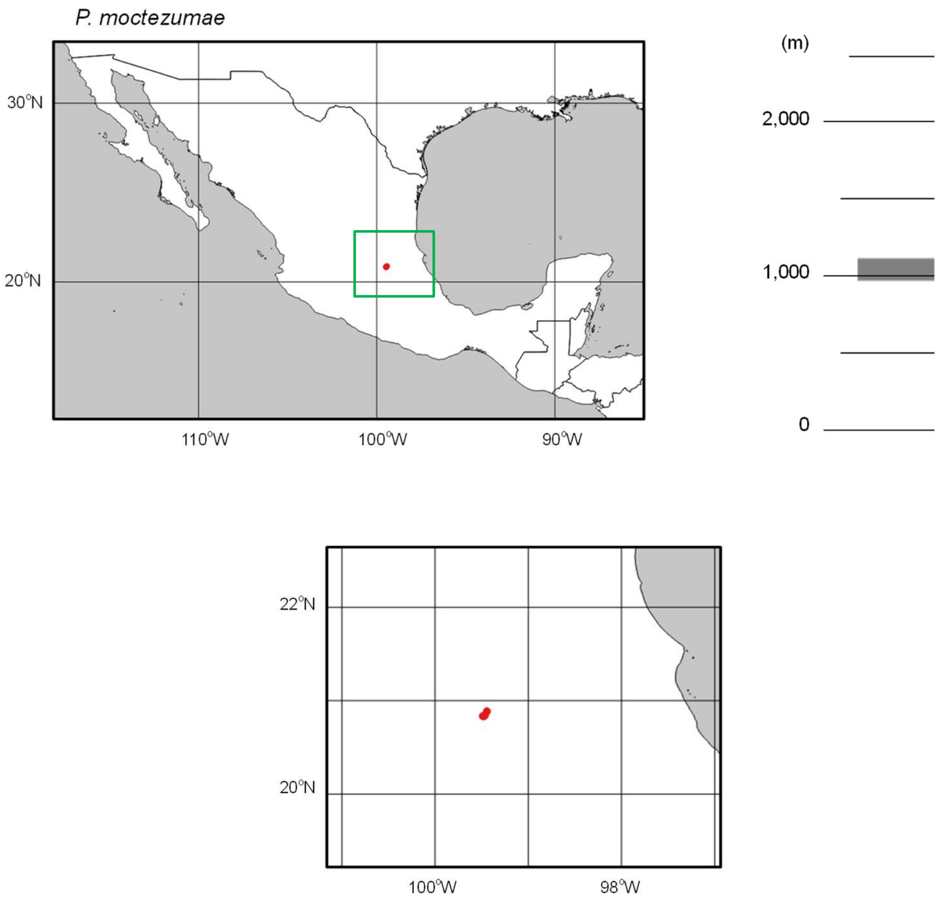
DISTRIBUTION: MEXICO (Hidalgo, Querétaro). A few localities have been recorded near the type locality, both Hidalgo and Querétaro sides of the Río Moctezuma. 950-1,150 m.

DISCUSSION: *Pinguicula moctezumae* is endemic to the Moctezuma Canyon, located on the state border of Hidalgo and Querétaro, Mexico. There have been herbarium records from both sides of the states. It forms a winter rosette only if the habitat is too dry for their constant growth (Zamudio and Ortega 1994). *P. moctezumae* is morphologically similar to *P. gypsicola*, but can be distinguished by having larger pinkish-purple flower and broader corolla lobes. Moreover, the distributions of the two are geographically isolated from each other. *P. moctezumae* seems to be abundant at microhabitats although the distribution area is highly restricted. The habitat of the species might have been disturbed by a construction of hydroelectric dam.

Plate 4.57. *Pinguicula moctezumae*

10 mm: 1, 2, 3, 4, 5
500 μm: 6

1. summer rosette in flower
2. summer leaf
3. flower, front view
4. flower, lateral view
5. capsule
6. seed


P. moctezumae
30°N
20°N
110°W
100°W
90°W
(m)
2,000
1,000
0
22°N
20°N
100°W
98°W

58. ***Pinguicula moranensis*** Kunth

a. ***Pinguicula moranensis*** Kunth **var. *moranensis*** Kunth, Nov. Gen. et Spec. 2 (1817) 226.

TYPE: MEXICO. Crescit locis temperatis prope Moran Mexicanorum, alt. 1340 hex. (temperate areas near Morán, alt. 1,340 m), s.d., *Humboldt & Bonpland 4117* (holotype: P!; isotype: P!).

SYNONYMS: *P. bakeriana* Sander, *P. bakeriana* Sprague, *P. caudata* Schlecht., *P. flos-mulionis* Morr., *P. rosei* Watson

DESCRIPTION: Very variable. Perennial herb. Root filiform, fragile. Stem very short. Leaf dimorphic, summer leaf 4-14, bright green or maroon, ovate, obovate, oblong or suborbicular, margin slightly involute, apex obtuse or sometimes rather acute, 30-100 mm long, 23-75 mm wide, winter leaf 30-120, spatulate, oblong-spatulate, lanceolate to oblong-lanceolate, thick, apex rather acute, 5-40 mm long, 2-10 mm wide. Winter rosette lenticular or acetabuliform. Scape 1-11, densely glandulous, 60-320 mm long. Calyx bilabiate, upper lip 3-lobed, lobes ovate to oblong-lanceolate, 3-4 mm long, lower lip 2-lobed, lobes smaller than uppers. Flower pink, pinkish-red, reddish-purple or purple, sometimes darker at base of lips, white spot or stripes at base of lower lip, or rarely entirely white.

Corolla bilabiate, 20-40 mm across, zygomorphic, 30-64 mm long including spur, upper lip 2-lobed, lobes oblong to obovate, oblong-lanceolate or cuneate, tip acute to obtuse or truncate, sometimes twisted at base, lower lip 3-lobed, lobes similar to uppers but slightly larger, lateral lobes sometimes reflexed to twisted, middle lobe rather cuneate, tip truncate to shallowly emarginate, tube very short, conical, spur yellowish-green, cylindrical, 15-38 mm long. Capsule subglobose. Seed narrowly ellipsoid, 840-1,050 X 200-250 µm. $2n = 22, 44$. (Plate 4.58).

PHENOLOGY: I, II, III, IV, V, VI, VII, VIII, IX, X, XI, XII. Scape arising from either winter or summer rosettes, depending on strains or localities.

ETYMOLOGY: native of Mina de Morán

HABITAT: Wet rocks (often steep to vertical limestone rocks) in forests, gorges, or along streams. Tolerant to low light intensity.

DISTRIBUTION: GUATEMALA (Baja Verapaz, Chimaltenango, El Quiché, Huehuetenango, Quetzaltenango, San Marcos, Totonicapán); MEXICO (Chiapas, Distrito Federal, Guanajuato, Guerrero, Hidalgo, México, Michoacán, Morelos, Nuevo León, Oaxaca, Puebla, Querétaro, San Luis Potosí, Tamaulipas, Tlaxcala, Veracruz). 470-3,600 m.

DISCUSSION: *Pinguicula moranensis* var. *moranensis* is morphologically very variable. It is widely distributed in Mexico and Guatemala. It is hard to describe a general outline for the taxon because of its morphological and ecological diversities. At the same time, the morphological diversities are often continuous among the populations; therefore, it is often impossible to divide it at intraspecific ranks. Furthermore, morphologically similar but unidentified taxa have been often included into *P. moranensis* sensu lato. Recently, Zamudio (1999b) attempted to divide *P. moranensis* to two varieties, *P. moranensis* var. *moranensis* and *P. moranensis* var. *neovolcanica*. According to Zamudio (1999b), *P. moranensis* var. *moranensis*, possessing spatulate to oblong-spatulate winter leaves with the obtuse tip, forms a more loosely imbricate winter rosette, compared with *P. moranensis* var. *neovolcanica*. *P. moranensis* var. *moranensis* is morphologically similar to a few other species, e.g. *P. potosiensis*, *P. rectifolia* or *P. zecheri.* Due to the great morphological diversities, it is often difficult to distinguish from other species. In fact, Zamudio (2001b) treated that *P. potosiensis* and *P. rectifolia* were synonymous with *P. moranensis* var. *moranensis*. Generally, *P. moranensis* var. *moranensis* has paler flower colour than *P. potosiensis*, and more cuneate with non-undulate corolla lobe tip than *P. rectifolia* or *P. zecheri* does. The populations in Nuevo León and Tamaulipas may need a review if those include *P. potosiensis*. *P. moranensis* var. *moranensis* is the most widespread taxon in Mexico and Guatemala and fairly common or abundant in many regions.

b. ***Pinguicula moranensis*** Kunth **var. *neovolcanica*** Zamudio, Acta Bot. Mex. 49 (1999) 27.

TYPE: MEXICO. *Hidalgo, Barrio Escobar, cerca de la Mina de Morán, municipio de Real del Monte, bosque de encino con Quercus mexicana, alt. 2500 m* (Hidalgo, Barrio Escobar, near ancient Mina de Morán, Municipality of Real del Monte, oak forest with *Quercus mexicana*, alt. 2,500 m), 17 August 1993, *Zamudio 9144* (holotype: IEB!; isotypes: IEB!, MEXU!, TEX!).

SYNONYM: *P. sodalium* Fourn.

DESCRIPTION: Similar to *P. moranensis* var. *moranensis*. Winter leaf 30-80 or more, lanceolate to oblong-lanceolate, thick, apex obtuse to acute, 10-30 mm long, 2-6 mm wide. Winter rosette subglobose.

PHENOLOGY: IV, V, VI, VII, VIII, IX, X. Scape arising mostly from summer rosette.

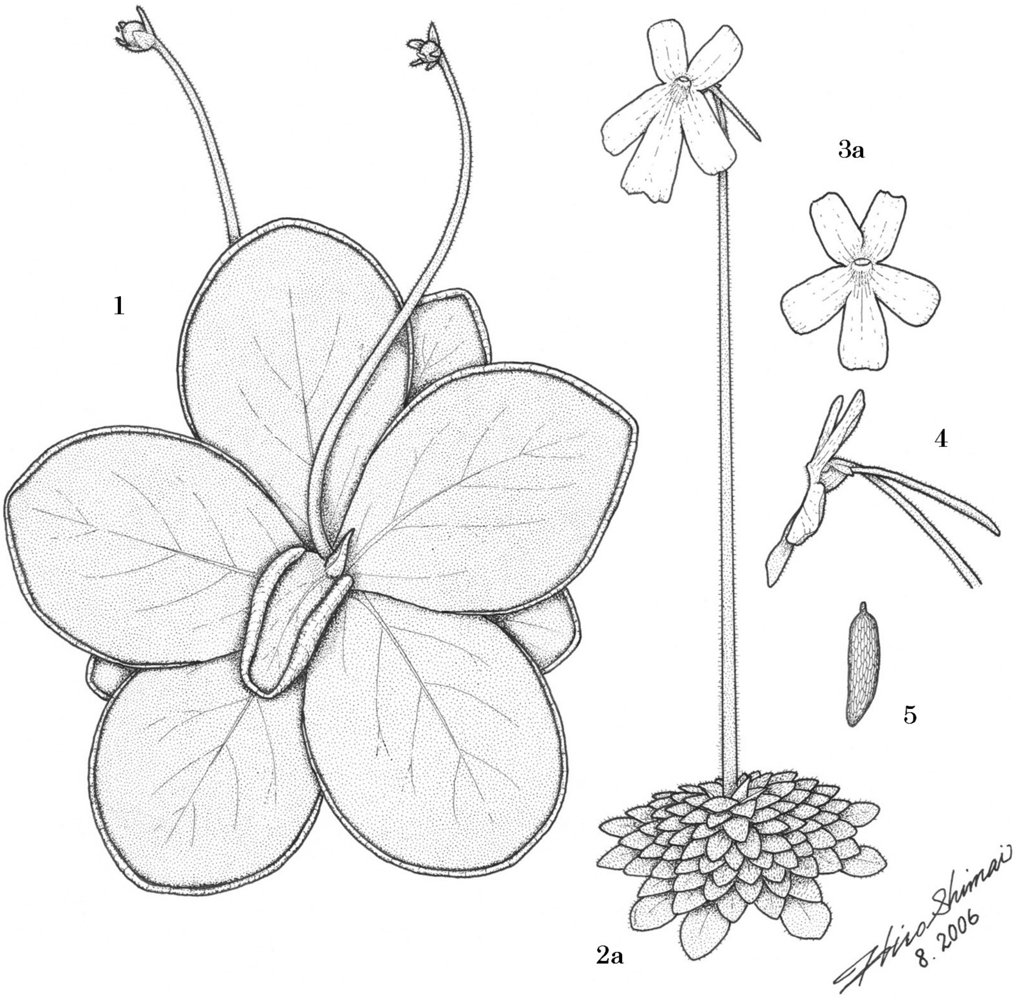
ETYMOLOGY: native of the Eje Neovolcánico Range

HABITAT: Volcanic rocks or sands in oak or pine forests. Tolerant to low light intensity.

DISTRIBUTION: MEXICO (Distrito Federal, Hidalgo, México, Michoacán, Morelos, Oaxaca, Puebla, Querétaro, Tlaxcala, Veracruz). 1,600-3,100 m.

DISCUSSION: *Pinguicula moranensis* var. *neovolcanica* was described by Zamudio (1999b) after examinations of a large number of herbarium specimens of *P. moranensis*. The distribution of the variety is restricted to the mountain areas of the Eje Volcánico Transversal or Eje Neovolcánico region, covering the States of Guerrero, Hidalgo, México, Michoacán, Morelos, Puebla, Tlaxcala, Veracruz, and Distrito Federal. The distribution more or less fits into the region; however, it is also overlapped with that of *P. moranensis* var. *moranensis*. Due to wider morphological variations within *P. moranensis* sensu lato, it is often difficult to divided it at the intraspecific ranks, but *P. moranensis* var. *neovolcanica*, possessing narrower winter leaves with the acute to obtuse tip, forms a more compact subglobose or bulb-like winter rosette than *P. moranensis* var. *moranensis* does (Zamudio 1999b). It is not possible to distinguish the two varieties with their summer rosettes.

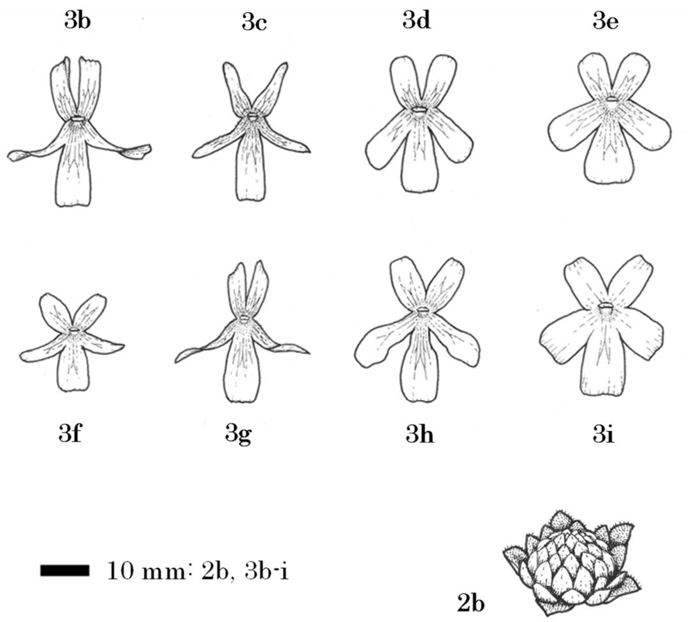
Plate 4.58. *Pinguicula moranensis*



10 mm: 1, 2a, 3a, 4
500 µm: 5

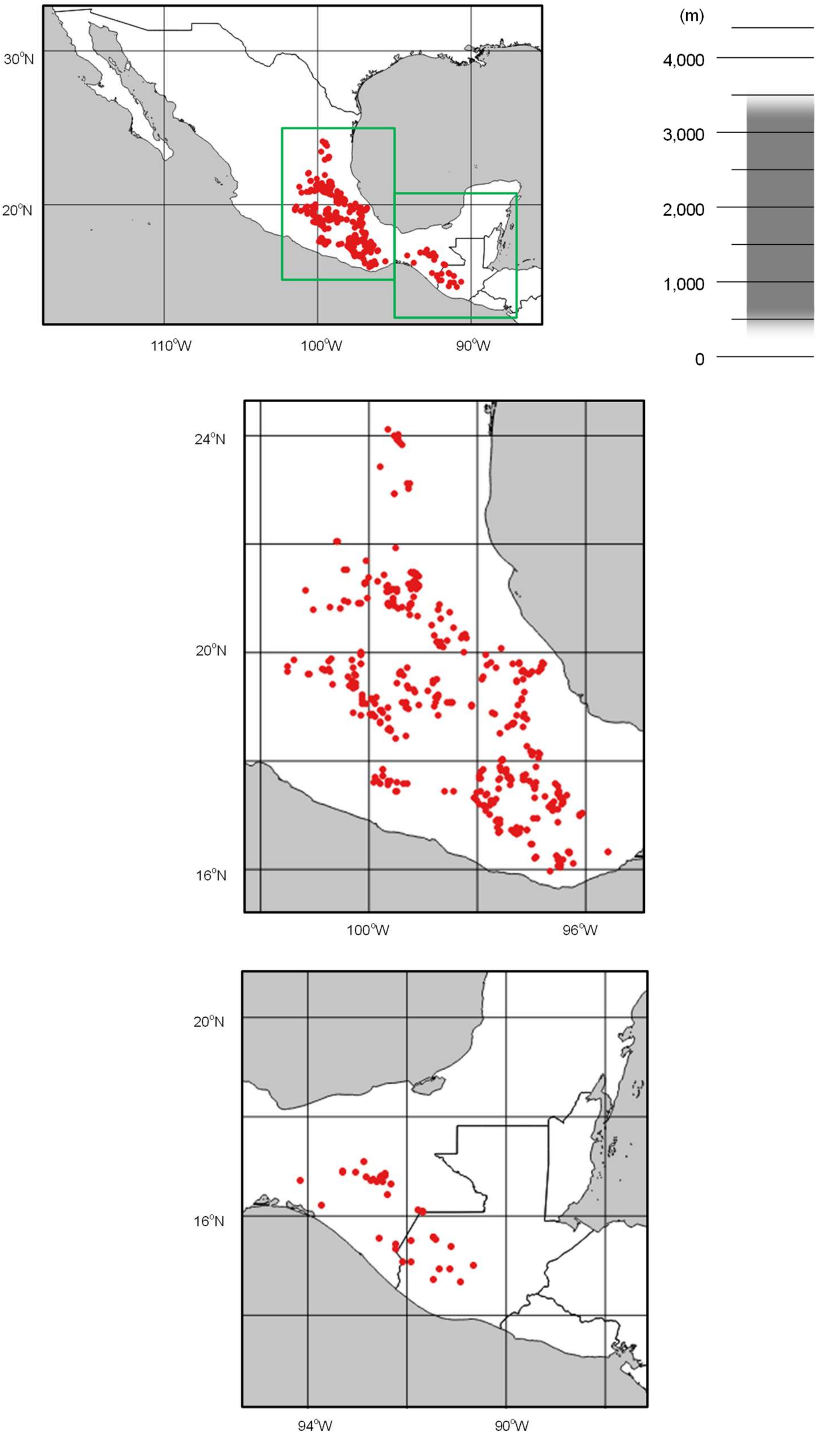
1. summer rosette with fruit
2a. winter rosette with flower
3a. flower, front view
4. flower, lateral view
5. seed
summer leaf (see Plate 4.90)

Plate 4.58. *Pinguicula moranensis* (continued)

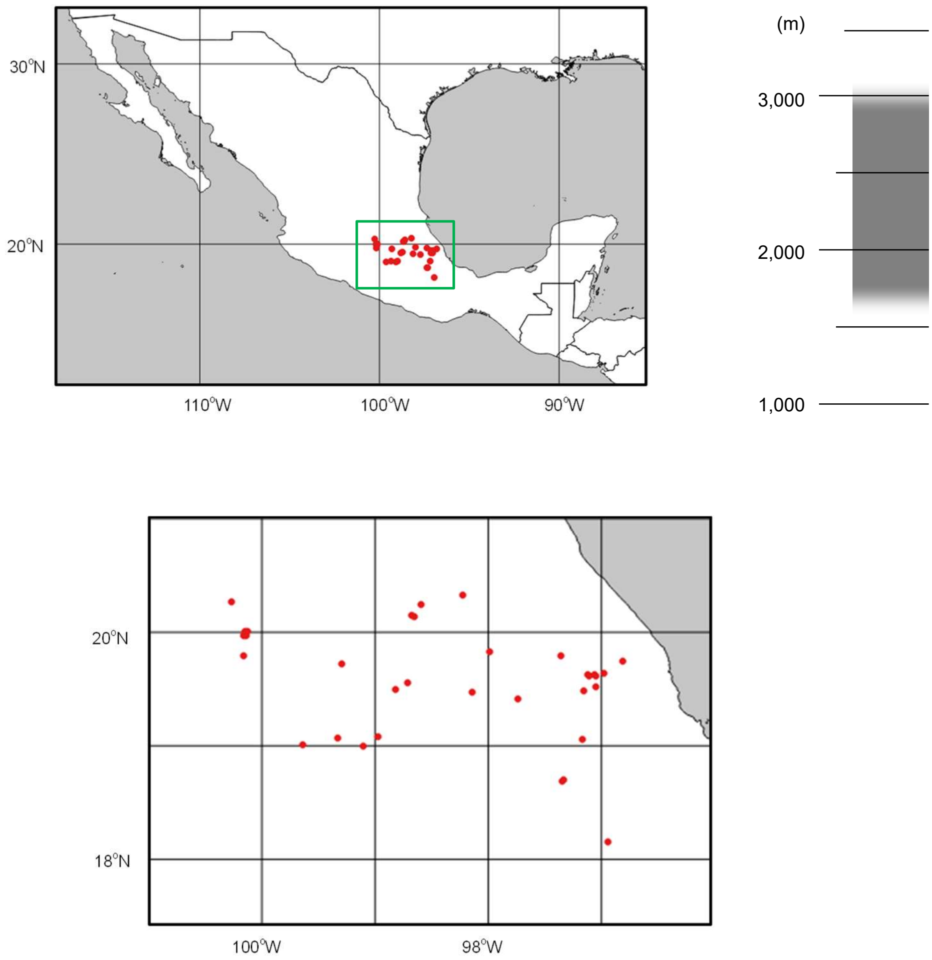


2b. winter rosette (*P. moranensis* var. *neovolcanica*)
3b-i. flower variations

P. moranensis var. *moranensis*



P. moranensis var. *neovolcanica*



59. ***Pinguicula nivalis*** Luhrs et Lampard, Carniv. Pl. Newslett. 35 (2006) 4.

TYPE: MEXICO. Nuevo León, distr. Zaragoza, gypsum hills between Carpinteria and Zaragoza, 1350-1400 m alt., 14 February 1994, *Luhrs & Lampard s.n.* (holotype: IEB!).

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf dimorphic, summer leaf 8-15, yellowish-green, outer margin sometimes maroon, obovate, apical margin narrowly involute, apex obtuse, base rather abruptly spatulate to cuneate, hairy at base, 4-10 mm long, 4-8 mm wide, winter leaf 13-19, oblong, thick, apex rather acute, hairy at margin near base, 4-6 mm long, 1-1.5 mm wide. Winter rosette subglobose, very hairy. Scape 1-2, glabrous, 20-70 mm long. Calyx bilabiate, upper lip 3-lobed, lobes oblong-ovoid, 1-2.5 mm long, lower lip 2-lobed, lobes slightly smaller than uppers. Flower white, yellowish-green in throat. Corolla bilabiate, 10-15 mm across, zygomorphic, 11-16 mm long including spur, upper lip 2-lobed, lobes broadly ovate, lower lip 3-lobed, lobes larger than uppers, lateral lobes obliquely obovate, middle lobe obovate to cuneate, tip emarginate, much wider than laterals, tube yellowish-green, very short, conical, spur yellowish-green, cylindrical, 3-5 mm long. Capsule globose. Seed unknown. $2n = 22$. (Plate 4.59).

PHENOLOGY: II, III. Scape arising from winter rosette.

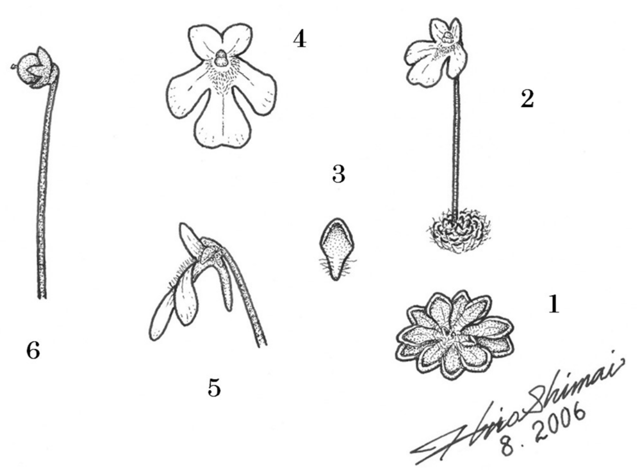
ETYMOLOGY: whitish (referring to the flower)

HABITAT: Dry gypsum hillside. Tolerant to various light intensities.

DISTRIBUTION: MEXICO (Nuevo León). 1,350-1,400 m.

DISCUSSION: *Pinguicula nivalis* is found only in the State of Nuevo León, Mexico. In February 1994, H. Luhrs and S. E. Lampard collected specimens and after careful observations, they concluded that it was morphologically different from *P. immaculata* but was a new species, i.e. *P. nivalis* (Luhrs and Lampard 2006). In comparison to *P. immaculata*, *P. nivalis* has larger lobes of the upper lip and more numbers of summer leaves. It is, however, often difficult to distinguish between *P. nivalis* and *P. immaculata* by specimens without flowers.

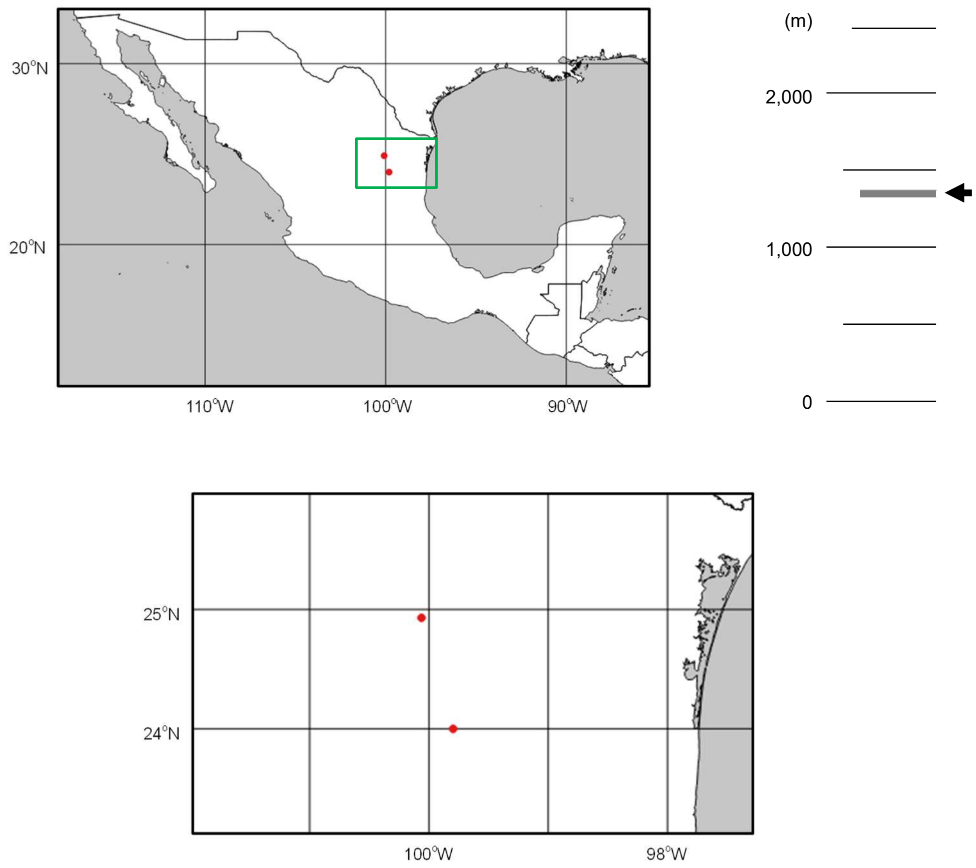
Plate 4.59. *Pinguicula nivalis*



10 mm: 1, 2, 3
5 mm: 4, 5, 6

1. summer rosette
2. winter rosette with flower
3. summer leaf
4. flower, front view
5. flower, lateral view
6. capsule

P. nivalis



60. ***Pinguicula oblongiloba*** DC., Prodr. 8 (1844) 27.

TYPE: in Calq. Dess. Fl. Mex. 2, Fig. 1071-2. (lectotype?: in De Candolle 1874!)

SYNONYMS: *P. caudata* Hemsley, *P. vulgaris* Sessé et Mociño

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf dimorphic, summer leaf 2-8, yellowish-green or maroon, ovate to suborbicular, margin narrowly involute, apex obtuse, 15-75 mm long, 12-55 mm wide, petiole up to 40 mm long, winter leaf up to 90, lanceolate, thick, apex acute to acuminate, 5-30 mm long, 2-10 mm wide. Winter rosette subglobose. Scape 1-6, densely glandulous, 50-230 mm long. Calyx bilabiate, upper lip 3-lobed, lobes lanceolate, 4-5 mm long, lower lip 2-lobed, lobes slightly smaller than uppers. Flower dark pink to pinkish-purple, white at base of lower lip, yellowish-green in throat. Corolla bilabiate, 25-35 mm across, zygomorphic, 28-42 mm long including spur, upper lip 2-lobed, lobes oblong-obovate to suborbicular, lower lip 3-lobed, lobes usually narrower and longer than uppers, obovate to oblong-obovate, lateral lobes often reflexed to twisted, tube pale purple, very short, conical, spur yellowish-green to pale purple, cylindrical, recurved, 13-30 mm long. Capsule subglobose. Seed ellipsoid. $2n = 22$. (Plate 4.60).

PHENOLOGY: V, VI, VII, VIII, IX, X. Scape arising from summer rosette.

ETYMOLOGY: oblong-lobed (referring to the flower)

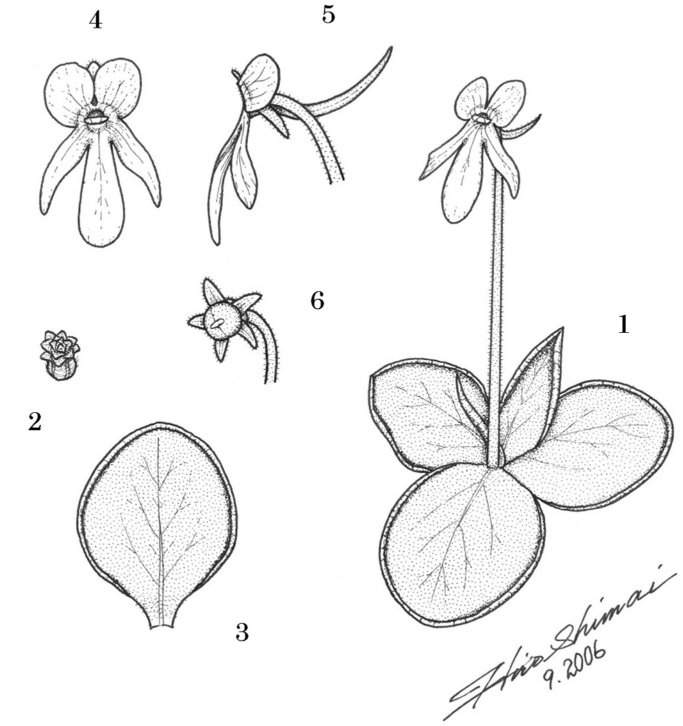
HABITAT: Mossy loam in slopes in pine forests. Moderate to low light intensity.

NATURAL HYBRID: X *P. parvifolia*?

DISTRIBUTION: MEXICO (Aguascalientes, Chihuahua, Colima, Durango, Guanajuato, Jalisco, México, Michoacán, Nayarit, Sonora, Zacatecas). 1,067-2,880 m.

DISCUSSION: *Pinguicula oblongiloba* is widely distributed in the Sierra Madre Occidental and stretching southeast to the States of Michoacán and México. Although it was described in an early time by De Candolle (1844) showing a wider distribution area, the species is poorly known even today. Historically, *P. oblongiloba* has been confused with a few other species, such as *P. macrophylla* or *P. orchidioides*. *P. oblongiloba* is a somewhat morphologically variable species, particularly in the shape of corolla lobes, but it basically has oblong lobes of the lower lip. *P. oblongiloba* has more pinkish flowers than *P. macrophylla*, which has more purple flowers. *P. oblongiloba* does not produce runners whereas *P. orchidioides* often produces them. The distribution area does not overlap with that of *P. orchidioides*.

Plate 4.60. *Pinguicula oblongiloba*

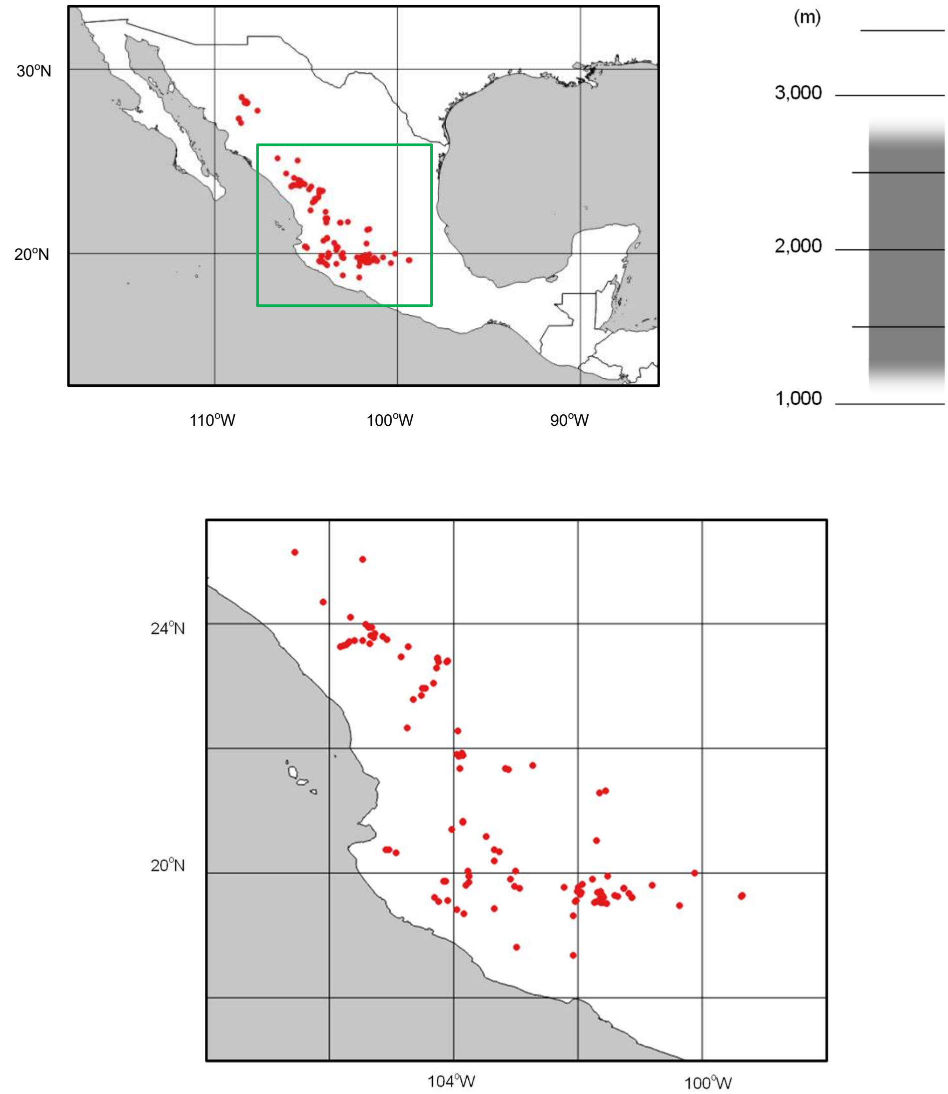


10 mm: 1, 2, 3

10 mm: 4, 5, 6

1. summer rosette with flower
2. winter rosette
3. summer leaf
4. flower, front view
5. flower, lateral view
6. capsule

P. oblongiloba



61. ***Pinguicula orchidioides*** DC., Prodr. 8 (1844) 27.

TYPE: MEXICO. *in humidis montis San Felipe Oaxacae Mexicanorum* (Oaxaca, in wet mountains Cerro San Felipe), *Andrieux 130* (holotype: G-DC!).

SYNONYM: *P. stolonifera* Luhrs

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf dimorphic, summer leaf 2-8, yellowish-green or maroon, oblong-ovate to oblong-lanceolate, margin often strongly involute, apex obtuse to rather acute, 18-46 mm long, 6-18 mm wide, petiole 10-40 mm long, hairy at margin, winter leaf 25-36, ovate to lanceolate, thick, apex acute to acuminate, hairy at margin, 5-11 mm long, 1-3 mm wide. Winter rosette subglobose. Runner aerial, producing clonal plantlet at apex. Scape 1-4, densely glandulous only upper part, 70-220 mm long. Calyx bilabiate, upper lip 3-lobed, lobes lanceolate, 2-3 mm long, lower lip 2-lobed, lobes smaller than uppers. Flower reddish-purple, white spot or stripe at base of lower lip. Corolla bilabiate, 25-35 mm across, zygomorphic, 30-51 mm long including spur, upper lip 2-lobed, lobes oblong ovate to oblong-lanceolate, lower lip 3-lobed, lobes elliptic to oblong-lanceolate, usually narrower than uppers, middle lobe larger than laterals, laterals often reflexed to twisted, tube pale purple with darker veins, very short, conical, spur pale purple, cylindrical, 16-30 mm long. Capsule ovoid. Seed ellipsoid, 520-840 X 150-200 µm. $2n = 22$. (Plate 4.61).

PHENOLOGY: V, VI, VII, VIII, IX, X. Scape arising from summer rosette.

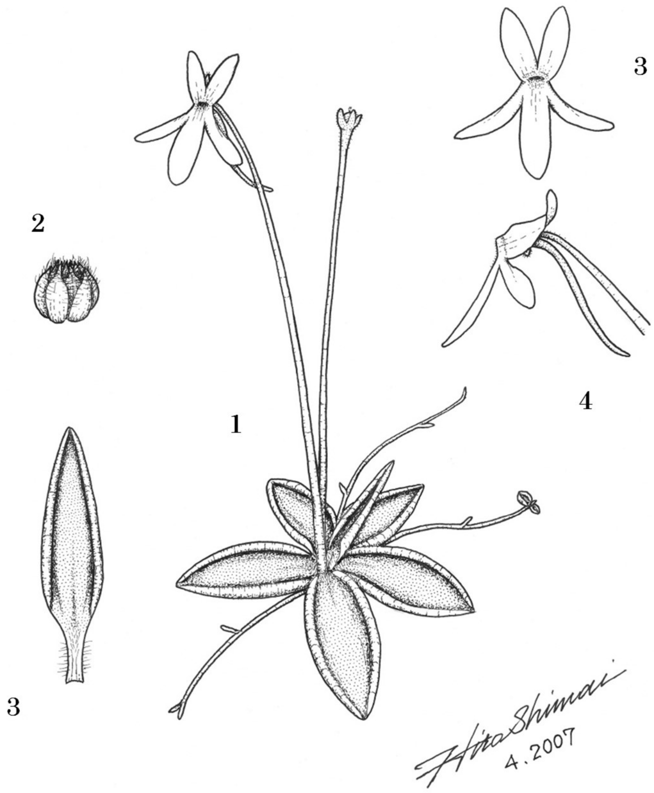
ETYMOLOGY: resembling the orchid (referring to the flower)

HABITAT: Wet rocks in slopes or on brown to reddish-brown clay or sandy clay soils in pine and oak forests. Low light intensity.

DISTRIBUTION: GUATEMALA (Sololá); MEXICO (Guerrero, Oaxaca). 1,000-3,000 m.

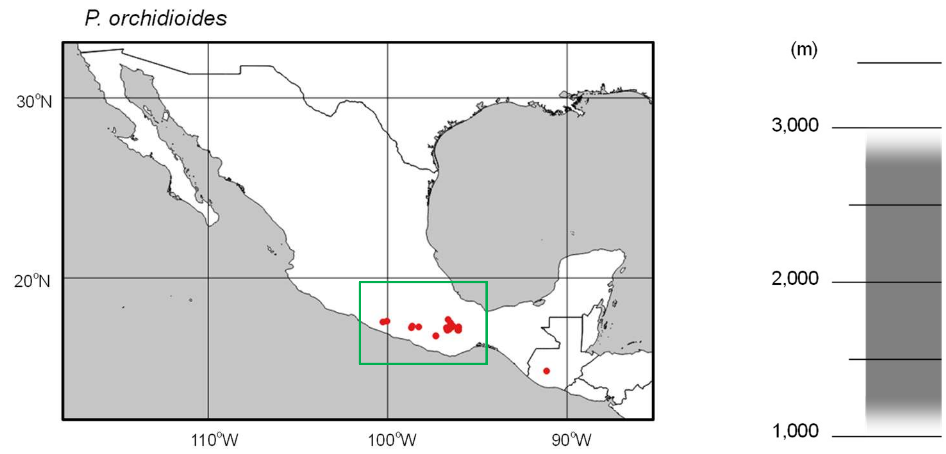
DISCUSSION: *Pinguicula orchidioides* is distributed in Mexico and Guatemala. This species was described by De Candolle (1844) based on the specimen collected at San Felipe, the neighbouring mountain area of the City of Oaxaca. Casper (1966a), however, did not recognise the species. More recently, Luhrs (1995a) described *P. stolonifera*, uniquely producing runners, from the material collected in the State of Oaxaca, but it is synonymous with *P. orchidioides* (Zamudio 1998). *P. orchidioides* is morphologically similar to *P. oblongiloba*, but *P. orchidioides* often has runners producing a plantlet at the apex and clonal plantlets at the base of winter rosette. It has been confirmed only in the States of Guerrero and Oaxaca in Mexico and the Department of Sololá in Guatemala.

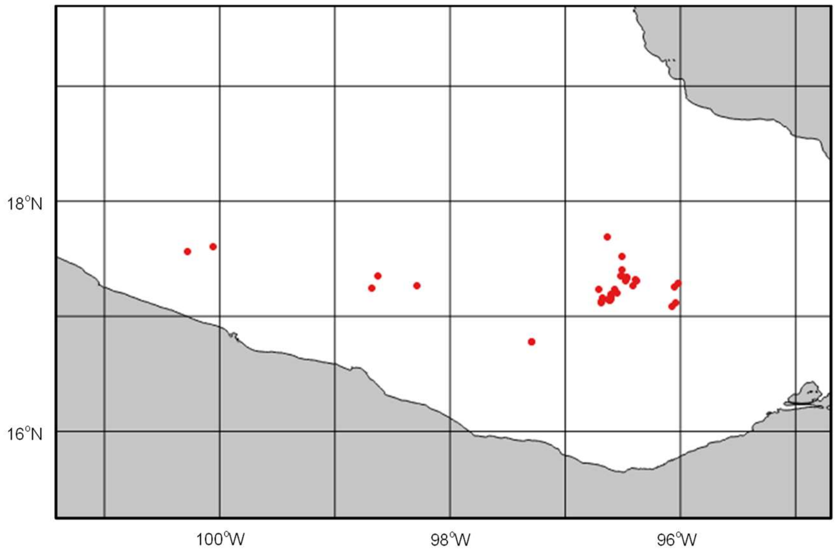
Plate 4.61. *Pinguicula orchidioides*



10 mm: 1, 2, 3
10 mm: 4, 5

1. summer rosette with flower and fruit
2. winter rosette
3. summer leaf
4. flower, front view
5. flower, lateral view


P. orchidioides
30°N
20°N
110°W
100°W
90°W
(m)
3,000
2,000
1,000


18°N
16°N
100°W
98°W
96°W

62. ***Pinguicula parvifolia*** Robinson, Proc. Am. Acad. Arts and Sci. 29 (1894) 320.

TYPE: MEXICO. collected on mossy gravel bluffs near Guadalajara, 23 June 1893, *Pringle 4397* (holotype?: ZT!; isotypes: BM!, BR!, COLO, E!, GOET!, IEB-photo ex-NY!, K!, LE!, MANCH!, MEXU!, MO!, MSC!, MU!, NY!, P!, WU!).

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf dimorphic, summer leaf 4-10, yellowish-green or maroon, oblong to oblong-ovate, margin narrowly involute, apex obtuse to rather acute, 8-30 mm long, 5-12 mm wide, hairy at base, petiole short but distinctive, winter leaf 10-15, oblong-lanceolate, apex acute to rather acuminate, 8-18 mm long, 3-6 mm wide. Winter rosette subglobose. Scape 1-3, glabrous, 30-100 mm long. Calyx bilabiate, upper lip 3-lobed, lobes lanceolate, ca. 3 mm long, connate at base, lower lip 2-lobed, lobes similar to uppers. Flower entirely white, or sometimes faintly pale lilac at lobe margins, purple in throat. Corolla bilabiate, 12-20 mm across, zygomorphic, 12-21 mm long including spur, upper lip 2-lobed, lobes oblong to obovate-oblong, lower lip 3-lobed, lobes similar to uppers but slightly larger, tube faintly pale purple, cylindrical, spur pale green, cylindrical, 2-5 mm long. Capsule subglobose. Seed unknown. (Plate 4.62).

PHENOLOGY: V, VI, VII, VIII. Scape arising from summer rosette.

ETYMOLOGY: small-leaved

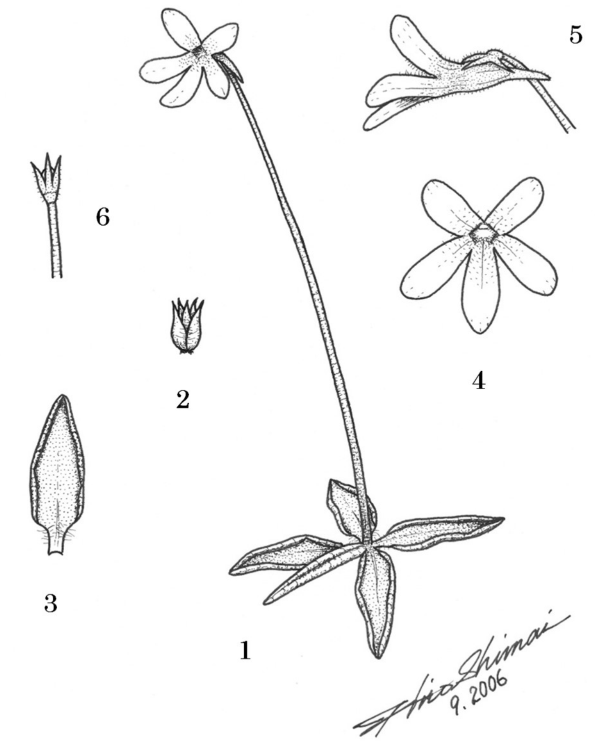
HABITAT: Mossy gravel bluffs. Low light intensity.

NATURAL HYBRID: X *P. oblongiloba*?

DISTRIBUTION: MEXICO (Durango, Jalisco, México, Michoacán, Morelos, Nayarit, Puebla, Sinaloa, Zacatecas). 1,372-2,750 m.

DISCUSSION: *Pinguicula parvifolia* is distributed in the Sierra Madre Occidental, Mexico. The first herbarium specimen was collected in June 1893 by C. G. Pringle, and it was described as a *P. parvifolia* in the following year by Robinson (1894). The species possesses narrower summer leaves with a more or less distinctive petiole at the base and white to faintly pale lilac flowers. The flower of the species is somewhat similar to that of *P. heterophylla* or *P. medusina*, but it can be distinguishable by their summer leaves. Despite its wider distribution area, information on the habitat is poorly known. According to Zamudio (per. com.), some populations having pale purple flowers may be hybrids with *P. oblongiloba*.

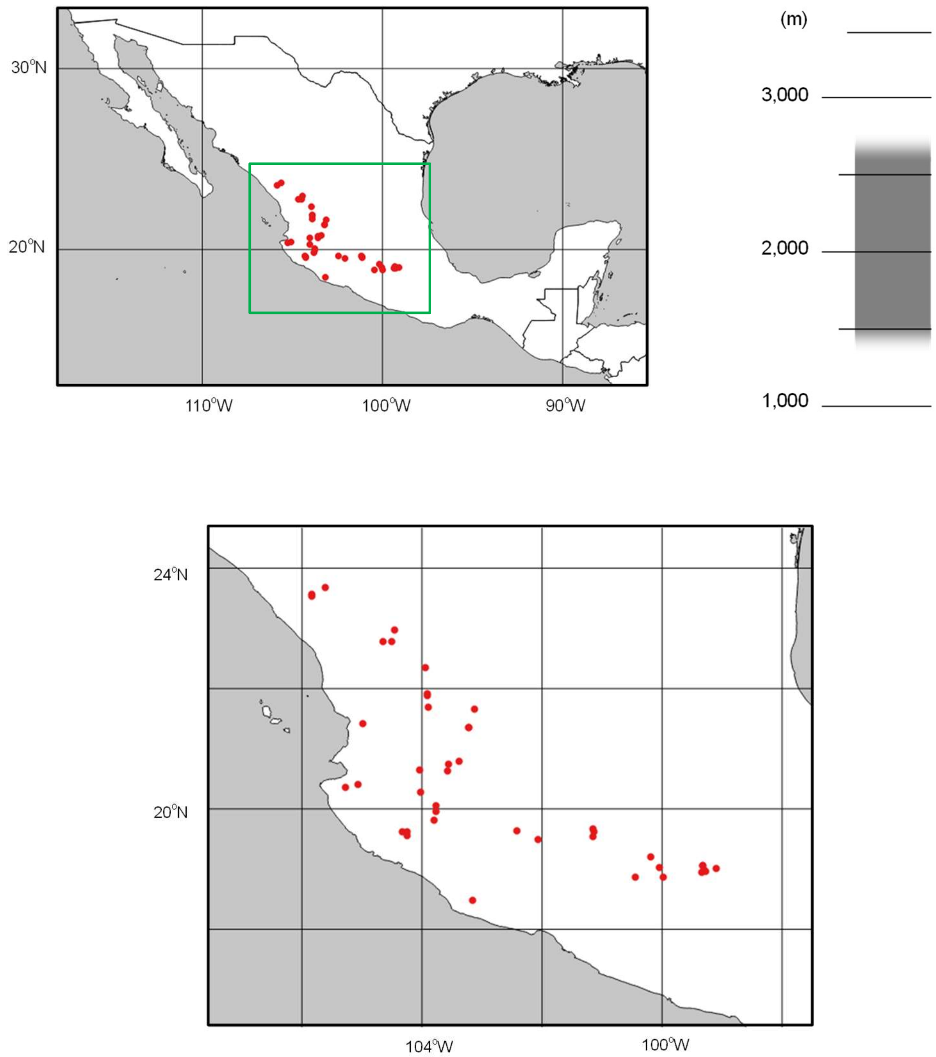
Plate 4.62. *Pinguicula parvifolia*



10 mm: 1, 2, 3
10 mm: 4, 5, 6

1. summer rosette with flower
2. winter rosette
3. summer leaf
4. flower, front view
5. flower, lateral view
6. capsule

P. parvifolia



63. ***Pinguicula pilosa*** Luhrs, Studnička et Gluch, Carniv. Pl. Newslett. 33 (2004) 43.

TYPE: MEXICO. Tamaulipas, distr. Casas, Sierra de Tamaulipas, near El Cabrito, A. Lau s.n., cultivated in the Botanical Garden of Liberec, 29 January 1996, *Studnička* (holotype: TEX!).

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf dimorphic, summer leaf 8-12, yellowish-green, rather thick, obovate to suborbicular, margin narrowly involute, apex obtuse, base spatulate to cuneate, 25-40 mm long, 20-30 mm wide, winter leaf 12-18, oblanceolate to spatulate, thick, apex obtuse, 10-20 mm long, 6-12 mm wide. Winter rosette acetabuliform. Scape 1-3, densely glandulous, 35-90 mm long. Calyx bilabiate, upper lip 3-lobed, lobes ovate to oblong, 2.5-3 mm long, connate at base, lower lip 2-lobed, lobes slightly longer than uppers. Flower faintly pale purple, paler at lower half of lobes, or sometimes entirely white, yellowish-green to yellow in throat. Corolla bilabiate, 17-20 mm across, subactinomorphic, 16-25 mm long including spur, surface of lobes pilose entirely, upper lip 2-lobed, lobes broadly obovate to cuneate, lower lip 3-lobed, lobes similar to uppers, lateral lobes rather oblique, tube yellowish-green, cylindrical, spur yellowish-green, cylindrical, slightly incurved, 4-5 mm long. Capsule subglobose. Seed unknown. $2n$ = 22. (Plate

4.63).

PHENOLOGY: No data (I—IV according to the original description). Scape arising from winter rosette.

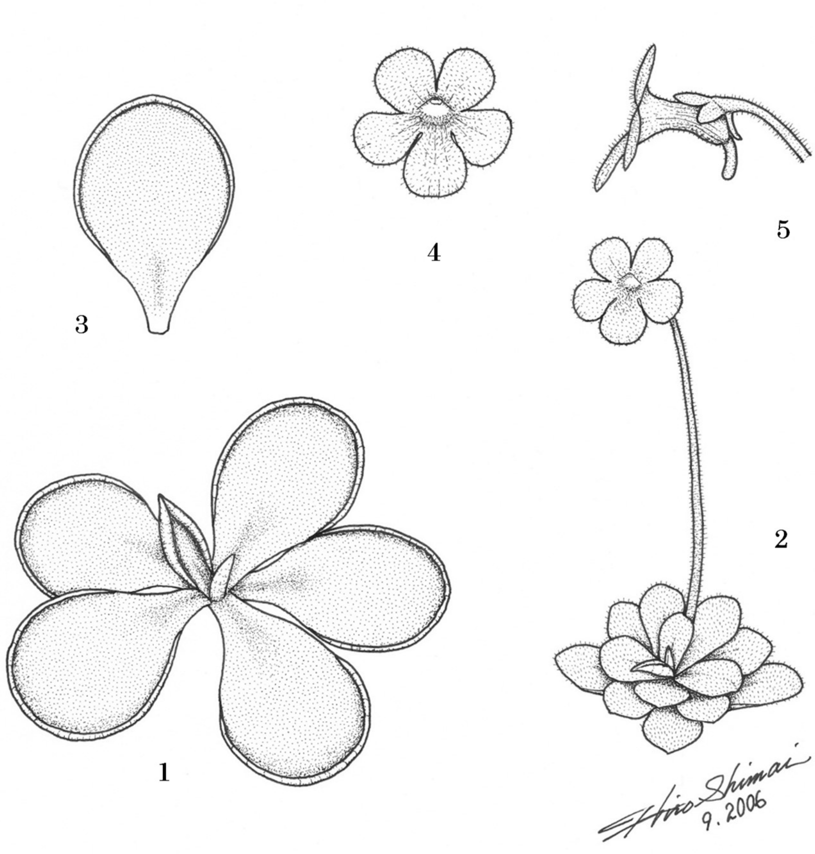
ETYMOLOGY: pilose (referring to the scape and calyx)

HABITAT: remote mountain range

DISTRIBUTION: MEXICO (Tamaulipas). Known only from the type locality.

DISCUSSION: *Pinguicula pilosa* is endemic to the State of Tamaulipas, Mexico, and has been hitherto known only from the type locality. It was initially collected by Alfred B. Lau and was cultivated among horticulturalists since around 1984 under various names, such as *P.* sp. "Sierra de Tamaulipas" or *P.* sp. "El Cabrito". To prevent possible future taxonomic confusions, Luhrs et al. (2004) described it as *P. pilosa* based on the materials cultivated at the Botanical Garden of Liberec, the Czech Republic. It is morphologically similar to a few other species, such as *P. conzattii* or *P. mirandae*, both of which are endemic to the State of Oaxaca, but *P. pilosa* can be distinguishable from them by having more rounded corolla lobes, densely and entirely covered by trichomes on the surface. The specific epithet refers to the hairy scape and calyx (Luhrs et al. 2004), but more characteristically the surface of the corolla lobes are hairy entirely. The current status at the habitat is unknown.

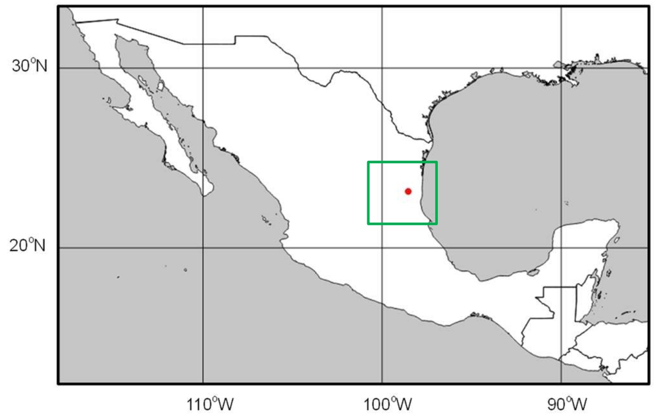
Plate 4.63. *Pinguicula pilosa*

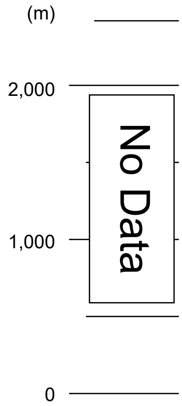


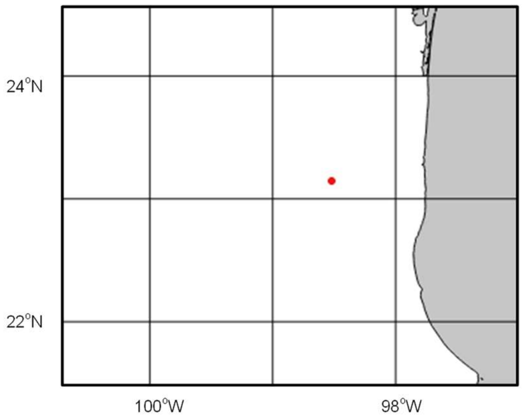
10 mm: 1, 2, 3
10 mm: 4, 5

1. summer rosette
2. winter rosette with flower
3. summer leaf
4. flower, front view
5. flower, lateral view

P. pilosa







64. ***Pinguicula potosiensis*** Speta et Fuchs, Phyton (Austria) 29 (1989) 100.

TYPE: MEXICO. *San Luis Potosí , 48 km östlich von San Luis Potosí in Richtung Río Verde, 1940 m* (San Luis Potosí, 48 km east of San Luis Potosí, way to Río Verde 1,940 m), Ehlers, cult. Botanical Garden of Linz, 9 April 1987, (holotype: Herb. Speta; isotype: LI?).

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf dimorphic, summer leaf 15-20, bright green or maroon, elliptic to oblong, margin narrowly involute, apex obtuse, base cuneate, 30-85 mm long, 25-40 mm wide, winter leaf 30-40, obovate, thick, apex acute, ca. 20 mm long, 6-9 mm wide. Winter rosette acetabuliform. Scape 2-5, densely glandulous, 80-260 mm long, Calyx bilabiate, upper lip 3-lobed, lobes oblong-lanceolate, ca. 4.5 mm long, lower lip 2-lobed, lobes smaller than uppers. Flower purple to reddish-purple, often darker at base of lips, white spots or stripes at base of lower lip. Corolla bilabiate, 30-40 mm across, zygomorphic, 35-40 mm long including spur, upper lip 2-lobed, lobes broadly obovate to oblong, tip obtuse to rather truncate, lower lip 3-lobed, lobes larger than uppers, often overlapping at base, lateral lobes obliquely oblong, middle lobe cuneate, tip truncate to shallowly emarginate, tube pale purple, very short, shortly conical, spur pale green, cylindrical, incurved to pendulous, 23-30 mm long. Capsule globose. Seed fusiform-ellipsoid, 840-1,050 X 150-210 μm. (Plate 4.64).

PHENOLOGY: No data (II—VII according to the original description). Scape arising from late winter rosette or summer rosette.

ETYMOLOGY: native of San Luis Potosí

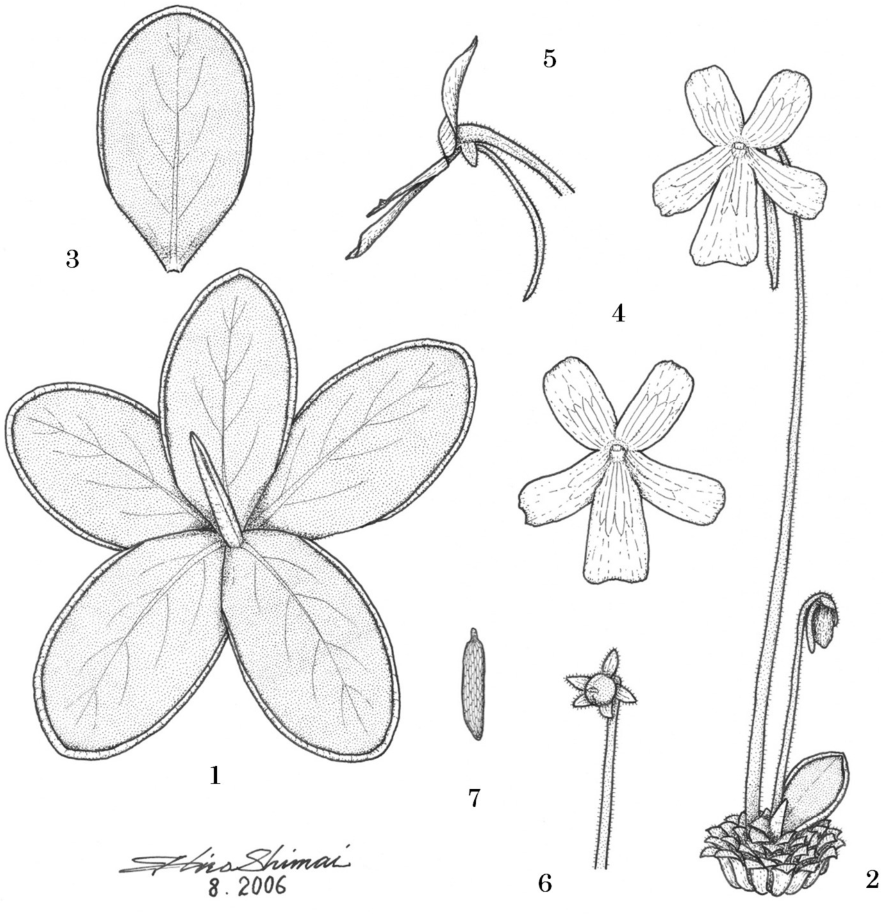
HABITAT: Mossy calcareous rocks in forests. Low light intensity.

DISTRIBUTION: MEXICO (San Luis Potosí). Known only from the type locality. 1,940 m.

DISCUSSION: *Pinguicula potosiensis* was first discovered by R. Ehlers in the State of San Luis Potosí, Mexico and described by Speta and Fuchs (1989) based on the cultivated materials. The type specimens are likely Franz Speta's personal collections and those are not seen in LI. It is morphologically very similar to *P. moranensis* var. *moranensis*, but can be distinguished by having a more compact winter rosette, narrower corolla lobes and darker purple flower colour (Speta and Fuchs 1989). Zamudio (2001b) treated it as a synonym of *P. moranensis* var. *moranensis*, but DNA sequences inferred that those might be different taxa, so that those are treated as different species here to avoid future possible confusions. The type locality is the only hitherto known locality but *P.*

moranensis var. *morenensis* recorded in Nuevo León and Tamaulipas may need a review. The current status of the species at the habitat is unknown.

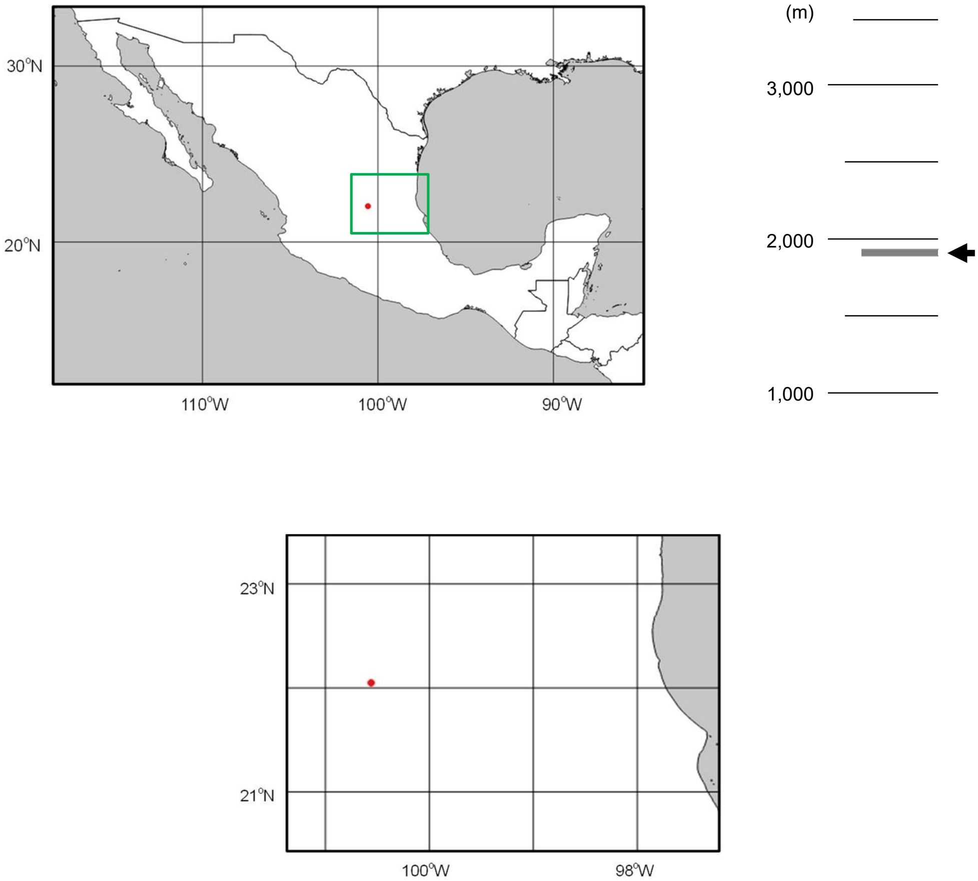
Plate 4.64. *Pinguicula potosiensis*



10 mm: 1, 2, 3, 4, 5, 6
500 µm: 7

1. summer rosette
2. winter rosette with flower
3. summer leaf
4. flower, front view
5. flower, lateral view
6. capsule
7. seed

P. potosiensis



65. ***Pinguicula rectifolia*** Speta et Fuchs, Phyton (Austria) 29 (1989) 97.

TYPE: MEXICO. Oaxaca, distr. Juxtlahuaca, Sierra Madre del Sur, Presa Morelos/Río Balsas, ca. 98°10'/17°20', NW Putla de Guerrero, 1340 m, Schatzl, cult. at Botanical Garden of Linz, 9 April 1987 & 2 July 1987 (holotype: Herb. Speta; isotype: LI?).

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf dimorphic, summer leaf 15-20, bright green, ovate to rhombate, margin narrowly involute, apex obtuse, 40-70 mm long, 20-37 mm wide, winter leaf 30-45, lanceolate, thick, apex obtuse to rather acute, 30-40 mm long, 10-14 mm wide. Winter rosette acetabuliform, leaves often subelect. Scape 1-7, densely glandulous, 80-160 mm long. Calyx bilabiate, upper lip 3-lobed, lobes elliptic-ovate, ca. 4 mm long, lower lip 2-lobed, lobes smaller than uppers, connate to middle. Flower pink to reddish-purple, darker purple veins at base of lips, white spots or stripes at base of lower lip. Corolla bilabiate, 25-35 mm across, zygomorphic, ca. 60 mm long including spur, upper lip 2-lobed, lobes elliptic-obovate to oblong-obovate, tip rather truncate and irregularly undulate, lower lip 3-lobed, similar to uppers but larger, irregularly undulate at tip, lateral lobes oblique and slightly twisted, middle lobe rather cuneate, tube pink, very short, shortly conical, spur faintly pale green to pale purple, cylindrical, incurved near tip, 18-30 mm long. Capsule subglobose, 900-1,050 X 180-260 µm. Seed narrowly ellipsoid. $2n = 22$. (Plate 4.65).

PHENOLOGY: No data (IV–XI according to the original description). Scape arising from summer rosette.

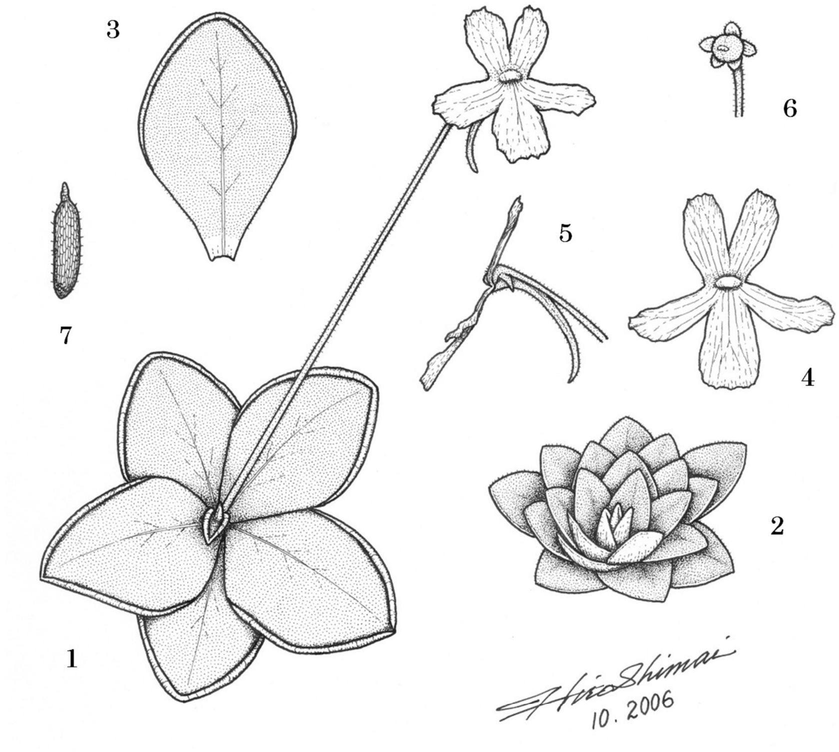
ETYMOLOGY: erect-leaved

HABITAT: Unknown

DISTRIBUTION: MEXICO (Oaxaca). Known only from the type locality. 1,340 m.

DISCUSSION: *Pinguicula rectifolia* has been recorded only from the State of Oaxaca, Mexico. It was originally collected at the area between Santiago Juxtlahuaca and Putla, close to the Oaxaca-Guerrero state border, by St. Schatal and was described as *P. rectifolia* based on the materials cultivated at the Botanical Garden of Linz, Austria, by Speta and Fuchs (1989). All type specimens are likely Franz Speta's personal collections and the isotype is not seen at LI. It is morphologically very similar to *P. moranensis* and actually Zamudio (2001b) treated it as synonymous with *P. moranensis*. The winter leaf is subelect and the tip of corolla lobes is undulate in *P. rectifolia* that can be distinguished from *P. moranensis*. In this study, *P. rectifolia* is considered to be a distinct species since closer phylogenetic relationships to other species have been implied rather than *P. moranensis*. The actual distribution range and the current status at the habitat remain unknown.

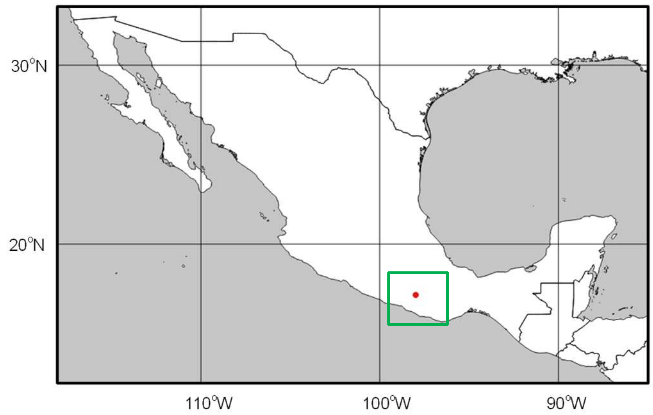
Plate 4.65. *Pinguicula rectifolia*

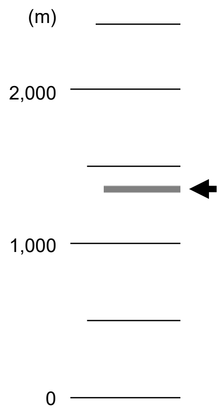


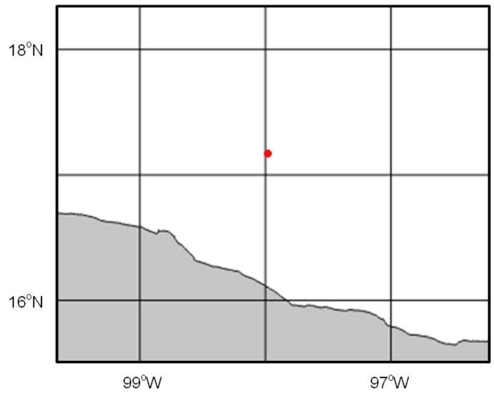
10 mm: 1, 2, 3
10 mm: 4, 5, 6
500 µm: 7

1. summer rosette with flower
2. winter rosette
3. summer leaf
4. flower, front view
5. flower, lateral view
6. capsule
7. seed

P. rectifolia







66. ***Pinguicula rotundiflora*** Studnička, Folia Geobot. Phytotax. 20 (1985) 201.

TYPE: MEXICO. *Oaxaca, prope Minas de Asbestos, 2200 m* (Oaxaca, near Minas de Asbestos, 2,200 m), leg R. Šubík & J. Říha (1977), cultivated at Liberec Botanical Garden, winter rosette, 20 January 1984, *Studnička s.n.* (holotype: LIM; isotype: PR).

SYNONYM: *P. jorgehintonii* Turner

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf dimorphic, summer leaf 10-16, yellowish-green, outer margin sometimes maroon, rather thick, obovate, apical margin narrowly involute, apex obtuse base rather abruptly cuneate, 5-16 mm long, 3-8 mm wide, winter leaf 30-50, spatulate, thick, apex obtuse, 3-15 mm long, 2-4 mm wide. Winter rosette acetabuliform. Scape 1-2, glabrous, 40-70 mm long. Calyx bilabiate, upper lip 3-lobed, lobes oblong-lanceolate, ca. 2 mm long, lower lip 2-lobed, lobes smaller than uppers. Flower white to faintly pale purple, sometimes pale yellow at base of lower lip, purple in throat. Corolla bilabiate, 13-20 mm across, subactinomorphic, ca. 16 mm long including spur, upper lip 2-lobed, lobes broadly obovate, tip truncate, lower lip 3-lobed, lobes similar to upper lips but only slightly larger, tube faintly pale purple with darker veins, subcylindrical, spur yellow or pale purple, cylindrical, 5-6 mm long. Capsule globose. Seed narrowly ellipsoid. $2n = 22$. (Plate 4.66).

PHENOLOGY: II, III, XI. Scape arising from winter rosette.

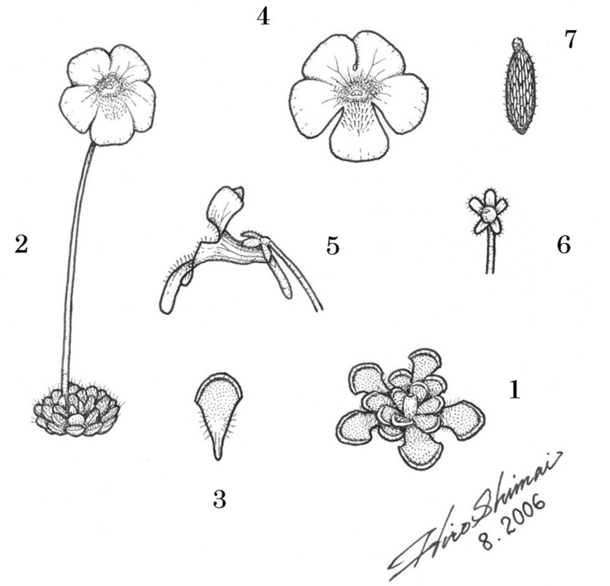
ETYMOLOGY: round-flowered

HABITAT: Calcareous rocks in a forest. Tolerant to low light intensity.

DISTRIBUTION: MEXICO (Nuevo León, Tamaulipas). 1,025-2,200 m.

DISCUSSION: *Pinguicula rotundiflora* is distributed in the States of Nuevo León and Tamaulipas, Mexico. The plant was initially collected by R. Šubík and J. Říha, Czechslovakian cactus collectors, in 1977, at Minas de Asbestos in the State of Tamaulipas [it was erroneously located in the state of Oaxaca in the original description by Studnička (1985), but was later corrected by Zamudio (1992), and was described as *P. rotundiflora*, based on the cultivated materials at the Botanical Garden of Liberec, the Czech Republic (Studnička 1985). Afterwards, Turner (1994) described *P. jorgentonii* from the State of Nuevo León, but Luhrs (1995a) suggested that it was synonymous with *P. rotundiflora*. It can be easily recognised by the flower which is more or less circular appearance. The actual distribution area and the current status at the habitat are poorly known.

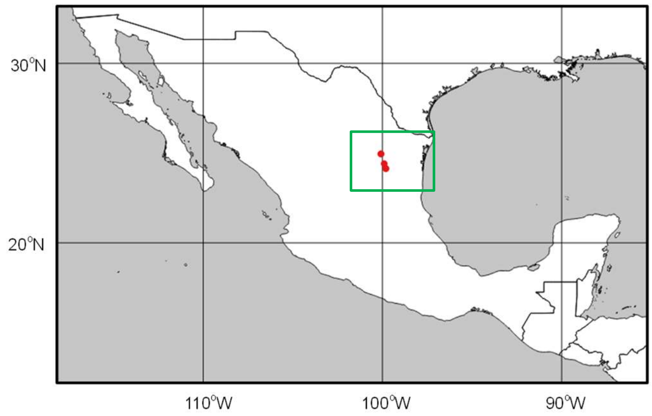
Plate 4.66. *Pinguicula rotundiflora*

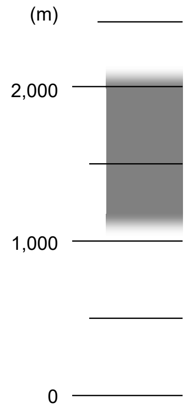


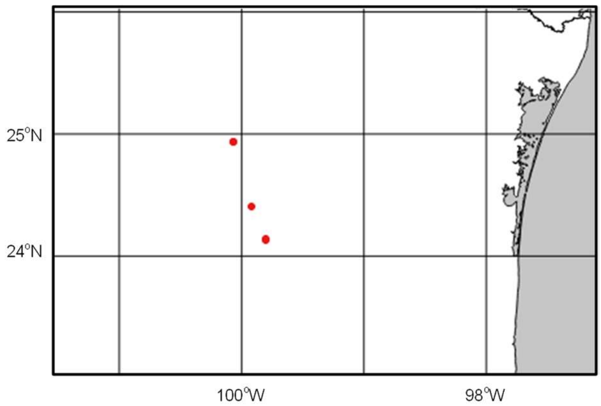
10 mm: 1, 2, 3
10 mm: 4, 5, 6
300 µm: 7

1. summer rosette
2. winter rosette with flower
3. summer leaf
4. flower, front view
5. flower, lateral view
6. capsule (immature)
7. seed

P. rotundiflora







67. ***Pinguicula utricularioides*** Zamudio et Rzedowski, Acta Bot. Mex. 14 (1991) 28.

TYPE: MEXICO. *Oaxaca, Cerro Azul al norte de Niltepec, alt. 6000-7000 ft.* (Oaxaca, Cerro Azul, north of Niltepec, alt. 2,000-2,300 m), 7 March 1956, *MacDougall s.n.* (holotype: MEXU!; isotype: IEB!).

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf dimorphic, summer leaf 1-4?, orbicular and deeply concave to saccate, 2-4 mm in diameter, petiolate, 10-25 mm long including petiole, winter leaf 14-23, spatulate, base petiolate, apex obtuse to rather acute, 5-20 mm long, 1-2.5 mm wide. Winter rosette lenticular? Scape 1, densely glandulous, 50-90 mm long. Calyx bilabiate, upper lip 3-lobed, lobes oblong, 2-3 mm long, lower lip lobe not divided, emarginate at tip, slightly larger than uppers. Flower reddish? Corolla bilabiate, ca. 15 mm across, zygomorphic, 27-37 mm long including spur, upper lip 2-lobed, lobes obovate-cuneate, tip emarginate, lower lip 3-lobed, lobes oblong-obovate, larger than uppers, tube thick, cylindrical, spur cylindrical, vaguely extending from tube, 5-8 mm long. Capsule subglobose? Seed unknown. (Plate 4.67).

PHENOLOGY: III. Scape arising from winter rosette?

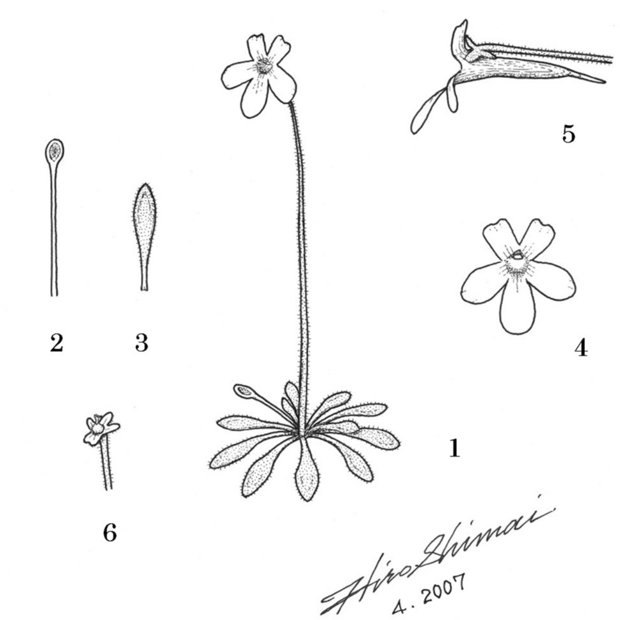
ETYMOLOGY: resembling the shape of *Utricularia*

HABITAT: Unknown

DISTRIBUTION: MEXICO (Oaxaca). Known only from the type locality. 2,000-2,300 m.

DISCUSSION: *Pinguicula utricularioides* is, no doubt, one of the most poorly known species in the genus. It was initially collected by T. MacDougall in March 1956, near Niltepec in the State of Oaxaca, Mexico. The herbarium specimen had not been identified until Zamudio and Rzedowski (1991) described it as *P. utricularioides*, based on the specimen. According to Zamudio and Rzedowski (1991), the species produces very unique summer leaves, which is a concave to saccate lamina (ca. 2-4 mm across in diameter) with a long petiole. However, it has not been confirmed whether it is truly a summer leaf regularly produced during the growth season or just an abnormal summer leaf since the species is known only from the specimens. The description in the current study basically follows that of Zamudio and Rzedowski (1991), but examinations of the live material will be highly necessary to understand the morphology of the species. Unfortunately, the locality is not easily accessible because of the public safety and limited accessibility (per. com., Zamudio). No information on the ecology can be available.

Plate 4.67. *Pinguicula utricularioides*

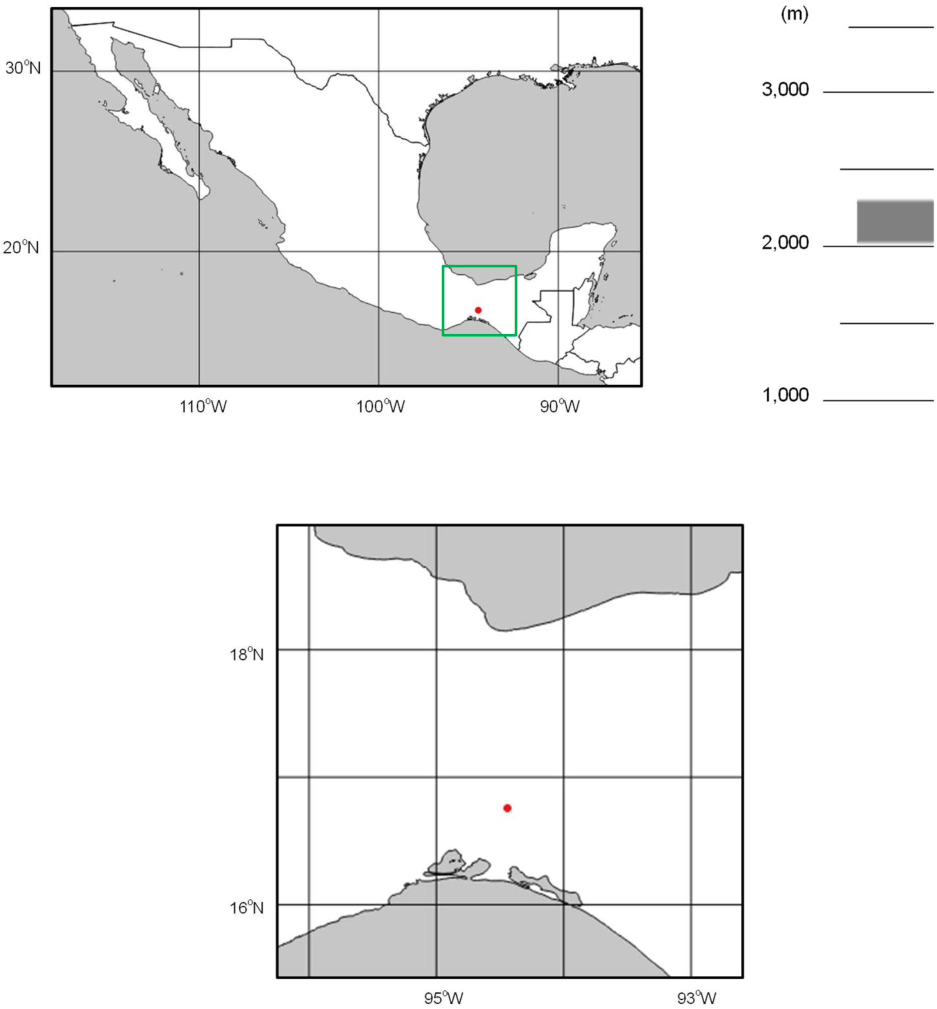


10 mm: 1, 2, 3

10 mm: 4, 5, 6

1. winter rosette with flower
2. summer leaf
3. winter leaf
4. flower, front view
5. flower, lateral view
6. capsule

P. utricularioides



68. ***Pinguicula zecheri*** Speta et Fuchs, Stapfia 10 (1982) 111.

TYPE: MEXICO. *Guerrero, Puerto de Gallo (100,1°/17,5°), 2400 m, an mit Moos überzogenen Felsen* [Guerrero, Puerto del Gallo (100,1°/17,5°), 2,400 m, on mossy rocks], St. Schatzl, cult. Bot. Garten of Linz, 28 August 1981 & 7 December 1981 (holotype: Herb. Speta).

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf dimorphic, summer leaf 10-15, bright green, ovate, margin narrowly involute, apex obtuse, base rather cuneate, 30-100 mm long, 20-75 mm wide, winter leaf 40-50, spatulate, thick, apex obtuse, 20-25 mm long, 3-5 mm wide. Winter rosette lenticular. Scape 1-4, densely glandulous, 70-180 mm long. Calyx bilabiate, upper lip 3-lobed, lobes oblong-ovate, 3-4 mm long, lower lip 2-lobed, lobes smaller than uppers, connate at base. Flower dark pink to reddish-pink or reddish-purple, often darker or with darker veins at base of lips, white spots or stripes at base of lower lip. Corolla bilabiate, 28-40 mm across, zygomorphic, up to 50 mm long including spur, upper lip 2-lobed, lobes obovate to obovate-oblong or oblong, tip rather truncate, irregularly serrate and undulate, lower lip 3-lobeed, lobes similar to uppers but slightly larger, margins often overlapping at base, tube reddish-purple, very short, shortly conical, spur faintly pale purple, subcylindrical, somewhat falcate, 25-40 mm long. Capsule subglobose. Seed fusiform-ellipsoid. $2n = 22$. (Plate 4.68).

PHENOLOGY: VI, VII, VIII, IX, X, XI, XII. Scape arising from summer rosette.

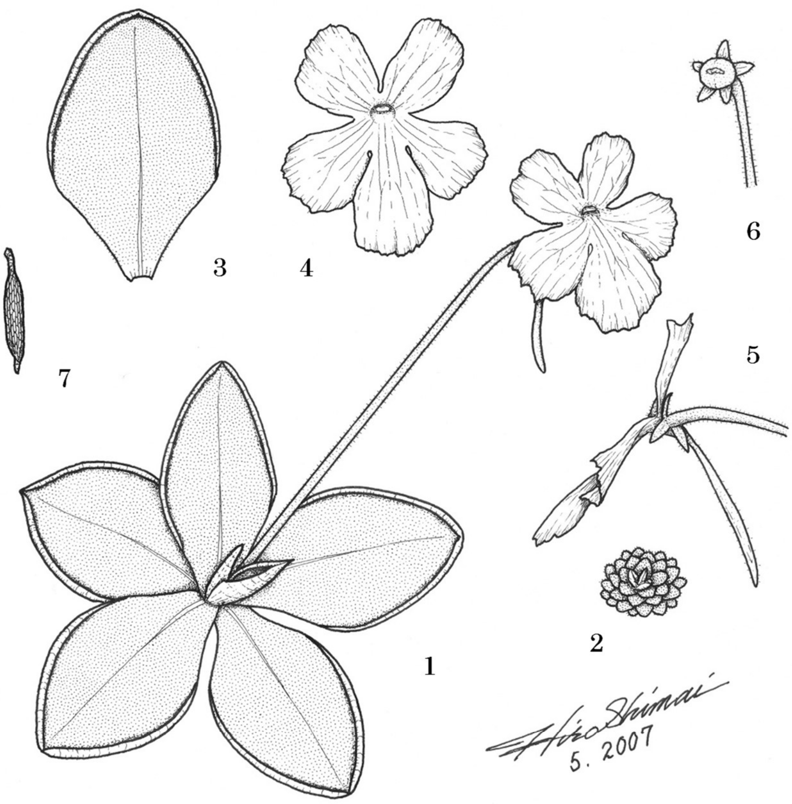
ETYMOLOGY: dedicated to Ernst Zecher

HABITAT: Wet rocks in steep slopes or on vertical cliffs, or mossy tree trunks. Low light intensity.

DISTRIBUTION: MEXICO (Guerrero, Michoacán). 1,772-2,600 m.

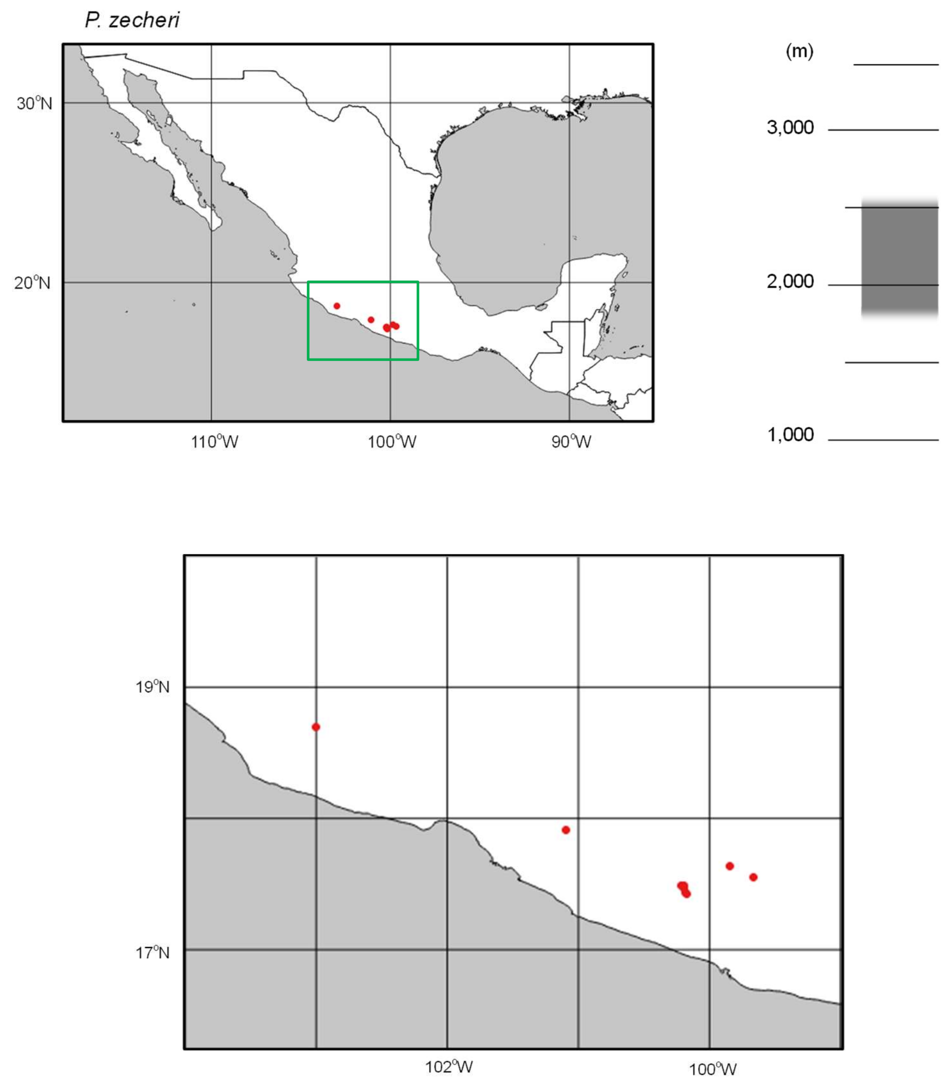
DISCUSSION: *Pinguicula zecheri* is distributed in the States of Guerrero and Michoacán, Mexico. It was initially collected by St. Schatzl at Puerto del Gallo in the State of Guerrero and was described as *P. zecheri* by Speta and Fuchs (1982) based on the materials cultivated at the Botanical Garden of Linz, Austria. The holotype specimen is Franz Speta's private collection. *P. zecheri* is morphologically very similar to a few other species, e.g. *P. moranensis* or *P. rectifolia*, but can be distinguished by having wider and irregularly waved corolla lobes. Also the winter rosette of *P. zecheri* is much smaller than that of *P. moranensis* var. *moranenisis*. It seems that the species is relatively abundant at the locality.

Plate 4.68. *Pinguicula zecheri*



10 mm: 1, 2, 3
10 mm: 4, 5, 6
500 µm: 7

1. summer rosette with flower
2. winter rosette
3. summer leaf
4. flower, front view
5. flower, lateral view
6. capsule
7. seed


P. zecheri
30°N
20°N
110°W
100°W
90°W
(m)
3,000
2,000
1,000
19°N
17°N
102°W
100°W

Sect. *Nana* Casper (1962) Feddes. Repert. 66, 41.

TYPE: *Pinguicula villosa* L.

SYNONYM: Ser. *Variegatae* Casper

69. ***Pinguicula algida*** Malysch., Novosti Sistematiki Visshikh Rasteniy (1966) 252.

TYPE: RUSSIA. *Montes Stanovoje Nagorje, jugum Kodar, as fonts fl. Apsat, in regione alpina, 1800 m s.m. in declivitate rupestri sphagnosa* (Stanovoje Nagorje Mts., Kodar Range, source of Apsat River, alpine region, 1,800 m), 11 VII 1964, fl., nº 220, *Malyschev et Petroczenko s.n.* (holotype: LE!; isotype: MAK!).

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf dimorphic, summer leaf 4-7, yellowish-green or maroon, ovate, margin strongly involute, apex obtuse, 4-15 mm long, 3-10 mm wide, winter leaf up to 15, ovate, concave, apex acute, very small. Hibernaculum subglobose. Scape 1, densely glandulous, sometimes bifurcate at above middle or near tip, 30-150 mm long. Calyx bilabiate, upper lip 3-lobed, lobes broadly ovate, ca. 1 mm long, lower lip 2-lobed, lobes similar to uppers. Flower purple, sometimes pale purple near tip of lobes, with dark purple veins, yellow spot at base of middle lobe. Corolla bilabiate, 5-8 mm across, zygomorphic, 4-10 mm long including spur, upper lip 2-lobed, lobes ovate to triangular, lower lip 3-lobed, lobes oblong-ovate, longer than uppers, middle lobe cuneate, tip rather truncate, irregularly undulate, tube purple with darker purple lines, conical, spur bright yellow, cylindrical to conical, 2-3 mm long. Capsule oblong-ovoid. Seed unknown. (Plate 4.69).

PHENOLOGY: VI, VII

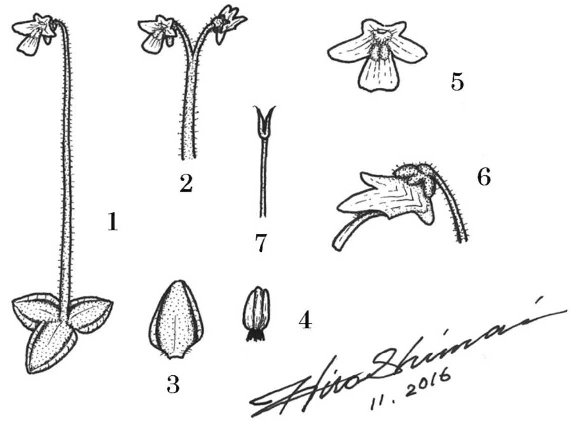
ETYMOLOGY: cold (referring to climate around the habitat of the species)

HABITAT: Wet gravelly soil or sphagnum in open slopes. Exposed to direct sunlight.

DISTRIBUTION: RUSSIA (Buryatia, Khabarovsk, Krasnoyarsk, Sakha, Zabaykalsk). 0-1,800 m.

DISCUSSION: *Pinguicula algida* is widely distributed in Eastern Russia. Although Malyschev and Petrochenko (1966) thought that *P. algida* was closely related to *P. villosa*, it is morphologically very similar to *P. spathulata*, but *P. algida* has a darker flower and sometimes has a bifurcate scape dividing above the middle or near the tip (not as often as *P. ramosa* does). It is sometimes difficult to distinguish between herbarium specimens of *P. algida* and those of *P. spathulata* particularly without flowers, but after examinations of type and general specimens, *P. algida* and *P. spathulata* are treated as different species here. The flower of *P. algida* is morphologically intermediate between *P. spathulata* and P*. villosa* in some degree, but it is often smaller than that of *P. spathulata*. The distribution area is less explored; therefore, outline of the distribution range is unclear. A further investigation will be needed for this species. This is one of the least known species.

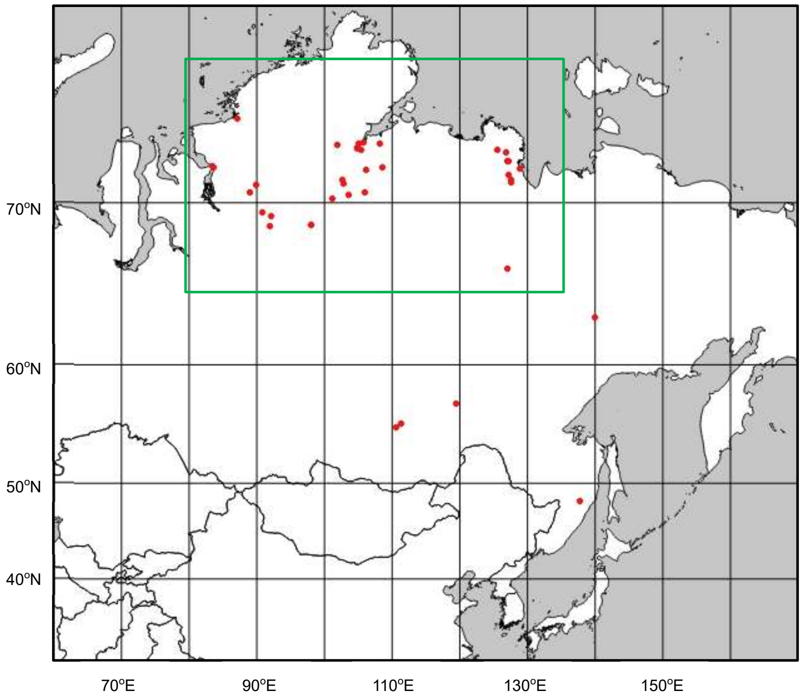
Plate 4.69. *Pinguicula algida*

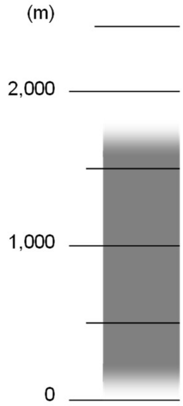


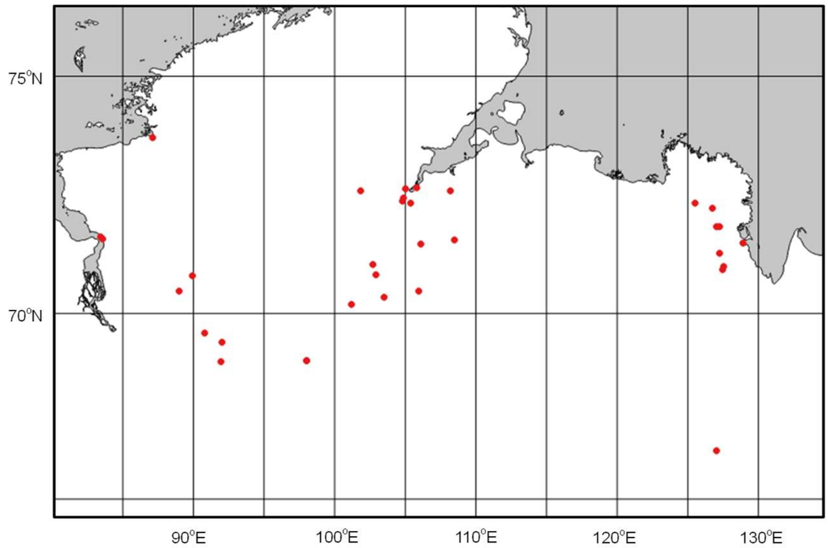
10 mm: 1, 2, 3, 4, 7
3 mm: 5, 6

1. rosette with flower
2. bifurcate scape
3. summer leaf
4. hibernaculum
5. flower, front view
6. flower, lateral view
7. capsule (dried)

P. algida


70°N
60°N
50°N
40°N
70°E
90°E
110°E
130°E
150°E


(m)
2,000
1,000
0


75°N
70°N
90°E
100°E
110°E
120°E
130°E

70. ***Pinguicula ramosa*** Miyoshi, Bot. Mag. Tokyo 4. (1890) 315.

TYPE: JAPAN. Mount Kōshin in the province of Shimotsuke, 9 August 1890, *Miyoshi s.n.* (holotype?: TI!).

SYNONYMS: *P. ramosa* Miyoshi f. *albiflora* Komiya, *P. villosa* L. var. *ramosa* (Miyoshi) Tamura

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf dimorphic, summer leaf 3-6, yellowish-green, ovate to elliptic, margin involute, apex obtuse, 6-15 mm long, 5-8 mm wide, winter leaf up to 15, ovate, apex acute, concave, very small. Hibernaculum subglobose. Scape 1, slightly S-shaped, often bifurcate or trifurcate at below middle or near base, 15-90 mm long. Calyx bilabiate, upper lip 3-lobed, lobes ovate, ca. 1 mm long, lower lip 2-lobed, lobes up to 2 mm, connate to middle. Flower pale purple, purple veins at base of lips to throat, yellow spot at base of middle lobe. Corolla bilabiate, 8-10 mm across, zygomorphic, 7-11 mm long including spur, upper lip 2-lobed, lobes ovate-oblong, lower lip 3-lobed, lobes larger than uppers, lateral lobes ovate to ovate-oblong, middle lobe ligulate, convex or with verrucose crests at base, slightly reflexed, tip truncate to emarginate, tube purple with darker veins, conical, dorsally compressed, spur bright yellow, cylindrical, 2-4 mm long. Capsule subglobose, upper margin rather flat. Seed fusiform-ellipsoid, 630-980 X 195-250 μm. $2n$ = 18. (Plate 4.70).

PHENOLOGY: V, VI, VII

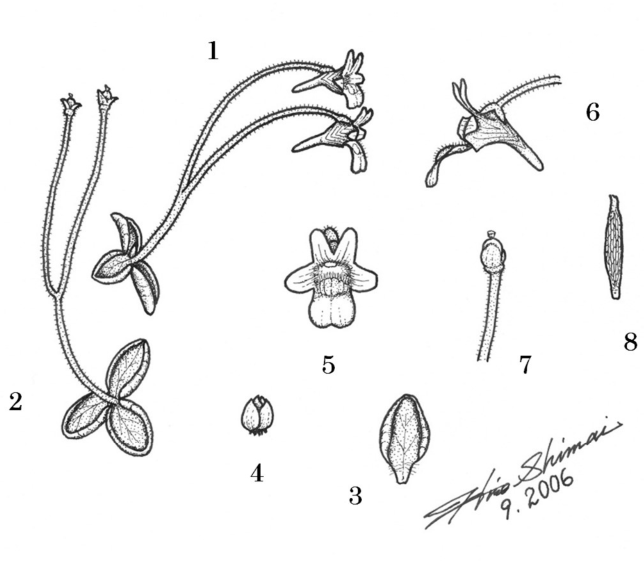
ETYMOLOGY: branched (referring to the scape)

HABITAT: Weathered volcanic rocks on cliffs (often vertical or overhanging) often below forest lines. Low light intensity.

DISTRIBUTION: JAPAN (Gunma, Tochigi). 1,441-2,300 m.

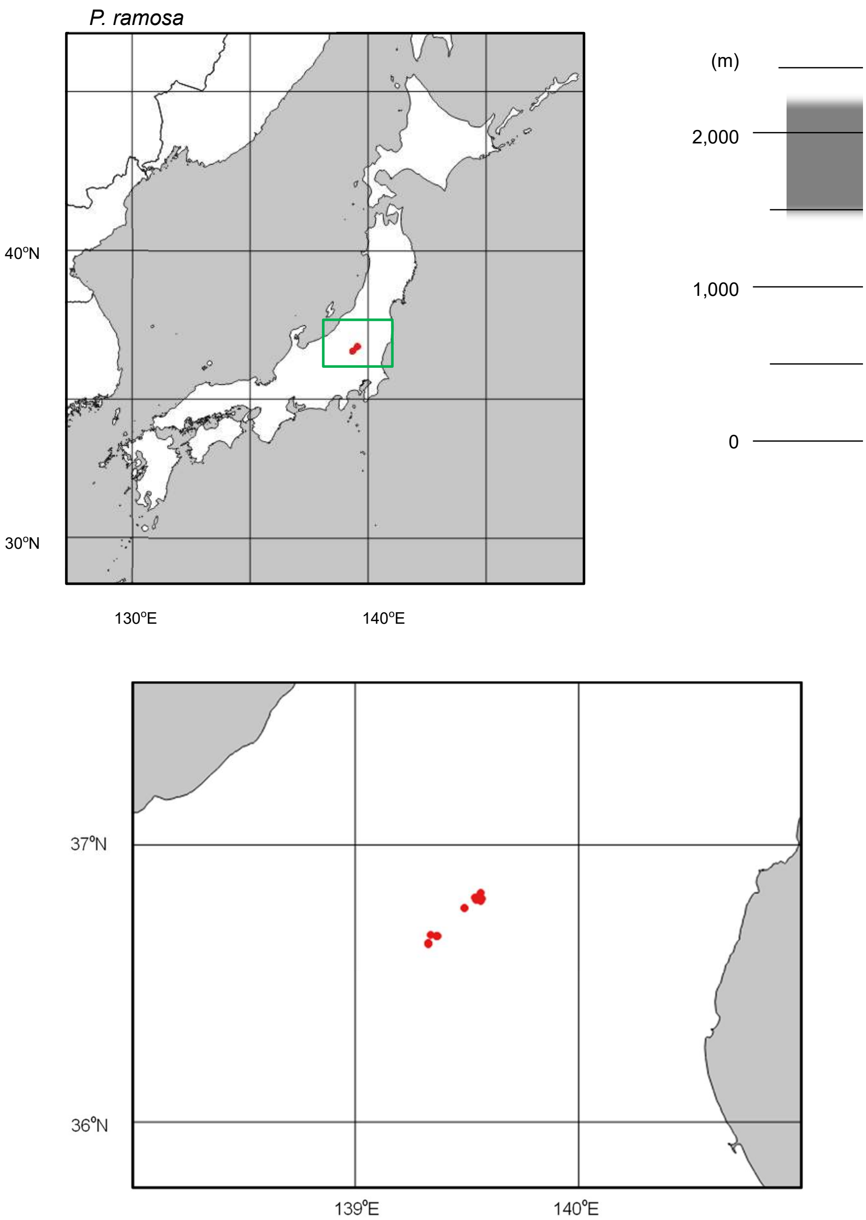
DISCUSSION: *Pinguicula ramosa* is endemic to the Prefectures of Tochigi and Gunma, Japan. The type locality mentioned in the original description as the Province of Shimotsuke is almost identical with Tochigi Prefecture at present. The distribution is highly restricted to subalpine zones of several mountains lying within ca. 30 km, including Mt. Nantai-san, Mt. Nyohō-san, Mt. Kesamaru-yama, and a few other mountains as well as the type locality of Mt. Kōshin-zan and those environments, around the City of Nikkō. It was initially discovered by Manabu Miyoshi at Mt. Kōshin-zan in August 1890, during his botanical expedition. The flowering season had already finished at the time of discovery, but Miyoshi (1890) immediately described it as *P. ramosa*. The earlier collection in July 1890 by Kinashi deposited at KYO was very likely misdated (per. com., Komiya). The species often has a bifurcate or a trifurcate scape, which is absolutely uncommon in the other species. Tamura (1953) treated as *P. villosa* var. *ramosa* and Ernst (1961) thought that *P. ramosa* was synonymous with *P. villosa*, but *P. ramosa* is clearly a distinct species. It forms relatively large colonies on slightly wet weathered volcanic rock cliffs, but has a higher risk of rapid decline of the population number at the habitat due to environmental stresses and/or climate changes. Details on this species were discussed by Shimai (2016).

Plate 4.70. *Pinguicula ramosa*



10 mm: 1, 2, 3, 4
10 mm: 5, 6, 7
300 μm: 8

1. rosette with flower
2. rosette with fruit
3. summer leaf
4. hibernaculum
5. flower, front view
6. flower, lateral view
7. capsule
8. seed


P. ramosa
40ºN
30ºN
130ºE
140ºE
(m)
2,000
1,000
0
37ºN
36ºN
139ºE
140ºE

71. ***Pinguicula spathulata*** Ledeb., Mém. Acad. Imp. Sci. St. Pétersbourg Hist. Acad. 5 (1815) 515.

TYPE: RUSSIA. In regione transbaicalensi (in the Transbaikal region), s.d., *leg. ign. s.n.* (holotype: LE!)

SYNONYMS: *P. glandulosa* Trautvetter et Meyer, *P. macroceras* Komarov, *P. spathulata* Ledeb. subsp. *variegata* (Turcz.) Khokhr. et Kuvaev, *P. spathulata* Ledeb. subsp. *variegata* (Turcz.) Khokhryakov et Kuvaev, *P. variegata* Turcz.

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf dimorphic, summer leaf 3-7, maroon to reddish-yellow or yellowish-green, ovate to orbicular, margin slightly involute, apex obtuse, 6-10 (-20) mm long, 5-7 mm wide, winter leaf up to 15, ovate, concave, apex acute, very small. Hibernaculum subglobose. Scape 1, densely glandulous, 30-250 mm long. Calyx bilabiate, upper lip 3-lobed, lobes ovate, ca. 1 mm long, lower lip 2-lobed, lobes smaller than uppers. Flower white to faintly pale purple, purple at base of lips, yellow spot at base of middle lobe. Corolla bilabiate, 3-10 mm across, zygomorphic, 4-17 mm long including spur, upper lip 2-lobed, lobes oblong, lower lip 3-lobed, lobes larger than uppers, lateral lobes ovate, middle lobe suborbicular, convex or with verrucose crests at base of middle lobe, tube purple with darker veins, conical, spur bright yellow, cylindrical, 2-4 mm long. Capsule obovoid. Seed fusiform-ellipsoid, 970-1,180 X 300-330 µm. $2n = 64$. (Plate 4.71).

PHENOLOGY: VI, VII, VIII

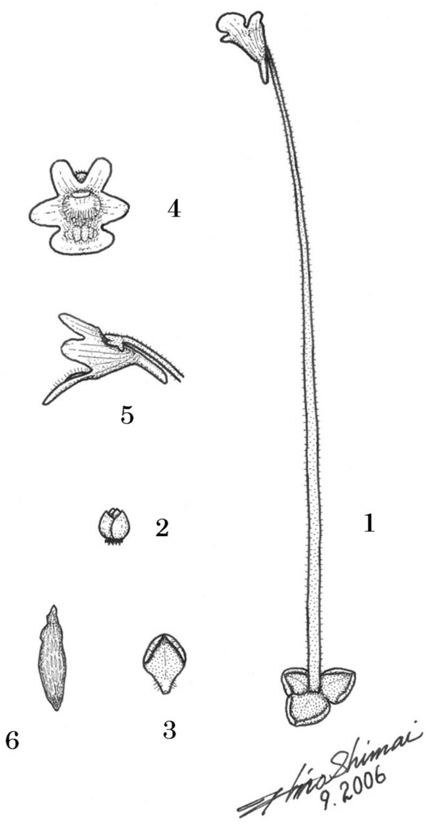
ETYMOLOGY: spatulate (referring to the leaf shape)

HABITAT: Wet gravelly serpentine in open slopes. Exposed to direct sunlight.

DISTRIBUTION: RUSSIA (Amur, Buryatia, Chukotka, Irkutsk, Kamchatka, Khabarovsk, Magadan, Sakha, Sakhalin). 0-1,600 m.

DISCUSSION: *Pinguicula spathulata* is widely distributed in eastern Russia, from the Lake Baikal region and stretching east to the Chukotka Autonomous District. The exact holotype locality is unknown. Observing the holotype specimen at LE, *P. spathulata* and *P. vareigata* seems to be identical. Casper (1966a) adopted that *P. variegata* was a valid name and rejected *P. spathulata*, but the latter could be a valid name because of the published date. This little known tiny species is morphologically similar to *P. algida* or *P. ramosa*. It can be distinguishable from the former by having paler flower colour, and from the latter by having a much longer scape without bifurcation. *P. spathulata* often forms a clump and can be found a large colony at the habitat. Due to a very short growth season and limited access to the habitat, an exact outline of the distribution area is not clearly known.

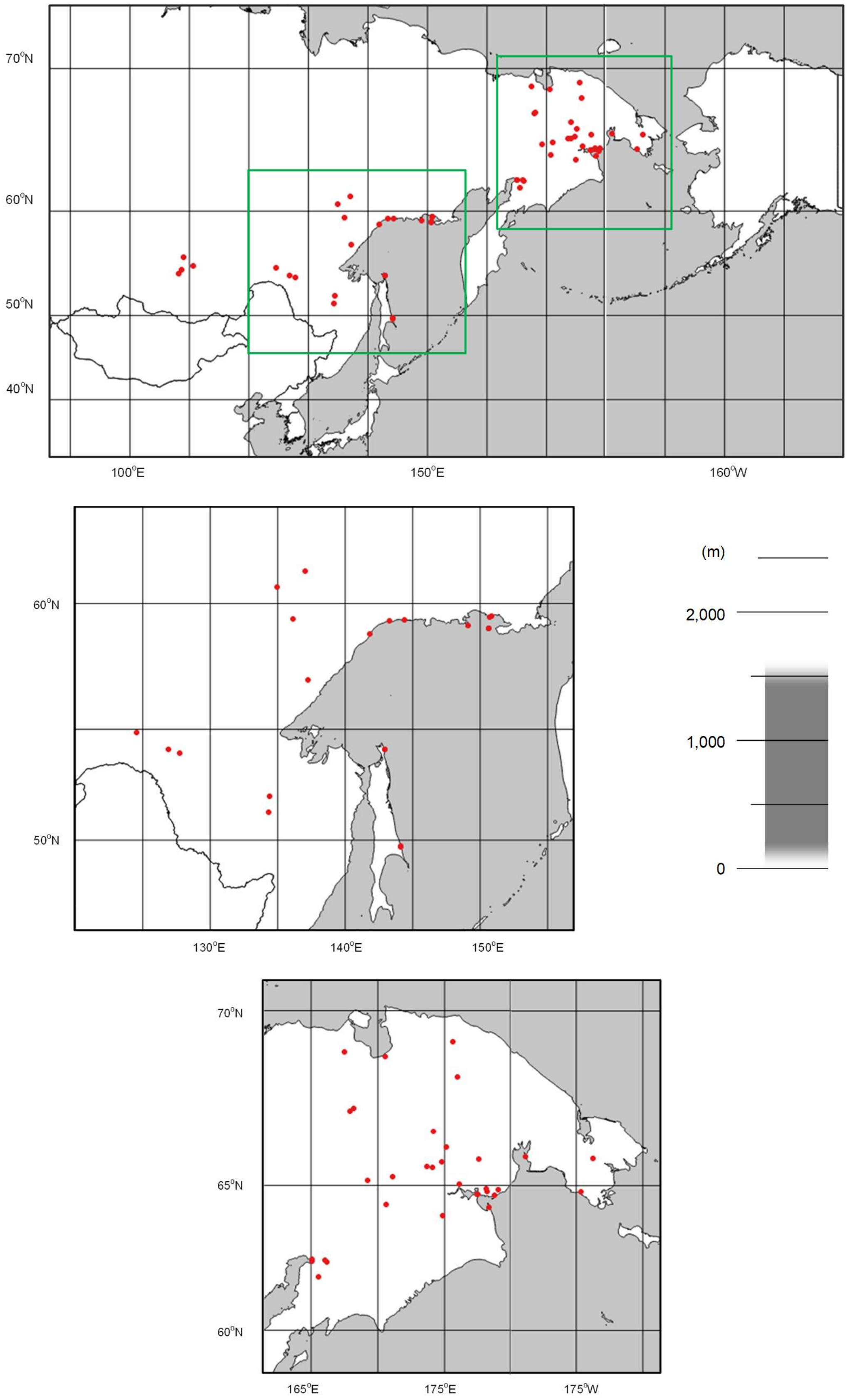
Plate 4.71. *Pinguicula spathulata*



10 mm: 1, 2, 3
10 mm: 4, 5
500 µm: 6

1. rosette with flower
2. hibernaculum
3. summer leaf
4. flower, front view
5. flower, lateral view
6. seed

P. spathulata



72. ***Pinguicula villosa*** L., Sp. Pl. 1 (1753) 17.

TYPE: *Linnaeus 33.3* (lectotype: LINN!).

SYNONYMS: *P. acutifolia* Michx., *P. involucrata* DC., *P. involuta* Schrank, *P. villosa* L. f. *albiflora* Froedin

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short or seasonally elongating. Leaf dimorphic, summer leaf 1-5, yellowish-green, outer margin sometimes maroon, elliptic, margin strongly involute, apex obtuse, base petiolate, 7-13 mm long, 3-7 mm wide, winter leaf up to 15, oblong, concave, apex obtuse, very small. Hibernaculum ellipsoid. Scape 1, densely covered by long glands, 15-95 mm long. Calyx bilabiate, upper lip 3-lobed, lobes oblong-lanceolate, ca. 1 mm long, lower lip 2-lobed, lobes smaller than uppers. Flower purple, with dark purple veins, yellow spot at base of middle lobe. Corolla bilabiate, 5-8 mm across, zygomorphic, 5-11 mm long including spur, upper lip 2-lobed, lobes oblong to obovate, lower lip 3-lobed, lobes larger than uppers, elliptic to ligulate, connate below middle, tube pale purple with darker veins, narrowly conical to subcylindrical, dorsally compressed, spur pale green to purple, cylindrical, 1-5 mm long. Capsule subglobose to obovoid, upper margin rather flat. Seed ellipsoid, 990-1,140 X 610-720 µm. $2n = 16$. (Plate 4.72).

PHENOLOGY: V, VI, VII, VIII

ETYMOLOGY: villous (referring to the scape)

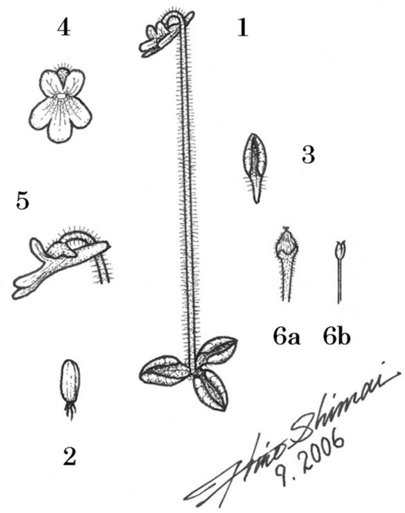
HABITAT: Sphagnum in bogs or open areas. Often exposed to direct sunlight.

DISTRIBUTION: Very widely distributed in the Arctic or colder regions of the Northern Hemisphere. CANADA (British Columbia, Manitoba, Newfoundland and Labrador, Northwest Territories, Nunavut, Ontario, Québec, Saskatchewan, Yukon Territory); CHINA (Nei Mongol); FINLAND (Kainuu, Lappi, Pohjois-Pohjanmaa); JAPAN (Hokkaidō); NORTH KOREA (Ryanggang-do); NORWAY (Finnmark, Hedmark, Oppland, Sør-Trøndelag); RUSSIA (Buryatia, Chukotka, Kamchatka, Khabarovsk, Komi, Krasnoyarsk, Magadan, Murmansk, Nenetsia, Sakha, Sakhalin, Tyumen, Yamalo-Nenets); SWEDEN (Dalarna, Jämtland, Norrbotten, Västerbotten, Wästernorrland); USA (Alaska). 0-1,900 m.

DISCUSSION: *Pinguicula villosa*, distributed in the circumpolar regions of Eurasia and North America, is one of the most widespread species in the genus. This is still a little known species in contrast to the wider distribution area. Because of the very tiny plant size, fewer leaf numbers (often 1-3), and very short growth season, the actual outline of the distribution is not clearly known.

P. villosa is often found on sphagnum mats, but it is very difficult to recognise at the habitat without flowers. In addition, it may not flower unless physiological and environmental conditions are optimum. This species is morphologically uniform among the populations, but it sometimes produces an abnormal flower, e.g. having 3-lobed or 4-lobed upper lip. It is locally common, but it seems that the species occurs less frequently and the population density is rather sparse at the habitat.

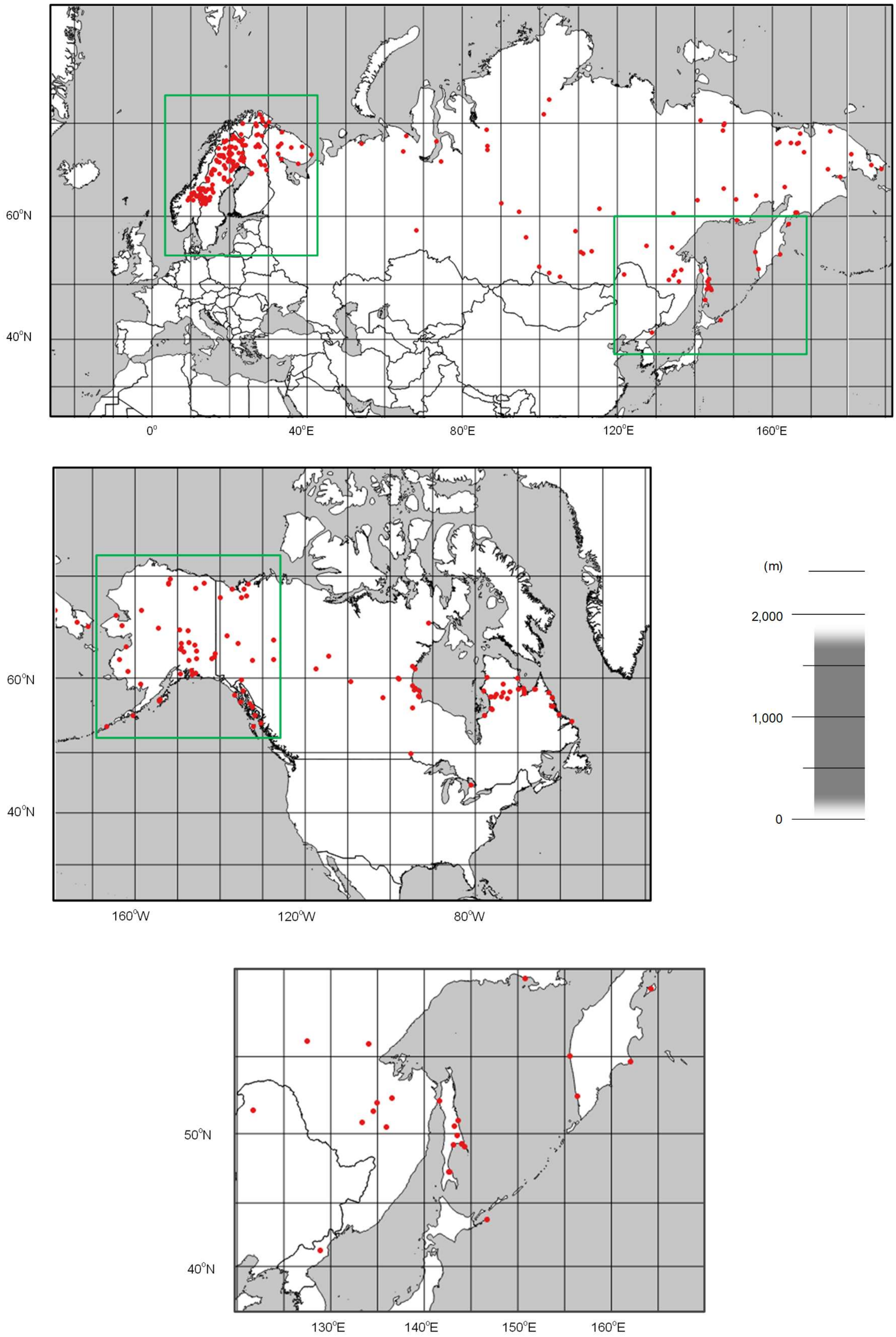
Plate 4.72. *Pinguicula villosa*

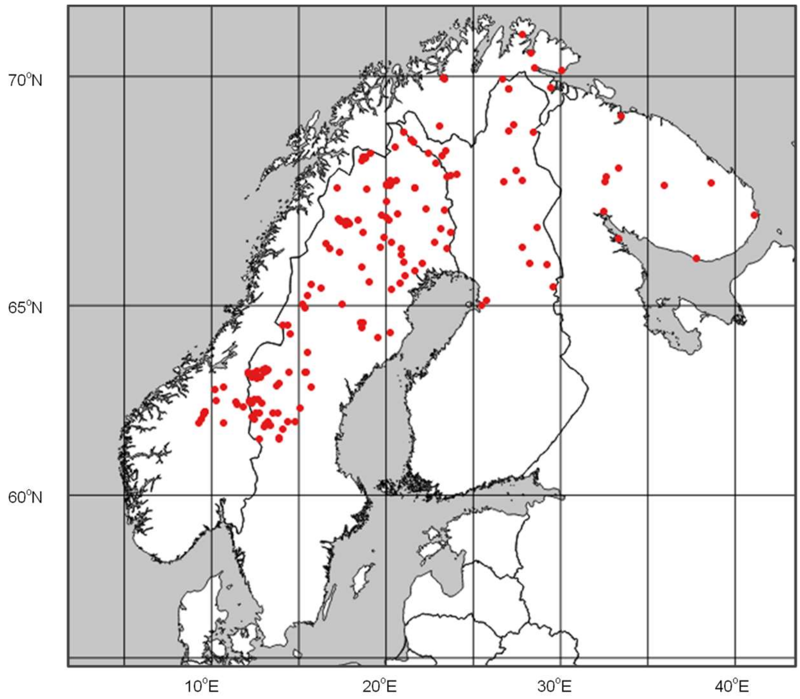


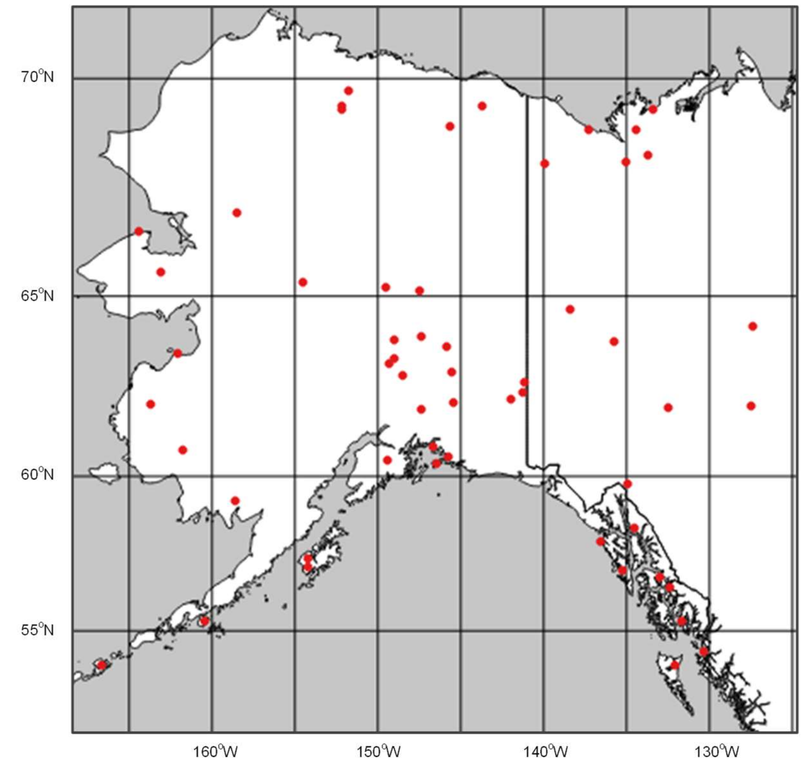
10 mm: 1, 2, 3
10 mm: 4, 5, 6a-b

1. rosette with flower
2. hibernaculum
3. summer leaf
4. flower, front view
5. flower, lateral view
6a. capsule
6b. capsule (dried)

P. villosa


60°N
40°N
0°
40°E
80°E
120°E
160°E
60°N
40°N
160°W
120°W
80°W
(m)
2,000
1,000
0
50°N
40°N
130°E
140°E
150°E
160°E


70°N
65°N
60°N
10°E
20°E
30°E
40°E


70°N
65°N
60°N
55°N
160°W
150°W
140°W
130°W

Sect. *Pinguicula* Casper (1963) Bot. Jb. 82, 327.

TYPE: *Pinguicula vulgaris* L.

SYNONYMS: Sect. *Pionophyllum* DC., Subgen. *Pionophyllum* Barnhart

73. ***Pinguicula balcanica*** Casper, Feddes Repert. Spec. Nov. 66 (1962) 105.

TYPE: ALBANIA. *nordostalbanische Alpen, zwischen den Ortschaften Prizren und Debra, Schneegipfel des Korab, an überrieselten Felsen an Nordhängen oberhalb der höchsten Doline beim Dorfe Radomir, Kalkboden, 2400 m* (Northeastern Albanian Alps, between Prizren and Debra, snowcapped mountains of the Korab, on wet rocks at the northern slope above the highest sinkhole near the Village of Radmir, calcareous soil, 2,400 m), 25 July 1918, *Kümmerle s.n.* (holotype: BP!).

SYNONYMS: *P. alpina* Baldacci, *P. balcana* Petrovic, *P. balcanica* Casper subsp. *pontica* Casper, *P. balcanica* Casper var. *tenuilaciniata* Casper, *P. grandiflora* Beck, *P. leptoceras* Grisebach, *P. leptoceras* Rohlena, *P. sempervivium* Janka, *P. vulgaris* Boissier, *P. vulgaris* L. var. *alpicola* Pontocsek, *P. vulgaris* L. var. *leptoceras* Stojanov et Stefanov

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf dimorphic, summer leaf 5-9, yellowish-green or maroon, elliptic-oblong to oblong, margin involute, apex obtuse, 20-50 mm long, 10-20 mm wide, winter leaf up to 15, ovate, concave, apex acute, small. Hibernaculum ovoid. Scape 1-5, densely glandulous, 20-100 mm long. Calyx bilabiate, upper lip 3-lobed, lobes ovate, ca. 3 mm long, connate at base, lower lip 2-lobed, lobes similar to uppers. Flower purple, white spots or stripes at base of lower lip. Corolla bilabiate, 15-20 mm across, zygomorphic, 14-23 mm long including spur, upper lip 2-lobed, lobes suborbicular, often overlapped each other, lower lip 3-lobed, lobes larger than uppers, obovate-oblong, middle lobe rather truncate, often overlapped with laterals, tube purple, conical, dorsally compressed, spur brownish-yellow with purple veins, cylindrical, 2-7 mm long. Capsule ovoid. Seed ellipsoid, 580-690 X 210-250 µm. $2n = 32$. (Plate 4.73).

PHENOLOGY: V, VI, VII, VIII, X

ETYMOLOGY: native of the Balkans

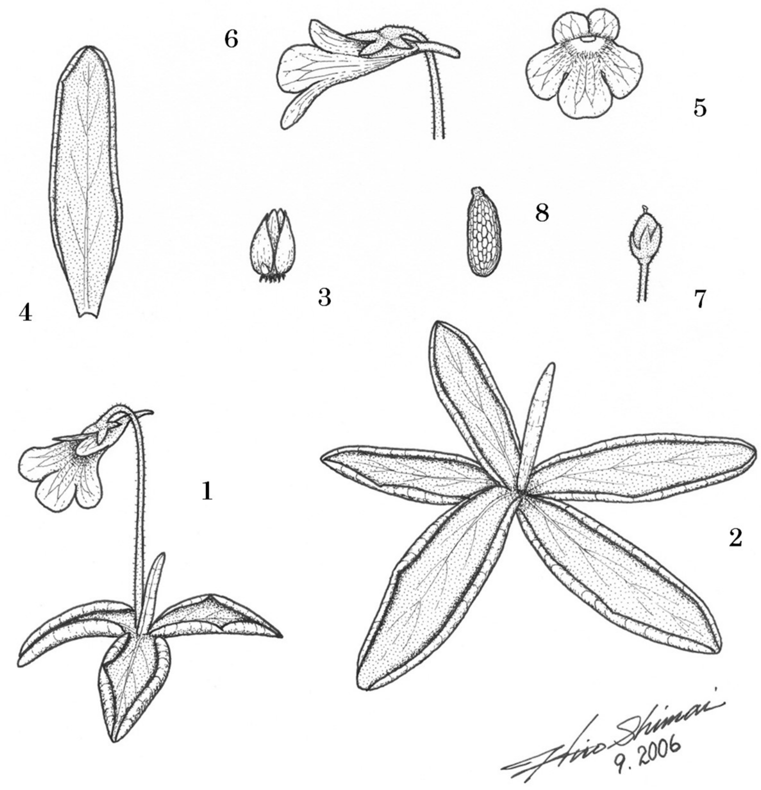
HABITAT: Wet calcareous or fine sandy soil in open grasslands. Often exposed to direct sunlight.

DISTRIBUTION: ALBANIA (Dibër, Elbasanit, Korçë, Kukësit, Shkodër); BOSNIA AND HERZEGOVINA (Federation of Bosnia and Herzegovina); BULGARIA

(Blagoevgrad, Gabrovo, Kyustendil, Lovech, Pazardžk, Pernik, Plovdiv, Smolyan, Sofia, Sofia City); GEORGIA (Abkhazia); GREECE (Fokída, Ioánina); KOSOVO (Ferizaj, Gjakovë, Pejë, Prizren); MACEDONIA (Bitola, Gevgelija, Jegunovce, Makedonski Brod, Mavrovo and Rostuša, Novaci, Studeničani, Tetovo); MONTENEGRO (Andrijevica, Kolašin, Plav, Podgorica); RUSSIA (Karachay-Cherkessia); SERBIA (Pirot); TURKEY (Adana, Artvin, Bursa, Erzurum, Gümüşhane, Niğde, Rize, Trabzon, Van). 600-3,000 m.

DISCUSSION: *Pinguicula balcanica* was described by Casper (1962a) based on herbarium materials labeled as *P. leptoceras* (the holotype locality should be near Radomira in Albania, between Prizren in Kosovo and Debar in Macedonia at present). Indeed, both species are morphologically very similar though their distributions are geographically isolated from each other. A middle lobe of lower lip in *P. balcanica* tends to be cuneate and rather truncate at tip, while those in *P. leptoceras* is rounded. *P. balcanica* is sometimes divided to two subspecies; *P. balcanica* subsp. *balcanica* distributed in the Balkans, and *P. balcanica* subsp. *pontica* in Turkey and the Caucasus, but the latter subspecies is not distinguished here. *P. balcanica* is often found at wet grasslands in alpine regions and locally abundant.

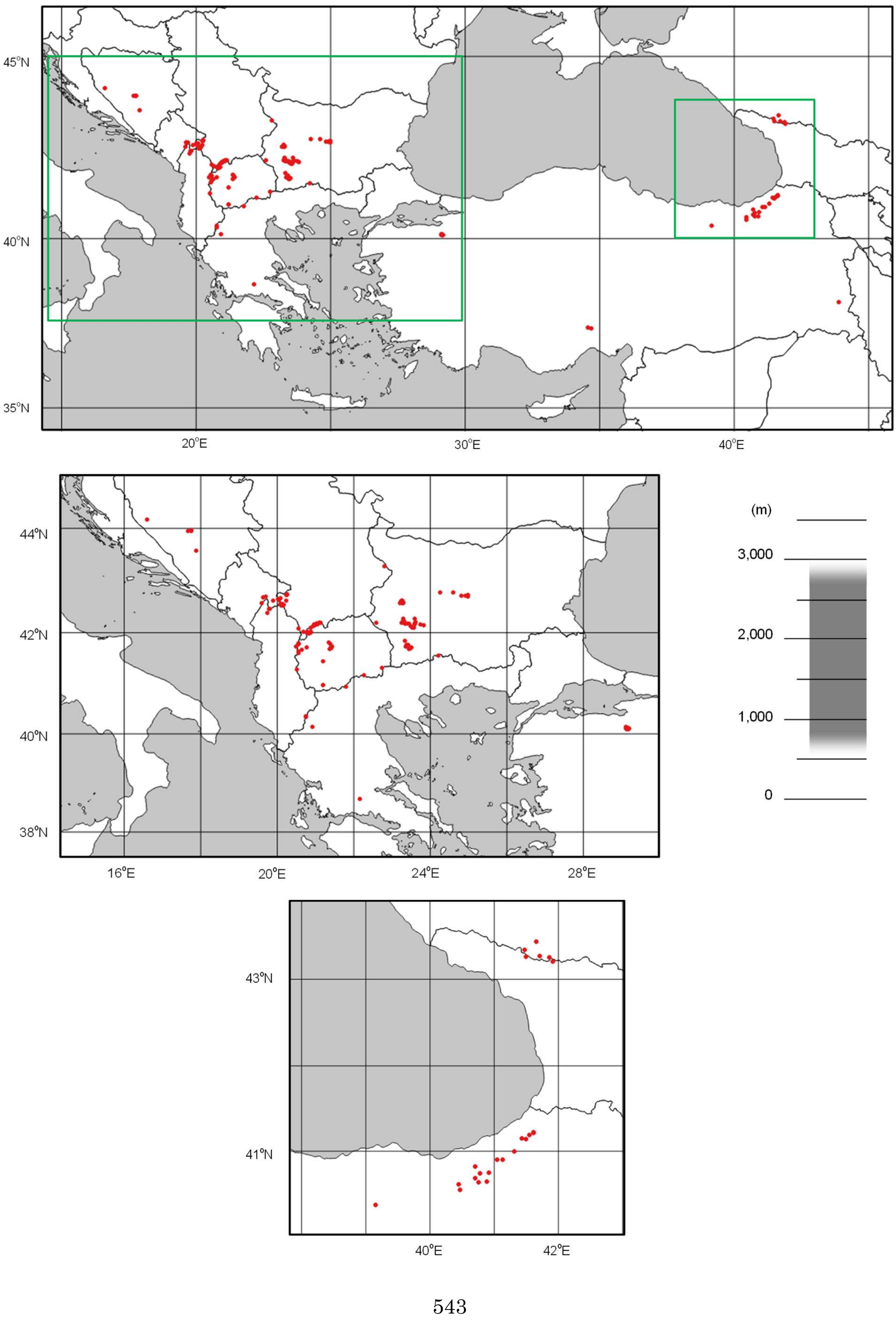
Plate 4.73. *Pinguicula balcanica*



10 mm: 1, 2, 3, 4
10 mm: 5, 6, 7
500 µm: 8

1. rosette with flower
2. rosette
3. hibernaculum
4. summer leaf
5. flower, front view
6. flower, lateral view
7. capsule
8. seed

P. balcanica


45°N
40°N
35°N
20°E
30°E
40°E
44°N
42°N
40°N
38°N
16°E
20°E
24°E
28°E
(m)
3,000
2,000
1,000
0
43°N
41°N
40°E
42°E

74. ***Pinguicula caussensis*** (Casper) Innangi, De Castro et Peruzzi, PLoS ONE 11 (12) (2016) epublished, 16.

TYPE: FRANCE. Aveyron, Vallée de la Dourbie, *Coste s.n.* (holotype: W?).

SYNONYMS: *P. grandiflora* Bras, *P. grandiflora* Lam. var. *longifolia* Grenier et Godron, *P. longifolia* Lamotte, *P. longifolia* Ram. ex DC. subsp. *caussensis* Casper, *P. longifolia* Ram. ex DC. var. *brevifolia* Genty ex Casper, *P. macrantha* Lamotte, *P. vulgaris* Bras

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf dimorphic, summer leaf 3-8, yellowish-green, obovate-oblong to oblong, margin slightly involute or revolute and undulate, apex obtuse, 15-80 mm long, 12-25 mm wide, winter leaf up to 15, ovate, apex acute, concave, small. Hibernaculum ovoid. Scape 1-5, densely glandulous, 60-150 mm long. Calyx bilabiate, upper lip 3-lobed, lobes oblong-lanceolate, 3-4 mm long, lower lip 2-lobed, lobes similar to uppers. Flower purple, white at base of middle lobe or sometimes base of lower lip, darker purple in throat. Corolla bilabiate, 15-25 mm across, zygomorphic, 15-38 mm long including spur, upper lip 2-lobed, lobes oblong, lower lip 3-lobed, lobes larger than uppers, lateral lobes oblong-ovate, middle lobe ovate to cuneate, often truncate to very shallowly retuse at tip, tube purple, conical, spur pale purple, cylindrical, 5-13 mm long. Capsule ovoid. Seed ellipsoid, 580-950 X 210-250 µm. $2n = 32$. (Plate 4.74).

PHENOLOGY: IV, V, VI

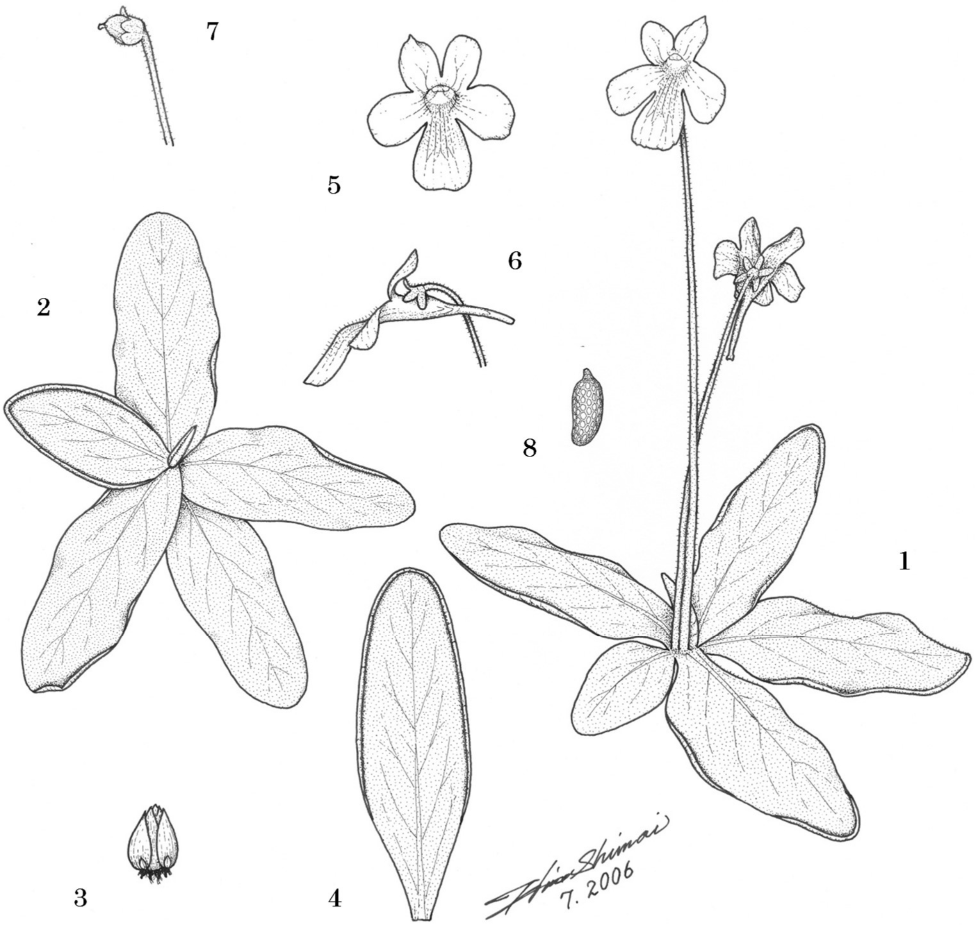
ETYMOLOGY: native of the Causse region

HABITAT: Calcareous sand or sandstone on cliffs (often vertical to overhanging). Tolerant to various light intensities.

DISTRIBUTION: FRANCE (Aveyron, Lozère, Puy-de-Dôme). 400-800 m.

DISCUSSION: *Pinguicula caussensis* is endemic to southern France. It is locally abundant particularly at gorges in the Causse (limestone plateau) region of Massif Central and commonly seen on limestone cliffs along roadsides. It has been historically included in *P. longifolia*. Casper (1962a, 1966a) considered that this was one of the subspecies of *P. longifolia* (i.e. *P. longifolia* subsp. *caussensis*) possessing longer leaves. However, *P. caussensis* has much shorter leaves and wider corolla lobes than *P. longifolia*, presenting apparently different morphological appearance. In addition, direct phylogenetic relationships between this taxon and *P. longifolia* have not been suggested; therefore, it is treated as an independent species. Roccia et al. (2016) described as *P. caussensis*, but it is likely invalid, although Roccia (2016) later annotated the error.

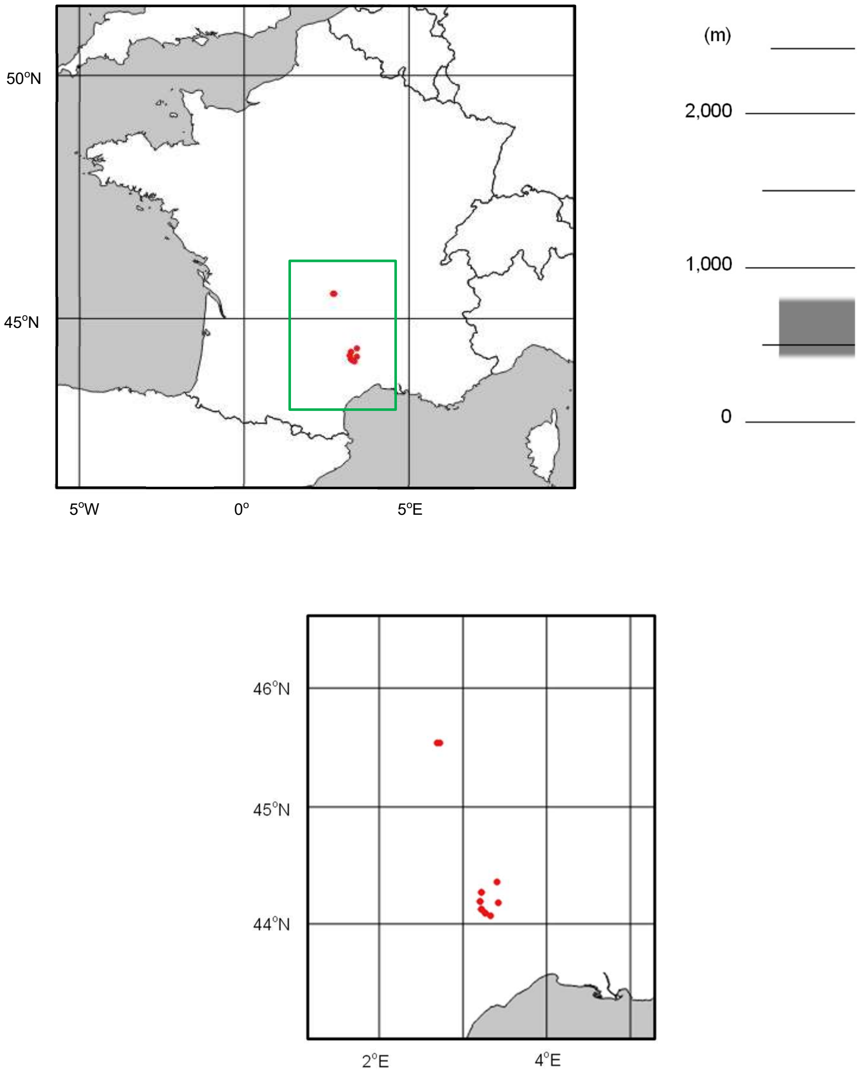
Plate 4.74. *Pinguicula caussensis*



10 mm: 1, 2, 3, 4
10 mm: 5, 6, 7
500 µm: 8

1. rosette with flower
2. rosette
3. hibernaculum
4. summer leaf
5. flower, front view
6. flower, lateral view
7. capsule
8. seed

P. caussensis



75. ***Pinguicula corsica*** Bernard et Gren. ex Gren. et Godr., Fl. France 2 (1850) 443.

TYPE: FRANCE. Corse mt., 1844, *Bernard s.n.* (holotype?: G-DC!).

SYNONYMS: *P. corsica* Bernard et Gren. ex Gren. et Godr. var. *coerulescens* Briquet, *P. corsica* Bernard et Gren. ex Gren. et Godr. var. *pallidula* Briquet, *P. grandiflora* Bertoloni, *P. leptoceras* DC., *P. leptoceras* Rchb. subsp. *corsica* Nyman, *P. lusitanica* Rchb., *P. vulgaris* L. var. *corsica* Cesati, Passerini et Gibelli, *P. vulgaris* L. var. *leptoceras* Cesati, Passerini et Gibelli, *P. vulgaris* L. var. *pusilla* Bertoloni, *P. vulgaris* Mutel

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf dimorphic, summer leaf 5-9, yellowish-green, oblong to oblong-ovate, margin involute and irregularly undulate, apex obtuse, 25-75 mm long, 15-40 mm wide, winter leaf up to 15, ovate, concave, apex acute, small. Hibernaculum ovoid. Scape 1-3, densely glandulous, 14-150 mm long. Calyx bilabiate, upper lip 3-lobed, lobes oblong-lanceolate, connate at base, ca. 3 mm long, lower lip 2-lobed, lobes similar to uppers. Flower faintly pale purple to pale lilac but occasionally dark purple, obscure purple stripes at base of lobes, purple in throat. Corolla bilabiate, 18-23 mm across, zygomorphic, 10-31 mm long including spur, upper lip 2-lobed, lobes oblong-ovate, lower lip 3-lobed, lobes larger than uppers, lateral lobes subquadrate to obovate, middle lobe cuneate, tip truncate to slightly emarginate, tube reddish-purple with darker veins, conical, dorsally compressed, spur pale purple, cylindrical, 3-9 mm long. Capsule ovoid. Seed ellipsoid, 750-950 X 200-350 µm. 2*n* = 16. (Plate 4.75).

PHENOLOGY: V, VI, VII, VIII

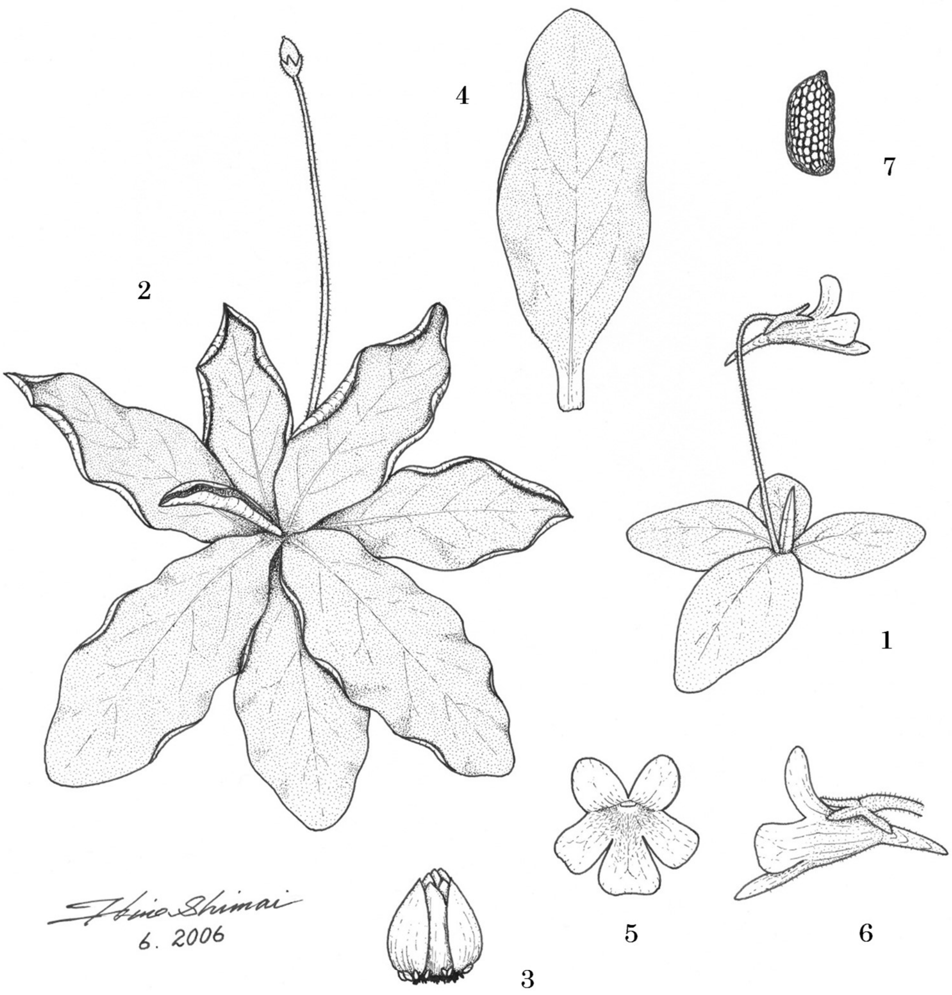
ETYMOLOGY: native of Corsica

HABITAT: Many wet places in open grassland, on granite rock walls, pond margins or along streams. Often exposed to direct sunlight.

DISTRIBUTION: FRANCE (Corse-du-Sud, Haute-Corse). 1,400-2,250 m.

DISCUSSION: *Pinguicula corsica* is confined to the mountain regions, mostly above forest lines, of Corsica. Although *P. corsica* had been historically treated as an intraspecific taxon of other species, such as *P. grandiflora* or *P. leptoceras*, it is a biogeographically well-defined species. It has prominently wavy summer leaves, larger summer basal rosettes and it often has paler flower colour compared with many other European species although the flower colour may vary from faintly pale purple to dark purple among habitats or clones. *P. corsica* is locally very common and abundant in many wet places including stream sides, pond margins, slopes or granite rock walls.

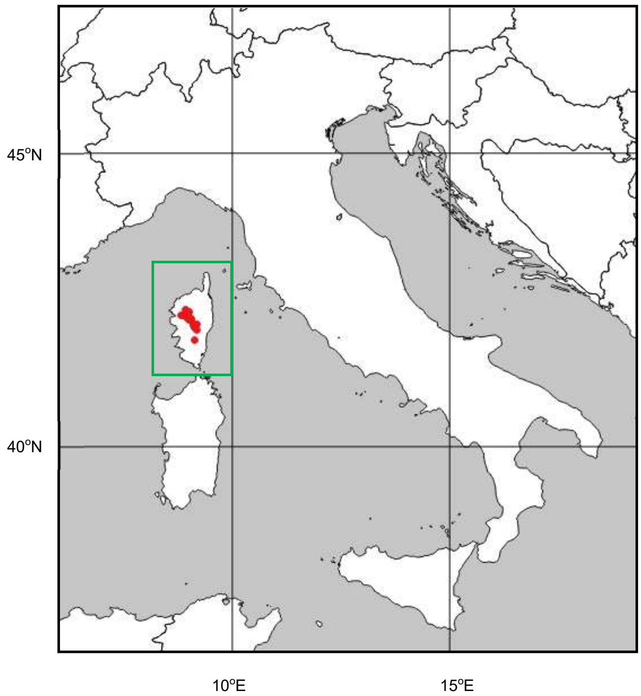
Plate 4.75. *Pinguicula corsica*

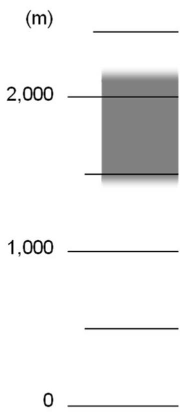


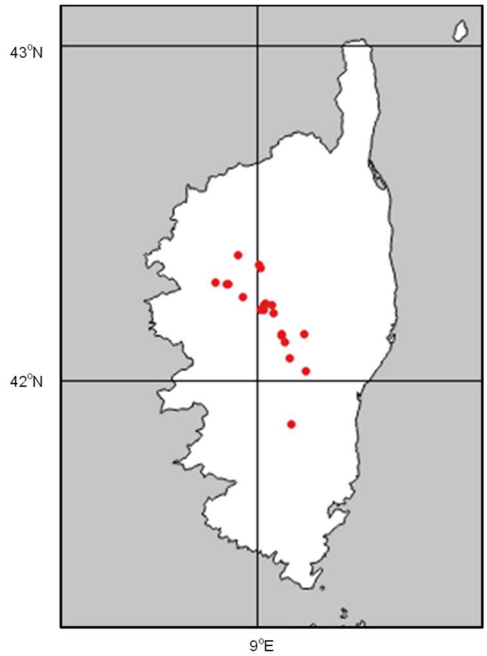
10 mm: 1, 2, 3, 4
10 mm: 5, 6
500 µm: 7

1. rosette with flower
2. rosette with fruit
3. hibernaculum
4. summer leaf
5. flower, front view
6. flower, lateral view
7. seed

P. corsica







76. ***Pinguicula dertosensis*** (Cañigueral) Mateo et Crespo, Fl. Abrev. Com. Valenciana (1995) 430.

TYPE: SPAIN. *rupium madidarum, in montibus dictis Ports de Tortosa, in altitudine 300 ad 600 m* (growing on wet cliffs, in mountains called Ports de Tortosa, at altitudes 300 to 600 m), April 1935, *Bartomeus 87830* (holotype: BC!).

SYNONYMS: *P. grandiflora* Lam. subsp. *dertosensis* (Cañigueral) Bolós et Vigo, *P. grandiflora* Lam. var. *dertosensis* Cañigueral, *P. longifolia* Ram. ex DC. subsp. *dertosensis* (Cañigueral) Schlauer, *P. submediterranea* Blanca, Jamilena, Ruiz-Rejón et Zamora

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf dimorphic, summer leaf 6-12, yellowish-green, elliptic-ovate to oblong, margin slightly involute or revolute, sometimes undulate, apex obtuse, 30-60 mm long, 10-35 mm wide, winter leaf up to 15, ovate, concave, apex acute, small. Hibernaculum ovoid. Scape 1-5, densely glandulous, 50-130 mm long. Calyx bilabiate, upper lip 3-lobed, lobes triangular to elliptic, 2.5-3.5 mm long, lower lip 2-lobed, lobes connate at base, smaller than uppers. Flower purple, white to faintly pale purple at base of lower lip. Corolla bilabiate, 12-16 mm across, zygomorphic, 20-43 mm long including spur, upper lip 2-lobed, lobes widely ovate to oblong, lower lip 3-lobed, lobes larger than uppers, often overlapping, obovate, middle lobe rather cuneate and wider than lateral lobes, tube purple with darker veins, conical, dorsally compressed, spur pale purple, cylindrical, 5-13 mm long. Capsule ovoid. Seed narrowly ellipsoid, 880-1,170 X 220-300 µm. $2n$ = 48, 64. (Plate 4.76).

PHENOLOGY: III, IV, VI

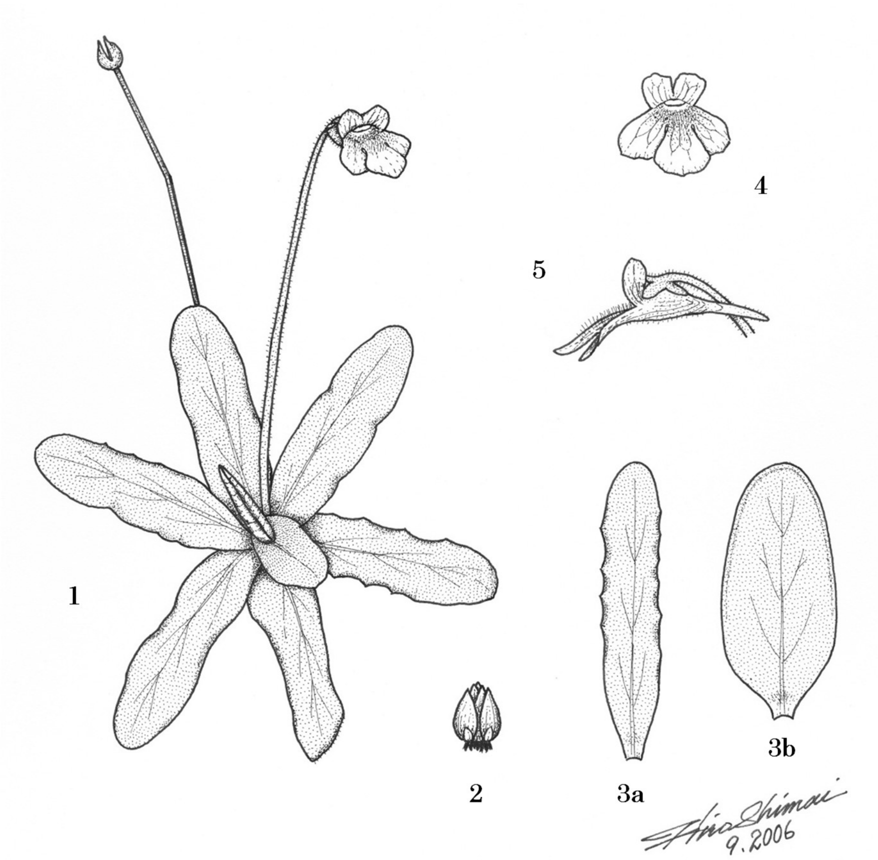
ETYMOLOGY: native of Dertosa, an ancient Roman name of Tortosa

HABITAT: Wet calcareous sandstone on cliffs (often vertical or overhanging). Tolerant to low light intensities.

DISTRIBUTION: SPAIN (Cuenca, Granada, Jaén, Tarragona, Teruel). 400-1,700 m.

DISCUSSION: *Pinguicula dertosensis*, having a complicated taxonomic history, is endemic to eastern and southern Spain. It was originally described as *P. grandiflora* var. *dertosensis* by Cañegueral (1957) based on the specimens corrected at the Ports de Tortosa (presumably identical with the Ports de Beseit), west of Tortosa in the Province of Tarragona, but Bolós and Vigo (1983) elevated it to a subspecific rank, i.e. *P. grandiflora* subsp. *dertosensis*. On the other hand, Shlauer (1994) treated as *P. longifolia* subsp. *dertosensis*. Zamora et al. (1996) described *P. submediterranea* based on the materials collected in the Province of Jaén, but Blanca et al. (1999) later admitted that it was synonymous with *P. dertosensis*, which had been upgraded to a specific rank by Mateo and Crespo (1995). A question remains whether the populations of Tarragona and those in other provinces are the same taxon, but it follows the taxonomic treatment proposed by Blanca et al. (1999) here.

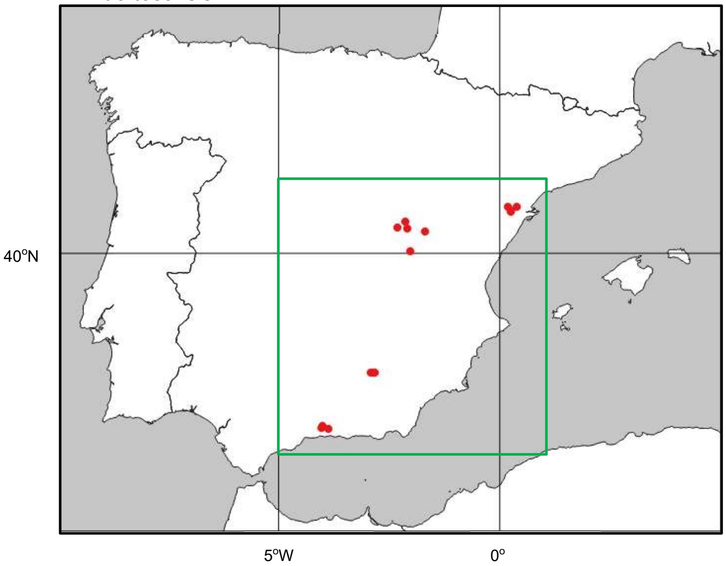
Plate 4.76. *Pinguicula dertosensis*

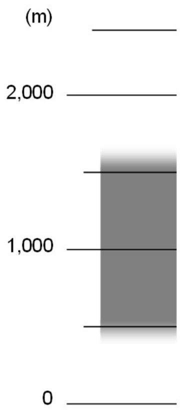


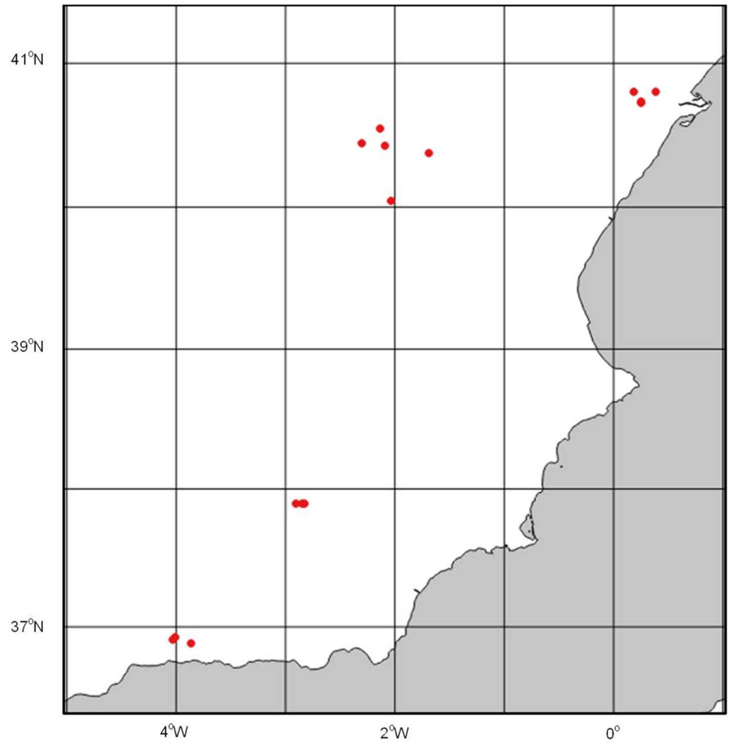
10 mm: 1, 2, 3a-b
10 mm: 4, 5

1. rosette with flower and dried capsule
2. hibernaculum
3a-b. summer leaf
4. flower, front view
5. flower, lateral view

P. dertosensis







77. ***Pinguicula fiorii*** Tammaro et Pace, Info. Bot. Italiano 19 (1987) 430.

TYPE: ITALY. *Versante orientale della Majella, località Cannelluccia di Bocca di Valle, in una forra, su rupi calcaree muschiose soggette a stillicilio, 750 m* (Eastern slope of the Majella, Cannelluccia di Bocca di Valle, in a gorge, on dripping limestone cliffs covered by mosses, 750 m), 30 May 1983, *Tammaro* (holotype: AQUI; isotypes: FI?, RO!).

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf dimorphic, summer leaf 7-8, yellowish-green, oblong-ovate to oblong, margin slightly involute, apex obtuse, 20-65 mm long, 9-25 mm wide, winter leaf up to 15, ovate, concave, apex acute, small. Hibernaculum ovoid. Scape 1-3, densely glandulous, 40-75 mm long. Calyx bilabiate, upper lip 3-lobed, lobes oblong-ovate, ca. 3 mm long, lower lip 2-lobed, lobes smaller than uppers, connate at base. Flower dark blue to violet. Corolla bilabiate, 16-20 mm across, zygomorphic, 15-20 mm long including spur, upper lip 2-lobed, lobes oblong, lower lip 3-lobed, lobes larger than uppers, obovate-oblong, middle lobe usually longer than laterals, tube dark purple to violet, conical, spur pale purple, cylindrical, dorsally compressed, 5-8 mm long. Capsule ovoid. Seed ellipsoid, 600-750 X 220-340 µm. $2n = 32, 64$. (Plate 4.77).

PHENOLOGY: V, VI, VII

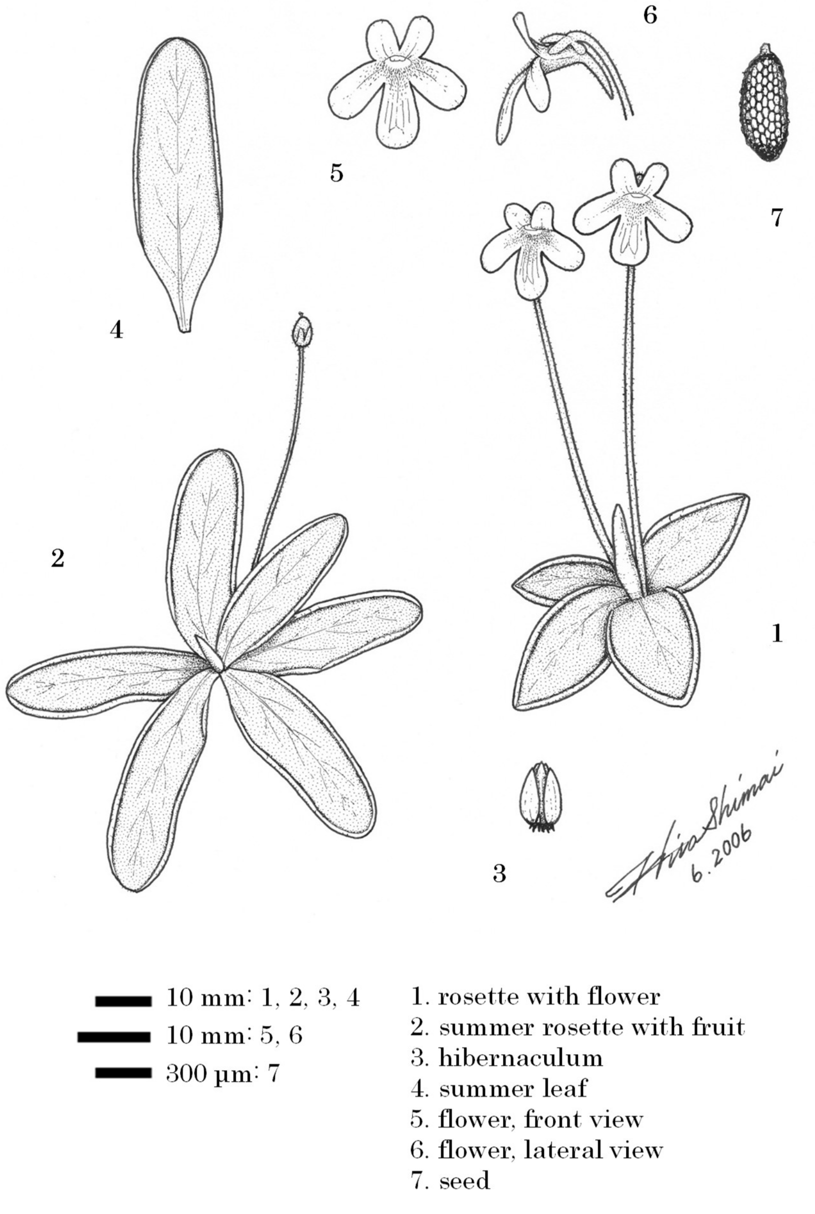
ETYMOLOGY: dedicated to Adriano Fiori (1865-1950), an Italian botanist

HABITAT: Wet mossy calcareous sandstone or limestone rocks in slopes or on cliffs. Tolerant to low light intensity.

DISTRIBUTION: ITALY (Abruzzo). Several localities have been recorded in the Maiella Mountains. 750-2,400 m.

DISCUSSION: *Pinguicula fiorii* is endemic to the Maiella (Majella) Mountains in the Region of Abruzzo, Italy. After morphological observations, compared with three other related taxa (*P balcanica, P. reichenbachiana* and *P. vulgaris*), Tammaro and Pace (1987) described *P. fiorii* as a new species from the Maiella population. Schlauer (1994), who thought that the population was identical with *P. longifolia* subsp. *reichenbachiana*, rejected their treatment, but *P. fiorii* is clearly a distinct species. The corolla is characteristically bluish-purple without any white spot on the lower lip whereas the base of lower lip is densely covered by white trichomes. Even though several localities have been recorded in the mountains, the number of population at each microhabitat is relatively small.

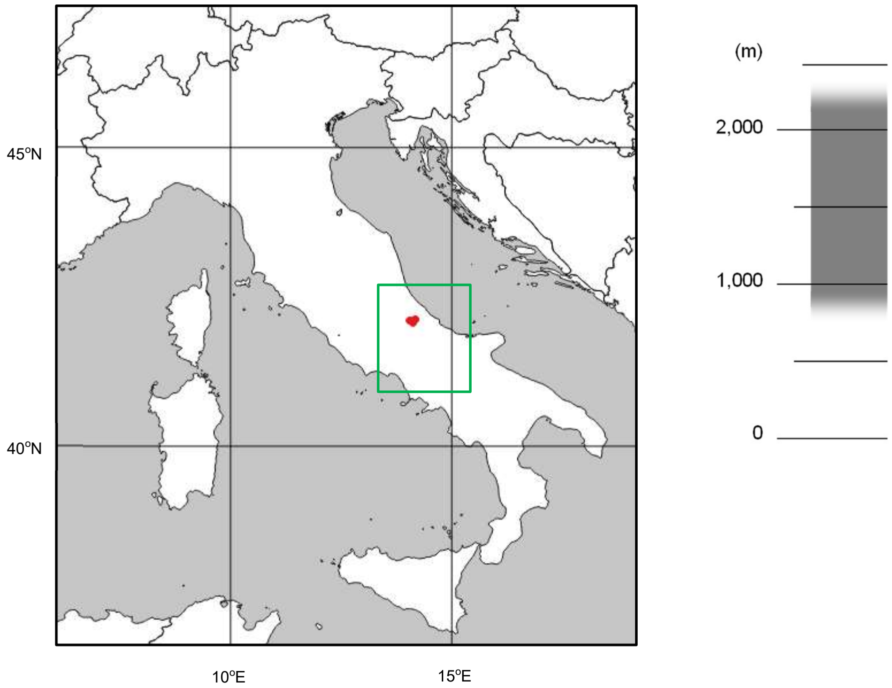
Plate 4.77. *Pinguicula fiorii*

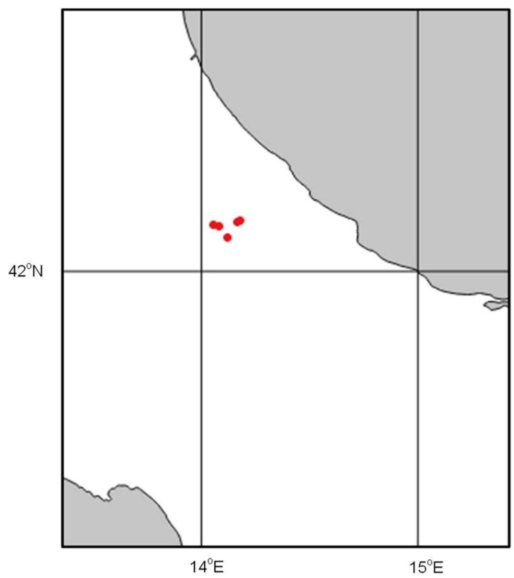


10 mm: 1, 2, 3, 4
10 mm: 5, 6
300 µm: 7

1. rosette with flower
2. summer rosette with fruit
3. hibernaculum
4. summer leaf
5. flower, front view
6. flower, lateral view
7. seed

P. fiorii





78. ***Pinguicula grandiflora*** Lam., Encycl. Méth. Bot. 3 (1789) 22.

TYPE: *s.a. Lamarck* (lectotype: designated by Blanca et al. 1999).

SYNONYMS: *P. eliae* Sennen, *P. grandiflora* Lam. subsp. *coenocantabrica* Rivas Martínez, Díaz, Prieto, Loidi et Penas, *P. grandiflora* Lam. subsp. *reuteri* Löve et Löve, *P. grandiflora* Lam. subsp. *rosea* (Mutel) Casper, *P. grandiflora* Lam. var. *albescens* Rouy, *P. grandiflora* Lam. var. *pallida* Gaudin, *P. grandiflora* Lam. var. *inaequilobata* (Sennen) Casper, *P. grandiflora* Lam. var. *pallida* Briquet, *P. grandiflora* Lam. var. *reuteri* (Genty) Ernst, *P. grandiflora* Lam. var. *rosea* Mutel, *P. grandiflora* Lam. f. *chionopetra* Nelson, *P. grandiflora* Lam. f. *pallida* (Gaudin) Casper, *P. inaequilobata* Sennen, *P. juratensis* Bernard, *P. leptoceras* Lamotte, *P. longifolia* Gaudin, *P. merinoana* Sennen, *P. reuteri* Genty, *P. reuteri* Schindler, *P. vulgaris* Bergeret, *P. vulgaris* L. subsp. *grandiflora* Magnin, *P. vulgaris* L. var. *grandiflora* Bentham et Hooker, *P. vulgaris* L. f. *grandiflora* St. Lager

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf dimorphic, summer leaf 5-9, yellowish-green, oblong to ovate, margin often slightly involute, apex obtuse, 30-60 mm long, 15-35 mm wide, winter leaf up to 15, ovate, concave, apex acute, small. Hibernaculum ovoid, numerous gemmae at base. Scape 1-5, densely glandulous, 40-200 mm long. Calyx bilabiate, upper lip 3-lobed, lobes elliptic-lanceolate, ca. 3 mm long, lower lip 2-lobed, lobes smaller than uppers. Flower bluish-purple to pale pink, pale purple or pale lilac, white stripes at base of middle lobe, rarely entirely white. Corolla bilabiate, 15-30 mm across, zygomorphic, 10-31 mm long including spur, upper lip 2-lobed, lobes obovate, obtuse to rather truncate tip, lower lip 3-lobed, lobes similar to uppers but slightly larger, tip obtuse to truncate, margin often irregularly undulate, tube pale purple, conical, dorsally compressed, spur pale purple with darker veins, cylindrical, 8-15 mm long. Capsule ovoid. Seed ellipsoid, 750-910 × 250-350 µm. $2n = 32$. (Plate 4.78).

PHENOLOGY: III, IV, V, VI, VII, VIII

ETYMOLOGY: large-flowered

HABITAT: Various soil types (fine sand, calcareous sandstone or limestone) in many wet places including open flat areas, slopes or cliffs. Tolerant to various light intensities.

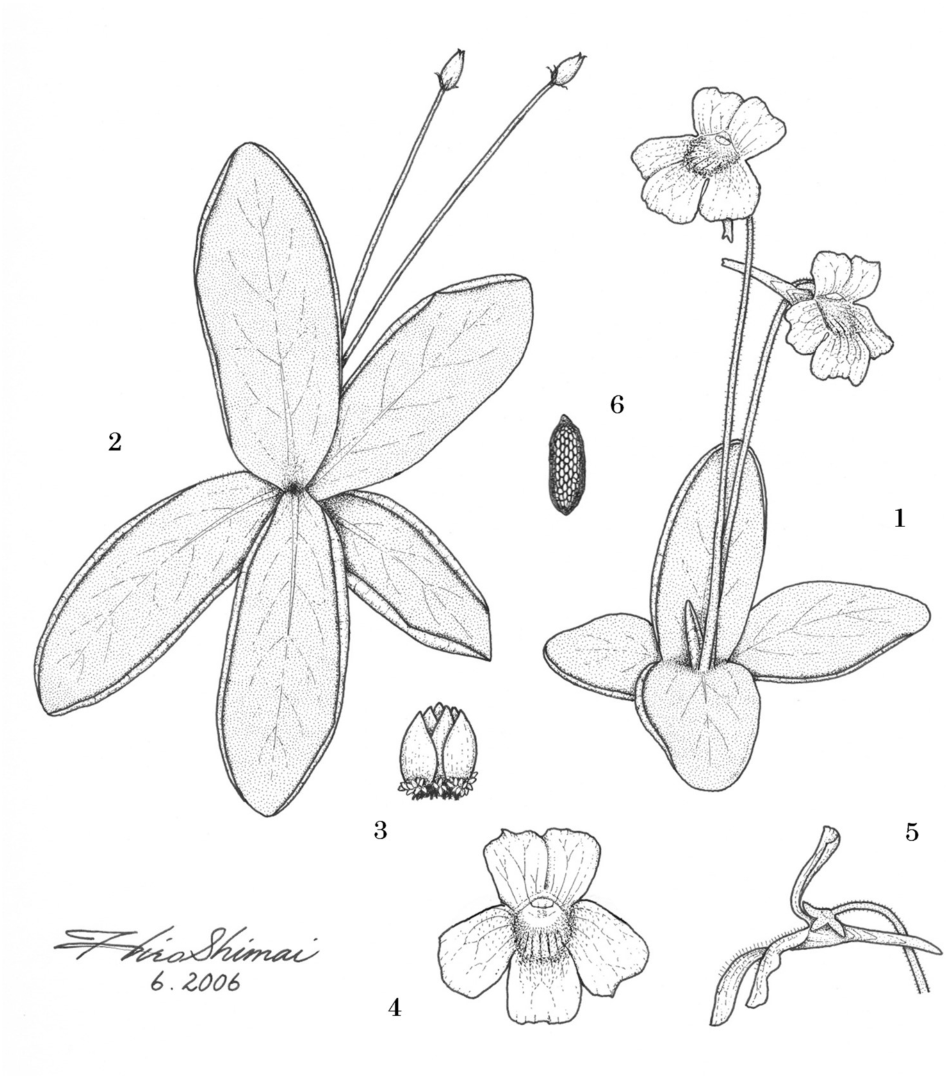
NATURAL HYBRID: × *P. longifolia*, × *P. vulgaris* (= *P.* × *scullyi* Druce)

DISTRIBUTION: ANDORRA (Canillo, Encamp, Ordino); FRANCE (Ain, Ariège, Aude, Cantal, Drôme, Haute-Garonne, Haute-Savoie, Hautes-Pyrénées, Isère, Jura, Puy-de-Dôme, Pyrénées-Atlantiques, Pyrénées-Orientales, Savoie); IRELAND (Clare, Cork, Dublin?, Kerry, Mimerick); MOROCCO (Taza-Al Hoceima-Taounate); SPAIN (Álava, Almería, Asturias, Barcelona, Burgos, Cantabria, Girona, Guipúzcoa, Huesca, León, Lleida, Lugo, Navarra, Soria, Zamora); SWITZERLAND (Vaud). 0-2,490 m.

DISCUSSION: *Pinguicula grandiflora*, having large flowers, is one of the widespread species in Western Europe. Casper (1962a, 1966a) recognised three intraspecific taxa which were *P. grandiflora* subsp. *grandiflora*, having bluish-purple flowers, distributed widely from Ireland to France, Spain, Switzerland (Jura Mountains) and extending to Morocco (Rif Mountains), *P. grandiflora* subsp. *resea*, having rose pink or pale purple flowers with slightly smaller corolla size, confined to eastern France, and *P. grandifola* f. *pallida*, having pale purple flowers, found in the Jura Mountains. Their distributions are not strictly isolated and a major attention for the taxonomy is their flower colours, as a result, the intraspecific division is not accepted here. Some populations of *P. grandiflora* are certainly found in Great Britain, including Cornwall, the Peak District, Wales, and a few other places. Although no apparent evidences have been documented in most cases, those populations in

Great Britain are often regarded as non-native, possibly naturalized by human (Heslop-Harrison 2004). Similarly, a naturalized population by human is seen in the Canton of Bern, Switzerland. *P. grandiflora* is considered to be one of the species of Lusitanian element, which is distributed in both Ireland and France but is absent from Great Britain (Heslop-Harrison 1962, 2004). The hibernacula characteristically bear numerous gemmae at the base. *P. grandiflora* is locally very common and profuse.

Plate 4.78. *Pinguicula grandiflora*

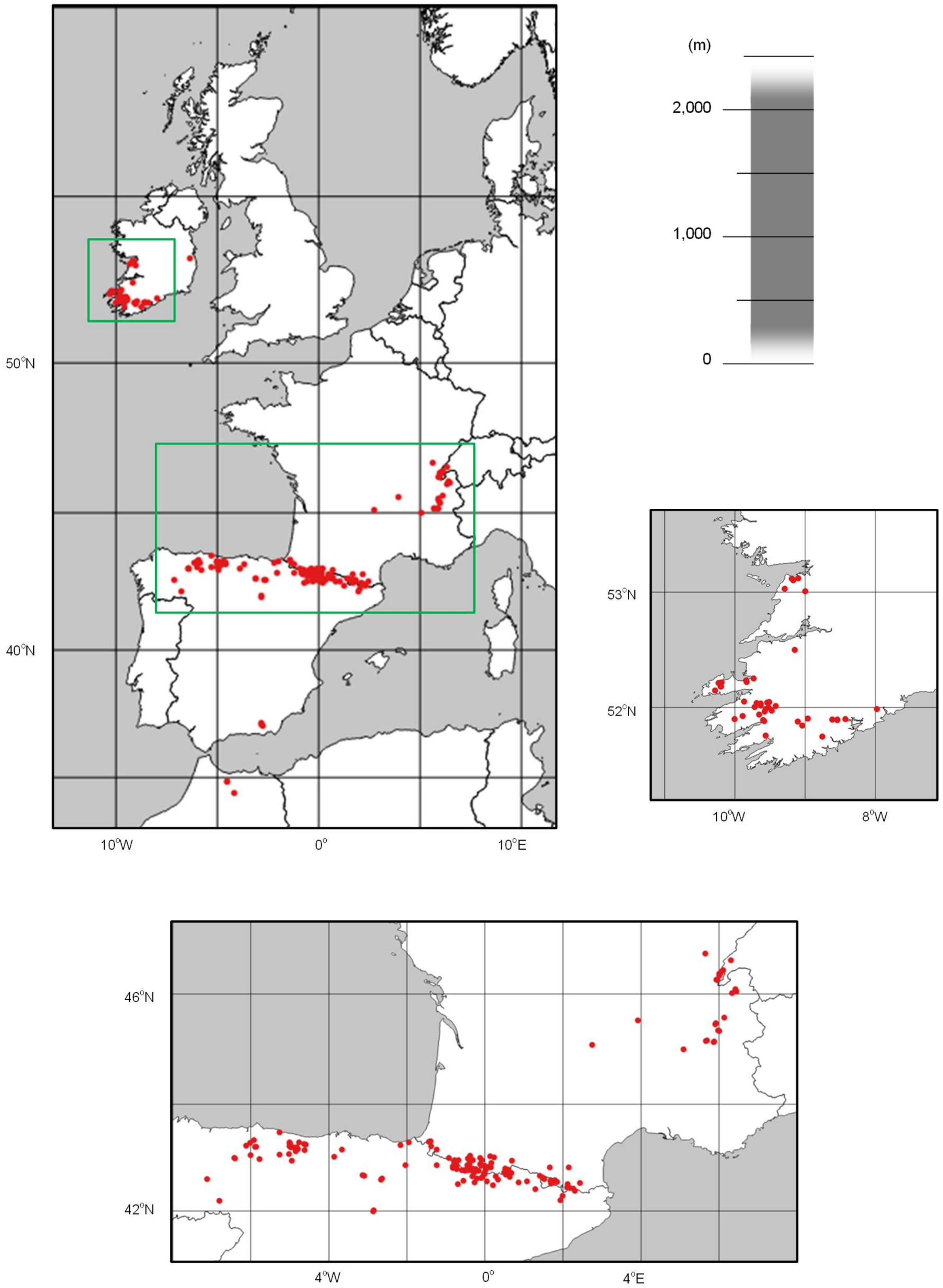


10 mm: 1, 2, 3
10 mm: 4, 5
500 µm: 6

1. rosette with flower
2. rosette with dried capsules
3. hibernaculum
4. flower, front view
5. flower, lateral view
6. seed

summer leaf (see Plate 4.90)

P. grandiflora



79. ***Pinguicula leptoceras*** Reichenbach, Iconogr. Pl. Crit. (1823) 69.

TYPE: SWITZERLAND. *in monte Grimsel in Helvetia* (mountain of Grimsel in Switzerland), *Groh s.n.* (holotype: DR, destroyed), 1927, *Groh* (neotype: ZT).

SYNONYMS: *P. arvetii* Genty, *P. grandiflora* Balbis, *P. grandiflora* Lam. var. *foliis-oblongis* Loiseleur, *P. hellwegeri* Murr, *P. leptoceras* Rchb. var. *hellwegeri* (Murr) Dalla Torre et Sarnthein, *P. leptoceras* Rchb. var. *lepontina* Chiovenda, *P. leptoceras* Rchb. var. *tridentina* Dalla Torre et Sarnthein, *P. leptoceras* Rchb. var. *typica* Chiovenda, *P. leptoceras* Rchb. var. *variegata* Schinz et Keller, *P. longifolia* Koch, *P. variegata* Arvet-Touvet, *P. vulgaris* Nyman, *P. vulgaris* L. subsp. *grandiflora* Thomé, *P. vulgaris* L. subsp. *leptoceras* Rübel, *P. vulgaris* L. var. *alpicola* Chenevard, *P. vulgaris* L. var. *grandiflora* Hausmann, *P. vulgaris* L. var. *grandiflora* Koch, *P. vulgaris* L. var. *grandiflora* Baroni, *P. vulgaris* L. var. *gypsophila* Bouvier, *P. vulgaris* L. var. *leptoceras* Cesati, Passerini et Gibelli, *P. vulgaris* L. var. *leptoceras* Chenevard, *P. vulgaris* L. var. *longifolia* Rapin, *P. vulgaris* L. var. *longifolia* Hausmann, *P. vulgaris* L. var. *longifolia* Koch

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf dimorphic, summer leaf 5-8, yellowish-green, outer margin sometimes maroon, oblong to oblong-lanceolate, margin slightly involute, apex obtuse to rather acute, 20-65 mm long, 6-22 mm wide, winter leaf up to 15, ovate, concave, apex acute, small. Hibernaculum ovoid. Scape 1-6, densely glandulous, 40-100 mm long. Calyx bilabiate, upper lip 3-lobed, lobes oblong-ovate to elliptic-ovate, ca. 3 mm long, lower lip 2-lobed, lobes smaller than uppers. Flower purple, white at base of lower lip or with white blotch at base of lower lip lobes. Corolla bilabiate, 13-20 mm across, zygomorphic, 10-31 mm long including spur, upper lip 2-lobed, lobes obovate, lower lip 3-lobed, lobes larger than uppers, often touching, obovate to suborbicular, middle lobe suborbicular, tip sometimes rather truncate, tube purple, conical, dorsally compressed, spur yellowish-green, cylindrical, 1-9 mm long. Capsule subglobose. Seed ellipsoid. $2n = 32$. (Plate 4.79).

PHENOLOGY: V, VI, VII, VIII

ETYMOLOGY: slender-spurred

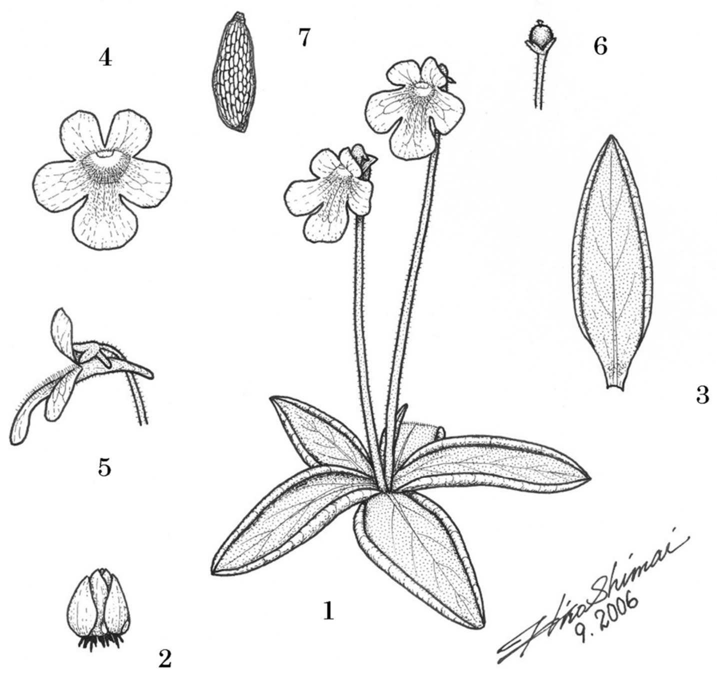
HABITAT: Wet calcareous sand or gravelly soil in open slopes. Often exposed to direct sunlight but tolerant to various light intensities.

NATURAL HYBRID: X *P. vulgaris*

DISTRIBUTION: AUSTRIA (Salzburg, Tirol, Vorarlberg); FRANCE (Alpes-Maritimes, Hautes-Alpes); ITALY (Lombardia, Piemonte, Trentino-Alto Adige, Valle d'Aosta, Veneto); SWITZERLAND (Bern, Graubünden, Ticino, Uri, Valais, Vaud). 900-3,000 m.

DISCUSSION: *Pinguicula leptoceras* is basically confined to higher elevations (often 1,500 m or higher) in the Alps and locally abundant. *P. leptoceras* is often confused with *P. vulgaris*. Although *P. vulgaris* is more commonly found at lower altitudes, the two species sometimes occur together in the same microhabitat and the vegetative and floral morphologies between the two are indeed very similar. In general, *P. leptoceras* has larger corolla diameter, broader and more rounded corolla lobes, and a larger white blotch at the base of lower lip than *P. vulgaris* does. A natural hybrid with *P. vulgaris* is occasionally found in the Alps (pers. observ., Shimai and Steiger). Casper (1962a, 1966a) included populations in the Apennine Mountains, Italy into *P. leptoceras*, but those are later divided to three other species, *P. apuana* and *P. mariae* (Ansaldi and Casper 2009), and *P. christinae* (Peruzzi and Gestri 2013).

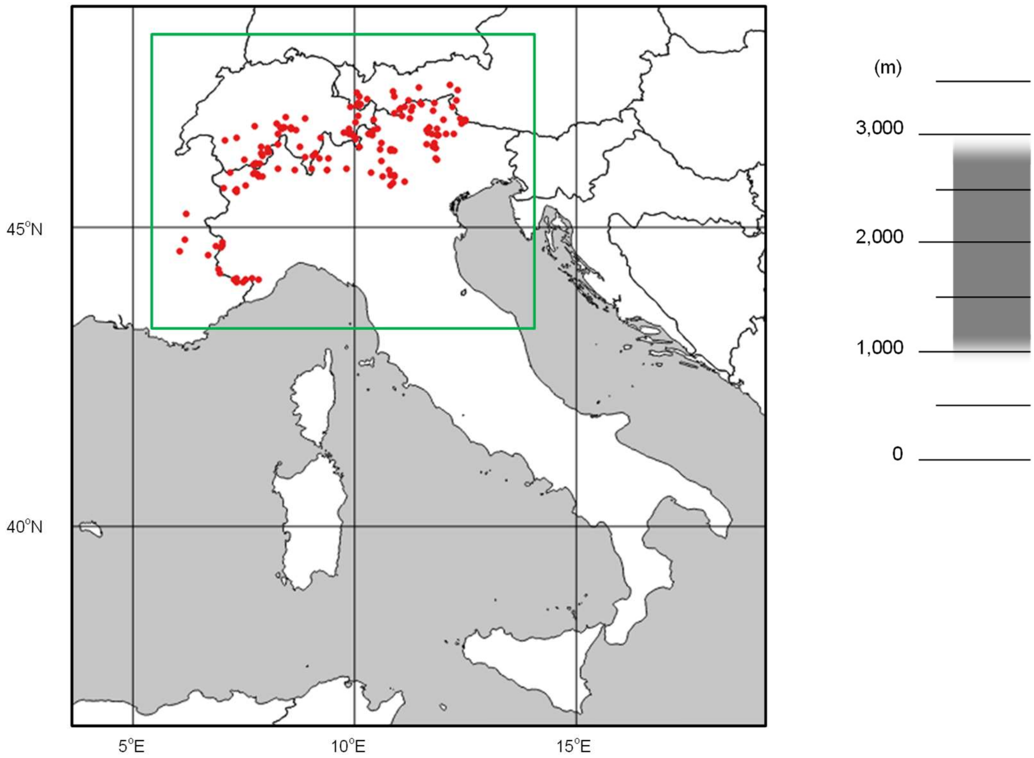
Plate 4.79. *Pinguicula leptoceras*

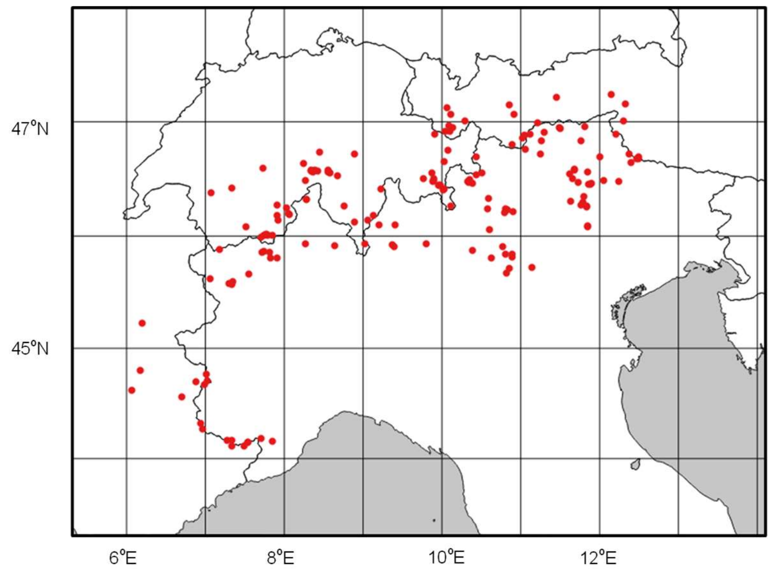


10 mm: 1, 2, 3
10 mm: 4, 5, 6
300 µm: 7

1. rosette with flower
2. hibernaculum
3. summer leaf
4. flower, front view
5. flower, lateral view
6. capsule
7. seed

P. leptoceras





80. ***Pinguicula longifolia*** Ram. ex DC., Fl. Françe ed. 3 (1805) 728.

TYPE: SPAIN. Rochers du Port de Pinède, 1798, *Ramond 001442* left specimen (lectotype: BBF, designated by Blanca et al. 1999); *Ramond 001442* right specimen (lectosyntype: BBF).

SYNONYMS: *P. grandiflora* Sprengel, *P. grandiflora* Lam. subsp. *longifolia* Nyman, *P. grandiflora* Lam. var. *longifolia* Bentham

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf dimorphic, summer leaf 5-10, yellowish-green or maroon, subelect to arcuate, oblong-oblanceolate to linear-oblanceolate, margin irregularly revolute, apex obtuse, 70-200 mm long, 15-25 mm wide, lower surface sparsely glandulous, winter leaf up to 15, ovate, concave, apex acute, small. Hibernaculum ovoid. Scape 1-5, densely glandulous, 50-170 mm long. Calyx bilabiate, upper lip 3-lobed, lobes triangular-elliptic, ca. 4 mm long, lower lip 2-lobed, lobes similar to uppers. Flower purple, white at base of lower lip, sometimes yellow at base of lower lip to throat. Corolla bilabiate, 18-25 mm across, zygomorphic, 20-46 mm long including spur, upper lip 2-lobed, lobes oblong to obovate-oblong, tip obtuse to truncate, lower lip 3-lobed, lobes similar to uppers but slightly larger, tube faintly pale purple with darker veins, conical, dorsally compressed, spur faintly pale purple, cylindrical, 9-18 mm long. Capsule globose. Seed ellipsoid, 620-900 X 240-300 µm. $2n = 32$. (Plate 4.80).

PHENOLOGY: III, IV, V, VI, VII, VIII

ETYMOLOGY: long-leaved

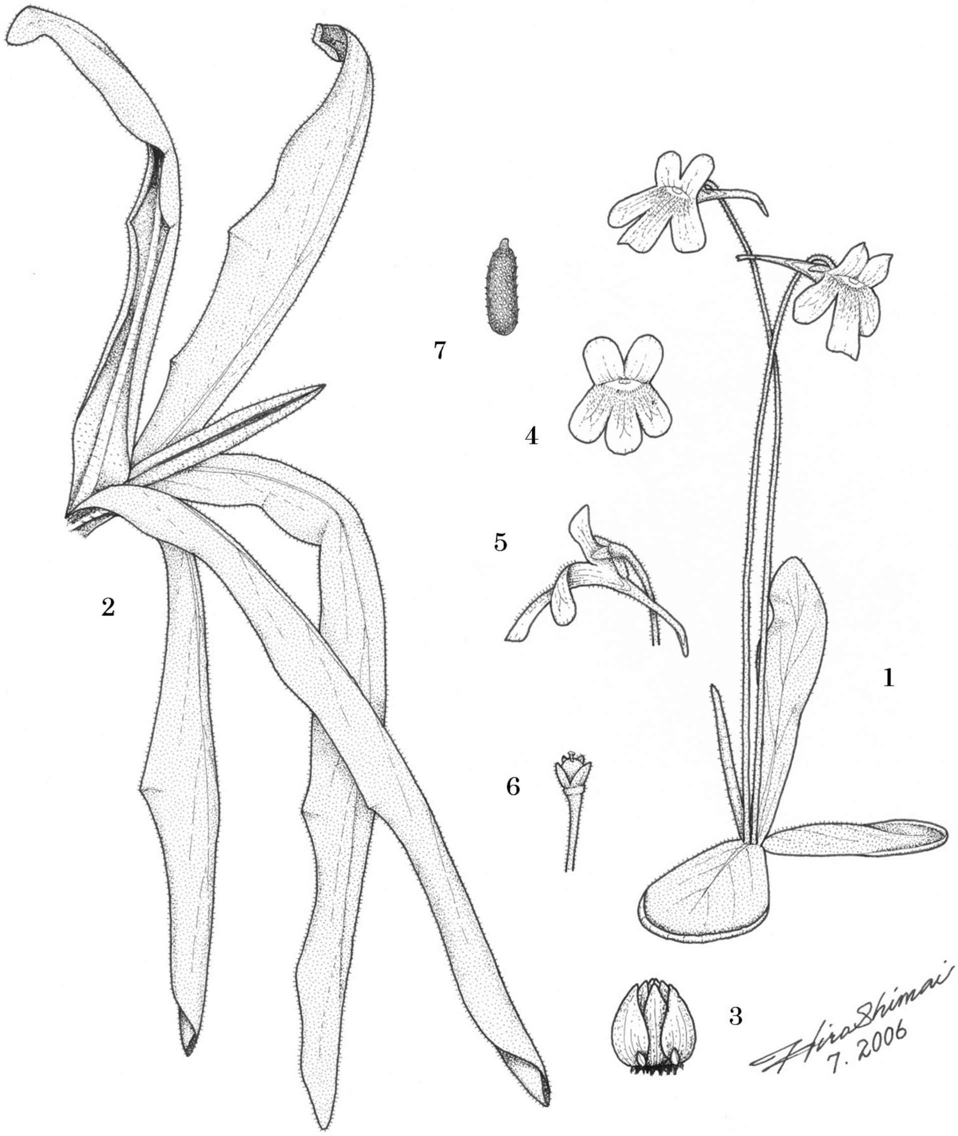
HABITAT: Wet calcareous sandstone or limestone cliffs (often vertical or overhanging). Tolerant to low light intensity.

NATURAL HYBRID: X *P. grandiflora*

DISTRIBUTION: FRANCE (Hautes-Pyrénées); SPAIN (Huesca). 620-2,230 m.

DISCUSSION: *Pinguicula longifolia* is endemic to the Pyrenees. Although herbarium records are seen in both French and Spanish sides of the Pyrenees, it seems the species is found only in the Spanish side at present and the French populations might have been lost. The population currently found in the French Pyrenees is highly likely a hybrid with *P. grandiflora* (i.e. *P. longifolia* X *P. grandiflora*). Casper (1962a, 1966a) recognised three subspecies of *P. longifolia* (*P. longifolia* subsp. *longifolia*, *P. longifolia* subsp. *caussensis* and *P. longifolia* subsp. *reichenbachiana*), but each of them are considered to be distinct species here; therefore, this species can be found only in Spain today. It is morphologically very similar to *P. vallisneriifolia*, but *P. longifolia* never produces runners. Furthermore, the lower surface of the summer leaf in *P. longifolia* is sparsely glandulous while that in *P. vallisneriifolia* is not. *P. longifolia* is locally abundant, whereas the distribution area is highly restricted.

Plate 4.80. *Pinguicula longifolia*

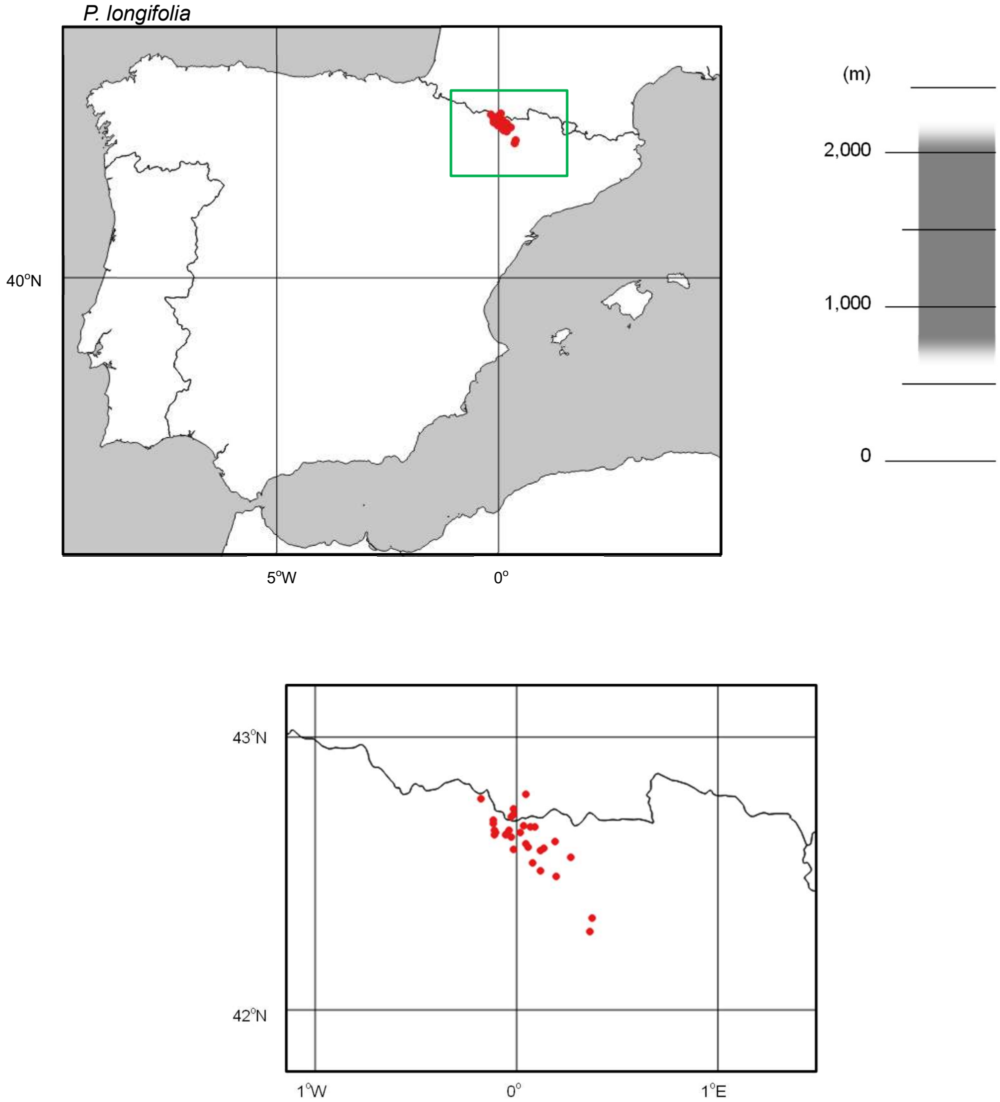


10 mm: 1, 2, 3, 4
10 mm: 5, 6
300 µm: 7

1. rosette with flower
2. rosette
3. hibernaculum
4. flower, front view
5. flower, lateral view
6. capsule
7. seed

summer leaf (see Plate 4.90)

P. longifolia



81. ***Pinguicula macroceras*** Link, Jahrb. Gewächskunde 1 (1820) 54.

TYPE: USA. Alaska, Unalaska, *Willdenow ex Pallas 422* (holotype: B, destroyed; see Casper 1962b).

SYNONYMS: *P. daurica* Link, *P. kamtschatica* Roemer et Schultes, *P. macroceras* Link var. *microceras* (Cham.) Casper, *P. microceras* Cham., *P. vulgaris* Hultén, *P. vulgaris* L. subsp. *macroceras* (Link) Calder et Taylor, *P. vulgaris* L. var. *floribunda* Watanabe et Takeda, *P. vulgaris* L. var. *macroceras* (Link) Herder, *P. vulgaris* L. f. *albiflora* Komiya

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf dimorphic, summer leaf 3-8, yellowish-green, ovate to oblong-ovate, margin sometimes slightly involute, apex obtuse to rather acute, 20-80 mm long, 7-28 mm wide, winter leaf up to 15, ovate, concave, apex acute, small. Hibernaculum ovoid. Scape 1-5, densely glandulous, 25-150 mm long. Calyx bilabiate, upper lip 3-lobed, lobes triangular-lanceolate, 3-5 mm long, lower lip 2-lobed, lobes smaller than uppers. Flower bluish-purple to reddish-purple, white at base of lower lip, or white to faintly pale purple, purple at base of lips to throat. Corolla bilabiate, 15-25 mm across, zygomorphic, 12-30 mm long including spur, upper lip 2-lobed, lobes ovate to oblong-ovate, lower lip 3-lobed, lobes larger than uppers, oblong to obovate-oblong, middle lobe usually longer than laterals, tube dark purple, conical, dorsally compressed, spur dark purple, cylindrical, 3-10 mm long. Capsule subovoid. Seed ellipsoid, 650-840 X 220-300 µm. $2n = 64$. (Plate 4.81).

PHENOLOGY: IV, V, VI, VII, VIII, IX, X

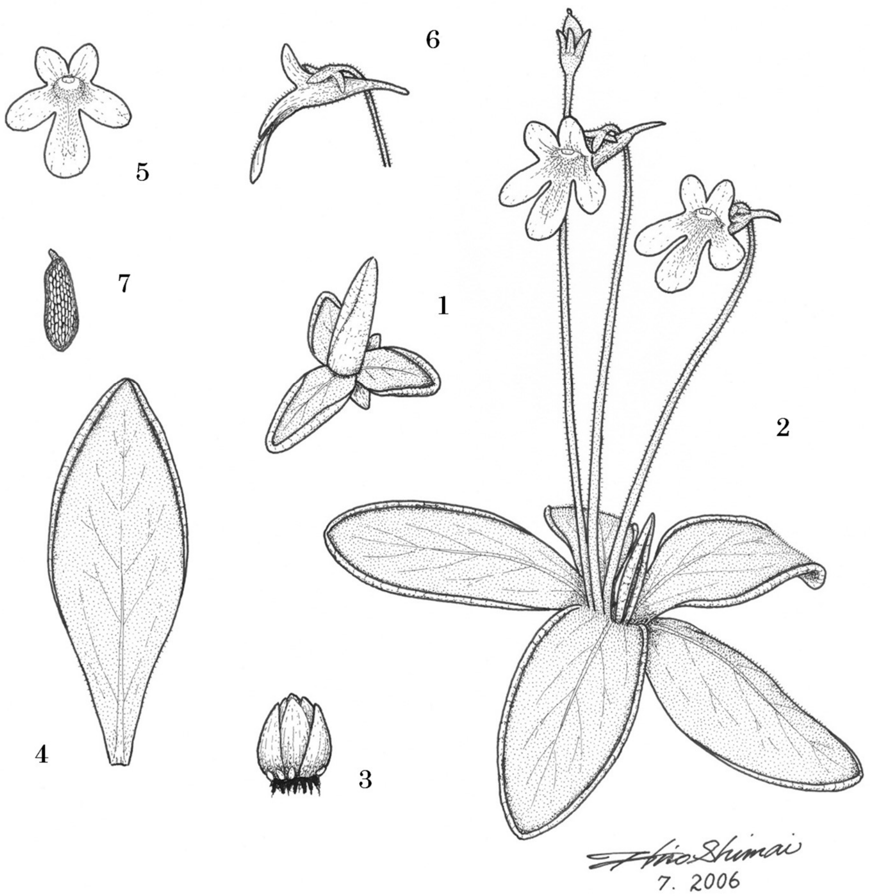
ETYMOLOGY: large-spurred

HABITAT: Various soil types (fine sand, gravelly soil, limestone or serpentine) in many wet places including flat areas, slopes or cliffs (sometimes vertical or overhanging). Tolerant to various light intensities.

DISTRIBUTION: CANADA (Alberta, British Columbia, Yukon Territory); JAPAN (Akita, Aomori, Fukui, Fukushima, Gifu, Gunma, Hokkaidō, Ishikawa, Iwate, Kōchi?, Mie, Miyagi, Nagano, Niigata, Saitama, Tochigi, Tokushima, Toyama, Yamagata, Yamanashi); RUSSIA (Kamchatka, Sakhalin); USA (Alaska, California, Montana, Oregon, Washington). 0-3,026 m.

DISCUSSION: *Pinguicula macroceras* is widely distributed in the northern Pacific Rim regions. This species has been often treated as an intraspecific taxon of *P. vulgaris*. The morphologies between the two are similar in some degree, and their partially overlapped distribution areas in northwestern North America cause confusions. Casper (1962b) explained morphological differences between the two, having different shapes of corolla lobes. In general, *P. macroceras* has wider and more rounded corolla lobes than *P. vulgaris*. *P. macroceras* is morphologically uniform except minor flower colour variations and plant sizes. In spite of little morphological differences, populations from Oregon and California were described as *P. macroceras* subsp. *nortensis* by J. H. Rondeau and J. F. Steiger (in International *Pinguicula* Study Group Newsletter Volume 8, February 1997); *P. macroceras* subsp. *nortensis* is not accepted here. *P. macroceras* is locally very common.

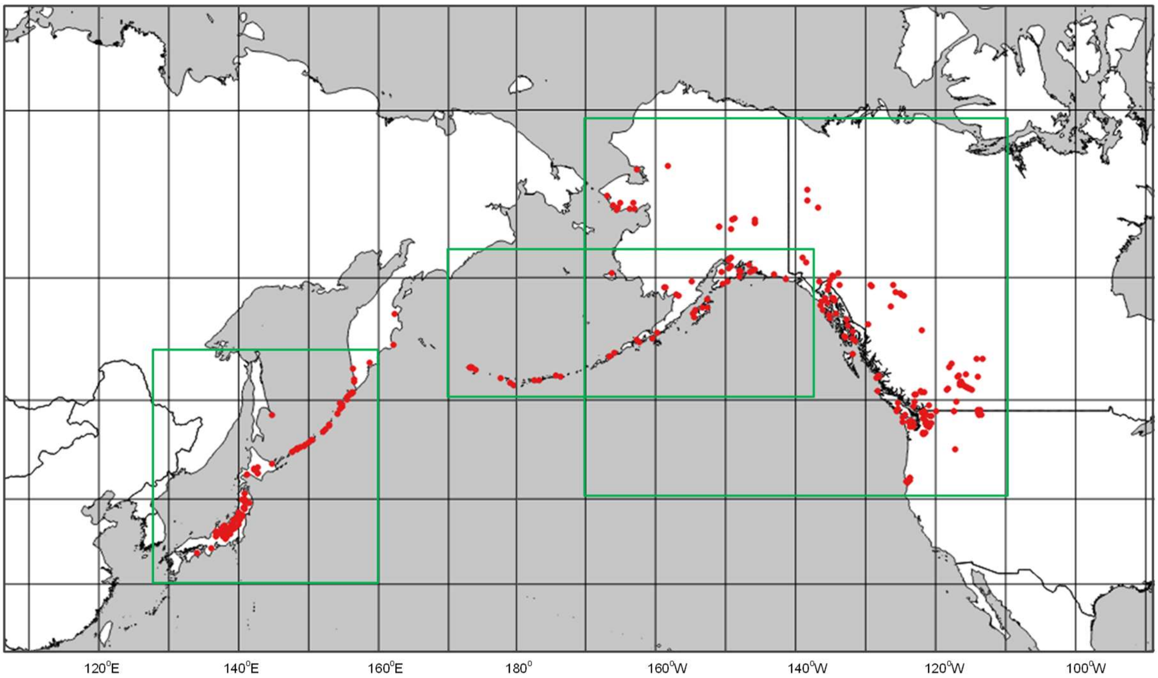
Plate 4.81. *Pinguicula macroceras*

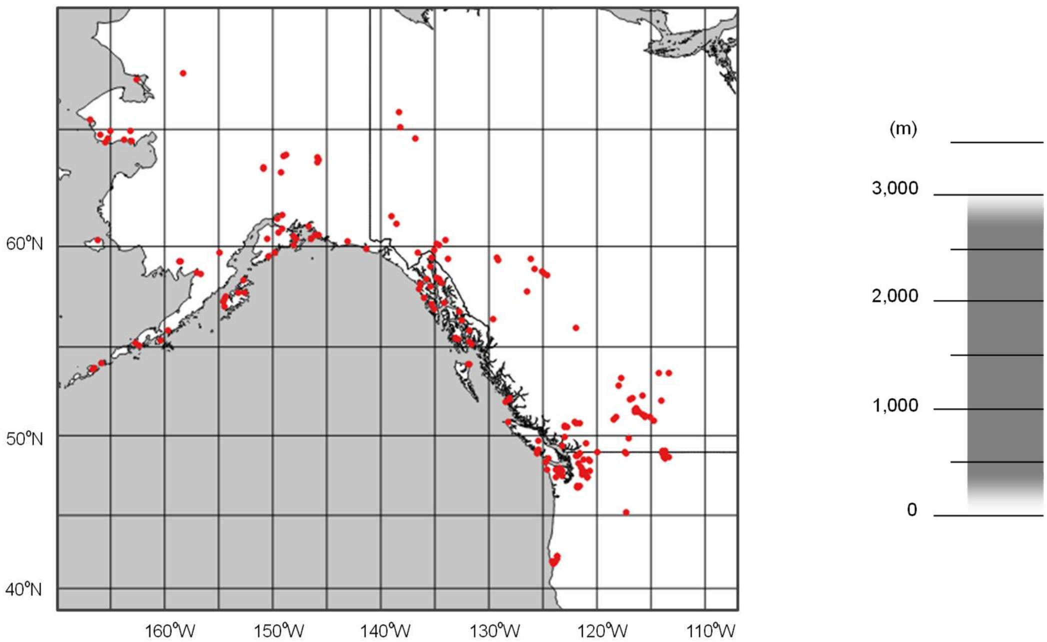


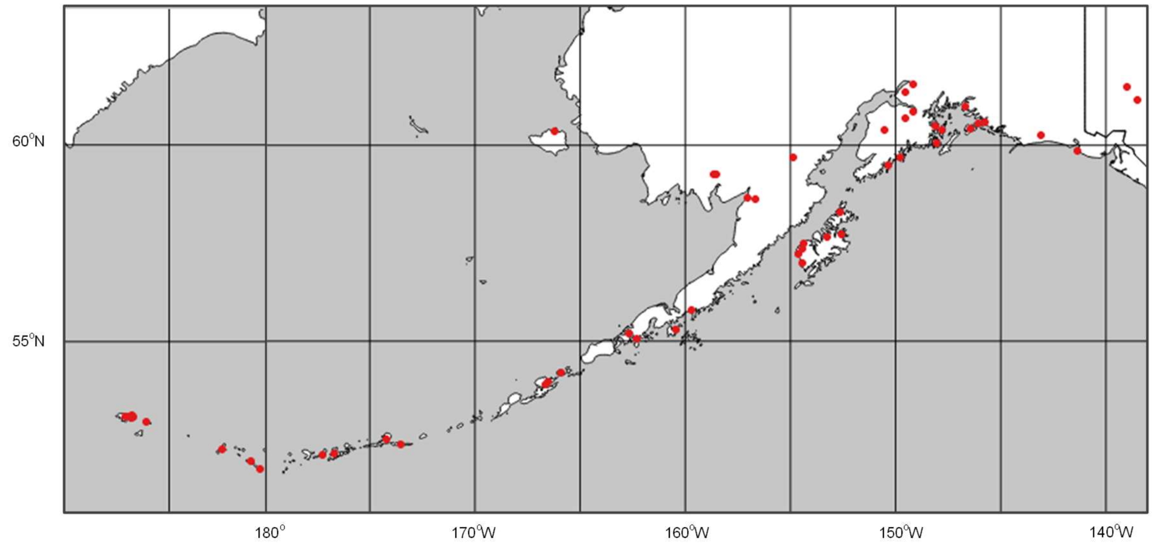
10 mm: 1, 2, 3, 4, 5, 6
500 µm: 7

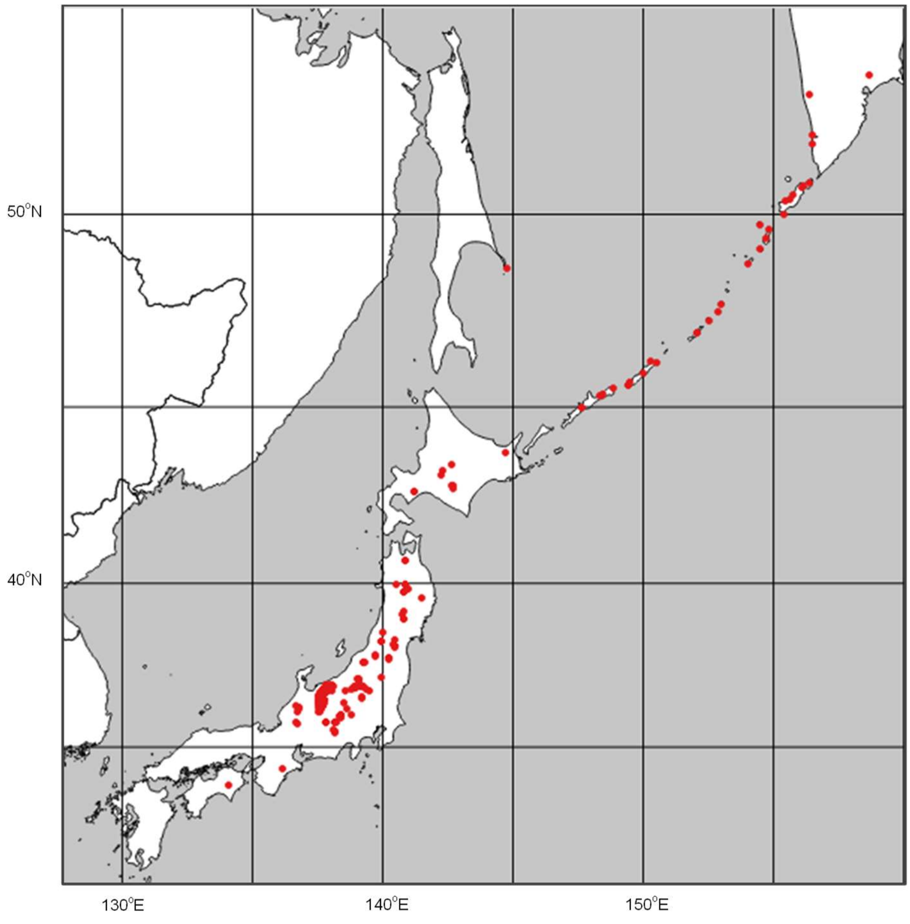
1. rosette
2. rosette with flower and fruit
3. hibernaculum
4. summer leaf
5. flower, front view
6. flower, lateral view
7. seed

P. macroceras






60°N
55°N
180°
170°W
160°W
150°W
140°W


50°N
40°N
130°E
140°E
150°E

82. ***Pinguicula mundi*** Blanca, Jamilena, Ruiz-Rejón et Zamora, Pl. Syst. Evol. 200 (1996) 58.

TYPE: SPAIN. *in orto fluminis Mundo, loco dicto Cueva de los Chorros, Sierra del Calar del Mundo, pr. Riòpar (Albacete provincial, Hispania), 1200m s.m. alt.* (the source of the Mundo River, place called Cueva de los Chorros, Sierra del Calar del Mundo, near Riópar, Province of Albacete, Spain, 1,200 m alt.), 15 June 1993, *Zamora 37729* (holotype: GDAC!).

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf dimorphic, summer leaf 5-15, yellowish-green, oblong to oblong-oblanceolate, base rather cuneate, margin irregularly undulate and slightly involute, apex obtuse, 50-120 mm long, 15-25 mm wide, winter leaf up to 15, ovate, concave, apex acute, small. Hibernaculum ovoid. Scape 1-10, densely glandulous, 50-120 mm long. Calyx bilabiate, upper lip 3-lobed, lobes elliptic, 2.5-3.5 mm long, lower lip 2-lobed, lobes similar to uppers but connate to middle. Flower purple, white at base of lower lip, dark purple in throat. Corolla bilabiate, 18-25 mm across, zygomorphic, 20-38 mm long including spur, upper lip 2-lobed, lobes oblong-obovate, lower lip 3-lobed, lobes similar to uppers but larger, lateral lobes rather oblique, tube purple with darker veins, conical, dorsally compressed, spur faintly pale purple, cylindrical, 8-13 mm long. Capsule subglobose. Seed ellipsoid, 950-690 X 250-270 µm. 2*n* = 48, 64. (Plate 4.82).

PHENOLOGY: V, VI, VII, VIII

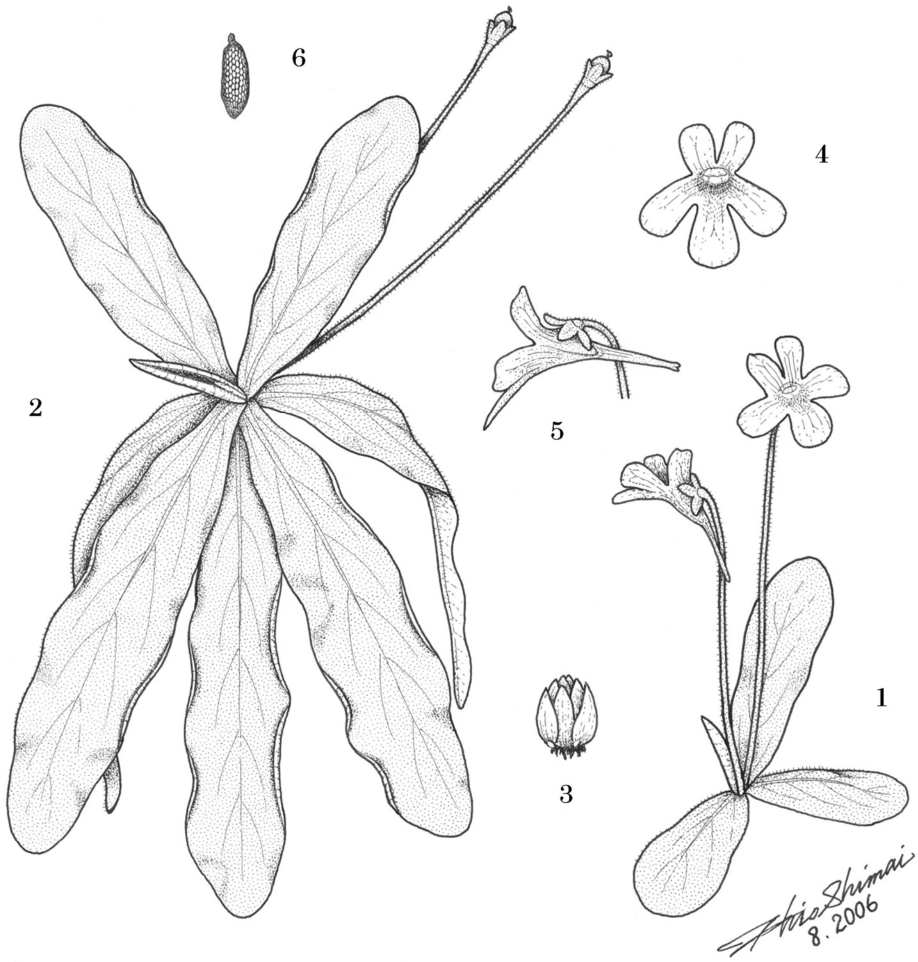
ETYMOLOGY: native of Río Mundo

HABITAT: Mossy wet limestone cliffs. Tolerant to low light intensity.

DISTRIBUTION: SPAIN (Albacete). 800-1,200 m.

DISCUSSION: *Pinguicula mundi* is endemic to the Province of Albacete, Spain. Although the oldest specimens were collected in 1850 at Riópar as *P. longifolia*, it was more recently described as *P. mundi* by Zamora et al. (1996). It is morphologically similar to *P. vallisneriifolia*, but *P. mundi* has wider and shorter summer leaves, and darker flower colour particularly upper lip. Zamora et al. (1996) stated that *P. mundi* produced runners, but it is doubtful. Sometimes populations in the Provinces of Guadalajara and Cuenca have been identified as *P. mundi* (e.g. Blanca et al. 1999), but those are likely *P. dertosensis*. Relatively a large number of plants are seen at the habitat, but it always has a risk of immediate decline of the population density due to environmental stresses and/or climate changes.

Plate 4.82. *Pinguicula mundi*

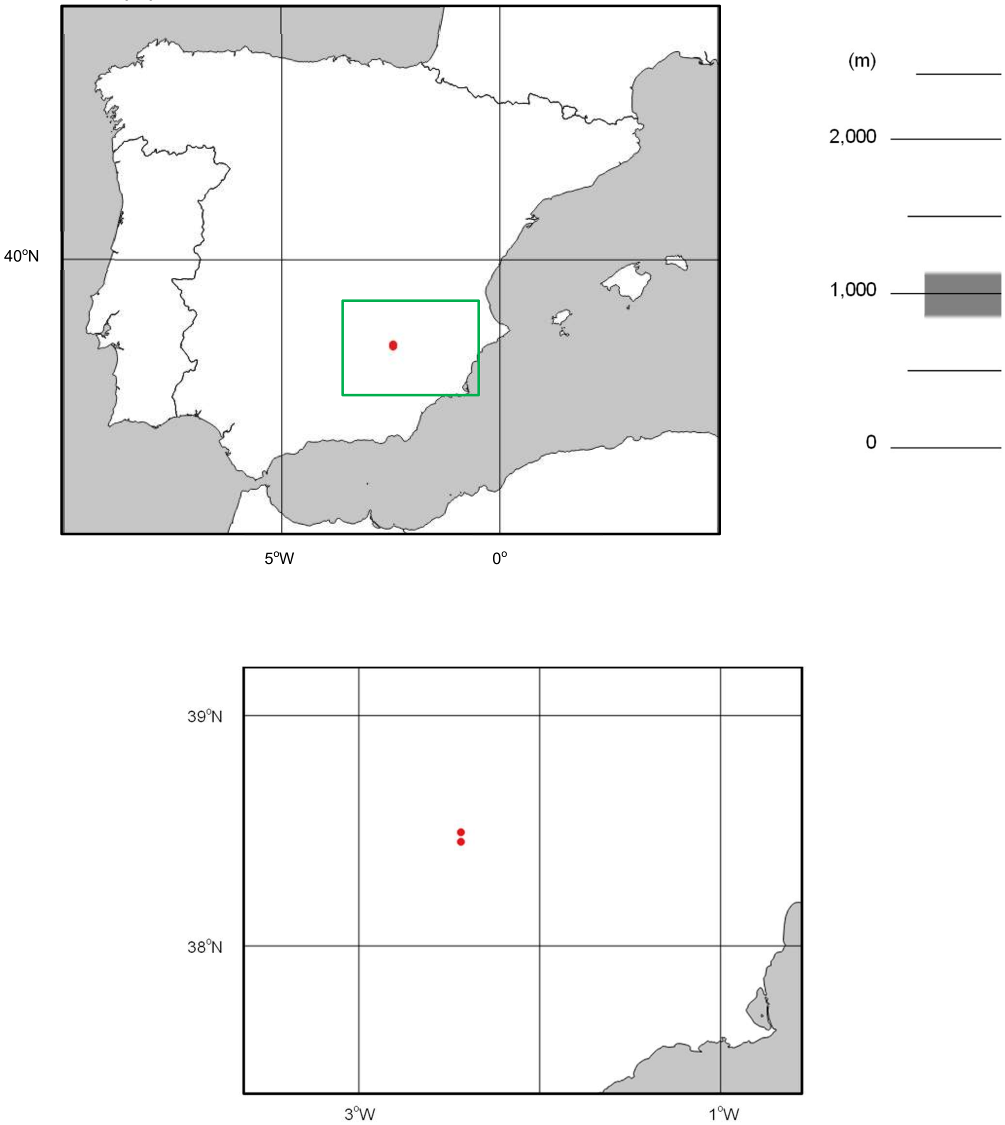


10 mm: 1, 2, 3
10 mm: 4, 5
500 µm: 6

1. rosette with flower
2. rosette with fruit
3. hibernaculum
4. flower, front view
5. flower, lateral view
6. seed

summer leaf (see Plate 4.90)

P. mundi



83. ***Pinguicula nevadensis*** (Lindberg) Casper, Feddes Repert. Spec. Nov. 66 (1962) 112.

TYPE: SPAIN. *Sierra Nevada, in turfosis humidis in declivi supra Laguna de las Yeguas, c. 2600 m* (Sierra Nevada, wet slopes above Laguna de las Yeguas, ca. 2,600 m), 22 July 1926, *Lindberg s.n.* (holotype: LD).

SYNONYMS: *P. leptoceras* Boissier, *P. vulgaris* Nyman, *P. vulgaris* L. subsp. *nevadensis* Lindberg

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf dimorphic, summer leaf 5-8, yellowish-green, outer margin sometimes maroon, ovate to suborbicular, margin involute, apex obtuse, 15-50 mm long, 7-25 mm wide, winter leaf up to 15, ovate, concave, apex acute, small. Hibernaculum ovoid. Scape 1-3, densely glandulous, 20-85 mm long. Calyx bilabiate, upper lip 3-lobed, lobes oblong-ovoid, 2-3 mm long, connate at base, lower lip 2-lobed, lobes smaller than uppers. Flower pale pink or pale lilac, darker at base of lips to throat. Corolla bilabiate, 14-17 mm across, zygomorphic, 10-16 mm long including spur, upper lip 2-lobed, lobes obovate-oblong to obovate, lower lip 3-lobed, lobes larger than uppers, quadrate-obovate, tip truncate to weakly emarginate, tube purple with darker veins, conical to shortly subcylindrical, dorsally compressed, spur purple, cylindrical, incurved to pendulous, 3-6 mm long. Capsule subglobose. Seed ellipsoid. $2n = 16, 32$. (Plate 4.83).

PHENOLOGY: VII

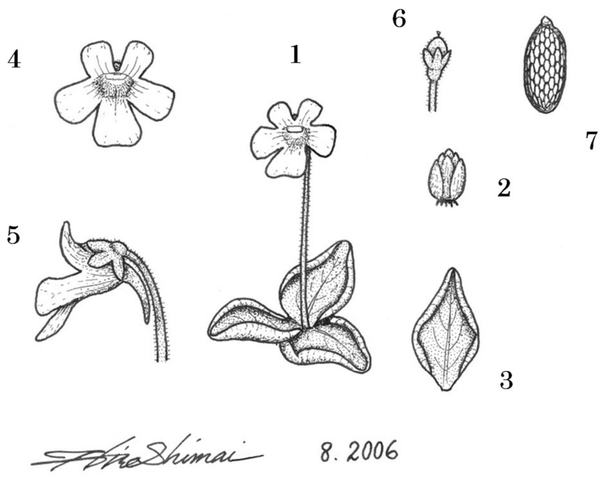
ETYMOLOGY: native of the Sierra Nevada

HABITAT: Wet fine sand in open grasslands with flows. Exposed to direct sunlight.

DISTRIBUTION: SPAIN (Granada). Endemic to the Sierra Nevada. 2,438-3,079 m.

DISCUSSION: *Pinguicula nevadensis* is endemic to the Sierra Nevada in the Province of Granada, Spain. It is found in wet open grasslands at higher altitudes of the mountains. Although it had been often identified as *P. leptoceras* or *P. vulgaris* before Casper (1962a) described *P. nevadensis*, the species is not confused with other *Pinguicula* species at the habitat since no other *Pinguicula* species can be found at higher elevations of the Sierra Nevada. This is a well-defined species both biogeographically and morphologically. *P. nevadensis* has much smaller rosette diameter (often ca. 30 mm across) than other related species seen in Europe. It forms relatively a large colony though the distribution area itself is very restricted in the higher altitudes in the mountains.

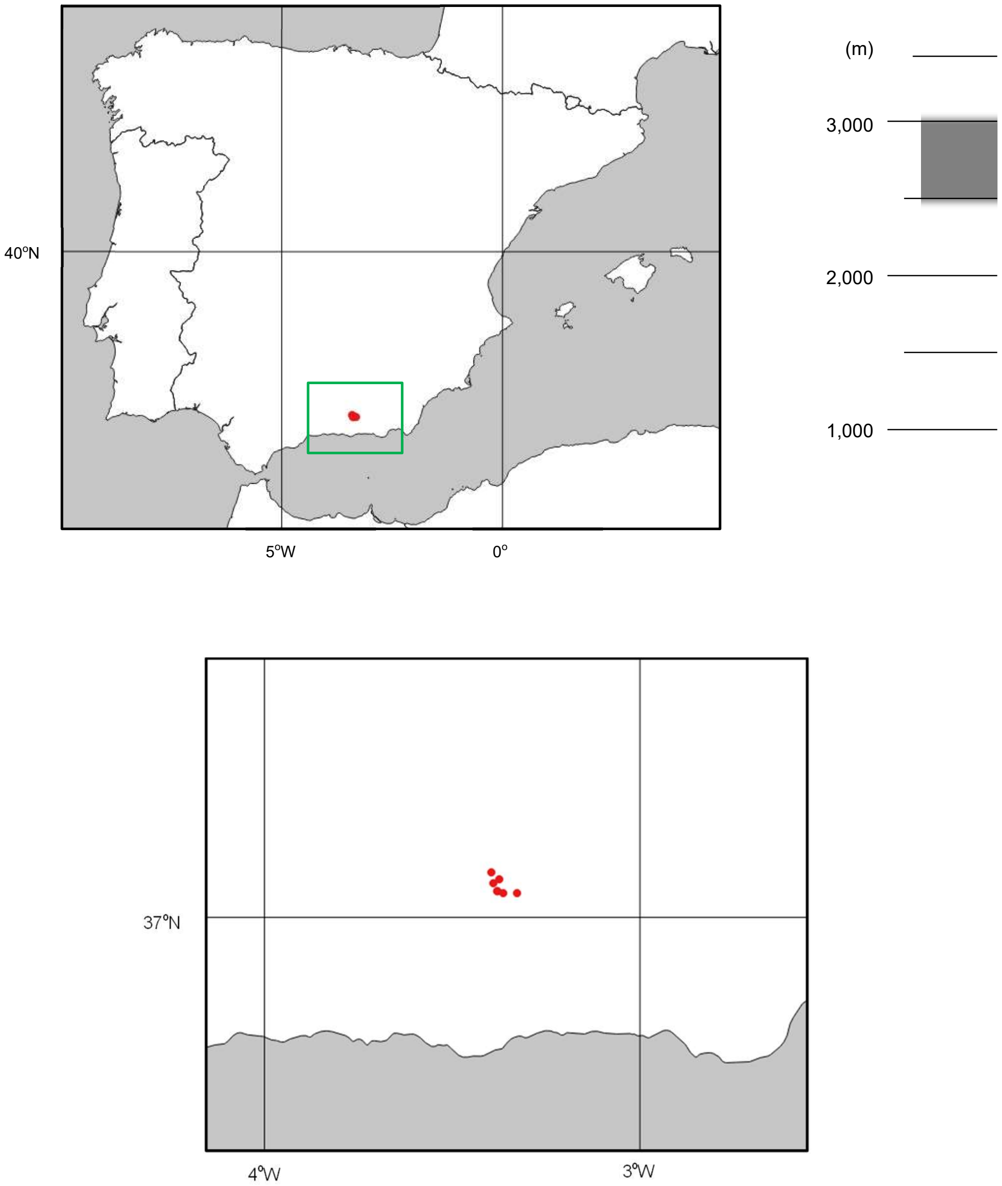
Plate 4.83. *Pinguicula nevadensis*



10 mm: 1, 2, 3
10 mm: 4, 5, 6
500 µm: 7

1. rosette with flower
2. hibernaculum
3. summer leaf
4. flower, front view
5. flower, lateral view
6. capsule
7. seed

P. nevadensis



84. ***Pinguicula poldinii*** Steiger et Casper, Wulfenia 8 (2001) 28.

TYPE: ITALY. *prov. Pordenone, Prealpi Carniche, Val de Cuna (Valle dell'Arzino), ca. 500 m s.m. in rupibus calcareo-dolomiticis madidis* (prov. Pordenone, Carnic Prealps, Val di Cuna (Valle dell'Arzino), ca. 500 m, wet dolomitic limestone rocks), May 1996, *Poldini* (holotype: TSB).

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf dimorphic, summer leaf 4-8, maroon or yellowish-green, oblong to obovate-oblong, margin slightly involute, apex obtuse, base cuneate, 30-50 mm long, 5-13 mm wide, winter leaf up to 15, ovate, concave, apex acute, small. Hibernaculum ovoid to subglobose. Scape 1-6, densely glandulous, 30-115 mm long. Calyx bilabiate, upper lip 3-lobed, lobes ovate-oblong, 2-3 mm long, lower lip 2-lobed, lobes smaller than uppers. Flower reddish-purple, base of lower lip white with fine reddish veins. Corolla bilabiate, 18-25 mm across, zygomorphic, 21-32 mm long including spur, upper lip 2-lobed, lobes oblong, tip obtuse to truncate, lower lip 3-lobed, lobes larger than uppers, obovate-oblong to obovate, tip obtuse to truncate, middle lobe larger than laterals, tube dark purple, conical, dorsally compressed, spur dark purple, cylindrical, 7-13 mm long. Capsule globose. Seed ellipsoid, 560-700 X 210-310 µm. $2n = 32$. (Plate 4.84).

PHENOLOGY: IV, V, VI, VII

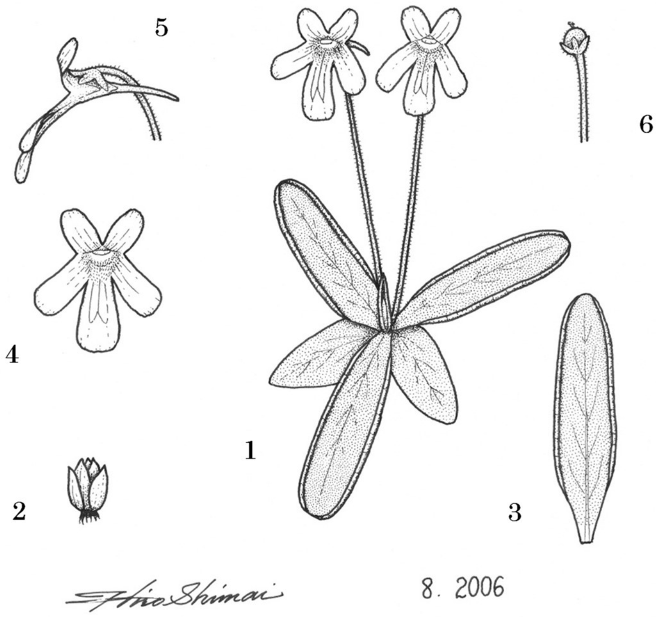
ETYMOLOGY: dedicated to Prof. Livio Poldini, who studied the flora of Friuli-Venezia Giulia

HABITAT: Wet calcareous sandstone or limestone cliffs. Tolerant to low light intensity.

DISTRIBUTION: ITALY (Friuli-Venezia Giulia, Veneto). 450-1,900 m.

DISCUSSION: *Pinguicula poldinii* is found in the Regions of Friuli-Venezia Giulia and Veneto, Italy. It was initially discovered in 1991 by Gianfranco Tonussi, who later reported it to Prof. Livio Poldini (Casper and Steiger 2001). It may be morphologically similar to *P. leptoceras* or *P. vulgaris* in some degree although there has been no record sharing the same microhabitat with them. In comparison to the two, *P. poldinii* has narrower leaves often suffused with maroon entirely, and fine purple stripes on the white background at the base of lower lip. *P. alpina* has been found within the same area, but can be easily distinguished by the flower colour. It was first thought to be an endemic to the Arzino Valley, the holotype locality (Casper and Steiger 2001), but other localities have been discovered since then (Giovagnoli and Tasinozzo 2012).

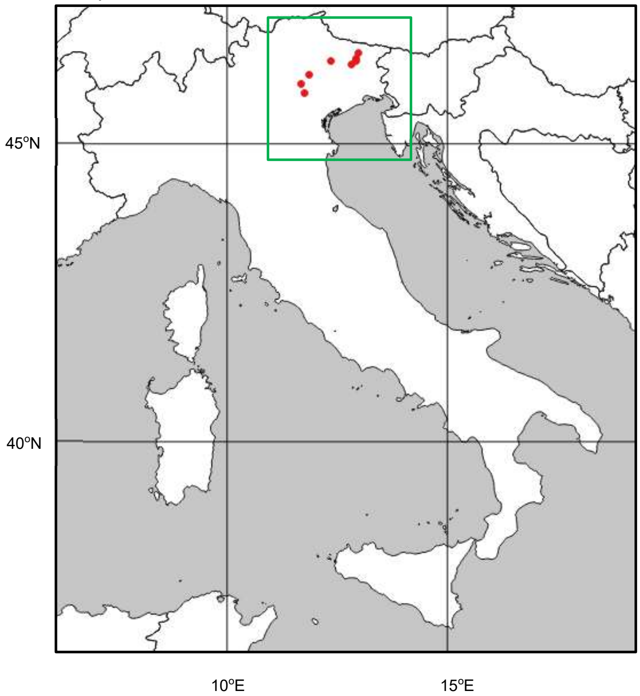
Plate 4.84. *Pinguicula poldinii*

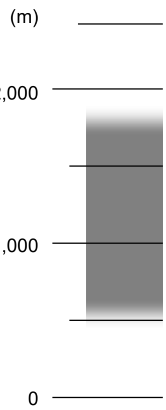


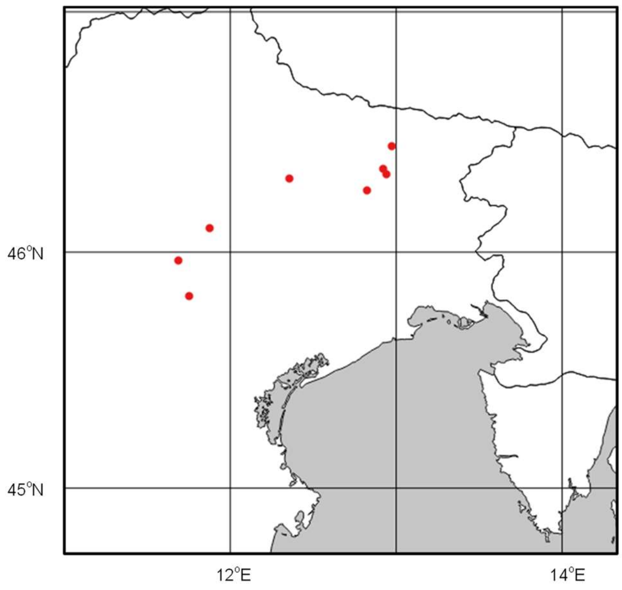
10 mm: 1, 2, 3
10 mm: 4, 5, 6

1. rosette with flower
2. hibernaculum
3. summer leaf
4. flower, front view
5. flower, lateral view
6. capsule

P. poldinii







85. ***Pinguicula reichenbachiana*** Schindler, Österr. Bot. Zeitschr. 58 (1908) 13.

TYPE: FRANCE. *Seealpen, Rojatal, zwischen Fontan und San Dalmazzo di Tenda* (Maritime Alps, Roya, between Fontan and St. Dalmas-de-Tende), May 1907, *Brunnthaler & Porsch s.n.* (lectotype: WU!; designated here from one of the syntype specimens #WU0071049 verified by Sonnleitner on 3 July 2013).

SYNONYMS: *P. grandiflora* Bertoloni, *P. grandiflora* Lam. subsp. *longifolia* Nyman, *P. grandiflora* Lam. var. *longifolia* Grenier et Godron, *P. leptoceras* Rchb. var. *longifolia* Reichenbach, *Pinguicula longifolia* Ram. ex DC. subsp. *reichenbachiana* (Schindler) Casper, *P. vulgaris* Parlatore, *P. vulgaris* L. var. *grandiflora* Fiori et Paoletti, *P. vulgaris* L. var. *grandiflora* Baroni, *P. vulgaris* L. var. *leptoceras* Baroni, *P. vulgaris* L. var. *leptoceras* Cesati, Passerini et Gibelli, *P. vulgaris* L. var. *longifolia* Arcangeli, *P. vulgaris* L. var. *reichenbachiana* Fiori

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf dimorphic, summer leaf 5-10, yellowish-green, oblanceolate to linear-oblanceolate, margin rather revolute and irregularly undulate, apex obtuse, 25-115 mm long, 5-20 mm wide, winter leaf up to 15, ovate, concave, apex acute, small. Hibernaculum ovoid. Scape 1-5, densely glandulous, 50-120 mm long. Calyx bilabiate, upper lip 3-lobed, lobes oblong lanceolate, ca. 3 mm long, lower lip 2-lobed, lobes smaller than uppers. Flower pale purple to bluish-purple, often darker at base of lips, white at base of lower lip. Corolla bilabiate, 18-28 mm across, zygomorphic, 16-44 mm long including spur, upper lip 2-lobed, lobes oblong to suborbicular, lower lip 3-lobed, lobes larger than uppers, obovate, tip obtuse to truncate, tube bluish-purple, conical, dorsally compressed, spur pale purple, cylindrical, 5-15 mm long. Capsule ovoid. Seed ellipsoid, 600-900 X 190-280 µm. $2n = 32$. (Plate 4.85).

PHENOLOGY: IV, V

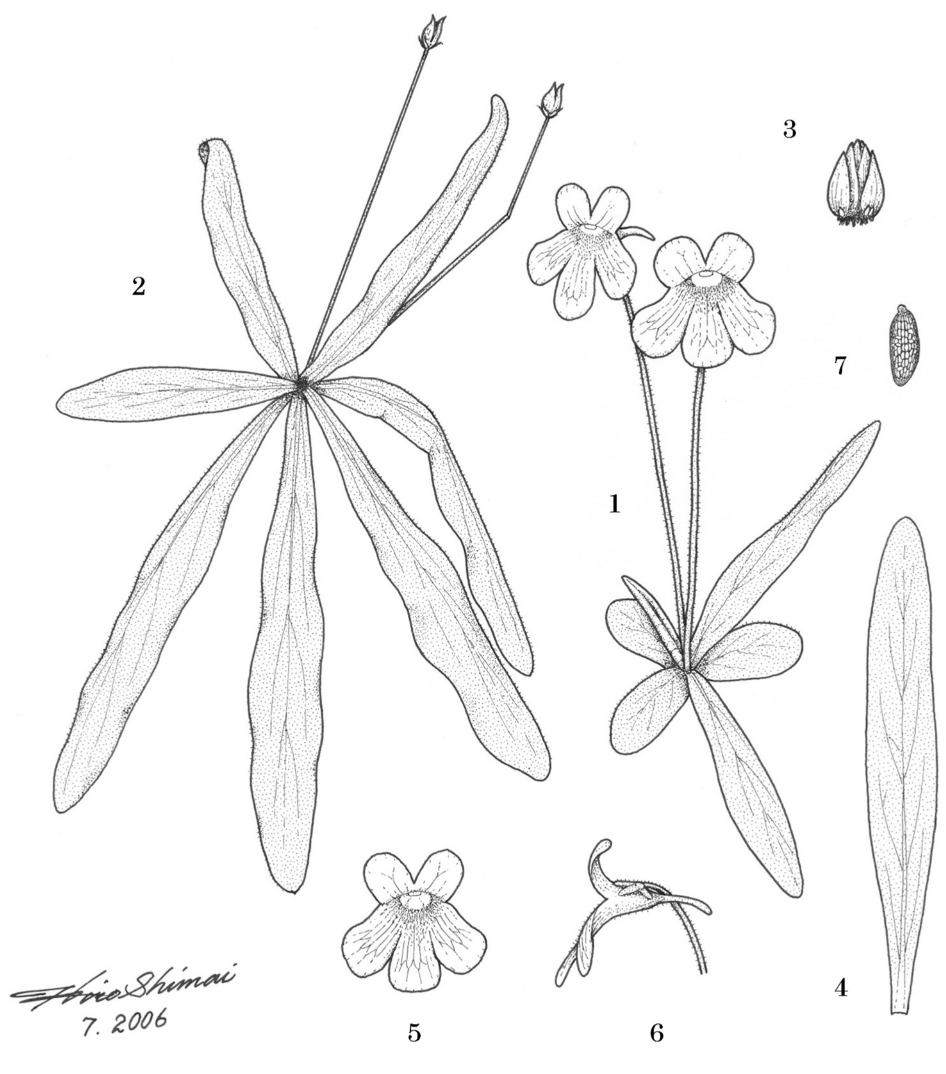
ETYMOLOGY: dedicated to Prof. Heinrich Gustav Reichenbach f. (1824-1889), at the University of Hamburg

HABITAT: Wet calcareous sandstone on cliffs (often vertical or overhanging). Tolerant to low light intensity.

DISTRIBUTION: FRANCE (Alpes-Maritimes); ITALY (Liguria). 128-500 m.

DISCUSSION: *Pinguicula reichenbachiana* is very narrowly found in Alpes-Maritimes, France and Liguria, Italy. It was initially described as a distinct species. Later, Casper (1962a, 1966a) treated as *P. longifolia* subsp. *reichenbachiana* and presented a wider distribution area extending to the Apennine Mountains in Italy. However, it has little morphological similarities, except having longer leaves, to *P. longifolia*. Furthermore, the populations in the Apennine Mountains, which Casper (1962a, 1966a) included into *P. longifolia* subsp. *reichenbachiana*, were recently divided to other species. An Italian population was recently found although more studies would be necessary whether it is the same taxon as the French population. It seems that the French habitat is regularly disturbed by collectors and the population density has being decreased.

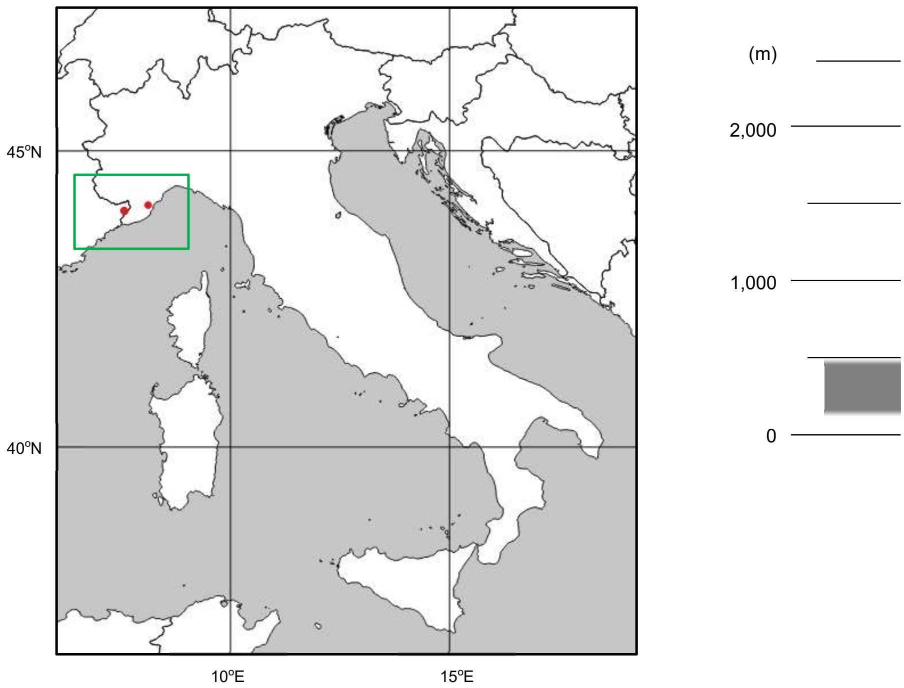
Plate 4.85. *Pinguicula reichenbachiana*

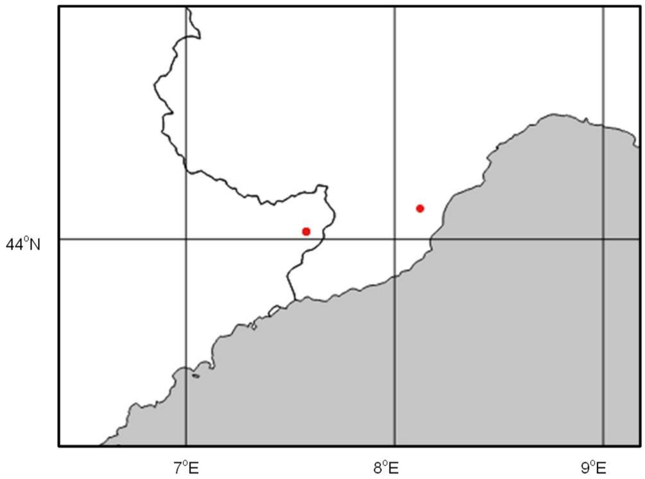


10 mm: 1, 2, 3, 4, 5, 6
500 µm: 7

1. rosette with flower
2. rosette with dried capsules
3. hibernaculum
4. summer leaf
5. flower, front view
6. flower, lateral view
7. seed

P. reichenbachiana





86. ***Pinguicula vallisneriifolia*** Webb, Otia Hispan. (1853) 48.

TYPE: SPAIN. *in montibus circa Velez Rubio* (in mountains near Velez Rubio), *s.a. Blanco,* (lectotype: FI!, designated by Blanca et al. 1999).

SYNONYM: *P. longifolia* Ram. ex DC. f. *vallisneriaefolia* Hervier

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf dimorphic, summer leaf 6-15, yellowish-green, subelect to arcuate or pendulous, linear-oblanceolate, margin rather revolute and irregularly undulate, apex obtuse, 50-250 mm long, 8-28 mm wide, winter leaf up to 15, ovate, concave, apex acute, small. Runner aerial, producing clonal plantlet at apex. Hibernaculum ovoid. Scape 1-8, densely glandulous, 50-175 mm long. Calyx bilabiate, upper lip 3-lobed, lobes triangular-lanceolate, 3-4 mm long, lower lip 2-lobed, lobes similar to uppers. Flower faintly pale purple to purple, white at base of lips, often with yellow trichomes at base of lower lip. Corolla bilabiate, 18-25 mm across, zygomorphic, 20-40 mm long including spur, upper lip 2-lobed, lobes oblong to obovate, lower lip 3-lobed, lobes larger than uppers, obovate-oblong to obovate, tube faintly pale purple with darker veins, conical, dorsally compressed, spur yellow, cylindrical, 9-18 mm long. Capsule subglobose. Seed narrowly ellipsoid to rather clavate, 830-1,000 X 210-270 μm. $2n$ = 32.

(Plate 4.86).

PHENOLOGY: V, VI, VII

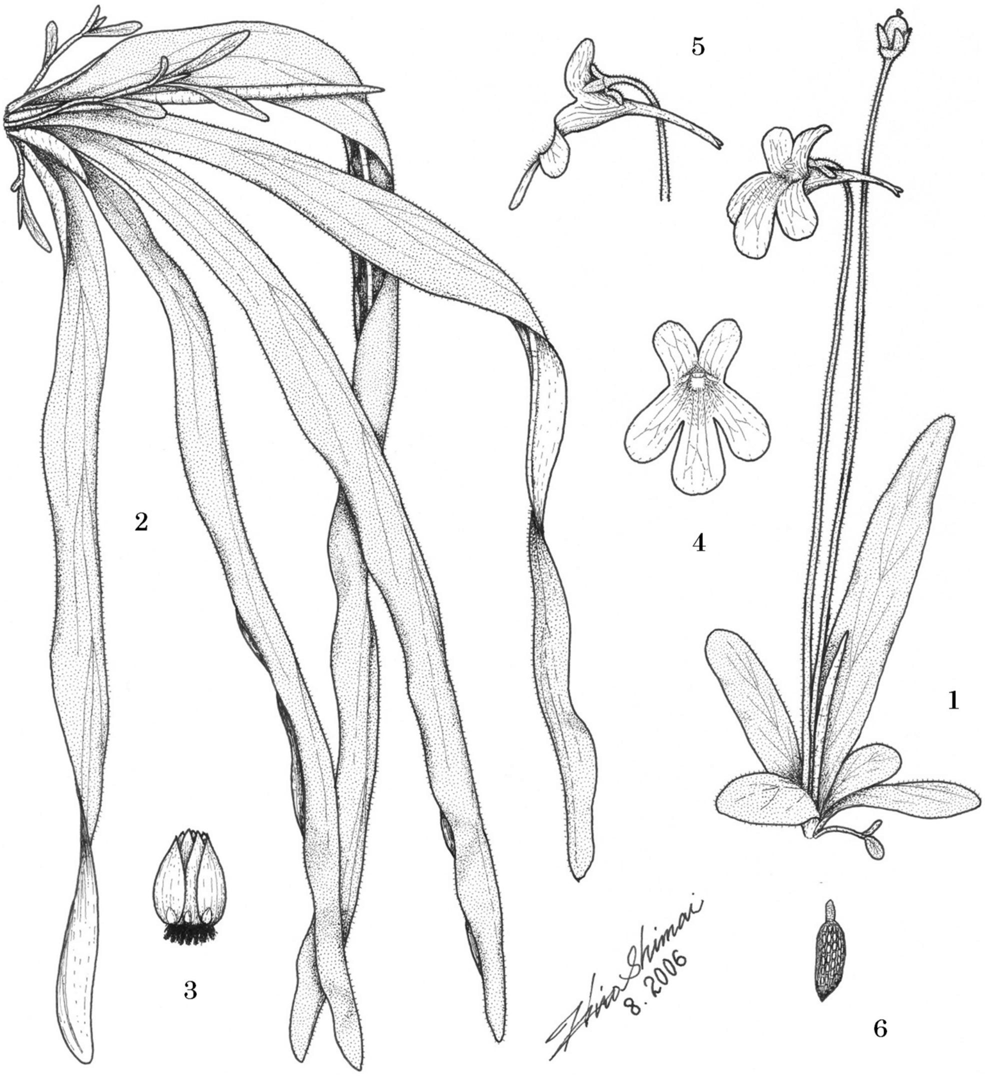
ETYMOLOGY: resembling the leaf of *Vallisneria* (Hydrocharitaceae)

HABITAT: Wet calcareous sandstone or limestone on cliffs (often vertical or overhanging). Tolerant to low light intensity.

DISTRIBUTION: SPAIN (Granada, Jaén). 600-1,700 m.

DISCUSSION: *Pinguicula vallisneriifolia*, spelled as *P. vallisneriifoliae* in the original description, seems to be restricted to the Sierras de Cazorla, Segura and Las Villas Natural Park in the Province of Jaén, and Sierras de Teheda in the Province of Granada, Spain. Although the lectotype locality of Velez Rubio cannot be detected, it is presumably identical with Espumaderas (Espumaedas in the original description) in the Sierra de Segura, Province of Jaén (Blanca et al. 1999). There are minor flower colour variations, purple to faintly pale purple, depending on the strains. It is morphologically very similar to *P. longifolia*, but *P. vallisneriifolia* characteristically has runners which produce a clonal plantlet at the apex. The distributions of both species have been geographically isolated, which results no taxonomic confusions at the habitat. Although *P. vallisneriifolia* often forms large colonies on wet limestone cliffs, the distribution area itself is highly restricted to small geographical regions. Due to relatively drier climate in the region, the population density may have a risk of rapid decline due to environmental stresses and/or environmental changes. A population naturalized by human is seen in the Canton of Bern, Switzerland.

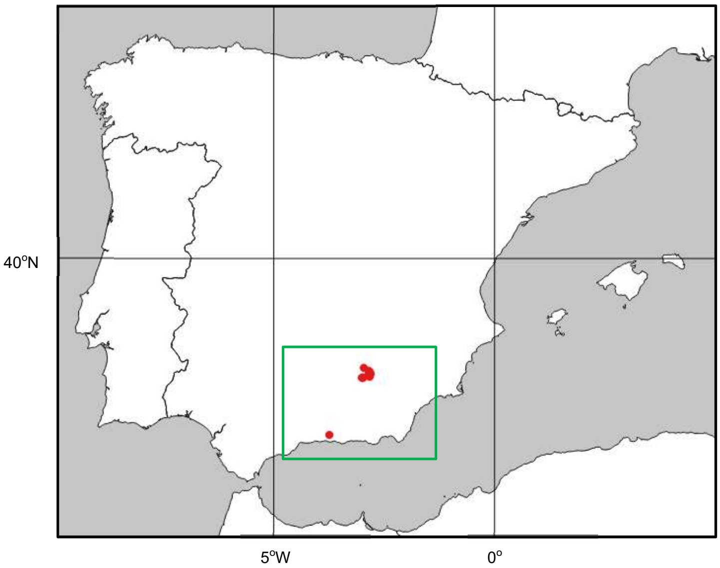
Plate 4.86. *Pinguicula vallisneriifolia*

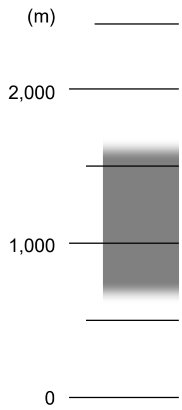


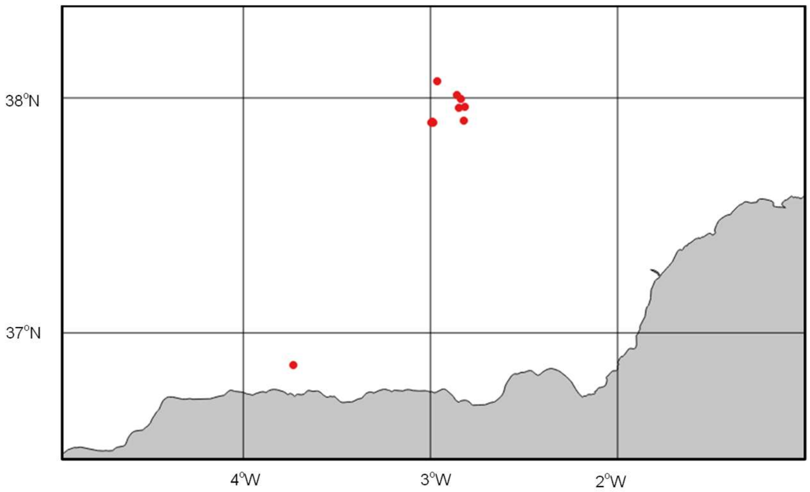
▬ 10 mm: 1, 2, 3
▬ 10 mm: 4, 5
▬ 500 μm: 6

1. rosette with flower and fruit
2. summer rosette
3. hibernaculum
4. flower, front view
5. flower, lateral view
6. seed
summer leaf (see Plate 4.90)

P. vallisneriifolia







87. ***Pinguicula vallis-regiae*** Conti et Peruzzi, Ann. Bot. Fennici 43 (2006) 329.

TYPE: ITALY. Abruzzo, Abruzzo National Park, Camosciara, Villetta Barrea (L'Aquila), dripping cliffs, 1073 m a.s.l., 41°45.925'N, 13°54.535'E, 26 May 1994, *Conti s.n.* (holotype: APP!).

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf dimorphic, summer leaf 5-9, yellowish-green, oblong-obovate, margin slightly involute, apex obtuse to rather acute, 30-72 mm long, 11-18 mm wide, winter leaf up to 15, ovate, concave, apex acute, small. Hibernaculum ovoid. Scape 1-2, densely glandulous, 75-170 mm long. Calyx bilabiate, upper lip 3-lobed, lobes elliptic-linear, 2.5-3.5 mm long, lower lip 2-lobed, lobes smaller than upper, connate at base. Flower bluish-purple, nearly white at base of lower lip with purple veins. Corolla bilabiate, 18-25 mm across, zygomorphic, 28-35 mm long including spur, upper lip 2-lobed, lobes oblong, suborbicular, tip sometimes rather truncate, lower lip 3-lobed, lobes oblong-obovate, middle lobe larger than laterals and somewhat spatulate, tube violet, conical, dorsally compressed, spur pale violet, cylindrical, 9-12 mm long. Capsule ovoid. Seed ellipsoid. (Plate 4.87).

PHENOLOGY: V

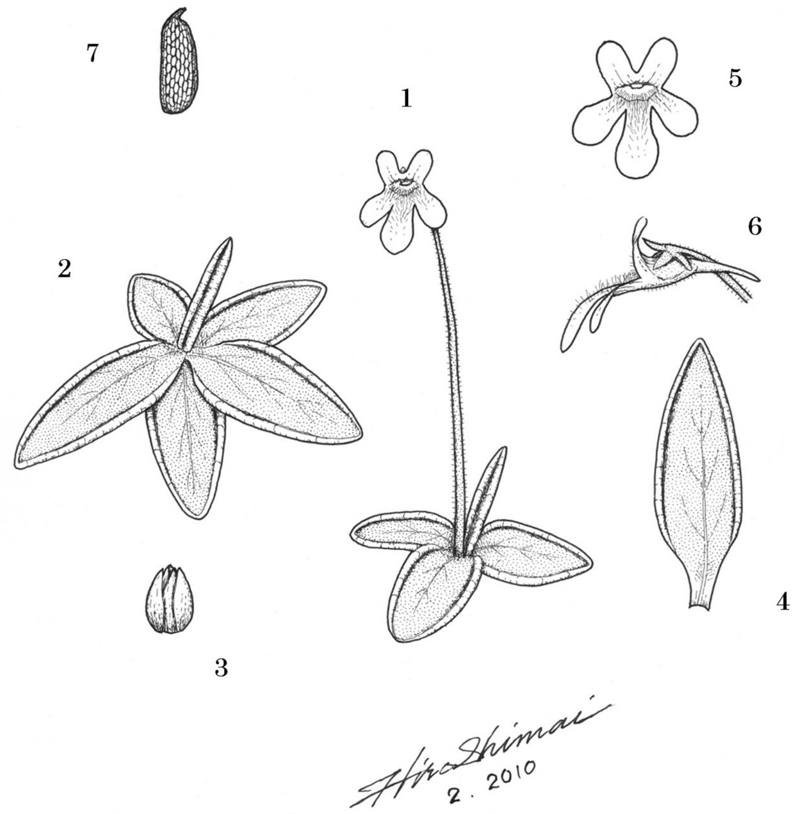
ETYMOLOGY: old medieval name of high Sangro Valley, from which also the name “Barrea” stems

HABITAT: Wet calcareous cliffs. Tolerant to various light intensities.

DISTRIBUTION: ITALY (Abruzzo). Known only from the type locality. 1,073 m.

DISCUSSION: *Pinguicula vallis-regiae* is endemic to the National Park of Abruzzo, Italy. It was previously treated as *P. longifolia* subsp. *reichenbachiana*, for example by Casper (1962a, 1966a). Conti and Peruzzi (2006) divided the population as a new species, i.e. *P. vallis-regiae*, having different morphological characteristics from the *P. reichenbachiana* population in the Roya Valley, France as well as the other Italian *Pinguicula* taxa. In comparison to *P. reichenbachiana*, *P. vallis-regiae* has well-divided corolla lobes, shorter and broader leaves. The geographical distributions of the two are also well-isolated from each other. *P. vallis-regiae* is restricted to a very small area within the National Park of Abruzzo, hitherto known only from the type locality, and the population is small.

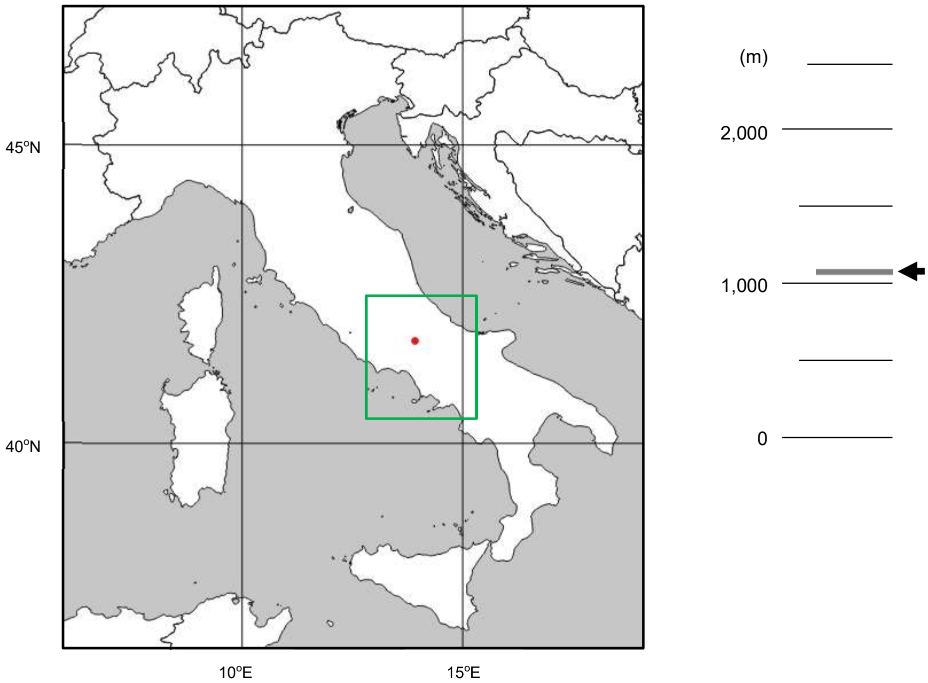
Plate 4.87. *Pinguicula vallis-regiae*

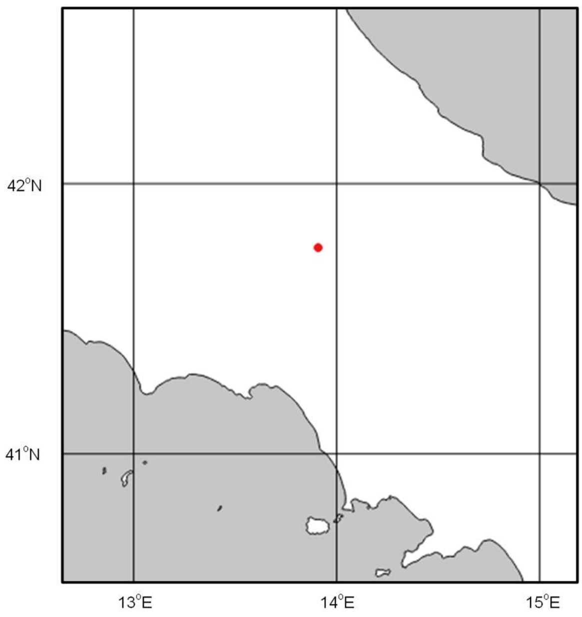


10 mm: 1, 2, 3, 4
10 mm: 5, 6
500 µm: 7

1. rosette with flower
2. rosette
3. hibernaculum
4. summer leaf
5. flower, front view
6. flower, lateral view
7. seed

P. vallis-regiae





88. ***Pinguicula vulgaris*** L., Sp. Pl. (1753) 17.

TYPE: *Linnaeus 33.1* (lectotype: LINN!).

SYNONYMS: *P. alpicola* Rouy, *P. alpina* Weber, *P. arctica* Eastwood, *P. bicolor* (Nordstedt ex Fries) Woloszczak, *P. bicolor* Nordstedt ex Freis f. *gorcensis* Kornas, *P. bohemica* Krajina, *P. borealis* Salisb., *Pinguicula fontiqueriana* Romo, Peris et Stübing, *P. grandiflora* Pollinius, *P. gypsophila* Wallroth, *P. leptoceras* Schur, *P. norica* Beck, *P. ovata* Stokes, *P. villosa* Gunner, *P. vulgaris* L. subsp. *alpicola* Rouy, *P. vulgaris* L. subsp. *bicolor* (Nordstedt) Löve et Löve, *P. vulgaris* L. subsp. *bohemica* (Krajina) Domin, *P. vulgaris* L. subsp. *euvulgaris* Dostál, *P. vulgaris* L. var. *albida* Behm, *P. vulgaris* L. var. *alpestris* Marçais, *P. vulgaris* L. var. *alpicola* Chenevard, *P. vulgaris* L. var. *alpicola* Koch, *P. vulgaris* L. var. *bicolor* Blytt, *P. vulgaris* L. var. *bicolor* Nordstedt, *P. vulgaris* L. var. *coerulea* Briquet, *P. vulgaris* L. var. *gaveana* Beauverd, *P. vulgaris* L. var. *genuina* Schinz et Keller, *P. vulgaris* L. var. *grandiflora* Cosson et Germain, *P. vulgaris* L. var. *gypsophila* Rchb., *P. vulgaris* L. var. *gypsophila* Fuss, *P. vulgaris* L. var. *leptoceras* Sampaio, *P. vulgaris* L. var. *macrantha* Lamotte, *P. vulgaris* L. var. *minor* Koch, *P. vulgaris* L. var. *minor* Mayer, *P. vulgaris* L. var. *obtusa* Sommerfelt, *P. vulgaris* L. var. *obtusata* Nordstedt, *P. vulgaris* L. var. *pallida*

Lange, *P. vulgaris* L. var. *pratensis* Koch, *P. vulgaris* L. var. *pratensis* Willkomm, *P. vulgaris* L. var. *sixtina* Briquet, *P. vulgaris* L. var. *tenuior* Fries, *P. vulgaris* L. var. *tenuior* Wahlenberg, *P. vulgaris* L. var. *transsilvanica* Krajina, *P. vulgaris* L. var. *uliginosa* Genty, *P. vulgaris* L. f. *albida* (Behm) Neumann, *P. vulgaris* L. f. *bicolor* (Nordstedt ex Fries) Neumann, *P. vulgaris* L. f. *coerulescens* Eklund, *P. vulgaris* L. f. *semiflava* Neumann

DESCRIPTION: Perennial herb. Root filiform, fragile. Stem very short. Leaf dimorphic, summer leaf 5-11, yellowish-green, ovate to ovate-oblong, margin slightly involute, apex obtuse to rather acute, 10-90 mm long, 7-26 mm wide, winter leaf up to 15, ovate, concave, apex acute, small. Hibernaculum ovoid. Scape 1-6, densely glandulous, 25-270 mm long. Calyx bilabiate, upper lip 3-lobed, lobes ovate to oblong-lanceolate, 2-3 mm long, connate at base, lower lip 2-lobed, lobes slightly smaller than uppers. Flower purple, white at base of lower lip, or occasionally white to faintly pale lilac, dark purple at base of lips and in throat. Corolla bilabiate, 10-15 mm across, zygomorphic, 9-29 mm long including spur, upper lip 2-lobed, lobes oblong, lower lip 3-lobed, lobes larger than uppers, obovate to rather cuneate, tube purple, conical, dorsally compressed, spur purple, cylindrical, 1-10 mm long. Capsule ovoid, 550-750 X

220-300 μm. Seed ellipsoid to pyriform. $2n = 32, 64$. (Plate 4.88).

PHENOLOGY: III, IV, V, VI, VII, VIII, IX, X

ETYMOLOGY: common (referring to the distribution)

HABITAT: Various soil types (sphagnum, peat, fine sand, gravelly soil, limestone or serpentine) in many wet places including flat areas, slopes or cliffs. Tolerant to various light intensities.

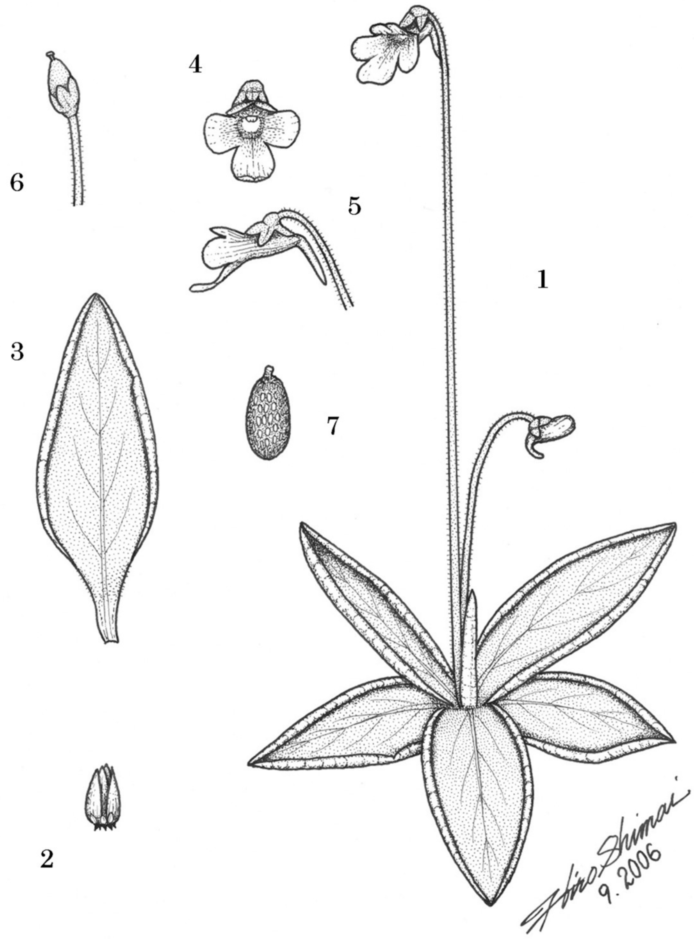
NATURAL HYBRID: X *P. alpina* (=*P.* X *hybrida* Wettstein)?, X *P. bohemica* (=*P.* X *dostalii* Bárta), X *P. grandiflora* (=*P.* X *scullyi* Druce), X *P. leptoceras*

DISTRIBUTION: Widely distributed in Eurasia and northern North America. ANDORRA (Encamp); AUSTRIA (Burgenland, Kärnten, Niederöstrreich, Oberösterreich, Salzburg, Steiermark, Tirol, Vorarlberg); BELARUS (Minsk); BELGIUM (Flanders); CANADA (Manitoba, New Brunswick, Newfoundland and Labrador, Northwest Territories, Nova Scotia, Nunavut, Ontario, Québec, Saskatchewan, Yukon Territory); CROATIA (Karlovac); CZECH REPUBLIC (Jihočeský kraj, Královéhradecký kraj, Liberecký kraj, Plzeňský kraj, Středočeský kraj, Ústecký kraj); DENMARK (Faroe Isls., Greenland, Midtjylland, Nordjylland, Sjaelland, Syddanmark); ESTONIA (Harju maakond, Hiiu maakond, Pärnu maakond, Saare maakond, Tartu maakond); FINLAND

(Ahvenanmaa, Kainuu, Lappi, Pirkanmaa, Pohjois-Karjala, Pohjois-Pohjanmaa); FRANCE (Ain, Alpes-de-Haute-Provence, Alpes-Maritimes, Bas-Rhin, Cantal, Doubs, Eure, Haute-Rhin, Haute-Savoie, Hautes-Alpes, Hautes-Pyrénées, Indre-et-Loire, Isère, Jura, Maine-et-Loire, Oise, Puy-de-Dôme, Pyrénées-Atlantiques, Pyrénées-Orientales, Sarthe, Savoie, Somme, Vosges); GERMANY (Baden-Württemberg, Bayern, Berlin, Brandenburg, Mecklenburg-Vorpommern, Nordrhein-Westfalen, Rheinland-Pfalz, Sachsen-Anhalt, Sachsen, Thüringen); HUNGARY (Győr-Moson-Sopron); ICELAND (Austurland, Höfuðborgarsvæði, Norðurland eystra, Suðurland, Vestfirðir, Vesturland); IRELAND (Clare, Cork, Donegal, Dublin, Galway, Kerry, Kildare, Limerick, Loais, Mayo, Roscommon, Tipperary, Westmeath, Wicklow); ITALY (Friuli-Venezia Giulia, Lombardia, Piemonte, Trentino-Alto Adige, Valle d'Aosta, Veneto); LATVIA (Jūrmala, Tukums); MONGOLIA (Khövsgöl); MOROCCO (Taza-Al Hoceima-Taounate); NETHERLANDS (Gelderland, Overijssel); NORWAY (Akershus, Aust-Agder, Buskerud, Finnmark, Hordaland, Møre og Romsdal, Nordland, Nord-Trøndelag, Oppland, Oslo, Sogn og Fjordane, Sør-Trøndelag, Telemark, Troms, Vest-Agder); POLAND (Lubelskie, Małopolskie, Opole, Świętokrzyskie, Zachodniopomorskie); PORTUGAL (Braga); ROMANIA (Braşov, Dâmbovița, Harghita, Neamț, Prahova, Sibiu, Suceava); RUSSIA (Arkhangelsk, Bashkortostan, Karelia, Khanty-mansi, Komi, Krasnodar, Krasnoyarsk, Leningrad, Murmansk, Nenetsia, Perm, Pskov, Sakha, St. Petersburg, Sverdlovsk, Yamalo-Nenets, Vologda); SLOVAKIA (Banskobystrický kraj, Bratislavský kraj, Košicky kraj, Prešovský kraj, Žilinský kraj); SLOVENIA (Bohinj, Gorje, Jesenice, Kamnik, Kranjska Gora, Ljubljana, Logatec, Mežica, Tržič, Železniki); SPAIN (Asturias, Girona, Guadalajara, Huesca, Teruel, Zamora); SWEDEN (Blekinge, Dalarna, Gotland, Gövleborg, Halland, Jämtland, Jönköping, Kalmar, Kronoberg, Norrbotten, Örebro, Östergötland, Skåne, Södermanland, Stockholm, Uppsala, Värmland, Västerbotten, Västernorrland, Västmanland, Västra Götland); SWITZERAND (Bern, Fribourg, Graubünden, Jura, Luzern, Neuchâtel, Schwyz, Ticino, Uri, Valais, Vaud, Zug, Zürich); UKRAINE (Lviv, Zakarpattia); UNITED KINGDOM ([ENGLAND] Cambridgeshire, Cheshire West and Chester, Cumbria, Derbyshire, Dorset, Durham, Gloucestershire, Greater London, Hampshire, Herefordshire, Lancashire, Lincolnshire, Merseyside, Norfolk, Northumberland, North Yorkshire, Oxfordshire, Somerset, Suffolk, West Midlands, West Yorkshire, Wrexham, Yorkshire; [ISLE OF MAN]; [NORTHERN IRELAND] Antrim, Belfast, Fermanagh, Londonderry, Tyrone; [SCOTLAND] Aberdeenshire, Angus, Argyll and Bute, Dumfries and Galloway, East Lothian, Edinburgh, Highland, Inverclyde, Moray, Na h-Eileanan Siar, North Ayrshire, Orkney, Perth and Kinross, Scottish Borders, Shetland Islands, Stirling; [WALES] Blaenau Gwent, Carmarthenshire, Ceredigion, Conwy, Denbighshire, Gwynedd, Isle of Anglesey, Monmouthshire, Neath Port Talbot, Pembrokeshire, Powys, Rhondda Cynon Taff, Torfaen, Vale of Glamorgan); USA (Alaska, Michigan, Minnesota, New Hampshire, New York, Vermont, Wisconsin). 0-2,500 m.

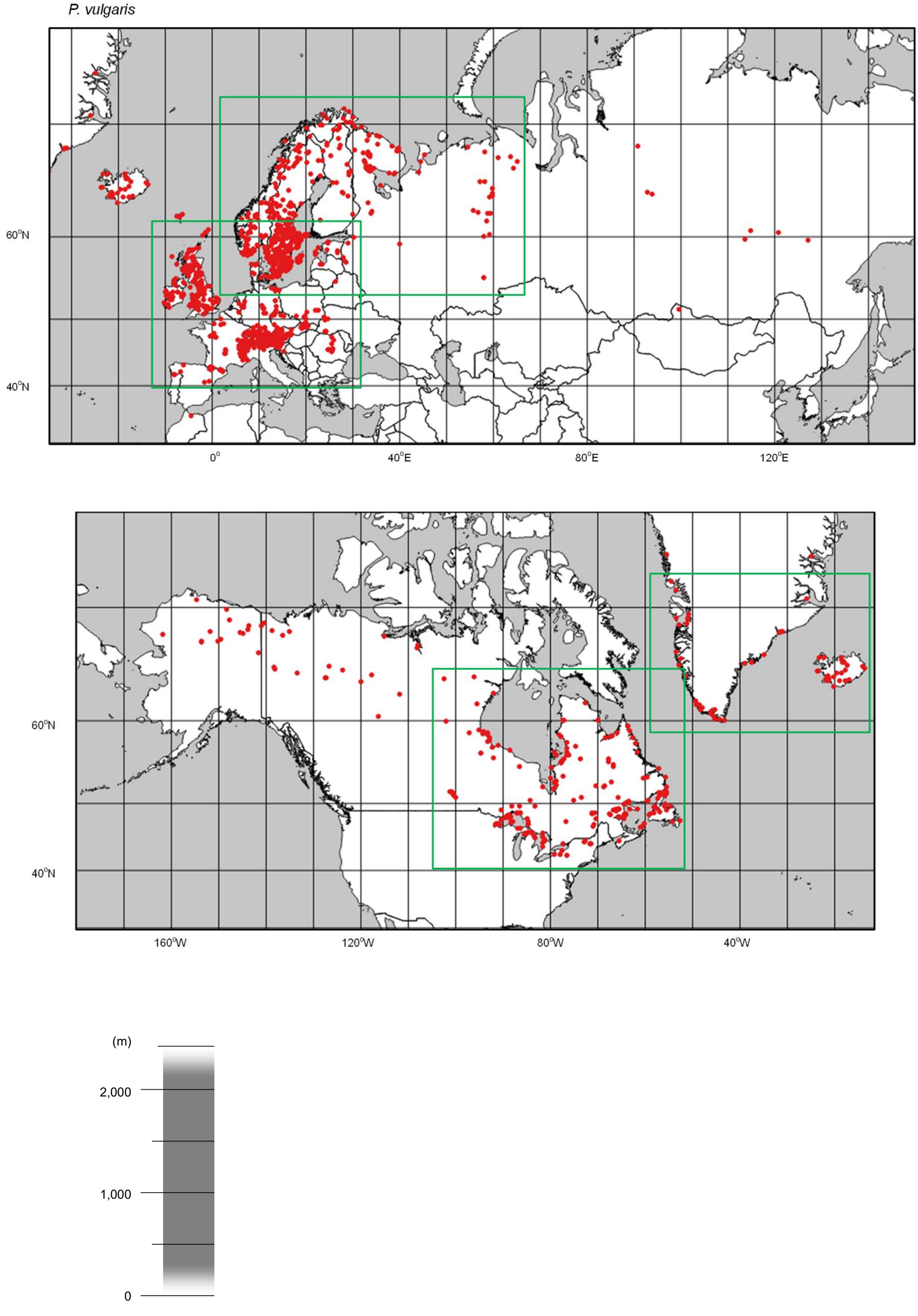
DISCUSSION: *Pinguicula vulgaris*, distributed in North America, Eurasia and Morocco, is one of the most widespread species in the genus. Despite its wider distribution and numerous synonyms, it is morphologically uniform. The flower colouration is basically purple with white at the base of lower lip. Occasionally, populations having different colourations can be found, for example white to faintly pale purple corolla lobes with dark purple at the base of lips and in the throat, and they are sometimes treated as *P. vulgaris* f. *bicolor*. However, those flower colour variations have not been accepted here. At the same time, the populations found in the northern part of the Czech Republic have been recognised as *P. bohemica* by some taxonomists (e.g. Krahulcová and Jarolímová 1991) though it is controversial whether it is a distinct species from *P. vulgaris* (Casper 1966a). *P. vulgaris* is morphologically very similar to *P. macroceras* and their distribution areas are partially overlapped in Alaska and Yukon Territory. The difference between the two was discussed in *P. macroceras* (species number 81). A natural hybrid between *P. vulgaris* and *P. leptoceras* is occasionally found in the Alps, at where the two species sometimes occur together at the same microhabitat. In some areas, *P. vulgaris* is locally sympatric with *P. grandiflora* and their hybrid (*P.* X *scullyi*) can be commonly generated. As the specific epithet "*vulgaris* (common)" suggesting, it is locally very common or profuse.

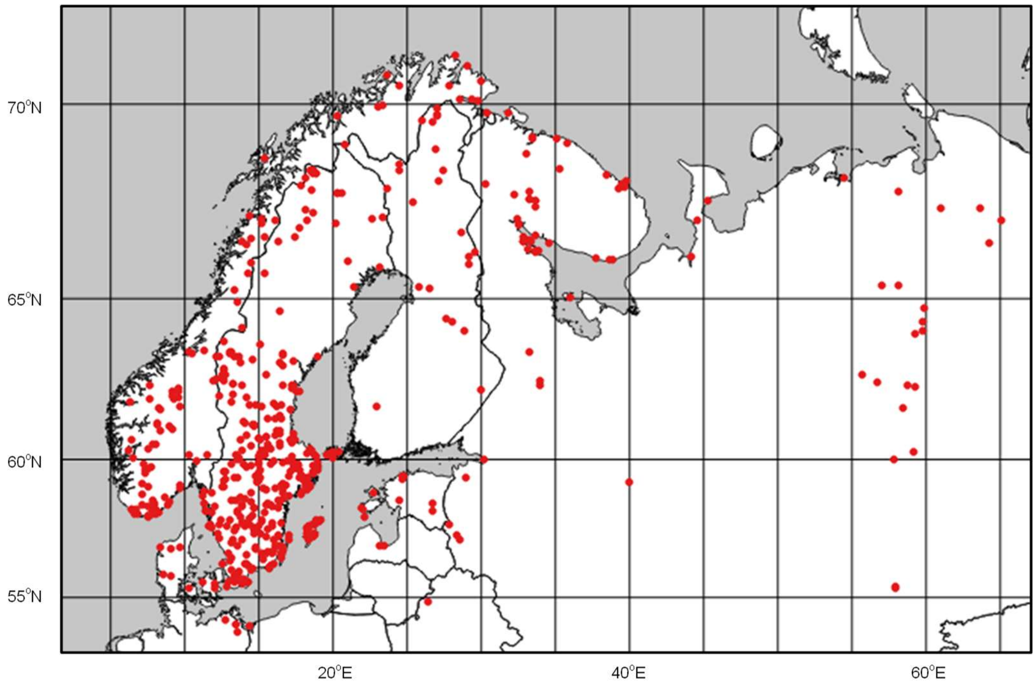
Plate 4.88. *Pinguicula vulgaris*

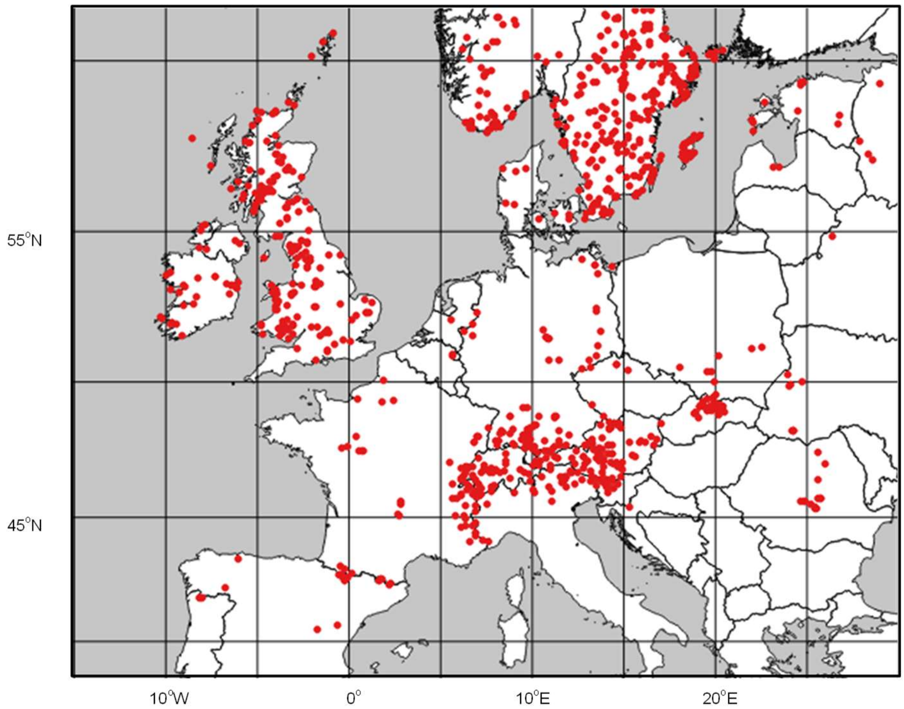


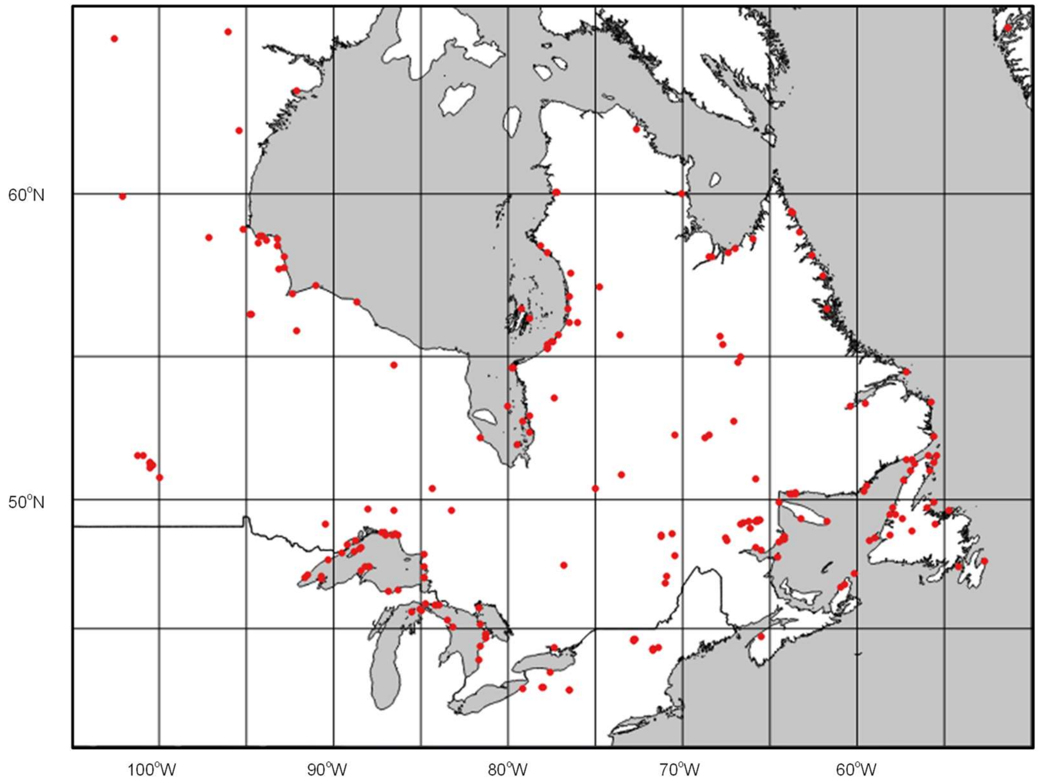
10 mm: 1, 2, 3
10 mm: 4, 5, 6
500 µm: 7

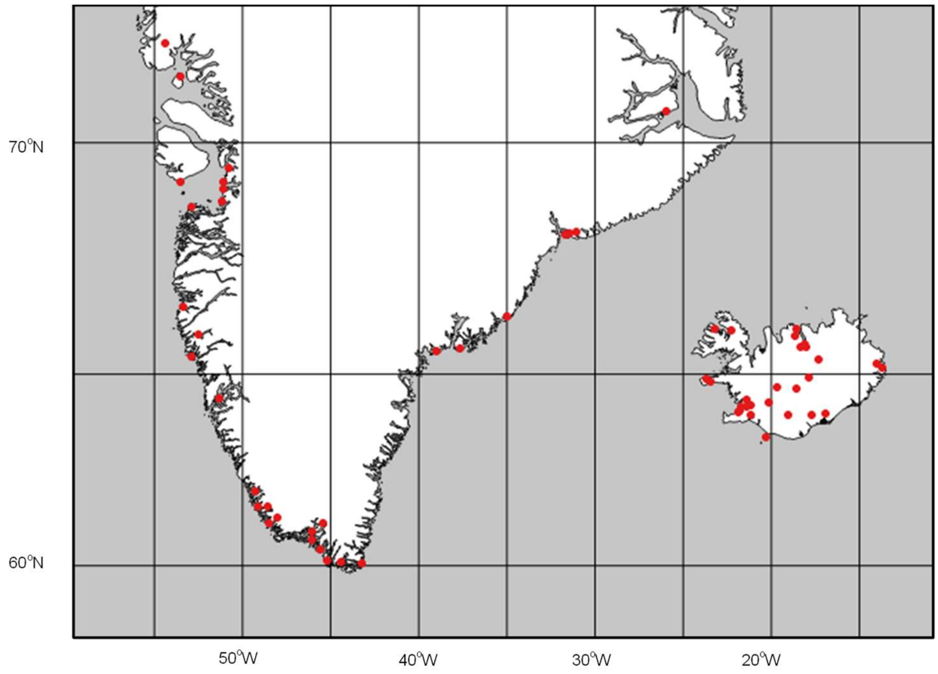
1. rosette with flower
2. hibernaculum
3. summer leaf
4. flower, front view
5. flower, lateral view
6. capsule
7. seed


P. vulgaris
60°N
40°N
0°
40°E
80°E
120°E
60°N
40°N
160°W
120°W
80°W
40°W
(m)
2,000
1,000
0


70°N
65°N
60°N
55°N
20°E
40°E
60°E


55°N
45°N
10°W
0°
10°E
20°E


60°N
50°N
100°W
90°W
80°W
70°W
60°W


70°N
60°N
50°W
40°W
30°W
20°W

Sect. *Pumiliformis* (Casper) Shimai, sect. nov.

TYPE: *Pinguicula lusitanica* L.

SYNONYMS: Subgen. *Isoloba* Barnhart, Sect. *Pionophyllum* DC., Subsect. *Pumiliformis* Casper

89. ***Pinguicula lusitanica*** L., Spec. Pl. 1 (1753) 17.

TYPE: PORTUGAL. *Habitat in arenosis humidis pr. S. Gens. Sta Cruz do Bispo, circa Porto* (growing in wet sand near S. Gens, Sta Cruz do Bispo, Porto), May 1883, *Johnston 2662* (neotype: BM, designated by Blanca et Jarvis in Blanca et al. 1999).

SYNONYMS: *P. alpina* Thoré, *P. subaequalis* Stokes, *P. villosa* Lightfoot, *P. vulgaris* Maulny

DESCRIPTION: Biannual herb. Root filiform, fragile. Stem very short. Leaf monomorphic, 5-12, yellowish-green to pale green or pale pink, with maroon veins, elliptic to oblong-ovate, margin strongly involute, apex obtuse to rather acute, 6-30 mm long, 3-8 mm wide. Scape 1-8, densely glandulous, 30-250 mm long. Calyx bilabiate, upper lip 3-lobed, lobes ovate, ca. 2 mm long, connate to middle, lower lip 2-lobed, lobes smaller than uppers. Flower white to faintly pale lilac or pink, yellowish at base of lips to throat. Corolla bilabiate, 5-10 mm across, subactinomorphic, 5-11 mm long including spur, upper lip 2-lobed, lobes obovate, tip emarginate to notched, lower lip 3-lobed, lobes similar to uppers but sometimes larger, trapeziform convex process in lower throat, tube white to pink or dark yellow with purple veins, cylindrical, spur purple or yellow, cylindrical, pendulous, 2-5 mm long. Capsule globose to subglobose. Seed pyriform to ovoid, 470-550 X 200-250 µm. $2n = 12$. (Plate 4.89).

PHENOLOGY: II, IV, V, VI, VII, VIII, IX, X

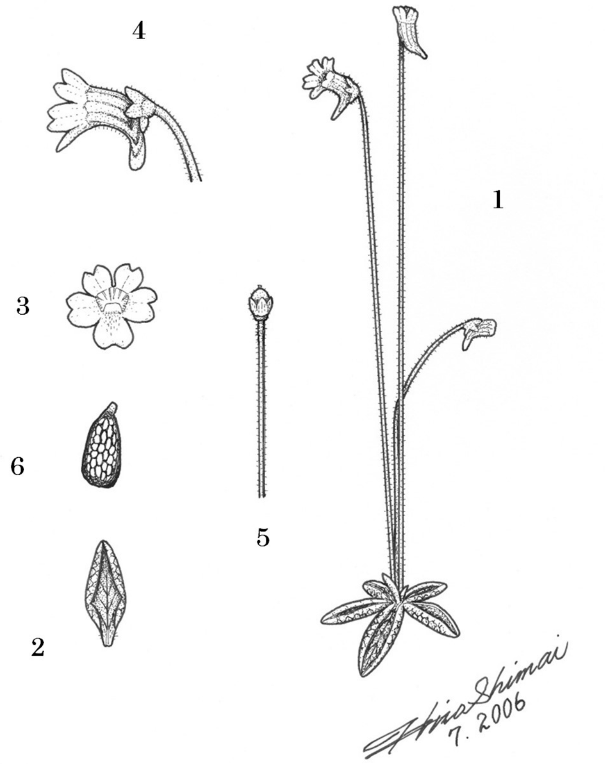
ETYMOLOGY: native of western Iberia or Portugal

HABITAT: Wet peat or fine sand in open grasslands or bogs. Often exposed to direct sunlight.

DISTRIBUTION: FRANCE (Calvados, Charente-Maritime, Cher, Dordogne, Eure, Finistère, Gers, Gironde, Ille-et-Vilaine, Indre-et-Loire, Landes, Loire-Atlantique, Loire-et-Cher, Maine-et-Loire, Manche, Mayenne, Morbihan, Orne, Pyrenées-Atlantiques, Sarthe, Vendée, Vienne); IRELAND (Carlow, Cork, Donegal, Dublin, Galway, Kerry, Kilkenny, Leitrim, Mayo, Waterford, Wicklow); MOROCCO (Tangier-Tetouan); PORTUGAL (Aveiro, Beja, Braga, Coimbra, Faro, Leiria, Lisboa, Portalegre, Porto, Santarém, Setúbal, Viseu); SPAIN (A Coruña, Asturias, Burgos, Cádiz, Cantabria, Guipúzcoa, Lugo, Malaga, Navarra); UNITED KINGDOM ([ENGLAND] Bournemouth, Cornwall, Devon, Dorset, Hampshire, Poole, Somerset, Southampton, Surrey, Isla of Wight, Wiltshire; [ISLE OF MAN]; [NORTHERN IRELAND] Antrim, Down, Fermanagh, Tyrone; [SCOTLAND] Angus, Argyll and Bute, Dumfries and Galloway, Highland, Na h-Eileanan Siar, North Ayrshire, Stirling; [WALES] Pembrokeshire). 0-1,450 m.

DISCUSSION: *Pinguicula lusitanica* is a wide-spread species in Western to Southern Europe and extending to the northern part of Africa. It was described by Linnaeus (1753) but the neotype was more recently designated by Blanca et Jarvis (Blanca et al. 1999). Unlike many other European *Pinguicula* species, *P. lusitanica* does not form any hibernacula. Basically this is a morphologically uniform species except slight flower colour variations among strains. The species is very likely a biannual or short-lived perennial, so that regular seed propagations at the habitat are necessary. Due to the smaller rosette having tiny whitish flowers, it cannot be confused with other species found in the same regions. This species is locally abundant particularly at peaty bogs in some regions, but the current status in the African habitats is unknown.

Plate 4.89. *Pinguicula lusitanica*



10 mm: 1, 2
10 mm: 3, 4, 5
300 µm: 6

1. habit with flower
2. leaf
3. flower, front view
4. flower, lateral view
5. capsule
6. seed

P. lusitanica

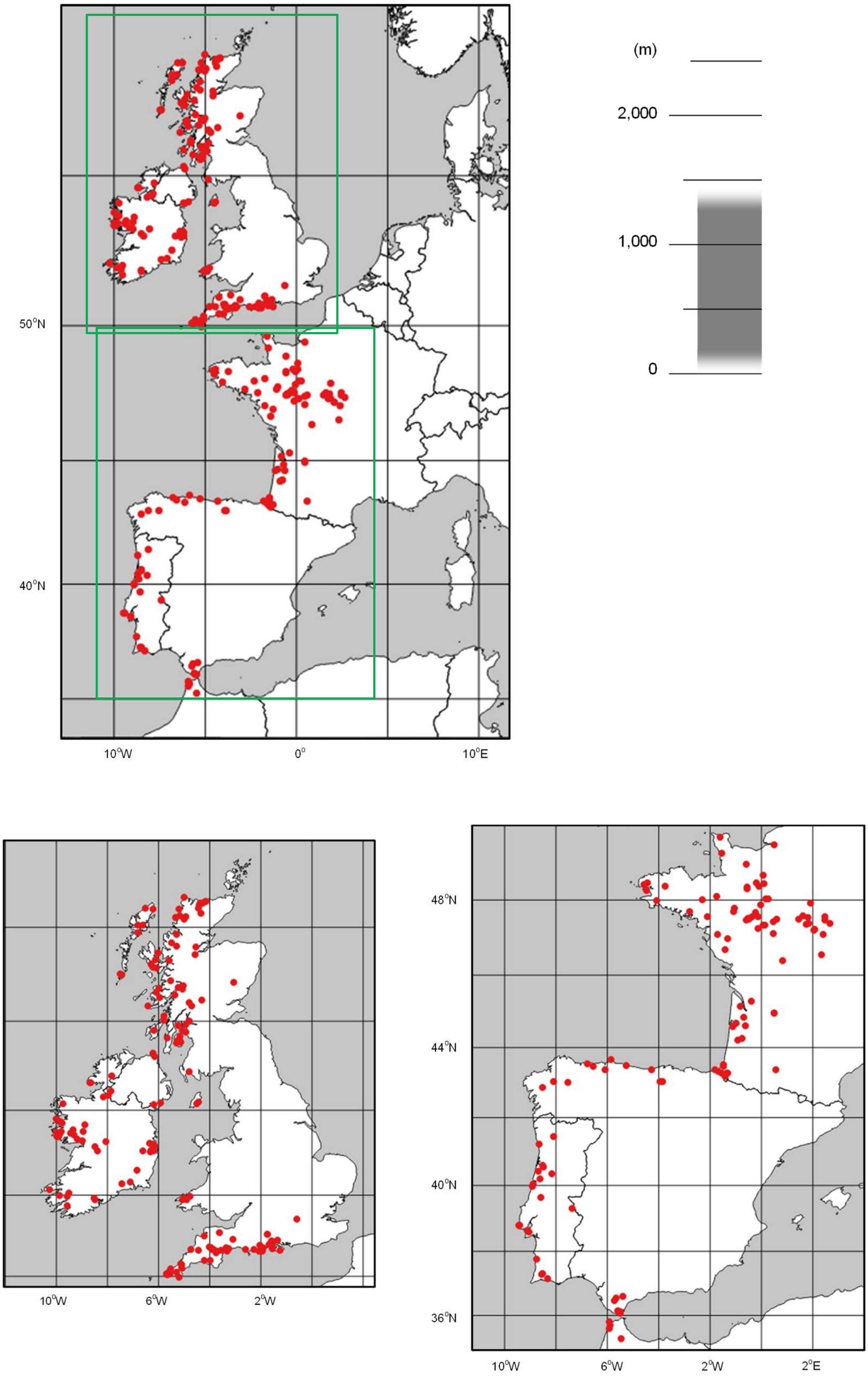
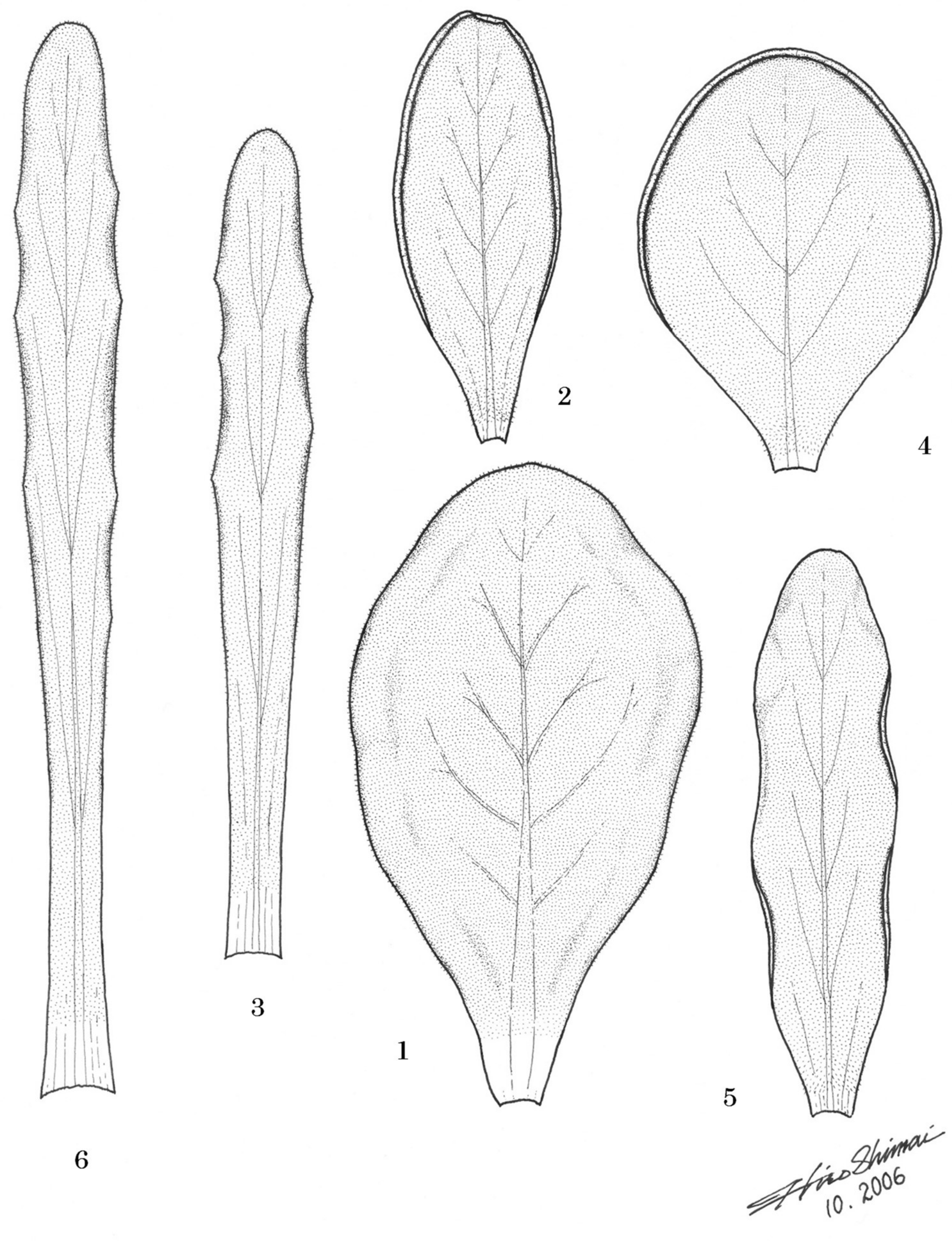


Plate 4.90. Summer leaf of six *Pinguicula* species



10 mm

1. *P. gigantea*, 2. *P. grandiflora*, 3. *P. longifolia*, 4. *P. moranensis*, 5. *P. mundi*, 6. *P. vallisneriifolia*

Nomen dubium

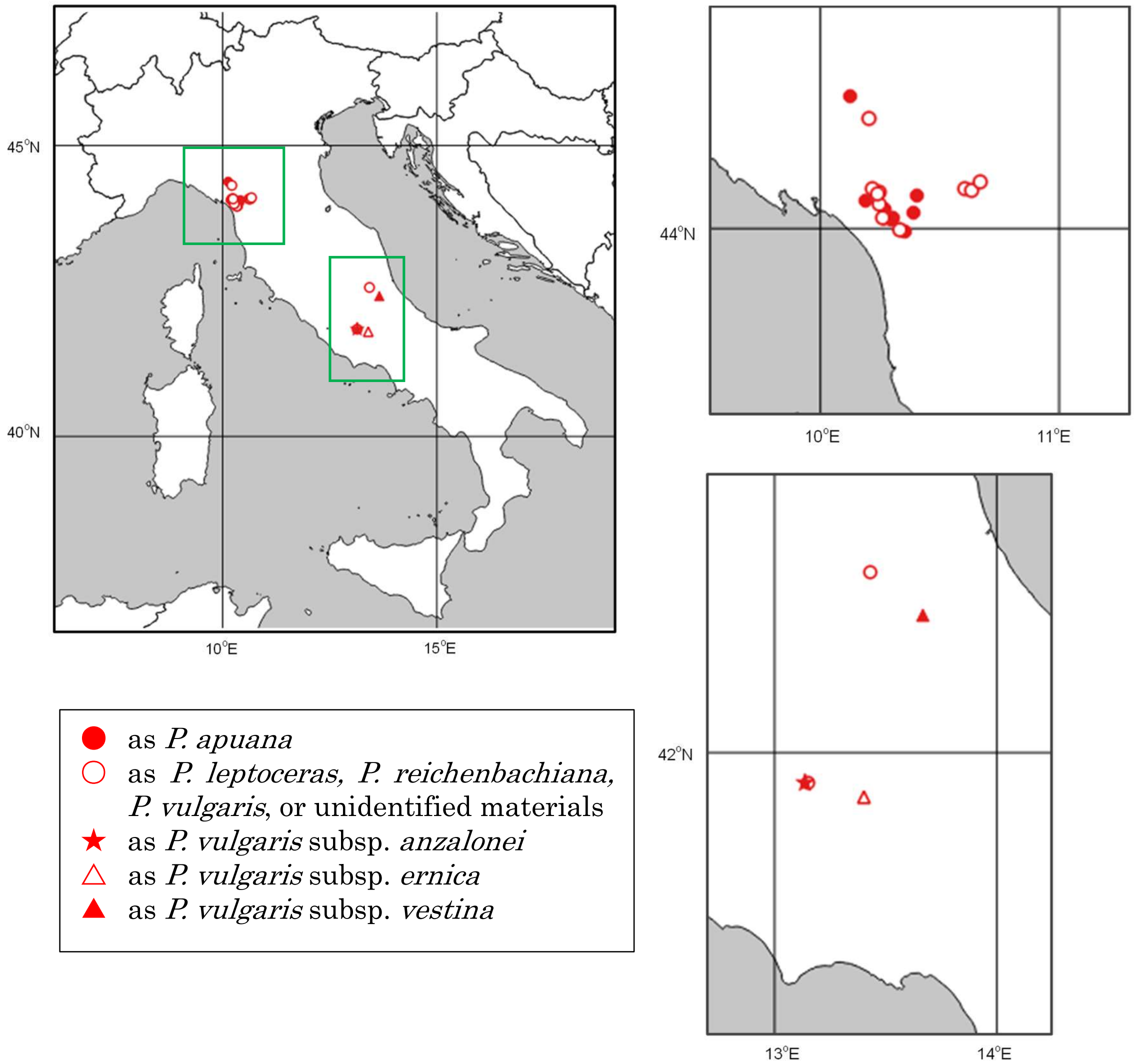
Pinguicula imitatrix Casper, Feddes Repertorium 67 (1963) 12.

TYPE: MEXICO. Guerrero: Distr. Galeana, Piedra Ancha, mossy boulder in oak and pine forest, alt. 3025 m, 2 May 1939, *Hinton et al. 14219* (holotype: UC!; isotypes: GBH!, IEB!, MICH!, MO!, NY!, P, TEX!, US!).

Some Italian Pinguicula taxa recently described

In recent years, some new taxa have been described from Italy. Many of those have previously been identified as various names (e.g. *P. leptoceras, P. reichenbachiana*, or *P. vulgaris*). In the Apennine Mountains, three taxa, *P. apuana, P. mariae* (Ansaldi and Casper 2009), and *P. christinae* (Peruzzi and Gestri 2013), have been reported, and their distribution areas are likely overlapped one another (Plate 4.91). Unfortunately, some herbarium specimens do not have flowers or do not present floral characteristics because of poor press condition. Those are morphologically very similar in some degree with some morphological diversity within each micropopulation. Moreover, those are morphologically intermediate between two taxa already known. In Abruzzo, three subspecies of *P. vulgaris* (subsp. *anzalonei*, subsp. *ernica*, and subsp. *vestina*) have been described by Conti and Peruzzi (2006). Concerning their floral morphology shown in the original description, it is somewhat questionable if those are intraspecific taxa of *P. vulgaris*. All those taxa mentioned above may need further studies. In this study, it is regret that there are not enough materials and information available to deal with them as distinct taxa. Observations on live materials preferably at habitats will be needed. Those distribution areas based on specimen observations are shown in the map. In addition, other new taxa *P. sehuensis* (Bacchetta et al. 2014) and *P. lattanziae* (De Castro et al. 2016) have been recently described from Sardinia and Liguria, respectively (spec. n.v.).

Plate 4.91. Distribution of some Italian taxa.



4.4. CONCLUSION

In this study 91 taxa (89 species and 2 varieties) are recognised after studying literature and herbarium specimens. There could be more species, particularly some Italian taxa described recently, but due to little available information and materials, those were unable to examine thoroughly here. There are also a few new species which will be described in the near future from Mexico and Central America. In conclusion, it is temporally 91 taxa recognised, but the number will increase.

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General conclusions

Taxonomy of Pinguicula

Before Linnaeus (1753), established the genus *Pinguicula* L. (Lentibulariaceae), described four European *Pinguicula* species, *P. alpina* L., *P. lusitanica* L., *P. villosa* L., and *P. vulgaris* L. in his “Species Plantarum”, *Pinguicula* had being used for medical purposes and producing curd milk products in Europe (Lloyd 1942, Juniper et al. 1989). De Candolle (1844) recognised 30 *Pinguicula* species and proposed three sectional delimitations in the genus. The most recent taxonomic treatment was attempted by Casper (1966), who recognised 46 species in 3 subgenera, *Isoloba, Pinguicula*, and *Temnoceras*, based on floral morphology, regardless of distribution areas. Casper (1966) broadened the knowledge of *Pinguicula* and his taxonomic treatment is widely accepted today. Since the taxonomic treatment by Casper, a number of new species have been described (e.g. Speta and Fuchs 1982, 1989, Zamudio and Rzedowski 1986, Zamudio 1988, 1991, Cheek 1994, Zamora et al. 1996) and the total number of species has been estimated to be almost double (Cieslak et al. 2005, Zamudio 2005, 2006). However, some morphologically similar taxa cause taxonomic confusion (e.g. *P. ehlersiae* Speta et Fuchs and *P. esseriana* Kirchner) (Zamudio 2001).

Chapter 1. Red List assessments of the genus Pinguicula L.

Many *Pinguicula* taxa are confined to a small geographical area and thus they are often endemic (Blanca et al. 1999, Espinosa-Matías et al. 2005, Shimai and Kondo 2007). Due to horticultural interest as a carnivorous plant, *Pinguicula* is illegally collected from the field and cultivated among amateur growers (Zamudio 1995). Currently *Pinguicula* are absent from the appendices of the Conservation on International Trade in Endangered Species of Wild Fauna and Flora (CITES) (von Arx et al. 2001; also see the CITES website for an up to date checklist). Currently the International Union for Conservation of Nature (IUCN) has evaluated only 7 *Pinguicula* taxa (only ca. 4 % of the whole genus), and 4 of them are categorised as Least Concern. Given levels of endemism within the genus it is very unlikely representing the whole genus. The current status of each *Pinguicula* taxa has to be clarified to provide an understanding of their conservation.

Red List assessments based on the IUCN criteria and categories have been performed in Chapter 1. In this study, over 6,800 herbarium specimens from 167 herbaria were examined as herbarium specimens represent some of the best available biological evidence for species distribution and occupancy (Willis et al. 2003, Rivers et al. 2011, Romeiras et al. 2014, Brummitt et al. 2015), and is often the only available data for rare species (Joppa et al. 2011, Rivers et al. 2011, Roberts et al. 2016). The Extent of Occurrence (EOO) and Area of Occupancy (AOO) was calculated for each of the recognized *Pinguicula* taxa (89 species and 2 varieties) using Geospatial Conservation Assessment Tool (GeoCAT) (Bachman et al. 2011). According to the results, 61 % of the 91 *Pinguicula* taxa are threatened with extinction. As suggested by Roberts et al. (2016), more recently described taxa had fewer localities also in the case of *Pinguicula*. Between the two biodiversity hotspots of *Pinguicula*, Mexico, with the proportion of endemism of 87 % (40 endemic taxa out of 46), has a higher extinction risk than Europe and Western Asia with 45 % endemism (9 endemic taxa out of 20).

The results suggest that many *Pinguicula* taxa are at risk of extinction. Although all results obtained are primary analyses using only criterion B, EOO and AOO, the necessity of urgent conservation actions for the protection of *Pinguicula* is clear, not only for the taxa but also the environment in which they occur.

Full Red List assessments requiring multi-year observations of the taxa within their habitat, however for *Pinguicula* this is likely to be difficult and not realistic (Rivers et al. 2011, Brummitt et al. 2015). However, investigating a few selected *Pinguicula* species may help provide an overall understanding of the threats the genus face. However, this lack of information should not be used as an excuse, and conservation measures should be put in place. Finally, the data obtained from herbarium specimens at museums, may still have sampling gaps in some regions that will impact particularly on AOO estimates. An additional study on the specimens would help fill these gaps.

Chapter 2. Phylogenetic analyses of the genus Pinguicula L.

While the genus *Pinguicula* is well defined, there is taxonomic confusion within the genus (Zamudio 2001). Espinosa-Matías et al. (2005) suggested that the subgeneric treatment by Casper (1966) is questionable. Recent phylogenetic studies (Cieslak et al. 2005, Shimai et al. 2007, Shimai and Kondo 2007, Beck et al. 2008) also suggested that *Pinguicula* is more or less monophyletic in each geographical area. Cieslak et al. (2005) analysed the gene region of *mat*K and *trn*K in chloroplast DNA (cpDNA) using 42 *Pinguicula* taxa. However, more samplings from wider geographical regions is necessary to support these results. Molecular systematics has become a standard method for inferring phylogenetic relationships among plant taxa in recent years (APG 1998, APG II 2003, APG III 2009). Clarifying the phylogenetic status is also informative for the taxonomy and conservation of *Pinguicula*.

In chapter 2, three regions of the *Pinguicula* gene, internal transcribed spacer

(ITS) in nuclear ribosomal DNA, *rpl32-trnL* and additional *mat*K and *trn*K in cpDNA (up to 80 taxa or ca. 88 % of all taxa within the genus) were sequenced. The ITS region result has suggested that clades are mostly agreed with geographical distribution area (e.g. temperate regions of the Northern Hemisphere, Southeastern USA, Mexico and Central America, Cuba, and South America). In other words, they are more or less monophyletic within each region although a few species (depending on gene regions) do not belong to any clade. Mexican taxa have been divided into 3 subgenera by Casper (1966), but these results suggest that they are phylogenetically monophyletic. The results of *mat*K and *trn*K and *rpl32-trnL* are partially, but not completely, in agreement with the result of ITS. It appears that ITS is more informative in inferring phylogenetic relationships at the specific rank than *mat*K and *trn*K (Degtjareva et al. 2006).

Chapter 3. The effect of geographical and environmental factors on patterns of species richness in the genus Pinguicula L.

Habitats of *Pinguicula* are often found in narrow geographical ranges (Casper 1966, Zamudio 2001). Although *Pinguicula* is usually found in wet soils (Darwin 1875, Lloyd 1942, Givnish 1989, Heslop-Harrison 2004), more occur in wet places surrounded by larger dry areas (Blanca et al. 1999). Species richness of *Pinguicula* is particularly seen in Mexico, and many of them are endemic (Espinosa-Matías 2005, Zamudio 2005); 40 endemics out of 46 (Chapters 1 and 4). The number of taxa in Mexico is much greater than that in Europe and Western Asia, having 20 taxa (9 endemics out of 20). What geographical and environmental factors affect species richness in the genus *Pinguicula* has not been previously studied.

In Chapter 3, which geographical and environmental factor more significantly affects species richness in *Pinguicula* has been explored. Although positive correlations are found in the all correlations between and the geographical and environmental factors, most of them are not significant. According to the results, species richness is significantly and positively correlated with land area, i.e. larger countries have more number of species. This may also suggest that large areas not just simply have more species, but there could be more habitats thus increasing species richness further. Species richness of *Pinguicula* is also positively correlated with climate B (dry-type climate category). The result supports that small wet areas surrounded by large dry climate area (a rare climate) affect species richness of the genus. The species richness in Northeastern Asia is also significantly and positively correlated with climate E (polar-type climate). Probably due to large distribution gaps (e.g. deserts) in the southern part, more number of species is found in the northern part of Northeastern

Asia. Interestingly, species richness is not significantly correlated with altitude in all regions.

According to the results, it is likely that speciation of *Pinguicula* has occurred in different regions independently (e.g. Mexico and the temperate Northern Hemisphere) to adapt to local environmental and geographical factors, particularly climate, i.e. many Mexican taxa form winter rosettes to resist dry winter while taxa in the temperate Northern Hemisphere forms hibernacula to resist low temperature (below 0°C). Ecological preference of *Pinguicula* is very narrow (Zamudio 2001, Heslop-Harrison 2004), therefore, more detailed and small scale variables will be needed for analyses instead of larger scales by country used in this study.

Chapter 4. A revision of the genus Pinguicula L.

Previous taxonomic studies by De Candolle (1844), Barnhart (1916), Ernst (1961), and Casper (1966), have largely been inconsistent in their infrageneric treatment of the genus. Because of taxonomic issues (Espinosa-Matías et al. 2005, Zamudio 2001), a revision of the genus *Pinguicula* is necessary. Roccia et al. (2016) have stated that the current taxonomy based on morphology requires a critical review since only the section *Pinguicula* is in agreement with phylogenetic results presented by

Cieslak et al. (2005), Degtjareva et al. (2006), Kondo and Shimai (2006), and Beck et al. (2008).

Based on herbarium specimen examinations performed in Chapter 1, ninety-one *Pinguicula* taxa (89 species and 2 varieties) have been recognised. Phylogenetic analyses inferred in Chapter 2 have suggested that there are disagreements between the current taxonomy based on morphology and the phylogeny. In Chapter 4, therefore, a revision of the genus *Pinguicula* has been presented based on the phylogeny and new sectional delimitations with 11 sections (3 of which are newly established in this study) are proposed. Keys to section and species, a brief description, botanical line drawings, and distribution maps for each taxon are provided to assist identifications.

Due to limited availability of materials, similar distribution areas, and difficulties of identification using herbarium specimens, some recently described Italian taxa (e.g. *P. apuana* Casper et Ansaldi, *P. christinae* Peruzzi et Gesteri, and *P. mariae* Casper) fall from this work. Furthermore, a few more species will be described from Mexico and Central America in the near future (per. com., Zamudio). Those have to be reviewed as well as the 91 taxa recognised in this chapter. Species having wider morphological diversity, such as *P. moranensis*, will be needed a further taxonomic study.

In spite of paraphyletic origins of some carnivorous plant families, many species are found in common ecological environments, such as acid wet soils with poor nutrition, and high light intensity (Givnish 1989, Juniper et al. 1989). However, *Pinguicula* can be often found in unique habitats, e.g. limestone or serpentine cliffs or slopes facing north with low light intensity (Zamudio 2001) as is particularly the case in Mexico (Espinosa-Matías et al. 2005, Zamudio 2005, Shimai and Kondo 2007). Biodiversity hotspots of carnivorous plants vary among genera; e.g. a number of *Drosera* species occur in Australia, Africa, and South America (Rivadavia et al. 2003) while many *Nepenthes* species are confined to Southeast Asia (Jebb and Cheek 1997). However, the family Lentibulariaceae, in which *Pinguicula* is placed, contains further two closely related genera, *Genlisea* and *Utricularia* that are carnivorous. What is interesting is that they possess totally different trapping mechanisms. This group has the potentially to act as a model system for understanding the geographical and environmental divers of their diversity in trapping mechanism but also the conservation challenges that lies ahead.

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Taxonomy and conservation ecology of the genus *Pinguicula* L. (Lentibulariaceae)

Volume 2.

Appendices

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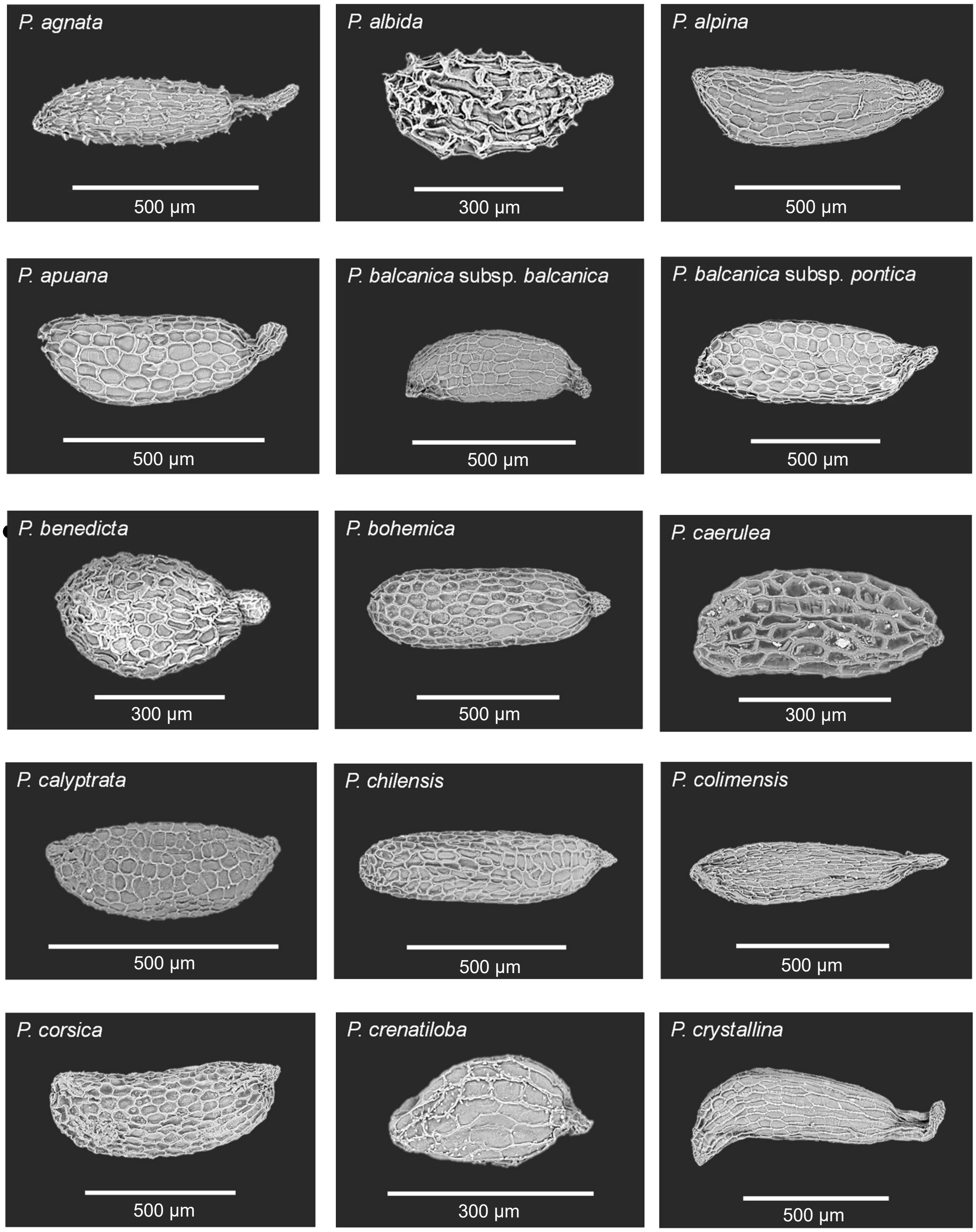
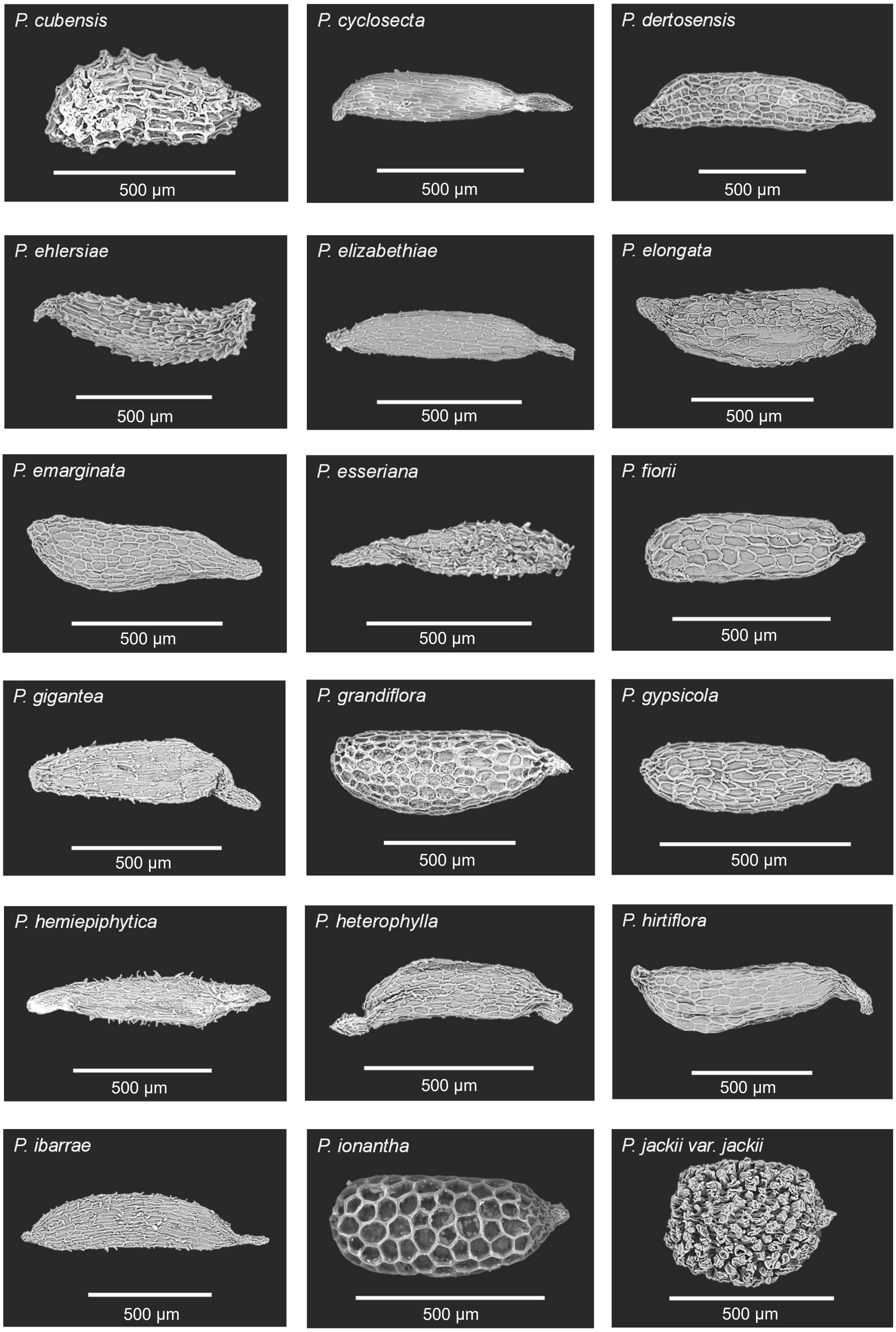
APPENDIX I

Seed morphology of *Pinguicula*

The seed of *Pinguicula* was imaged using Miniscopes® TM3000 and TM3030 Plus (Hitachi High-Technologies Co., Tokyo, Japan) by Kaori Ichikawa and Hiro Shimai. The images are sorted in alphabetical order under the sample name obtained, but it is not necessarily all taxa are accepted in this study.




P. cubensis
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P. cyclosecta
500 µm
P. dertosensis
500 µm
P. ehlersiae
500 µm
P. elizabethiae
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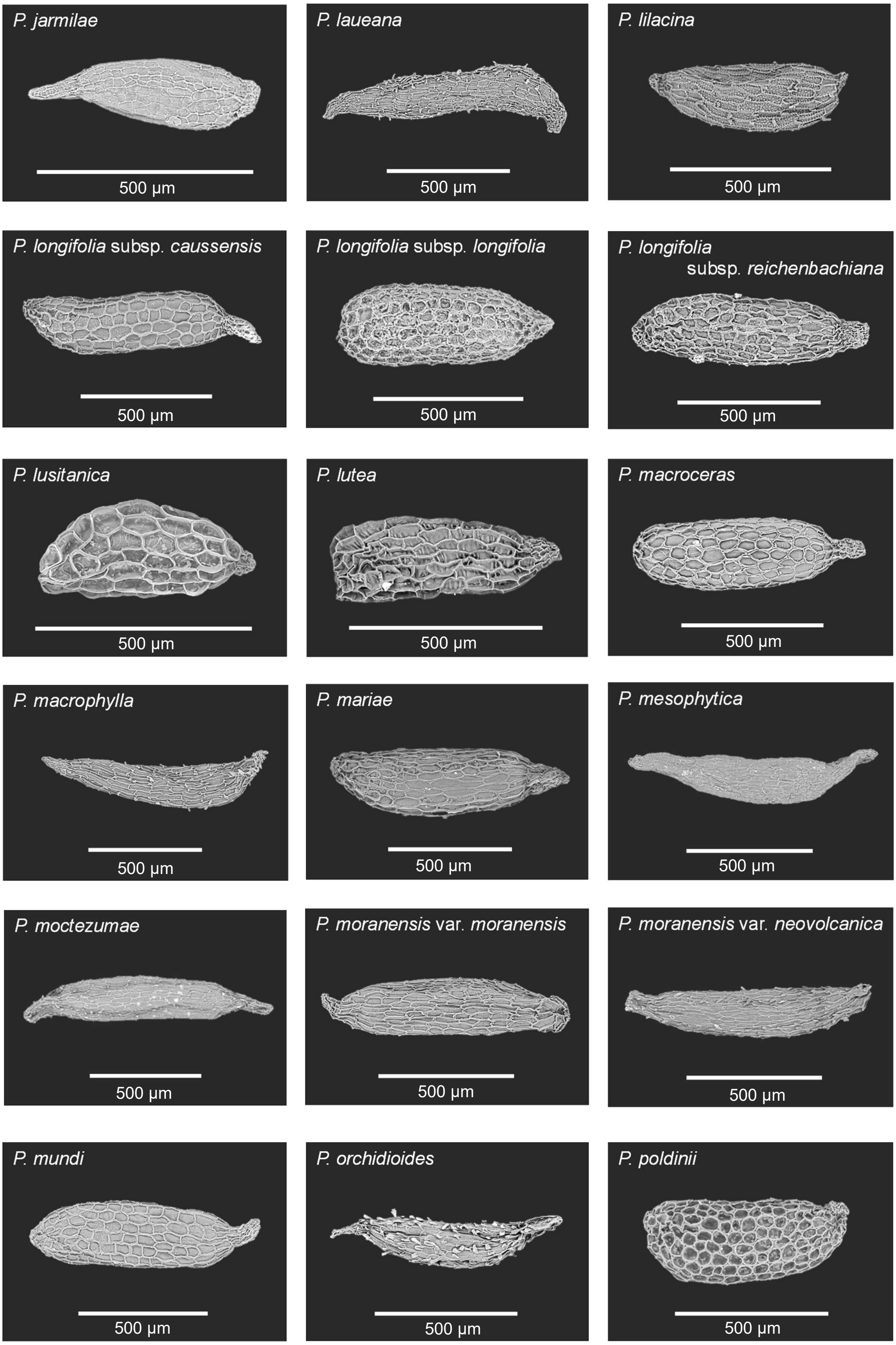
P. elongata
500 µm
P. emarginata
500 µm
P. esseriana
500 µm
P. fiorii
500 µm
P. gigantea
500 µm
P. grandiflora
500 µm
P. gypsicola
500 µm
P. hemiepiphytica
500 µm
P. heterophylla
500 µm
P. hirtiflora
500 µm
P. ibarrae
500 µm
P. ionantha
500 µm
P. jackii var. jackii
500 µm


P. jarmilae
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P. laueana
500 µm
P. lilacina
500 µm
P. longifolia subsp. caussensis
500 µm
P. longifolia subsp. longifolia
500 µm
P. longifolia subsp. reichenbachiana
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P. lusitanica
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P. lutea
500 µm
P. macroceras
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P. macrophylla
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P. mariae
500 µm
P. mesophytica
500 µm
P. moctezumae
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P. moranensis var. moranensis
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P. moranensis var. neovolcanica
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P. mundi
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P. orchidioides
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P. poldinii
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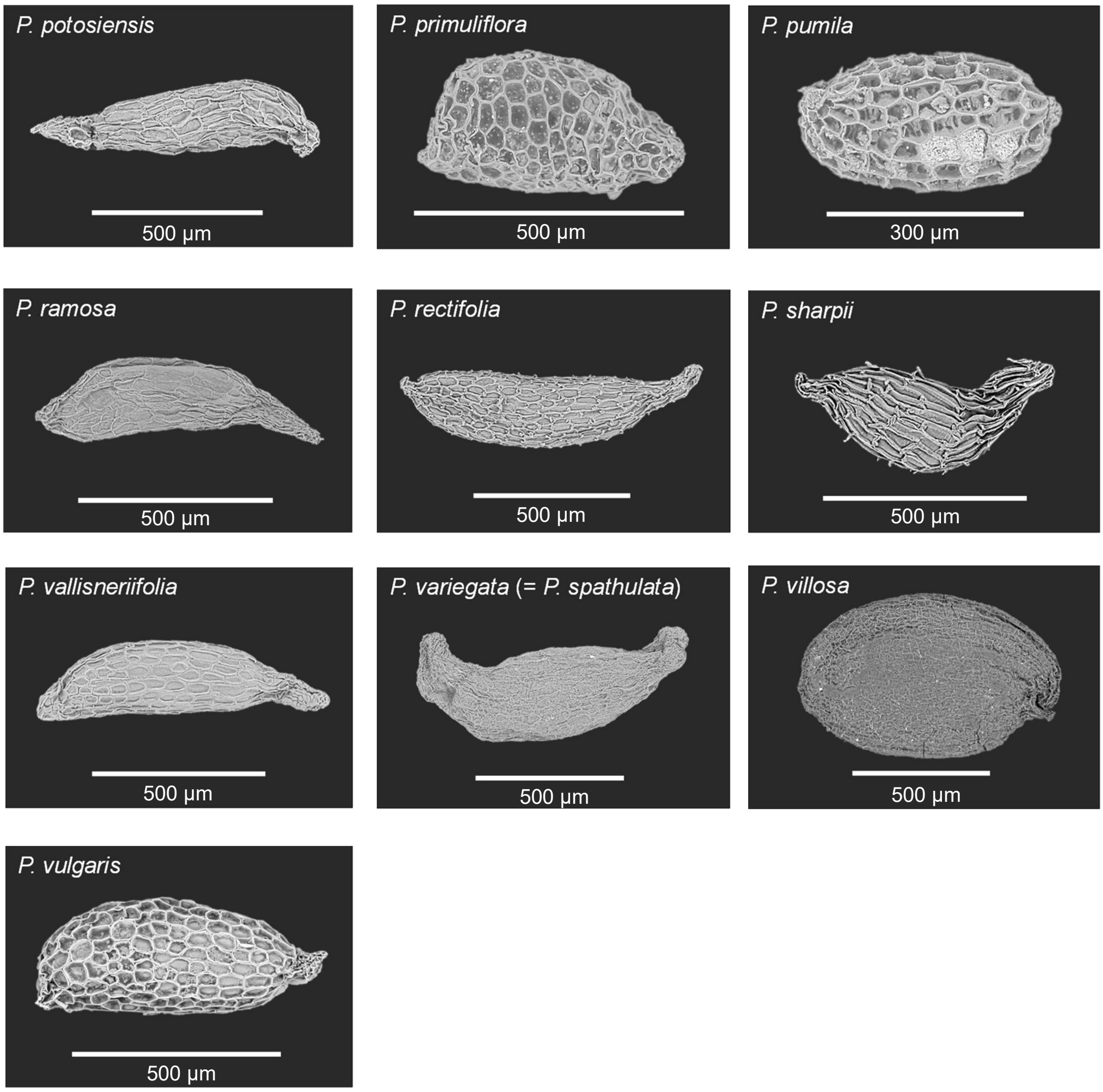
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P. primuliflora
500 µm
P. pumila
300 µm
P. ramosa
500 µm
P. rectifolia
500 µm
P. sharpii
500 µm
P. vallisneriifolia
500 µm
P. variegata (= P. spathulata)
500 µm
P. villosa
500 µm
P. vulgaris
500 µm

APPENDIX II

Specimens examined

Pinguicula acuminata Bentham

MEXICO. Distrito Federal:

Hidalgo:

REDACTED

México:

Michoacán:

Querétaro:

Tlaxcala:

Misc.

Pinguicula agnata Casper

MEXICO. Guanajuato:

Hidalgo:

Querétaro:

Pinguicula albida Wright ex Griseb.

CUBA. Pinar del Río:

Misc.

Pinguicula algida Malysch.

RUSSIA. Buryatia:

Khabarovsk:

Krasnoyarsk:

Sakha

(Yakutia):

Zabaykalsk:

Pinguicula alpina L.

AUSTRIA. Kärnten:

Niederösterreich:

Oberösterreich:

Salzburg:

Steiermark:

Tirol:

Vorarlberg:

BHUTAN. Bumthang:

Lhuntse:

Paro:

Thimpu:

Trashiyangtse:

CHINA. Chongqing:

Gansu:

Guizhou:

Hubei:

Qinghai:

Shaanxi:

Sichuan:

Xizang (Tibet):

Yunnan:

CROATIA. Karlovac:

Primorje-Gorski Kotar:

ESTONIA. Harju maakond:

Saare maakond:

Tartu maakond:

FINLAND.

Lappi:

Pohjois-Pohjanmaa:

FRANCE.

Ain:

Haute-Garonne:

Haute-Savoie:

Hautes-Alpes:

Hautes-Pyrénées:

Isère:

Pyrénées-Orientales:

Savoie:

GERMANY. Baden-Württemberg:

Bayern:

HUNGARY. Veszprém:

INDIA. Arunachal

Pradesh:

Assam:

Sikkim:

Uttarakhand:

ITALY. Friuli-Venezia Giulia:

Lombardia:

Piemonte:

Trentino-Alto Adige:

Valle d'Aosta:

Veneto:

Misc. **LIECHTENSTEIN.**

Triesenberg:

MONGOLIA. Khövsgöl:

MYANMAR (BURMA). Kachin:

NEPAL.

Bagmati:

Dhawalagiri:

Gandaki:

Karnali:

Kosi:

Mahakali:

NORWAY. Finnmark:

Nordland:

Oppland:

Sør-Trøndelag:

Svalbard:

Troms:

POLAND. Małopolskie:

ROMANIA. Alba:

Argeş:

Bistriţa-Năsăud:

Braşov:

Caraş-Severin:

Dâmboviţa:

Maramureş:

Neamţ:

Prahova:

Sibiu:

Suceava:

RUSSIA. Buryatia:

Irkutsk:

Khanty-mansi (Yugra):

Komi:

Krasnoyarsk:

Leningrad:

Murmansk:

(Yakutia):

Nenetsia:

Sakha

(Yakutia):

Yamalo-Nenets:

SLOVAKIA. Prešovský

kraj:

Žilinský kraj:

SLOVENIA. Bled:

Bloke:

Bohinj:

Borovnica:

Bovec:

Brezovica:

Cerklje na Gorenjskem:

Cerknica: Črna na Koroškem:

Idrija:

Jesenice:

Jezersko:

Kamnik:

Kranj:

Kranjska Gora:

Ljubljana:

Nova Gorica:

Radece:

Sodražica:

Solčava:

Tržič:

Velike Lašče:

Vojnik:

Železniki:

Žirovnica:

SPAIN. Huesca:

Lleida:

Navarra:

SWEDEN. Gotland:

Jämtland:

Norrbotten:

Västerbotten:

SWITZERLAND. Appenzell-Innerrhoden:

Bern:

Fribourg:

Genève:

Graubünden:

Obwalden:

Schwyz:

Ticino:

Uri:

Valais:

Vaud:

Zürich:

UKRAINE. Zakarpattia Oblast (Transcarpatia):

UNITED KINGDOM. [SCOTLAND] Highlands:

Misc.

Pinguicula antarctica Vahl

ARGENTINA. Neuquén:

Río Negro:

Tierra del Fuego:

CHILE. IX (La Araucanía):

XII

(Magallanes y de la Antártica Chilena):

Misc.

Pinguicula balcanica Casper

ALBANIA. Dibër:

Elbasanit:

Korçë:

Kukësit:

Shkodër:

BOSNIA AND HERZEGOVINA. Federation of Bosnia and Herzegovina:

BULGARIA. Blagoevgrad:

Gabrovo:

Kyustendil:

Lovech:

Pazardžk:

Pernik: Plovdiv:

Smolyan: Sofia:

Sofia City:

Misc.

GEORGIA (*P. balcanica* subsp. *pontica*?). Abkhazia:

GREECE. Fokída:

Ioánina:

KOSOVO.

Ferizaj:

Gjakovë:

Pejë:

Prizren:

REPUBLIC OF MACEDONIA (FYROM). Bitola:

Gevgelija:

Jegunovce:

Makedonski Brod:

Mavrovo and Rostuša:

Novaci:

Studeničani:

Tetovo:

MONTENEGRO. Andrijevica:

Kolašin:

Plav:

Podgorica:

RUSSIA (*P. balcanica* subsp. *pontica*?). Karachay-Cherkessia:

SERBIA. Pirot:

TURKEY (*P. balcanica* subsp. *pontica*?). Adana:

Artvin:

Bursa:

Erzurum:

Gümüşhane:

İzmir (mislabelled?):

Niğde:

Rize:

Trabzon:

Van:

Pinguicula benedicta Barnhart

CUBA. Guantánamo:

Holguín:

Santiago de

Cuba:

Pinguicula caerulea Walter

USA. Florida:

Georgia:

North Carolina:

South Carolina:

Pinguicula calderoniae Zamudio

MEXICO. Querétaro:

San Luis Potosí:

Pinguicula calyptrata Kunth

COLOMBIA. Cauca:

ECUADOR. Azuay:

Carchi:

Chimborazo:

El Oro:

Loja:

Morona-Santiago:

Napo:

Pichincha:

Sucumbíos:

Tungurahua:

Pinguicula casabitoana Jiménez

DOMINICAN REPUBLIC. La Vega:

Monseñor Nouel:

Peravia:

San Juan:

Pinguicula caussensis (Casper) Innangi, De Castro et Peruzzi
FRANCE. Aveylon:

Lozère:

Puy-de-Dôme:

Pinguicula chilensis Clos
ARGENTINA. Neuquén:

Río Negro:

Misc.

CHILE. IX (La Araucanía):

X (Los Lagos):

XIV (Los Ríos):

Pinguicula clivorum Standley et Steyermark

GUATEMALA. Huehuetenango:

MEXICO. Chiapas:

Pinguicula colimensis McVaugh et Mickel

MEXICO. Colima:

Pinguicula conzattii Zamudio et van Marm

MEXICO. Oaxaca:

Pinguicula corsica Bernard et Gren. ex Gren. et Godr.

FRANCE. Corsica Isl.:

Pinguicula crassifolia Zamudio

MEXICO. Hidalgo:

Pinguicula crenatiloba DC.

COSTA RICA. San José:

EL SALVADOR.

Chalatenango:

Santa Ana:

GUATEMALA. Chiquimula:

Jalapa (Santa Rosa?):

HONDURAS. Comayagua:

El Paraíso:

Francisco Morazán:

Ocotepeque:

Olancho:

Misc.

MEXICO. Chiapas:

Guerrero:

Jalisco:

México:

Michoacán:

Nayarit:

Oaxaca:

Sinaloa:

Sonora:

PANAMA. Chiriquí:

Coclé:

Ngöbe Buglé:
Panamá:

Veraguas:

Pinguicula crystallina Smith
CYPRUS.

TURKEY. Adana:
Antalya:
Burdur:

Denizli:

Hatay:

Isparta:

Kütahya:

Muğla:

Uşak:

Pinguicula cubensis Urquiola et Casper

CUBA. Pinar del Río:

Pinguicula cyclosecta Casper

MEXICO. Nuevo León:

Tamaulipas:

Pinguicula debbertiana Speta et Fuchs
MEXICO. San Luis Potosí:

Pinguicula dertosensis (Cañigueral) Mateo et Crespo
SPAIN. Cuenca:

Granada:

Jaén:

Tarragona:

Teruel:

Pinguicula ehlersiae Speta et Fuchs

MEXICO. Nuevo León:

San Luis Potosí:

Misc.

Pinguicula elizabethiae Zamudio

MEXICO. Hidalgo:

Querétaro:

Pinguicula elongata Banjamin

COLOMBIA. Arauca:

Bogotá (D.C.):

Boyacá:

Cesar:

Cundinamarca:

La Guajira:

Magdalena:

Santander:

Misc.

VENEZUELA. Apre:

Mérida:

Pinguicula emarginata Zamudio et Rzedowski
MEXICO. Puebla:

Veracruz:

Pinguicula esseriana Kirchner
MEXICO. Hidalgo:

Nuevo León:

Querétaro:

San Luis Potosí:

Tamaulipas:

Pinguicula filifolia Wright ex Griseb.
CUBA. Isla de la Juventud:

Pinar del Río:

Misc.

Pinguicula fiorii Tammaro et Pace

ITALY. Abruzzo:

Misc.

Pinguicula gigantea Luhrs

MEXICO. Oaxaca:

Pinguicula gracilis Zamudio

MEXICO. Coahuila:

Nuevo León:

Tamaulipas:

Pinguicula grandiflora Lam.
ANDORRA. Canillo:

Ordino:

FRANCE. Ain:

Ariège:

Aude:

Cantal:

Drôme:

Haute-Garonne:

Haute-Savoie:

Hautes-Pyrénées:

Isère:

Jura:

Puy-de-Dôme:

Pyrénées-Atlantiques:

Pyrénées-Orientales:

Savoie:

IRELAND. Clare:

Cork:

Dublin (naturalized?):

Kerry:

Limerick:

MOROCCO. Taza-Al Hoceima-Taounate:

Misc.

SPAIN. Álava:

Almería:

Asturias:

Barcelona:

Burgos:

Cantabria:

Girona:

Guipúzcoa:

Huesca:

León:

Lleida:

Lugo:

Navarra:

Soria:

Zamora:

SWITZERLAND. Bern (naturalized):

Vaud:

UNITED KINGDOM (naturalized). [ENGLAND] Cornwall:

Derbyshire:

[WALES] Gwynedd:

Monmouthshire:

Pinguicula greenwoodii Cheek

MEXICO. Oaxaca:

Pinguicula gypsicola Brandegee
MEXICO. San Luis Potosí:

Pinguicula hemiepiphytica Zamudio et Rzedowski
MEXICO. Oaxaca:

México:

Pinguicula heterophylla Bentham
MEXICO. Guerrero:

México:

Michoacán:

Morelos:

Oaxaca:

Misc.

Pinguicula hirtiflora Tenore

ALBANIA. Berat:

Dibër:

Durrës:

Elbasanit:

Korçë:

Kukës:

Shkodrës:

Tiranë:

Vlorë:

Misc.

BOSNIA AND HERZEGOVINA. Republika Srpska:

FRANCE. Alpes-Maritimes:

GREECE. Achaïa:

Árta:

Évia:

Evritanía:

Fokída:

Grevená:

Ioánina:

Kardítsa:

Korinthia:

Messinia:

Pieriá:

Tríkala:

Viotia:

ITALY. Calabria:

Campania:

KOSOVO. Deçan:

Gjakovë:

REPUBLIC OF MACEDONIA (FYROM). Bitola:

Pinguicula ibarrae Zamudio

MEXICO. Hidalgo:

Querétaro:

Pinguicula immaculata Zamudio et Lux

MEXICO. Nuevo León:

Pinguicula involuta Ruíz et Pavón

BOLIVIA. Cochabamba:

PERU. Amazonas:

Cuzco:

Huánuco:

Lambayeque:

Pasco:

Piura:

San Martín:

Misc.

Pinguicula ionantha Godfrey

USA. Florida:

Pinguicula jackii Barnhart **var. *jackii*** Barnhart
CUBA. Cienfuegos:

Pinguicula jackii Barnhart **var. *parviflora*** Ernst
CUBA. Cienfuegos:

Pinguicula jaraguana Casper

Cuba. Holguín:

Pinguicula jarmilae Halda et Malina

BOLIVIA. Chuquisaca:

Pinguicula kondoi Casper

MEXICO. Nuevo León:

San Luis Potosí:

Tamaulipas:

Pinguicula laueana Speta et Fuchs
MEXICO. Oaxaca:

Pinguicula laxifolia Luhrs
MEXICO. Tamaulipas:

Pinguicula leptoceras Reichenbach
AUSTRIA. Salzburg:
Tirol:

Vorarlberg:

FRANCE. Alpes-Maritimes:

Hautes-Alpes:

ITALY. Lombardia:

Piemonte:

Trentino-Alto Adige:

Valle d'Aosta:

Veneto:

SWITZERLAND. Bern:

Valais:

Graubünden:

Ticino:

Uri:

Valais:

Vaud:

Pinguicula lignicola Barnhart
CUBA. Guantánamo:

Holguín:

Pinguicula lilacina Schlecht. et Cham.

GUATEMALA. Alta Verapaz:

Baja Verapaz:

Huehuetenango:

HONDURAS.

Isla de La Bahía:

MEXICO. Chiapas:

Jalisco:

Nayarit:

Oaxaca:

Puebla:

Querétaro:

San Luis Potosí:

Sinaloa:

Tamaulipas:

Veracruz:

Misc.

Pinguicula longifolia Ram. ex DC.

FRANCE. Hautes-Pyrénées:

SPAIN. Huesca:

Pinguicula lusitanica L.

FRANCE. Calvados:

Charente-Maritime: Cher:

Dordogne:

Eure:

Finistère:

Gers: Gironde:

Ille-et-Vilaine:

Indre-et-Loire:

Landes:

Loire-Atlantique:

Loire-et-Cher:

Maine-et-Loire:

Manche:

Mayenne:

Morbihan:

Orne:

Pyrenées-Atlantiques:

Sarthe:

Vendée:

Vienne:

Misc.

IRELAND. Carlow:

Cork:

Donegal:

Dublin:

Galway:

Kerry:

Kilkenny:

Leitrim:

Mayo:

Waterford:

Wicklow:

MOROCCO. Tangier-Tetouan:

PORTUGAL. Aveiro:

Beja:

Braga:

Coimbra:

Faro:

Leiria:

Lisboa:

Portalegre:

Porto:

Santarém:

Setúbal:

Viseu:

SPAIN. A Coruña:

Asturias:

Burgos:

Cádiz:

Cantabria:

Guipúzcoa:

Lugo:

Malaga:

Navarra:

UNITED KINGDOM. [ENGLAND] Bournemouth:

Cornwall:

Devon:

Dorset:

Hampshire:

Poole:

Somerset:

Southampton:

Surrey:

Isla of Wight:

Wiltshire:

[ISLE OF MAN]:

[NORTHERN IRELAND] Antrim:

Down:

Fermanagh:

Tyrone:

[SCOTLAND] Angus:

Argyll and Bute:

Dumfries and Galloway:

Highland:

Na h-Eileanan Siar (Western Isles):

North Ayrshire:

Stirling:

[WALES] Pembrokeshire:

Pinguicula lutea Walter

USA. Alabama:

Florida:

Georgia:

Louisiana:

Mississippi:

North Carolina:

South Carolina:

Misc.

Pinguicula macroceras Link

CANADA. Alberta:

British Columbia:

Yukon Territory:

JAPAN. Akita:

Aomori:

Fukui:

Fukushima:

Gifu:

Gunma:

Hokkaidō:

Ishikawa:

Iwate:

Kōchi (Tokushima side?):

Mie:

Miyagi:

Niigata:

Saitama:

Tochigi:

Tokushima:

Toyama:

Yamagata:

Yamanashi:

RUSSIA. Kamchatka:

Sakhalin:

USA. Alaska:

California:

Montana:

Oregon:

Washington:

Pinguicula macrophylla Kunth

MEXICO. Guanajuato:

San Luis Potosí:

Querétaro:

Pinguicula martinezii Zamudio

MEXICO. Querétaro:

Pinguicula medusina Zamudio et Studnička

MEXICO. Oaxaca:

Pinguicula mesophytica Zamudio

EL SALVADOR. Santa Ana:

GUATEMALA.

Chimaltenango:

Huehuetenango:

Sololá:

HONDURAS. Intibucá:

Lempira:

Ocotepeque:

Santa Bárbara:

MEXICO. Chiapas:

Pinguicula mirandae Zamudio et Salinas

MEXICO. Oaxaca:

Pinguicula moctezumae Zamudio et Ortega

MEXICO. Hidalgo:

Querétaro:

Pinguicula moranensis Kunth **var. *moranensis*** Kunth

GUATEMALA. Baja Verapaz:

Chimaltenango:

El Quiché:

Huehuetenango:

Quetzaltenengo:

San Marcos:

Totonicapán:

MEXICO. Chiapas:

Distrito Federal:

Guanajuato:

Guerrero:

Hidalgo:

México:

Michoacán:

Morelos:

Nuevo León:

Oaxaca:

Puebla:

Querétaro:

San Luis Potosí:

Tamaulipas:

Tlaxcala:

Veracruz:

P. moranensis Kunth **var. *neovolcanica*** Zamudio
MEXICO. Distrito Federal:

Hidalgo:

México:

Michoacán:

Morelos:

Oaxaca:

Puebla:

Querétaro:

Tlaxcala:

Veracruz:

Pinguicula mundi Blanca, Jamilena, Ruiz-Rejón et Zamora
SPAIN. Albacete:

Pinguicula nevadensis (Lindberg) Casper
SPAIN. Granada:

Pinguicula nivalis Luhrs et Lampard

MEXICO. Nuevo León:

Pinguicula oblongiloba DC.

MEXICO. Aguascalientes:

Chihuahua:

Colima:

Durango:

Guanajuato:

Jalisco:

México:

Michoacán:

Nayarit:

Sonora:

Zacatecas:

Pinguicula orchidioides DC.

GUATEMALA. Sololá:

MEXICO. Guerrero:

Oaxaca:

Misc.

Pinguicula parvifolia Robinson
MEXICO. Durango:

Jalisco:

México:

Michoacán:

Morelos:

Nayarit:

Puebla (Morelos?):

Sinaloa:

Zacatecas:

Pinguicula pilosa Luhrs, Studnička et Gluch
MEXICO. Tamaulipas:

Pinguicula planifolia Chapman
USA. Alabama:

Florida:

Mississippi:

Pinguicula poldinii Steiger et Casper
ITALY. Friuli-Venezia Giulia:

Veneto:

Pinguicula potosiensis Speta et Fuchs
non visus

Pinguicula primuliflora Wood et Godfrey
JAPAN (naturalized). Aichi:

Okayama:

Shizuoka:

USA. Alabama:

Florida:

Georgia:

Mississippi:

Pinguicula pumila Michx.

BAHAMAS. Andros Isl.:

Grand

Bahama Isl.: 7

Great Abaco Isl.:

USA. Florida:

Georgia:

Louisiana:

North Carolina:

South Carolina:

Texas:

Pinguicula ramosa Miyoshi

JAPAN. Gunma:

Pinguicula rectifolia Speta et Fuchs
non visus

Pinguicula reichenbachiana Schindler
FRANCE. Alpes-Maritimes:

ITALY. Liguria:

Pinguicula rotundiflora Studnička
MEXICO. Nuevo León:

Pinguicula sharpii Casper et Kondo
non visus

Pinguicula spathulata Ledeb.
RUSSIA. Amur:

Buryatia:

Chukotka:

Irkutsk:

Kamchatka:

Khabarovsk:

Magadan:

Sakha (Yakutia):

Sakhalin:

Misc.

Pinguicula takakii Zamudio et Rzedowski

MEXICO. San Luis Potosí:

Pinguicula utricularioides Zamudio et Rzedowski

MEXICO. Oaxaca:

Pinguicula vallisneriifolia Webb

SPAIN. Granada:

Jaén:

Misc.

SWITZERLAND (naturalized). Bern:

Pinguicula vallis-regiae Conti et Peruzzi

ITALY. Abruzzo:

Pinguicula villosa L.

CANADA. British Columbia:

Manitoba:

Newfoundland and Labrador:

Northwest Territories:

Nunavut:

Ontario:

Québec:

Saskatchewan:

Yukon Territory:

CHINA. Nei Mongol

(Inner Mongolia):

FINLAND. Kainuu:

Lappi:

Pohjois-Pohjanmaa:

JAPAN. Hokkaidō:

NORTH KOREA (DPRK). Ryanggang-do:

NORWAY. Finnmark:

Hedmark:

Oppland:

Sør-Trøndelag:

RUSSIA.

Buryatia:

Chukotka:

Irkutsk:

Kamchatka:

Khabarovsk:

Komi:

Krasnoyarsk:

Magadan:

Murmansk:

Nenetsia:

Sakha (Yakutia):

Sakhalin:

Tyumen:

Yamalo-Nenets:

SWEDEN. Dalarna:

Jämtland:

Norrbotten:

Västerbotten:

Wästernorrland:

Misc.

USA. Alaska:

Misc.

Pinguicula vulgaris L.

ANDORRA. Encamp:

AUSTRIA. Burgenland:

Kärnten:

Niederöstrreich:

Oberösterreich:

Salzburg:

Steiermark:

Tirol:

Vorarlberg:

BELARUS. Minsk:

BELGIUM. Flanders:

Misc.

CANADA. Manitoba:

New Brunswick:

Newfoundland and Labrador:

Northwest Territories:

Nunavut:

Ontario:

Québec:

Saskatchewan:

Yukon Territory:

CROATIA. Karlovac:

CZECH REPUBLIC. Jihočeský kraj (South Bohemia):

Královéhradecký kraj:

Liberecký kraj:

Plzeňský kraj:

Středočeský kraj (Central Bohemia):

Ústecký kraj:

DENMARK. [FÆRØERNE (FAROE ISLS.)]:

[GRØNLAND (GREENLAND)]:

Midtjylland:

Nordjylland:

Sjaelland:

Syddanmark:

ESTONIA. Harju maakond:

Hiiu maakond:

Pärnu maakond:

Saare maakond:

Tartu maakond:

FINLAND.

Ahvenanmaa (Åland):

Kainuu:

Lappi:

Pirkanmaa:

Pohjois-Karjala:

Pohjois-Pohjanmaa:

FRANCE. Ain:

Alpes-de-Haute-Provence:

Alpes-Maritimes:

Bas-Rhin:

Cantal:

Doubs:

Eure:

Haute-Rhin:

Haute-Savoie:

Hautes-Alpes:

Hautes-Pyrénées:

Indre-et-Loire:

Isère:

Jura:

Maine-et-Loire:

Oise:

Puy-de-Dôme:

Pyrénées-Atlantiques:

Pyrénées-Orientales:

Sarthe:

Savoie:

Somme:

Vosges:

GERMANY. Baden-Württemberg:

Bayern:

Berlin:

Brandenburg:
Mecklenburg-Vorpommern:

Nordrhein-Westfalen:

Rheinland-Pfalz:

Sachsen-Anhalt:

Sachsen:

Thüringen:

HUNGARY. Győr-Moson-Sopron:

ICELAND. Austurland:

Höfuðborgarsvæði:

Norðurland eystra:

Suðurland:

Vestfirðir:

Vesturland:

Misc.

IRELAND. Clare:

Donegal:

Dublin:

Galway:

Kerry:

Kildare:

Limerick:

Loais:

Mayo:

Roscommon:

Tipperary:

Westmeath:

Wicklow:

ITALY. Friuli-Venezia Giulia:

Lombardia:

Piemonte:

Trentino-Alto Adige:

Valle d'Aosta:

Veneto:

LATVIA. Jūrmala:

Tukums:

MONGOLIA. Khövsgöl:

MOROCCO. Taza-Al Hoceima-Taounate:

NETHERLANDS. Gelderland:

Overijssel:

Misc.

NORWAY. Akershus:

Aust-Agder:

Buskerud:

Finnmark:

Hordaland:

Møre og Romsdal:

Nordland:

Nord-Trøndelag:

Oppland:

Oslo:

Sogn og Fjordane:

Sør-Trøndelag:

Telemark:

Troms:

Vest-Agder:

POLAND. Lubelskie:

Małopolskie:

Opole:

Zachodniopomorskie:

PORTUGAL. Braga:

ROMANIA. Braşov:

Dâmboviţa:

Harghita:

Neamţ:

Prahova:

Sibiu:

Suceava:

RUSSIA. Arkhangelsk:

Bashkortostan:

Karelia:

Khanty-mansi (Yugra):

Komi:

Krasnodar:

Krasnoyarsk:

Leningrad:

Murmansk:

Nenetsia:

Perm:

Pskov (Pskow):

Sakha (Yakutia):

St. Petersburg:

Sverdlovsk:

Yamalo-Nenets:

Vologda:

SLOVAKIA. Banskobystrický kraj:

Bratislavský kraj:

Košicky kraj:

Prešovský kraj:

Žilinský kraj:

SLOVENIA.

Bohinj:

Jesenice:

Kamnik:

Kranjska Gora:

Ljubljana:

Logatec:

Mežica:

Tržič:

Železniki:

SPAIN. Asturias:

Girona:

Guadalajara:

Huesca:

Teruel:

Zamora:

SWEDEN. Blekinge:

Dalarna:

Gotland:

Gövleborg:

Halland:

Jämtland:

Jönköping:

Kalmar:

Kronoberg:

Norrbotten:

Örebro:

Östergötland:

Skåne:

Södermanland:

Stockholm:

Uppsala:

Värmland:

Västerbotten:

Västernorrland:

Västmanland:

Västra

Götland:

SWITZERLAND. Bern:

Fribourg:

Graubünden:

Jura:

Luzern:

Neuchâtel:

Schwyz:

Ticino:

Uri:

Valais:

Vaud:

Zug:

Zürich: **UKRAINE.** Lviv:

Zakarpattia:

UNITED KINGDOM. [ENGLAND] Cambridgeshire:

Cheshire West and Chester:

Cumbria:

Derbyshire:

Dorset:

Durham:

Gloucestershire:

Greater London:

Hampshire:

Herefordshire:

Lancashire:

Lincolnshire:

Merseyside:

Norfolk:

Northumberland:

North

Yorkshire:

Oxfordshire:

Somerset:

Suffolk:

West Midlands:

West Yorkshire:

Wrexham:

Yorkshire:

[ISLE OF MAN]

[NORTHERN IRELAND] Antrim:

Belfast:

Fermanagh:

Londonderry:

Tyrone:

[SCOTLAND]

Aberdeenshire:

Angus:

Argyll and Bute:

Dumfries and Galloway:

East Lothian:

Edinburgh:

Highland:

Inverclyde:

Moray:

Na h-Eileanan Siar

(Western Isles):

North Ayrshire:

Orkney:

Perth and Kinross:

Scottish Borders:

Shetland Islands.:

Stirling:

[WALES] Blaenau Gwent:

Carmarthenshire:

Ceredigion:

Conwy:

Denbighshire:

Gwynedd:

Isle of Anglesey:

Monmouthshire:

Neath Port Talbot:

Pembrokeshire:

Powys:

Rhondda Cynon Taff:

Torfaen:

Vale of Glamorgan:

USA. Alaska:

Michigan:

Minnesota:

New Hampshire:

New York:

Vermont:

Wisconsin:

Misc.

Pinguicula zecheri Speta et Fuchs
MEXICO. Guerrero:

Michoacán:

NATURAL HYBRID

P. grandiflora Lam. **X *P. longifolia*** Ram. ex DC.
FRANCE. Hautes-Pyrénées:

SPAIN. Huesca:

P. grandiflora Lam. **X *P. vulgaris*** L. **(= *P.* X *scullyi*** Druce**)**
ANDORRA. Encamp:

FRANCE. Hautes-Pyrénées:

Pyrénées-Orientales:

IRELAND. Clare:

Kerry:

SPAIN. Huesca:

Lleida:

P. gypsicola Brandegee **X *P. takakii*** Zamudio et Rzedowski
MEXICO. San Luis Potosí:

P. oblonbiloba DC. **X *P. parvifolia*** Robinson **?**
MEXICO. Durango:

P. apuana Casper et Ansaldi (not sure if species)
ITALY. Toscana:

***Pinguicula* spp. (Italian taxa)**
ITALY. Abruzzo:

Emilia-Romagna:

Lazio:

Toscana:

[Note] Local names, particularly political units, have been updated whenever possible. Specimen ID numbers given by each herbarium were omitted unless requested to mention them by the herbarium. All specimens deposited at the Department of Biology, Nippon Dental University were transferred to TNS in 2013.

Herbarium code

A: Harvard University (Massachusetts, USA)
AAU: Aarhus University (Denmark)
ABS: University of Wales (Wales, UK)
ACAD: Acadia University (Nova Scotia, Canada)
ALA: University of Alaska Museum of the North (Alaska, USA)
AMD: National Herbarium of the Netherlands, Hugo de Vries-Laboratory (Netherlands)
AO: Museo Regionale di Scienze Naturali della Valle d'Aosta (Italy)
APP: Parco Nazionale del Gran Sasso e Monti della Laga - Università di Camerino (Italy)
ARIZ: University of Arizona (Arizona, USA)
ASU: Arizona State University (Arizona, USA)
BAA: Universidad de Buenos Aires (Argentina)
BABY: Yukon Government (Yukon, Canada)
BASSA: Museo Civico (Vicenza, Italy)
BC: Institut Botànic de Barcelona (Spain)
BEI: American University of Beirut (Lebanon)
BEO: Natural History Museum (Serbia)
BERN: University of Bern (Switzerland)
BIRM: University of Birmingham (England, UK)
BKL: Brooklyn Botanic Garden (New York, USA)
BM: The Natural History Museum (England, UK)
BOLO: Università di Bologna (Italy)
BP: Hungarian Natural History Museum (Hungary)
BR: Botanic Garden Meise (Belgium)
BUF: Buffalo Museum of Science (New York, USA)
BVS: Transylvania University of Brasov (Romania)
CGE: Cambridge University (England, UK)
CHRB: Rutgers University (New Jersey, USA)
CINC: University of Cincinnati (Ohaio, USA)
CLF: Institut des Herbiers Universitaires de Clermont-Ferrand (France)
CLU: Università della Calabria (Italy)
CONN: University of Connecticut (Connecticut, USA)
CR: Museo Nacional de Costa Rica (Costa Rica)

DBN: National Botanic Gardens (Ireland)
DES: Desert Botanical Garden (Arizona, USA)
E: Royal Botanic Garden Edinburgh (Scotland, UK)
EAP: Escuela Agrícola Panamericana (Honduras)
EGE: Ege University (Turkey)
ENCB: Instituto Politécnico Nacional (Mexico)
FCO: Universidad de Oviedo (Spain)
FIAF: Università degli Studi di Firenze (Italy)
FLAS: Florida Museum of Natural History (Florida, USA)
FRP: Palmengarten (Germany)
GAZI: Gazi Üniversitesi (Turkey)
GBH: Herbarium of Geo. B. Hinton (Mexico)
GDAC: Universidad de Granada (Spain)
G-DC: Conservatoire et Jardin botaniques de la Ville de Genève (Switzerland)
GMNHJ: Gunma Museum of Natural History (Japan)
GOET: Universität Göttingen (Gernamy)
GR: University Grenoble Alpes (France)
GZU: Karl-Franzens-Universität Graz (Austria)
HAJU: Herbario Dr. Armando Jesus Urquiola (Cuba)
HAL: Martin-Luther-Universität (Germany)
HAM: Royal Botanical Gardens (Ontario, Canada)
HAST: Biodiversity Research Center, Academia Sinica (Taiwan)
HEM: Universidad de Ciencias y Artes de Chiapas (Mexico)
HUB: Hacettepe University (Turkey)
I: "Alexandru Ioan Cuza" University (Romania)
ID: University of Idaho (Idaho, USA)
IEB: Instituto de Ecología, A.C. (Mexico)
IJ: Natural History Museum of Jamaica (Jamaica)
ISKW: Ishikawa Museum of Natural History (Japan)
ISTF: Istanbul University (Turkey)
JACA: Instituto Pirenaico de Ecología, C.S.I.C. (Spain)
JE: Friedrich-Schiller-Universität Jena (Germany)
JEPS: University of California (California, USA)
K: Royal Botanic Gardens, Kew (England, UK)
KANA: Kanazawa University (Japan)
KMN: Adger Museum of Natural History and Botanical Garden (Norway)

KWHU: O. V. Fomin Botanical Garden of National Taras Schevchenko, National University of Kyiv (Ukraine)

KYO: Kyoto University (Japan)

LAGU: Asociación Jardín Botánico La Laguna, Urbanización Plan de La Laguna (El Salvador)

LE: V. L. Komarov Botanical Institute (Russia)

LEA: University of Lethbridge (Alberta, Canada)

LI: Oberösterreichischen Landesmuseums (Austria)

LINN: Linnean Society of London (England, UK)

LISU: Museu Nacional de História Natural e da Ciência (Portugal)

LJS: Scientific Research Centre (Slovenia)

LJU: University of Ljubljana (Slovenia)

LUG: Museo cantonale di storia natural (Switzerland)

MAK: Tokyo Metropolitan University (Japan)

MANCH: University of Manchester (England, UK)

MARS: Aix-Marseille Université (France)

MARY: University of Maryland (Maryland, USA)

MASS: University of Massachusetts (Massachusetts, USA)

MERL: Instituto Argentino de Investigaciones de las Zonas Áridas (IADIZA, CRICYTME) (Argentina)

MEXU: Universidad Nacional Autónoma de México (Mexico)

MGC: Universidad de Málaga (Spain)

MHA: Main Botanical Garden of the Russian Academy of Sciences (Russia)

MKNH: Institute of Biology (Republic of Macedonia)

MMMN: The Manitoba Museum (Manitoba, Canada)

MO: Missouri Botanical Garden (Missouri, USA)

MONTU: University of Montana (Montana, USA)

MRSN: Museo Regionale di Scienze Naturali (Italy)

MSC: Michigan State University (Michigan, USA)

MSNM: Museo Civico di Storia Naturale di Milano (Italy)

MU: Miami University (Ohio, USA)

MW: Moscow State University (Russia)

NAP: Università Degli Studi di Napoli Federico II (Italy)

NCY: Conservatoire et Jardins Botaniques de Nancy (France)

NHA: University of New Hampshire (New Hampshire, USA)

NHMF: Natural History Museum Fribourg (Switzerland)

NMW: National Museum Wales (Wales, UK)
NSPM: The Nova Scotia Museum, Collections (Nova Scotia, Canada)
NY: The New York Botanical Garden (New York, USA)
NYS: New York State Museum (New York, USA)
OLYM: Olympic National Park (Washington, USA)
O: Botanical Museum, University of Oslo (Norway)
OXF: University of Oxford (England, UK)
P: Muséum National d'Histoire Naturelle (France)
PAD: Università degli Studi di Padova (Italy)
PE: Institute of Botany, Chinese Academy of Sciences (China)
PH: Academy of Natural Sciences (Pennsylvania, USA)
PLU: Pacific Lutheran University (Washington, USA)
PRA: Institute of Botany, Academy of Sciences (Czech Republic)
QCA: Pontificia Universidad Católica del Ecuador (Ecuador)
QFA: Université Laval (Québec, Canada)
QK: Queen's University (Ontario, Canada)
REG: Regensburgische Botanische Gesellschaft (Germany)
RO: Università degli Studi di Roma La Sapienza (Italy)
S: Swedish Museum of Natural History (Sweden)
SAPS: Hokkaido University Museum (Japan)
SAV: Slovak Academy of Sciences (Slovakia)
SB: Saint Bernard Abbey (Alabama, USA)
SHIN: Shinshu University (Japan)
SNU: Seoul National University (Korea)
SO: Sofia University (Bulgaria)
SOC: Southern Oregon University (Oregon, USA)
SOM: Bulgarian Academy of Sciences (Bulgaria)
SRP: Boise State University (Idaho, USA)
STR: Institut de Botanique (France)
STU: Staatliches Museum für Naturkunde (Gernamy)
TAA: Estonian University of Life Sciences (Estonia)
TEX: University of Texas at Austin (Texas, USA)
TI: University of Tokyo (Japan)
TL: Université Paul Sabatier (France)
TNS: National Museum of Nature and Science (Japan)
TSM: Museo Civico di Storia Naturale (Italy)

TUS: Tohoku University (Japan)
UBC: University of British Columbia (British Columbia, Canada)
UDM: Museo Friulano di Storia Naturale (Italy)
UNA: University of Alabama (Alabama, USA)
UPA: University of Patras (Greece)
UPS: Museum of Evolution (Sweden)
US: Smithsonian Institution (Washington DC, USA)
USF: University of South Florida (Florida, USA)
UTC: Utah State University (Utah, USA)
UWSP: University of Wisconsin-Stevens Point (Wisconsin, USA)
VAL: Universitat de València (Spain)
VT: University of Vermont (Vermont, USA)
WA: University of Warsaw (Poland)
WI: Vilnius University (Lithuania)
WIN: University of Manitoba (Manitoba, Canada)
WIS: University of Wisconsin (Wisconsin, USA)
WTU: University of Washington (Washington, USA)
WU: Universität Wien (Austria)
WVA: West Virginia University (West Virginia, USA)
WWB: Western Washington University (Washington, USA)
ZA: University of Zagreb (Croatia)
ZAHO: University of Zagreb (Croatia)
ZT: Eidgenössische Technische Hochschule Zürich (Switzerland)

Eastern Washington University (Washington, USA)
Fukui City Museum of Natural History (Japan)
Nippon Dental University (Japan)
Okayama University (Japan)
Slater Museum of Natural History (Washington, USA)
Tochigi Prefectural Museum (Japan)
herb. Dr Garrett Crow (New Hampshire, USA)

APPENDIX III

Index to scientific names

Isoloba elatior (Michx.) Raf. = Pinguicula caerulea Walter

Isoloba lutea (Walter) Raf. = Pinguicula lutea Walte

Isoloba pumila (Michx.) Raf. = Pinguicula pumila Michx.

Isoloba recurva Raf. = Pinguicula lutea Walte

Pinguicula acuminata Bentham

Pinguicula acutifolia Michx. = Pinguicula villosa L.

Pinguicula agnata Casper

Pinguicula alba Kuchl = Pinguicula alpina L.

Pinguicula albanica Griseb. = Pinguicula hirtiflora Tenore

Pinguicula albida Wright ex Griseb.

Pinguicula albiflora Cariot et St. Lager = Pinguicula alpina L.

Pinguicula albiflora Cariot et St. Lager var. villosa Cariot et St. Lager
= Pinguicula alpina L.

Pinguicula algida Malyschev

Pinguicula alpestris Persoon = Pinguicula alpina L.

Pinguicula alpicola Rouy = Pinguicula vulgaris L.

Pinguicula alpina Baldacci = Pinguicula balcanica Casper

Pinguicula alpina L.

Pinguicula alpina L. subsp. gavei Beauverd = Pinguicula alpina L.

Pinguicula alpina L. var. bimaculata Wahlenberg = Pinguicula alpina L.

Pinguicula alpina L. var. flavescens Steudel et Hochstetter = Pinguicula alpina L.

Pinguicula alpina L. var. lendneri Beauverd = Pinguicula alpina L.

Pinguicula alpina L. var. lendneri Perrier = Pinguicula alpina L.

Pinguicula alpina L. var. villosa Villars = Pinguicula alpina L.

Pinguicula alpina Thoré = Pinguicula lusitanica L.

Pinguicula alpina Weber = Pinguicula vulgaris L.

Pinguicula antarctica Donat = Pinguicula chilensis Clos

Pinguicula antarctica Fernández-Pérez = Pinguicula calyptrata Kunth

Pinguicula antarctica Thomsson = Pinguicula chilensis Clos

Pinguicula antarctica Vahl

Pinguicula apuana Casper et Ansaldi ➔ review needed

Pinguicula arctica Eastwood = Pinguicula vulgaris L.

Pinguicula arvetii Genty = Pinguicula leptoceras Reichenbach

Pinguicula auricolor Arv. Touv. = Pinguicula alpina L.

Pinguicula australis Chapman = Pinguicula caerulea Walter

Pinguicula australis Nutt. = Pinguicula pumila Michx.

Pinguicula bakeriana Sander = Pinguicula moranensis Kunth var. moranensis Kunth
Pinguicula bakeriana Sprague = Pinguicula moranensis Kunth var. moranensis Kunth
Pinguicula balcana Petrovic = Pinguicula balcanica Casper
Pinguicula balcanica Casper
Pinguicula balcanica Casper subsp. pontica Casper = Pinguicula balcanica Casper
Pinguicula balcanica Casper var. tenuilaciniata Casper = Pinguicula balcanica Casper
Pinguicula barbata Zamudio et Rzedowski
= Pinguicula clivorum Standley et Steyermark
Pinguicula barkeriana Sprague = Pinguicula macrophylla Kunth
Pinguicula benedicta Barnhart
Pinguicula bicolor (Nordstedt ex Fries) Woloszczak = Pinguicula vulgaris L.
Pinguicula bicolor Nordstedt ex Freis f. gorcensis Kornas = Pinguicula vulgaris L.
Pinguicula bissei Casper = Pinguicula benedicta Barnhart
Pinguicula bohemica Krajina = Pinguicula vulgaris L.
Pinguicula borealis Salisb., Peris et Stübing = Pinguicula vulgaris L.
Pinguicula brachyloba Ledebour = Pinguicula alpina L.
Pinguicula caerulea Walter
Pinguicula caerulea Walter f. leucantha Schnell = Pinguicula caerulea Walter
Pinguicula calderoniae Zamudio
Pinguicula calyptrata Kunth
Pinguicula campanulata Lam. = Pinguicula lutea Walte
Pinguicula caryophyllacea Casper = Pinguicula benedicta Barnhart
Pinguicula casabitoana Jiménez
Pinguicula caudata Hemsley = Pinguicula macrophylla Kunth
Pinguicula caudata Hemsley = Pinguicula oblongiloba DC.
Pinguicula caudata Schlecht.
= Pinguicula moranensis Kunth var. moranensis Kunth
Pinguicula caussensis (Casper) Innangi, De Castro et Peruzzi
Pinguicula chilensis Clos
Pinguicula christinae Peruzzi et Gestri ➔ review needed
Pinguicula chuquisacensis Beck, Fleischm. et Borsch
= Pinguicula jarmilae Halda et Malina
Pinguicula cladophila Ernst = Pinguicula casabitoana Jiménez
Pinguicula clivorum Standley et Steyermark
Pinguicula colimensis McVaugh et Mickel
Pinguicula conzattii Zamudio et van Marm

Pinguicula corsica Bernard et Gren. ex Gren. et Godr.

Pinguicula corsica Bernard et Gren. ex Gren. et Godr. var. coerulescens Briquet

= Pinguicula corsica Bernard et Gren. ex Gren. et Godr.

Pinguicula corsica Bernard et Gren. ex Gren. et Godr. var. pallidula Briquet

= Pinguicula corsica Bernard et Gren. ex Gren. et Godr.

Pinguicula crassifolia Zamudio

Pinguicula crenatiloba DC.

Pinguicula crystallina Smith

Pinguicula crystallina Smith subsp. hirtiflora (Tenore) Strid

= Pinguicula hirtiflora Tenore

Pinguicula cubensis Urquiola et Casper

Pinguicula cyclosecta Casper

Pinguicula daurica Link = Pinguicula macroceras Link

Pinguicula debbertiana Speta et Fuchs

Pinguicula dertosensis (Cañigueral) Mateo et Crespo

Pinguicula diversifolia Cuatrecasas = Pinguicula elongata Benjamin

Pinguicula X dostalii Bárta = Pinguicula bohemica Krajina X Pinguicula vulgaris L.

Pinguicula edentula Hook. = Pinguicula lutea Walte

Pinguicula ehlersae Speta et Fuchs = Pinguicula ehlersiae Speta et Fuchus

Pinguicula ehlersiae Speta et Fuchs

Pinguicula elatior Michx. = Pinguicula caerulea Walter

Pinguicula eliae Sennen = Pinguicula grandiflora Lam.

Pinguicula elizabethiae Zamudio

Pinguicula elongata Benjamin

Pinguicula emarginata Zamudio et Rzedowski

Pinguicula esseriana Kirchner

Pinguicula esseriana Kirchner var. ehlersiae (Speta et Fuchs) Zamudio

= Pinguicula ehlersiae Speta et Fuchs

Pinguicula filifolia Wright ex Griseb.

Pinguicula filifolia Wright ex Griseb. subsp. alba Dominguez, Panfet et Miranda

= P. filifolia Wright ex Griseb.

Pinguicula fiorii Tammaro et Pace

Pinguicula flavescens Floerke = Pinguicula alpina L.

Pinguicula floridensis Chapman = Pinguicula pumila Michx.

Pinguicula flos-mulionis Morr. = Pinguicula moranensis Kunth var. moranensis Kunth

Pinguicula fontiqueriana Romo, Peris et Stübing = Pinguicula vulgaris L.

Pinguicula gelida Schur = Pinguicula alpina L.

Pinguicula gigantea Luhrs

Pinguicula glandulosa Trautvetter et Meyer = Pinguicula spathulata Ledeb.

Pinguicula gracilis Zamudio

Pinguicula grandiflora Balbis = Pinguicula leptoceras Reichenbach

Pinguicula grandiflora Beck = Pinguicula balcanica Casper

Pinguicula grandiflora Bertoloni
= Pinguicula corsica Bernard et Gren. ex Gren. et Godr.

Pinguicula grandiflora Bertoloni = Pinguicula reichenbachiana Schindler

Pinguicula grandiflora Bras = Pinguicula caussensis (Casper) Shimai

Pinguicula grandiflora Lam.

Pinguicula grandiflora Lam. subsp. coenocantabrica Rivas Martínez, Díaz, Prieto, Loidi et Penas = Pinguicula grandiflora Lam.

Pinguicula grandiflora Lam. subsp. dertosensis (Cañigueral) Bolós et Vigo
= Pinguicula dertosensis (Cañigueral) Mateo et Crespo

Pinguicula grandiflora Lam. subsp. longifolia Nyman
= Pinguicula longifolia Ram. ex DC.

Pinguicula grandiflora Lam. subsp. longifolia Nyman
= Pinguicula reichenbachiana Schindler

Pinguicula grandiflora Lam. subsp. reuteri Löve et Löve = Pinguicula grandiflora Lam.

Pinguicula grandiflora Lam. subsp. rosea (Mutel) Casper = Pinguicula grandiflora Lam.

Pinguicula grandiflora Lam. var. albescens Rouy = Pinguicula grandiflora Lam.

Pinguicula grandiflora Lam. var. dertosensis Cañigueral
= Pinguicula dertosensis (Cañigueral) Mateo et Crespo

Pinguicula grandiflora Lam. var. foliis-oblongis Loiseleur
= Pinguicula leptoceras Reichenbach

Pinguicula grandiflora Lam. var. inaequilobata (Sennen) Casper
= Pinguicula grandiflora Lam.

Pinguicula grandiflora Lam. var. longifolia Bentham
= Pinguicula longifolia Ram. ex DC.

Pinguicula grandiflora Lam. var. longifolia Grenier et Godron
= Pinguicula caussensis (Casper)

Pinguicula grandiflora Lam. var. longifolia Grenier et Godron
= Pinguicula reichenbachiana Schindler

Pinguicula grandiflora Lam. var. pallida Briquet = Pinguicula grandiflora Lam.

Pinguicula grandiflora Lam. var. pallida Gaudin = Pinguicula grandiflora Lam.

Pinguicula grandiflora Lam. var. reuteri (Genty) Ernst = Pinguicula grandiflora Lam.

Pinguicula grandiflora Lam. var. rosea Mutel = Pinguicula grandiflora Lam.

Pinguicula grandiflora Lam. f. chionopetra Nelson = Pinguicula grandiflora Lam.

Pinguicula grandiflora Lam. f. pallida (Gaudin) Casper = Pinguicula grandiflora Lam.

Pinguicula grandiflora Pollinius = Pinguicula vulgaris L.

Pinguicula grandiflora Sprengel = Pinguicula longifolia Ram. ex DC.

Pinguicula greenwoodii Cheek

Pinguicula X gresivaudanica Roccia

= Pinguicula grandiflora Lam. subsp. rosea (Mutel) Casper X Pinguicula vulgaris L.

Pinguicula gypsicola Brandegee

Pinguicula gypsophila Wallroth = Pinguicula vulgaris L.

Pinguicula habilii Yıldırım, Şenol, et Pirhan = P. crystallina

Pinguicula hellwegeri Murr = Pinguicula leptoceras Reichenbach

Pinguicula hemiepiphytica Zamudio et Rzedowski

Pinguicula heterophylla Bentham

Pinguicula hintoniorum Turner = Pinguicula ehlersiae Speta et Fuchs

Pinguicula hirtiflora Tenore

Pinguicula hirtiflora Tenore subsp. megaspilaea Nyman = Pinguicula hirtiflora Tenore

Pinguicula hirtiflora Tenore var. decipiens Bornmüller = Pinguicula hirtiflora Tenore

Pinguicula hirtiflora Tenore var. euboea Beauverd et Topali

= Pinguicula hirtiflora Tenore

Pinguicula hirtiflora Tenore var. gionae Contandriopoulos et Quézel

= Pinguicula hirtiflora Tenore

Pinguicula hirtiflora Tenore var. louisii (Markgr.) Ernst = Pinguicula hirtiflora Tenore

Pinguicula hirtiflora Tenore var. megaspilaea (Boiss. et Heldr.) Schindler

= Pinguicula hirtiflora Tenore

Pinguicula hirtiflora Tenore f. pallida Casper = Pinguicula hirtiflora Tenore

Pinguicula huilensis Cuatrecasas = Pinguicula calyptrata Kunth

Pinguicula X hybrida Wettstein = Pinguicula alpina L. X Pinguicula vulgaris L.

Pinguicula hyperborea Gandoger = Pinguicula alpina L.

Pinguicula ibarrae Zamudio

Pinguicula imitatrix Casper = nomen dubium

Pinguicula immaculata Zamudio et Lux

Pinguicula inaequilobata Sennen = Pinguicula grandiflora Lam.

Pinguicula infundibuliformis Casper = Pinguicula benedicta Barnhart

Pinguicula involucrata DC. = Pinguicula villosa L.

Pinguicula involuta Ruíz et Pavón

Pinguicula ionantha Godfrey

Pinguicula jackii Barnhart var. ***jackii*** Barnhart

Pinguicula jackii Barnhart var. ***parviflora*** Ernst

Pinguicula jaraguana Casper

Pinguicula jarmilae Halda et Malina

Pinguicula jaumavensis Debbert = Pinguicula esseriana Kirchner

Pinguicula jorgehintonii Turner = Pinguicula rotundiflora Studnička

Pinguicula juratensis Bernard = Pinguicula grandiflora Lam.

Pinguicula kamtschatica Roemer et Schultes = Pinguicula macroceras Link

Pinguicula kondoi Casper

Pinguicula laeta Pantocsek = Pinguicula hirtiflora Tenore

Pinguicula lateciliata McVaugh et Mickel = Pinguicula cyclosecta Casper

Pinguicula lattanziae Peruzzi et Gestri ➔ not studied in this work

Pinguicula laueana Speta et Fuchs

Pinguicula lavalvae Innangi et Izzo = Pinguicula hirtiflora Tenore

Pinguicula laxifolia Luhrs

Pinguicula leptoceras Boissier = Pinguicula nevadensis (Lindberg) Casper

Pinguicula leptoceras DC. = Pinguicula corsica Bernard et Gren. ex Gren. et Godr.

Pinguicula leptoceras Grisebach = Pinguicula balcanica Casper

Pinguicula leptoceras Lamotte = Pinguicula grandiflora Lam.

Pinguicula leptoceras Reichenbach

Pinguicula leptoceras Rchb. subsp. corsica Nyman
    = Pinguicula corsica Bernard et Gren. ex Gren. et Godr.

Pinguicula leptoceras Rchb. var. hellwegeri (Murr) Dalla Torre et Sarnthein
    = Pinguicula leptoceras Reichenbach

Pinguicula leptoceras Rchb. var. lepontina Chiovenda
    = Pinguicula leptoceras Reichenbach

Pinguicula leptoceras Rchb. var. longifolia Reichenbach
    = Pinguicula reichenbachiana Schindler

Pinguicula leptoceras Rchb. var. tridentina Dalla Torre et Sarnthein
    = Pinguicula leptoceras Reichenbach

Pinguicula leptoceras Rchb. var. typica Chiovenda
    = Pinguicula leptoceras Reichenbach

Pinguicula leptoceras Rchb. var. variegata Schinz et Keller

= Pinguicula leptoceras Reichenbach

Pinguicula leptoceras Rohlena = Pinguicula balcanica Casper

Pinguicula leptoceras Schur = Pinguicula vulgaris L.

Pinguicula lignicola Barnhart

Pinguicula lilacina Schlecht. et Cham.

Pinguicula lilacina Seemann = Pinguicula crenatiloba DC.

Pinguicula lippoldii Casper = Pinguicula benedicta Barnhart

Pinguicula lithophytica Panfet-Valdés et Temple

= Pinguicula jackii Barnhart var. parviflora Ernst

Pinguicula longifolia Gaudin = Pinguicula grandiflora Lam.

Pinguicula longifolia Koch = Pinguicula leptoceras Reichenbach

Pinguicula longifolia Lamotte = Pinguicula caussensis (Casper)

Pinguicula longifolia Ram. ex DC.

Pinguicula longifolia Ram. ex DC. subsp. caussensis Casper

= Pinguicula caussensis (Casper)

Pinguicula longifolia Ram. ex DC. subsp. dertosensis (Cañigueral) Schlauer

= Pinguicula dertosensis (Cañigueral) Mateo et Crespo

Pinguicula longifolia Ram. ex DC. subsp. reichenbachiana (Schindler) Casper

= Pinguicula reichenbachiana Schindler

Pinguicula longifolia Ram. ex DC. var. brevifolia Genty ex Casper

= Pinguicula caussensis (Casper)

Pinguicula longifolia Ram. ex DC. f. vallisneriaefolia Hervier

= Pinguicula vallisneriifolia Webb

Pinguicula louisii Markg. = Pinguicula hirtiflora Tenore

Pinguicula lusitanica Allioni = Pinguicula alpina L.

Pinguicula lusitanica L.

Pinguicula lusitanica Rchb. = Pinguicula corsica Bernard et Gren. ex Gren. et Godr.

Pinguicula lutea Walte

Pinguicula lutea Walter var. edentula (Hook.) DC. = Pinguicula lutea Walte

Pinguicula lutea Walter var. minor DC. = Pinguicula lutea Walte

Pinguicula lutea Walter f. alba Folkerts et Freeman = Pinguicula lutea Walte

Pinguicula macrantha Lamotte = Pinguicula caussensis (Casper) Shimai

Pinguicula macroceras Komarov = Pinguicula variegata Turcz.

Pinguicula macroceras Link

Pinguicula macroceras Link var. microceras (Cham.) Casper

= Pinguicula macroceras Link

Pinguicula macrophylla Kunth

Pinguicula macrostyla Benjamin = Pinguicula involuta Ruíz et Pavón

Pinguicula magellanica Commerson ex Franchet = Pinguicula antarctica Vahl

Pinguicula mariae Casper ➔ review needed

Pinguicula martinezii Zamudio

Pinguicula medusina Zamudio et Studnička

Pinguicula megaspilaea Boiss. et Herder. = Pinguicula hirtiflora Tenore

Pinguicula merinoana Sennen = Pinguicula grandiflora Lam.

Pinguicula mesophytica Zamudio

Pinguicula microceras Cham. = Pinguicula macroceras Link

Pinguicula mirandae Zamudio et Salinas

Pinguicula moctezumae Zamudio et Ortega

Pinguicula moranensis Kunth var. ***moranensis*** Kunth

Pinguicula moranensis Kunth var. ***neovolcanica*** Zamudio

Pinguicula mundi Blanca, Jamilena, Ruiz-Rejón et Zamora

Pinguicula nana Mart. et Gal. ex Hemsley = Pinguicula crenatiloba DC.

Pinguicula nevadensis (Lindberg) Casper

Pinguicula nivalis Luhrs et Lampard

Pinguicula norica Beck = Pinguicula vulgaris L.

Pinguicula oblongiloba DC.

Pinguicula obtusa Herb. Banks ex Benjamin = Pinguicula antarctica Vahl

Pinguicula obtusiloba DC. = Pinguicula lilacina Schlecht. et Cham.

Pinguicula occyptera Rchb. ex Benj. = Pinguicula oxyptera Rchb. ex Benj.

Pinguicula oxyptera Rchb. ex Benj. = nomen dubium

Pinguicula orchidioides DC.

Pinguicula ovata Stokes = Pinguicula vulgaris L.

Pinguicula pallida Turczaninov = Pinguicula alpina L.

Pinguicula parvifolia Robinson

Pinguicula pilosa Luhrs, Studnička et Gluch

Pinguicula planifolia Chapman

Pinguicula poldinii Steiger et Casper

Pinguicula potosiensis Speta et Fuchs

Pinguicula primuliflora Wood et Godfrey

Pinguicula pumila Michx.

Pinguicula pumila Michx. f. alba Moldenke = Pinguicula pumila Michx.

Pinguicula pumila Michx. var. buswellii Moldenke = Pinguicula pumila Michx.

Pinguicula purpurea Willdenow = Pinguicula alpina L.

Pinguicula pygmaea Rivadavia, Read et Fleishm. ➔ not studied in this work

Pinguicula ramosa Miyoshi

Pinguicula ramosa Miyoshi f. albiflora Komiya = Pinguicula ramosa Miyoshi

Pinguicula rectifolia Speta et Fuchs

Pinguicula reichenbachiana Schindler

Pinguicula reticulata Schlauer = Pinguicula kondoi Casper

Pinguicula reuteri Genty = Pinguicula grandiflora Lam.

Pinguicula reuteri Schindler = Pinguicula grandiflora Lam.

Pinguicula rosei Watson = Pinguicula moranensis Kunth var. moranensis Kunth

Pinguicula rotundiflora Studnička

Pinguicula scopulorum Brandegee = Pinguicula lilacina Schlecht. et Cham.

Pinguicula X scullyi Druce = Pinguicula grandiflora Lam. X Pinguicula vulgaris L.

Pinguicula sehuensis Bacch., Cannas et Peruzzi ➔ not studied in this work

Pinguicula sempervivium Janka = Pinguicula balcanica Casper

Pinguicula sharpii Casper et Kondo

Pinguicula sibiricaVest = nomen dubium (Pinguicula alpina?)

Pinguicula sodalium Fourn. = Pinguicula moranensis Kunth var. neovolcanica Zamudio

Pinguicula spathulata Ledeb.

Pinguicula spathulata Ledeb. subsp. variegata (Turcz.) Khokhryakov et Kuvaev
= Pinguicula spathulata Ledeb.

Pinguicula stolonifera Luhrs = Pinguicula orchidioides DC.

Pinguicula subaequalis Stokes = Pinguicula lusitanica L.

Pinguicula submediterranea Blanca, Jamilena, Ruiz-Rejón et Zamora
= Pinguicula dertosensis (Cañigueral) Mateo et Crespo

Pinguicula takakii Zamudio et Rzedowski

Pinguicula toldensis Casper = Pinguicula benedicta Barnhart

Pinguicula utricularioides Zamudio et Rzedowski

Pinguicula vallisneriifolia Webb

Pinguicula vallisneriifoliae Webb = Pinguicula vallisneriifolia Webb

Pinguicula vallis-regiae Conti et Peruzzi

Pinguicula variegata Arvet-Touvet = Pinguicula leptoceras Reichenbach

Pinguicula variegata Turcz. = Pinguicula spathulata Ledeb.

Pinguicula villosa Gunner = Pinguicula vulgaris L.

Pinguicula villosa L.

Pinguicula villosa L. f. albiflora Froedin = Pinguicula villosa L.

Pinguicula villosa L. var. ramosa (Miyoshi) Tamura = Pinguicula ramosa Miyoshi
Pinguicula villosa Lightfoot = Pinguicula lusitanica L.
Pinguicula villosa Sessé et Mociño = Pinguicula crenatiloba DC.
Pinguicula villosa Villars = Pinguicula alpina L.
Pinguicula vulgaris Bergeret = Pinguicula grandiflora Lam.
Pinguicula vulgaris Boissier = Pinguicula balcanica Casper
Pinguicula vulgaris Bras = Pinguicula caussensis (Casper) Shimai
Pinguicula vulgaris Hultén = Pinguicula macroceras Link
Pinguicula vulgaris L.
Pinguicula vulgaris L. subsp. alpicola Rouy = Pinguicula vulgaris L.
Pinguicula vulgaris L. subsp. anzalonei Peruzzi et Conti ➔ review needed
Pinguicula vulgaris L. subsp. bicolor (Nordstedt) Löve et Löve = Pinguicula vulgaris L.
Pinguicula vulgaris L. subsp. bohemica (Krajina) Domin = Pinguicula vulgaris L.
Pinguicula vulgaris L. subsp. ernica Peruzzi et Conti ➔ review needed
Pinguicula vulgaris L. subsp. euvulgaris Dostál = Pinguicula vulgaris L.
Pinguicula vulgaris L. subsp. grandiflora Magnin = Pinguicula grandiflora Lam.
Pinguicula vulgaris L. subsp. grandiflora Thomé = Pinguicula leptoceras Reichenbach
Pinguicula vulgaris L. subsp. leptoceras Rübel = Pinguicula leptoceras Reichenbach
Pinguicula vulgaris L. subsp. macroceras (Link) Calder et Taylor
    = Pinguicula macroceras Link
Pinguicula vulgaris L. subsp. nevadensis Lindberg
    = Pinguicula nevadensis (Lindberg) Casper
Pinguicula vulgaris L. subsp. vestina Conti et Peruzzi ➔ review needed
Pinguicula vulgaris L. var. albida Behm = Pinguicula vulgaris L.
Pinguicula vulgaris L. var. alpestris Marçais = Pinguicula vulgaris L.
Pinguicula vulgaris L. var. alpicola Chenevard = Pinguicula leptoceras Reichenbach
Pinguicula vulgaris L. var. alpicola Chenevard = Pinguicula vulgaris L.
Pinguicula vulgaris L. var. alpicola Koch = Pinguicula vulgaris L.
Pinguicula vulgaris L. var. alpicola Pontocsek = Pinguicula balcanica Casper
Pinguicula vulgaris L. var. bicolor Blytt = Pinguicula vulgaris L.
Pinguicula vulgaris L. var. bicolor Nordstedt = Pinguicula vulgaris L.
Pinguicula vulgaris L. var. coerulea Briquet = Pinguicula vulgaris L.
Pinguicula vulgaris L. var. corsica Cesati, Passerini et Gibelli
    = Pinguicula corsica Bernard et Gren. ex Gren. et Godr.
Pinguicula vulgaris L. var. floribunda Watanabe et Takeda
    = Pinguicula macroceras Link

Pinguicula vulgaris L. var. gaveana Beauverd = Pinguicula vulgaris L.
Pinguicula vulgaris L. var. genuina Schinz et Keller = Pinguicula vulgaris L.
Pinguicula vulgaris L. var. grandiflora Baroni = Pinguicula leptoceras Reichenbach
Pinguicula vulgaris L. var. grandiflora Baroni = Pinguicula reichenbachiana Schindler
Pinguicula vulgaris L. var. grandiflora Bentham et Hooker
= Pinguicula grandiflora Lam.
Pinguicula vulgaris L. var. grandiflora Cosson et Germain = Pinguicula vulgaris L.
Pinguicula vulgaris L. var. grandiflora Fiori et Paoletti
= Pinguicula reichenbachiana Schindler
Pinguicula vulgaris L. var. grandiflora Hausmann = Pinguicula leptoceras Reichenbach
Pinguicula vulgaris L. var. grandiflora Koch = Pinguicula leptoceras Reichenbach
Pinguicula vulgaris L. var. gypsophila Bouvier = Pinguicula leptoceras Reichenbach
Pinguicula vulgaris L. var. gypsophila Fuss = Pinguicula vulgaris L.
Pinguicula vulgaris L. var. gypsophila Rchb. = Pinguicula vulgaris L.
Pinguicula vulgaris L. var. hirtiflora Cesati, Passerini et Gibelli
= Pinguicula hirtiflora Tenore
Pinguicula vulgaris L. var. leptoceras Baroni = Pinguicula reichenbachiana Schindler
Pinguicula vulgaris L. var. leptoceras Cesati, Passerini et Gibelli
= Pinguicula corsica Bernard et Gren. ex Gren. et Godr.
Pinguicula vulgaris L. var. leptoceras Cesati, Passerini et Gibelli
= Pinguicula leptoceras Reichenbach
Pinguicula vulgaris L. var. leptoceras Cesati, Passerini et Gibelli
= Pinguicula reichenbachiana Schindler
Pinguicula vulgaris L. var. leptoceras Chenevard
= Pinguicula leptoceras Reichenbach
Pinguicula vulgaris L. var. leptoceras Sampaio = Pinguicula vulgaris L.
Pinguicula vulgaris L. var. leptoceras Stojanov et Stefanov
= Pinguicula balcanica Casper
Pinguicula vulgaris L. var. longifolia Arcangeli = Pinguicula reichenbachiana Schindler
Pinguicula vulgaris L. var. longifolia Hausmann = Pinguicula leptoceras Reichenbach
Pinguicula vulgaris L. var. longifolia Koch = Pinguicula leptoceras Reichenbach
Pinguicula vulgaris L. var. longifolia Rapin = Pinguicula leptoceras Reichenbach
Pinguicula vulgaris L. var. macrantha Lamotte = Pinguicula vulgaris L.
Pinguicula vulgaris L. var. macroceras (Link) Herder = Pinguicula macroceras Link
Pinguicula vulgaris L. var. minor Koch = Pinguicula vulgaris L.
Pinguicula vulgaris L. var. minor Mayer = Pinguicula vulgaris L.

Pinguicula vulgaris L. var. obtusa Sommerfelt = Pinguicula vulgaris L.
Pinguicula vulgaris L. var. obtusata Nordstedt = Pinguicula vulgaris L.
Pinguicula vulgaris L. var. pallida Lange = Pinguicula vulgaris L.
Pinguicula vulgaris L. var. pratensis Koch = Pinguicula vulgaris L.
Pinguicula vulgaris L. var. pratensis Willkomm = Pinguicula vulgaris L.
Pinguicula vulgaris L. var. pusilla Bertoloni
= Pinguicula corsica Bernard et Gren. ex Gren. et Godr.
Pinguicula vulgaris L. var. reichenbachiana Fiori
= Pinguicula reichenbachiana Schindler
Pinguicula vulgaris L. var. sixtina Briquet = Pinguicula vulgaris L.
Pinguicula vulgaris L. var. tenuior Fries = Pinguicula vulgaris L.
Pinguicula vulgaris L. var. tenuior Wahlenberg = Pinguicula vulgaris L.
Pinguicula vulgaris L. var. transsilvanica Krajina = Pinguicula vulgaris L.
Pinguicula vulgaris L. var. uliginosa Genty = Pinguicula vulgaris L.
Pinguicula vulgaris L. f. albida (Behm) Neumann = Pinguicula vulgaris L.
Pinguicula vulgaris L. f. albiflora Komiya = Pinguicula macroceras Link
Pinguicula vulgaris L. f. bicolor (Nordstedt ex Fries) Neumann = Pinguicula vulgaris L.
Pinguicula vulgaris L. f. coerulescens Eklund = Pinguicula vulgaris L.
Pinguicula vulgaris L. f. grandiflora St. Lager = Pinguicula grandiflora Lam.
Pinguicula vulgaris L. f. semiflava Neumann = Pinguicula vulgaris L.
Pinguicula vulgaris Maulny = Pinguicula lusitanica L.
Pinguicula vulgaris Mutel = Pinguicula corsica Bernard et Gren. ex Gren. et Godr.
Pinguicula vulgaris Nyman = Pinguicula leptoceras Reichenbach
Pinguicula vulgaris Nyman = Pinguicula nevadensis (Lindberg) Casper
Pinguicula vulgaris Parlatore = Pinguicula reichenbachiana Schindler
Pinguicula vulgaris Petangna = Pinguicula hirtiflora Tenore
Pinguicula vulgaris Sessé et Mociño = Pinguicula oblongiloba DC.
Pinguicula zecheri Speta et Fuchs

APPENDIX IV

List of vernacular names

There could be two or more vernacular names for one species within a country, or the same vernacular name may be applied for two or more species. Some names may be used only in a very small region or specific references. It is also possible that some names may not be used anymore. The names have been collected from various sources and were inquired to local botanists.

Genus/species	Country, Region	Vernacular name
Pinguicula L.	Albania	Pinguikulë
	Austria	Fettkraut
	Bulgaria	Петлюга (Petluga)
	Canada (English)	Butterwort
	Canada (French)	Grassette
	China	捕虫堇 (Bu chong jin)
	Croatia	Masnica
	Croatia	Tustica
	Czech Republic	Tučnice
	Denmark	Vibefedt
	Estonia	Võipätakas
	France	Grassette
	Finland	Yökönlehdet
	Germany	Fettkraut
	Ireland (English)	Butterwort
	Ireland (Gaelic)	Leith uisce
	Italy	Pinguicola
	Japan	ムシトリスミレ (Mushitori-sumire)
	Norway	Tettegras
	Romania	Foaie grasă
	Russia	Жирянка (Zhirjanka, Zhiryanka)
	Slovakia	Tučnica
	Spain	Atrapamoscas
	Spain	Flor de fuentes
	Spain	Grasilla
	Spain	Violeta de agua
	Spain (Catalan)	Pingüícula
	Spain (Catalan)	Viola d'aigua
	Sweden	Tätörter

Pinguicula L.	Switzerland	Fettkraut
	UK	Butterwort
	USA	Butterwort
	Hungary	Hízóka
P. alpina	Austria	Alpen-Fettkraut
	China	高山捕虫堇（Gao shan bu chong jin)
	Croatia	Alpska tustica
	Croatia	Planinska tustica
	Croatia	Žutkasta tustica
	Estonia	Alpi võipätakas
	Finland	Valkoyökönlehti
	France	Grassette des alpes
	Germany	Alpen-Fettkraut
	Hungary	Havasi hízóka
	Italy	Pinguicola bianca
	Norway	Fjelltettegras
	Russia	Жирянка альпийкая (Zhirjanka al'pijskaya)
	Slovakia	Tučnica alpínska
	Spain	Atrapamoscas
	Spain	Grasilla
	Spain	Tiraña alpina
	Spain (Catalan)	Tiranya alpina
	Sweden	Fjälltätört
	Switzerland	Alpen-Fettkraut
	UK	Alpine butterwort
P. antarctica	Chile	Flor del pantano
		Grasilla
P. balcanica	Bulgaria	Петлюга (Petluga)
P. bohemica	Czech Republic	Tučnice česká
P. caelurea	USA	Blueflower butterwort
P. chilensis	Chile	Violeta cimarrona
		Violetilla del pantano
P. corsica	France (French)	Grassette de Corse
P. dertosensis	Spain (Catalan)	Grasilla
	Spain (Catalan)	Violeta de font
P. filifolia	Cuba	Grasilla

P. grandiflora	France	Grassette à grandes fleurs
	Ireland (English)	Bog violet
	Ireland (Gaelic)	Leith uisce
	Spain	Biola d'aigua
	Spain	Flor de las fuentes
	Spain	Atrapamoscas
	Spain	Grasilla
	Spain	Grasilla de flor grande
	Spain	Pedorrera
	Spain	Tiraña
	Spain	Tirigaña
	Spain	Violeta de agua
	Spain (Basque)	Ametz-bedarr
	Spain (Basque)	Mokobedarr
	Spain (Basque)	Muki-belar
	Spain (Basque)	Muki-belarra
	Spain (Catalan)	Herba de tall
	Spain (Catalan)	Pingüícula de flor gran
	Spain (Catalan)	Pingüícula grandiflora
	Spain (Catalan)	Tiranya
	Spain (Catalan)	Viola d'aigua de fulla gran
	Switzerland	Großblütiges Fettkraut
	UK	Great butterwort
	UK	Large-flowered butterwort
P. ionantha	USA	Godfrey's butterwort
	USA	Panhandle butterwort
	USA	Violet butterwort
P. leptoceras	Austria	Dünnsporn-Fettkraut
	Austria	Großblütiges Fettkraut
	France	Grassette à éperon étroit
	France	Grassette à éperon grêle
	Italy	Pinguicola grandiflora
	Switzerland	Dünnsporniges Fettkraut
P. longifolia	France	Grassette à longues feuilles
	Spain	Atrapamoscas
	Spain	Grasilla

P. longifolia	Spain	Grasilla de hoja larga
	Spain (Catalan)	Pingüícula longifòlia
P. lusitanica	France	Grassette du Portugal
	Ireland (English)	Pale butterwort
	Ireland (Gaelic)	Leith uisce beag
	Spain	Grasilla pálida
	Spain (Gallego)	Pinguícula
	UK	Pale butterwort
P. lutea	USA	Yellow butterwort
	USA	Yellow-flowered butterwort
P. macroceras	Japan	ムシトリスミレ (Mushitori-sumire)
P. macroceras	USA	California butterwort
P. planifolia	USA	Chapman's butterwort
	USA	Swamp Butterwort
P. primuliflora	USA	Primrose-flowered butterwort
	USA	Southern butterwort
P. pumila	USA	Dwarf butterwort
	USA	Small butterwort
P. ramosa	Japan	コウシンソウ (Kōshin-sō)
P. vallisneriifolia	Spain	Atrapamoscas
	Spain	Grasilla
	Spain	Grasilla de Andalucía
	Spain	Tiraña
P. variegata	Japan	マルバムシトリスミレ (Maruba-mushitori-sumire)
P. villosa	China	北捕虫堇 (Bei bu chong jin)
	Finland	Karvayökönlehti
	Japan	カラフトムシトリスミレ (Karafuto-mushitori-sumire)
	Norway	Dvergtettegras
	Sweden	Dvärgtätört
	USA	Hairy butterwort
P. vulgaris	Austria	Gewöhnliches Fettkraut
	Austria	Gewöhnliche-Fettkraut
	Croatia	Ljubičasta tustica
	Croatia	Masnica

P. vulgaris	Croatia	Obična tustika
	Croatia	Tučnica
	Croatia	Tustica kukcolovka
	Czech Republic	Tučnice obecná
	Denmark	Vibefedt
	Estonia	Harilik võipätakas
	Finland	Siniyökönlehti
	France	Grassette commune
	Germany	Echtes Fettkraut
	Hungary	Lápi hízóka
	Hungary	Közönséges hízóka
	Ireland (English)	Common butterwort
	Ireland (Gaelic)	Bodán meascáin
	Italy	Erba-unta comune
	Italy	Erba-unta dei tagli
	Italy	Pinguicola
	Italy, Brescia	Erba da cai
	Italy, Brescia	Erba da taì
	Italy, Como	Erba da taglio
	Italy, Como	Erba grassa
	Italy, Modena	Erba oliosa
	Italy, Novara	Erba olearia
	Italy, Ponti di Nava	Erba unta
	Italy, Val S. Martino	Erbo de la tailleuiro
	Italy, Valtellina	Erba del taj
	Italy, Verona	Balsemina
	Italy, Verona	Erba del tajo
	Italy, Verona	Lunaria del grasso
	Norway	Tettegras
	Portugal	Grasseta
	Portugal	Pinguicula
	Russia	Жирянка обыкновенная (Zhirjanka obyknovennaya)
	Slovakia	Tučnica obyčajná
	Spain	Atrapamoscas
	Spain	Grasilla

P. vulgaris	Spain	Grassula
	Spain	Hierba del enteco
	Spain	Ropa blanca
	Spain	Tiraña
	Spain	Tirigaña
	Spain	Yerba d'as Furicadas
	Spain (Basque)	Ametz-bedar
	Spain (Basque)	Ametz-bedarra
	Spain (Basque)	Moko-bedar
	Spain (Basque)	Moko-bedarra
	Spain (Catalan)	Pingüícula comuna
	Spain (Catalan)	Pingüícula vulgar
	Spain (Catalan)	Plantatge blanc
	Spain (Catalan)	Viola d'aigua de fulla petita
	Spain (Gallego)	Grasilla
	Spain (Gallego)	Moruja de agua
	Sweden	Tätört
	Switzerland	Gemeines Fettkraut
	UK	Common butterwort
	USA	Butterwort
	USA	Common butterwort
	USA	Northern butterwort