

## Carnivorous Plants: Physiology, ecology, and evolution

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### CHAPTER

## 6 Systematics and evolution of Lentibulariaceae: I. *Pinguicula*

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### Abstract

Systematics and evolution of *Pinguicula* (butterworts) (Lentibulariaceae) are treated. Vegetative and generative morphology of the genus are illustrated and interpreted in the light of available phylogenetic evidence. A new infrageneric classification is proposed for *Pinguicula*; a simplified phylogenetic tree and detailed distribution maps are provided. Evolutionary history and phylobiogeography are briefly discussed together with the habitats, ecology, and conservation of the genus.

**Keywords:** [Adhesive trap](#), [distribution](#), [diversification](#), [infrageneric classification](#), [Lentibulariaceae](#), [morphology](#), [Pinguicula](#), [phylogeny](#)

**Subject:** [Plant Sciences and Forestry](#), [Animal Pathology and Diseases](#)

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### 6.1 Introduction

Lentibulariaceae is a monophyletic family within the Lamiales in the asterid crown-group of eudicots (APG IV 2016), that includes  $\approx 360$  species (Appendix). It is a derived and comparatively young family that originated  $\approx 42$ – $28$  Mya (upper and lower limits of divergence time from molecular clock estimations of Wikström et al. 2001 and Bell et al. 2010, respectively).

The family comprises three carnivorous genera, *Pinguicula*, *Genlisea*, and *Utricularia*. All are hygrophilous herbs; several species of the rootless *Genlisea* (Chapter 7) and *Utricularia* (Chapter 8) are hydrophytes that grow as submerged, affixed water plants (“rhizophytic aquatics”) or as aquatics freely floating underneath the water surface (“mesopleustophytes”).

## 6.2 Life history and morphology

*Pinguicula* comprises ≈96 currently recognized species (Roccia et al. 2016, Rivadavia et al. 2017; Appendix). All are rosette-forming, herbaceous carnivorous plants, with typical lamiales, bilabiate, tubular flowers (Figure 6.1). Although the general morphology is fundamentally similar in all species, the species display a wide range of life-history strategies, leaf shapes, and corolla morphologies that have evolved in adaptation to different habitats and perhaps also to varying types of prey.

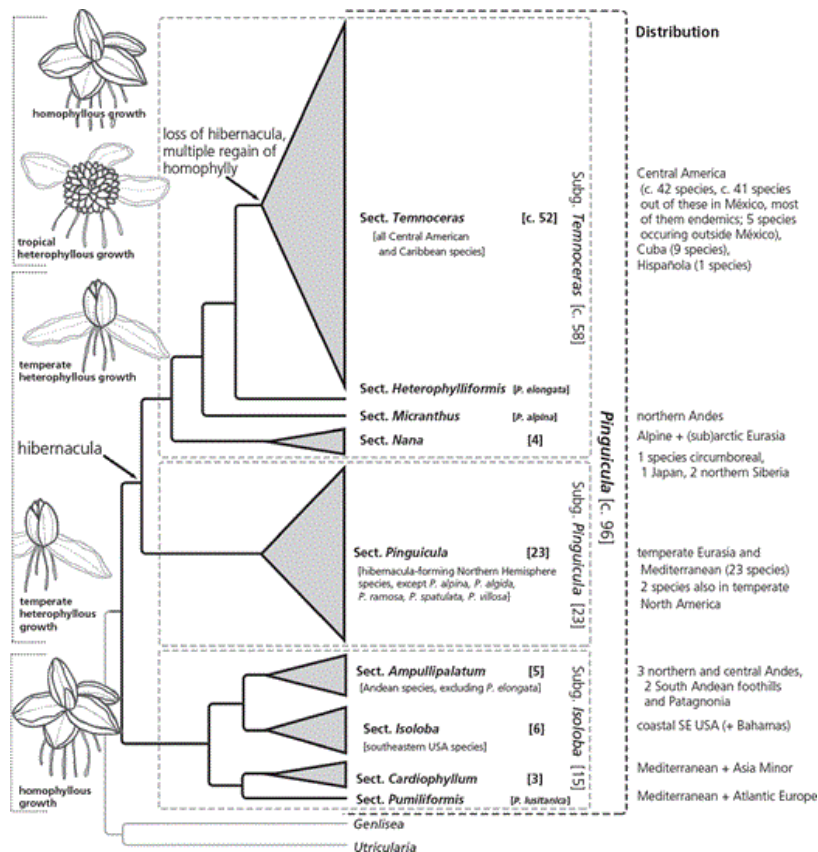


**Plate 6.** (Figure 6.1 on page 71). Morphological diversity and growth types of *Pinguicula*. A lithophytic habit with strap-shaped leaves has evolved in parallel in all three subgenera: (a) *P. megaspilaea* (*P. subg. Isoloba*); (b) *P. mundi* (*P. subg. Pinguicula*); (c) *P. calderoniae* (*P. subg. Temnoceras*). Those three species flower from the carnivorous rosettes. In contrast, (d) flowering from the noncarnivorous winter rosettes in *P. rotundiflora* (frequent in Mexican members of *P. subg. Temnoceras*); (e) sprouting hibernaculum of *P. grandiflora* (*P. subg. Pinguicula*). (f) *P. alpina* with hibernaculum formed in the center of a rosette of carnivorous leaves. (g) The (facultative) therophyte *P. lusitanica* has small leaves with strongly involute margins. (h) In most species, such as this *P. jarmilae*, the leaf margins are motile, enrolling over caught prey. (i) Species with thread-like leaves and revolute margins, such as this *P. heterophylla*, cannot move.

Photographs (b, e) by Aymeric Roccia, (c) by Fernando Rivadavia, and remaining photos by Andreas Fleischmann.

6.2.1 Life-history strategies

Most species are perennials; <10% (10 species) are either facultative or obligate annuals. Two of these are in the phylogenetically early-branching *Pinguicula* subg. *Isoloba* (*P. pumila* in the North American *P.* sect. *Isoloba* and *P. lusitanica*, the sole member of the Mediterranean-Atlantic *P.* sect. *Pumiliformis*; Figure 6.2 and §6.3). The others are Neotropical species in the derived *P.* sect. *Temnoceras* (Casper 1966, Domínguez et al. 2014, Lampard et al. 2016).



**Figure 6.2** Simplified phylogeny of the genus *Pinguicula*, based on plastid DNA data (Beck et al. 2008, Fleischmann 2011b).

Illustration by Andreas Fleischmann.

The perennials include “homophyllous” plants that produce only carnivorous leaves throughout the year and “heterophyllous” (*sensu* Rocchia et al. 2016) hemicryptophytes and cryptophytes that produce both carnivorous and noncarnivorous leaves during a single growth cycle (Figure 6.2). The heterophyllous species produce carnivorous leaves only when growing actively and survive a dry or cold period either as hibernacula (condensed resting buds formed from scale-like leaves: “temperate heterophyllous growth type” in all members of *P.* sects. *Pinguicula*, *Nana*, *Micranthus*, and *Heterophylliformis*; Figures 6.1, 6.2), or as open, compact rosettes or subterranean bulbs formed of more or less succulent, noncarnivorous leaves, usually with greatly reduced lamina (“tropical heterophyllous growth type” in the Central American and Caribbean *P.* sect. *Temnoceras*). Within that section, intermediate forms between the noncarnivorous “winter rosettes” and bulb-like rosettes, and several reversals to homophyllous growth also have occurred (Cieslak et al. 2005, Kondo and Shimai 2006; Figure 6.2).

## 6.2.2 Leaves

The leaves of *Pinguicula* are entire, more or less succulent to membranous, usually inconspicuously petiolate to sessile; the lamina is of various shape, most frequently broadly oblanceolate to ovate (usually when the leaves are appressed to the ground), or oblong, narrowly oblanceolate to linear or filiform, in which case they usually are held upright or hang down when the plant is growing on vertical habitats. The upper surface of the lamina of all species is lined densely with two types of non-vascularized, carnivorous glands (stalked and sessile; Chapters 13, 14); in few species (e.g., *P. gigantea*, *P. longifolia*) the lower leaf surface also is glandular. The leaf margins generally are slightly or conspicuously involute (the latter usually in species with leaves flat on the ground), but a few species have either flattened or revolute leaf margins (the latter being those species with upright or hanging leaves). In most species, the leaf margins enfold over captured prey (Figure 6.1; Chapter 14), but in species with filiform, upright leaves or species with flattened leaf margins (e.g., *P. agnata*, *P. gigantea*), the leaves are immobile.

p. 72 The carnivorous leaves of both homophyllous and heterophyllous species can be either uniform in shape throughout (“isophyllous”) or vary distinctively in size and shape during the growing season (“anisophyllous”). Examples of the latter include the flat rosetted and long strap-shaped leaves produced by homophyllous *P. megaspilaea* <sup>1</sup> and by heterophyllous *P. vallisneriifolia*. Casper (1966) used the term “temperate-heterophyllous” for the former growth type, although it is not a case of true heterophylly. Rather, it is a heterophyllous species in terms of carnivorous and noncarnivorous foliage. It also produces anisophyllous carnivorous leaves.

## 6.2.3 Inflorescences and flowers

p. 73 A solitary scape arises from the rosette among either the carnivorous leaves during active growth or the noncarnivorous leaves during dormancy. In *P. alpina* and the three members of *P. sect. Nana*, the flower buds develop in the dormant hibernacula at <sup>1</sup> the end of the previous growing season (the autumn in advance of flowering); the inflorescence emerges early in the season together with the newly formed leaves. In contrast, flower bud initiation in *P. sect. Pinguicula* takes place in the same year of vegetative growth (Degtjareva and Sokoloff 2012).

The underlying basic inflorescence type of *Pinguicula* is a few-flowered, sessile, frondulose terminal umbel (sometimes reduced to a solitary flower; Degtjareva and Sokoloff 2012) with inconspicuous, small scale-like, flower-subtending bracts hidden at the base of the foliar leaves (technically, therefore, the scapes of the flowers, often referred to as “peduncles” are actually pedicels). Shoot growth always terminates with an inflorescence, and new vegetative shoot growth resumes from a dormant lateral bud in the axil of the ultimate foliar leaf below the umbel (Degtjareva and Sokoloff 2012). Because of the compact rosette habit of *Pinguicula* (densely condensed shoots lacking any obvious internodes), the terminal inflorescence nature with resumed lateral growth is rarely obvious.

Flowers in all but two species are solitary on their scapes; the closely-related *P. algida* and *P. ramosa* (*P. sect. Nana*) normally have apically bifurcate scapes supporting two (or rarely more) flowers (Casper 1966). The flowers themselves are hermaphroditic, pentamerous, and tetracyclic. They are zygomorphic, with a sympetalous, tubular corolla typical of the Lamiales, including a nectariferous spur. The five sepals are basally adnate and form either a bilabiate (three sepals forming the upper, and two the lower, lip) or spreading calyx, which is persistent in fruit. The five petals are fused to a bilabiate, spurred, throat-like corolla: two petal lobes form the upper lip and three form the lower lip. The corolla shape is either distinctly zygomorphic with the lower lip spreading widely from the upper lip (flowers typically held vertically) or nearly isolobous and radial (flowers frequently facing sky). Corolla color and overall size, size and shape of its tube, shape and hair cover of the palate, patterns of nectar guides, and shape and length of the nectar

p. 74 spur vary widely between species, and  $\hookleftarrow$  appear to reflect adaptation to different pollinators (Fleischmann 2016b) rather than taxonomic affinity. Early classifications relied on corolla morphology (e.g., Casper 1996), but it has proven rather unreliable for infrageneric classification because of the large overlap of floral characters and parallel evolution of corolla design in distantly related groups (Cieslak et al. 2005, Beck et al. 2008).

In all three genera of Lentibulariaceae, the androecium is reduced to two anterior stamens, each with bithecate anthers and curved, dilatated filaments that clasp the superior ovary. The thecae are located on the infertile rear surface of the bilabiate stigma, and thus cannot touch with its receptive surface (“herkogamy,” which mechanically avoids self-pollination). However, some annual and small-flowered perennial *Pinguicula* species facultatively self-pollinate at the end of anthesis by growth of the filaments or style, so that the thecae touch the stigma (Chapter 22). The subglobose ovary has central placentation and its short bilabiate style is persistent in fruit. The fruit is a dry capsule with bivalvate dehiscence (Casper 1966). The small seed (0.4–1.0 mm long) is ellipsoidal to fusiform with a micropylar appendage and a reticulate testa in most species (Degtjareva et al. 2004); false vivipary can be observed in the two epiphytic Caribbean species, *P. lignicola* and *P. casabitoana* (Lampard et al. 2016). Cotyledon number of the embryo and seedling varies between species from two to one (by reduction of the second cotyledon), but this does not correlate either with taxonomic affinity or habitat (Haccius and Hartle-Baude 1957, Degtjareva et al. 2004).

#### 6.2.4 Chromosome numbers

Chromosome numbers range from  $2n = 16$  to  $2n = 128$ ; species are diploids ( $2n$ ), tetraploids ( $4n$ ), octoploids ( $8n$ ), and hexadecaploids ( $16n$ ), based on estimated chromosome base numbers of  $x = 6, 8, 9, 11$ , and  $14$  (Casper and Stimpert 2006, 2009). Chromosome numbers do not correspond to phylogenetic clades and they are rather unusable characters for infrageneric classification (§6.3). Different ploidy levels and “base numbers” *sensu* Casper and Stimpert (2009) occur within each major clade, possibly indicating reticulate evolution. In contrast to the ultra-small genomes (<100 Mbp) reported for some *Genlisea* and *Utricularia* species (Chapters 7, 8), the genomes of their common sister *Pinguicula* are of medium-size (Greilhuber et al. 2006, Veleba et al. 2014).

#### 6.2.5 Clonal growth

Vegetative propagation (clonal growth) occurs in some species. For example, *P. primuliflora* (*P.* sect. *Isoloba*) frequently forms adventitious plantlets from the tips of its leaves. Many species produce new plantlets from the base of the leaf petiole (especially in hibernacula of *P.* subg. *Pinguicula*; Heslop-Harrison 1962) or the lamina surface of dissected leaves (e.g. the succulent noncarnivorous leaves of most Mexican species, some of which easily detach from the mother rosette). Other species multiply by division from the center of the growing rosette. Adventitious plantlets formed at the tips of stolon runners have been reported for the European *P. vallisneriifolia* and *P. longifolia* (*P.* sect. *Pinguicula*; Casper 1966, Rocca et al. 2016), the Andean *P. jarmilae* and *P. calyptrata* (*P.* sect. *Ampullipalatum*; Fleischmann 2011b, Lampard et al. 2016), and the Mexican *P. stolonifera* and *P. gigantea* (*P.* sect. *Temnoceras*; Fleischmann 2011b, Lampard et al. 2016). These species all are matt-forming lithophytes that grow on vertical cliffs or exposed rock. However, many other lithophytic species do not form runners; this mode of clonal growth has evolved several times in the genus and appears to be unrelated to habitat preferences (Fleischmann 2011b).



## 6.3 Phylogeny and taxonomy

### 6.3.1 Phylogeography

The genus is assumed to have originated in temperate Eurasia, followed by an Early Tertiary migration to North America (the “boreotropics” hypothesis; Jobson et al. 2003). During the evolutionary history of the genus, at least five radiations in distinct geographical regions have happened, leading to the present-day diversity of *Pinguicula* (Cieslak et al. 2005). Incongruences have been found between plastid and nuclear marker datasets. However, both show the Eurasian Alpine *P. alpina* as sister to a Central American clade (Cieslak et al. 2005, Degtjareva et al. 2006, Kondo and Shimai 2006). Both datasets further revealed the boreal-subarctic *P. villosa* as sister to *P. ramosa* + *P. spathulata* (as *P. variegata*), but not assigned closely to *P. sect. Pinguicula*, where it was placed by Casper (1966). All show *P. sects. Cardiophyllum* and *Isoloba* as monophyletic, early-branching, and closely related to *P. lusitanica*, whose phylogenetic position differs between nuclear and plastid datasets.

It is reasonable to assume that early-branching *P. subg. Isoloba* is phylogenetically old among *Pinguicula*, judging from its long branch lengths (substitutions) and odd biogeography (Cieslak et al. 2005, Beck et al. 2008). This subgenus comprises a Mediterranean clade (*P. lusitanica* and *P. sect. Cardiophyllum*) as immediate sister to a New World clade (*P. sects. Isoloba* and *Ampullipalatum*).

Hibernacula are found in all members of the grade comprising *P. sects. Pinguicula*, *Nana*, *Micranthus*, and *Heterophylliformis* (Figure 6.2), implying that hibernacula evolved only once in the genus. They apparently were lost (or evolved into bulb-like organs or succulent winter rosettes) in *P. sect. Temnoceras* as it adapted to warmer, seasonally dry climates in Central America. In contrast, homophyllous growth is not a monophyletic trait in the genus, but rather is an apomorphy of *P. subg. Isoloba* (hence could be considered a plesiomorphic state), and evolved again in *P. subg. Temnoceras sect. Temnoceras* (Figure 6.2). In *P. sect. Temnoceras*, homophylly most likely evolved several times, either as an adaptation to stable environmental conditions—e.g., in *P. emarginata* from México and several Cuban species that grow in permanently wet habitats—or connected to annual life strategy.

The hibernacula-forming species are basal to the most diverse and species-rich clade of the genus, *P. sect. Temnoceras* (equivalent to the “Mexican–Central American–Caribbean clade” of Cieslak et al. 2005; Figure 6.2). This lineage seems to have diversified in concert with the biogeography of the region: the rich mosaic of closely co-occurring, heterogeneous topographies and climatic conditions in the Mexican Highlands have been considered the major factors driving speciation there (Zamudio 2001, 2005, Cieslak et al. 2005). This would represent a case of geographic/climatic radiation *sensu* Simões et al. (2016), and phylogeographic analyses of the Trans–Mexican Volcanic Belt showed that the climatic and geological changes associated with the volcanic transformation of the Mexican Highlands during the Pleistocene led to the present topography and climate. These were followed by rich allopatric and parapatric speciation of montane plants that are significantly associated with the rich plant biodiversity in that region (Myers et al. 2000, Mastretta–Yanes et al. 2015). Unfortunately, phylogenetic relationships within the species-rich, monophyletic *P. sect. Temnoceras* are not yet fully resolved, but it is clear that the taxonomic subgroups of earlier authors (e.g., Casper 1966) are largely para- or polyphyletic (Cieslak et al. 2005, Shimai and Kondo 2007). Reticulate evolution and hybrid speciation seem to account for part of the species richness in Europe and México (Cieslak et al. 2005, Degtjareva et al. 2006, Kondo and Shimai 2006), and most of the European populations are likely to be of post-glacial origin, reflected in polyploid complexes, hybrid swarms, and ongoing speciation (Casper 1966, Casper and Stimpert 2006, 2009, De Castro et al. 2016, Rocca et al. 2016).

### 6.3.2 Infrageneric classification

The following changes to the infrageneric classification of Casper (1966) are proposed to achieve monophyly of all groups. We consider the three major clades evident from phylogenetic reconstructions (Cieslak et al. 2005, Degtjareva et al. 2006, Beck et al. 2008) to be subgenera; species concepts (Appendix) follow Roccia et al. (2016).

*Pinguicula* subg. *Isoloba* Barnhart, Mem. N.Y. Bot. Gard. 6: 47 (1916), emend. Casper, Bot. Jb. 82: 329 (1963). Type: *Pinguicula pumila* Michx.

It is redefined here to include:

- (1) *P. sect. Isoloba* Casper, Bot. Jb. 82: 330 (1963). Casper's (1966) *P. subsection Pumiliformis* is excluded to become a distinct section.
- (2) *P. sect. Cardiophyllum* Casper, Feddes Repert. spec. nov. 66: 34 (1962).
- (3) *P. sect. Pumiliformis* (Casper) Roccia & A. Fleischm. stat. nov. Basionym: *P. subsect. Pumiliformis* Casper, Bibliotheca Botanica 127/128: 71 (1966). Type: *P. lusitanica* L.
- (4) *P. sect. Ampullipalatum* Casper, Bot. Jb. 82: 334 (1963).

p. 76 This section is moved from *P. subg. Temnoceras sensu* Casper (1966). *Pinguicula elongata* now is excluded from this section, which was polyphyletic in the circumscription of Casper (1966). This species was revealed in phylogenetic reconstructions (Beck et al. 2008) as sister to the Central American species here classified as *P. sect. Temnoceras* in *P. subg. Temnoceras*.

*Pinguicula* sects. *Heterophyllum*, *Agnata*, and *Discoradix* are excluded from *P. subg. Isoloba* because they fall within a single major clade in phylogenetic reconstructions (Cieslak et al. 2005, Shimai and Kondo 2007, Shimai et al. 2007) that does not include the subgeneric type *P. pumila* nor any other *Isoloba*-members *sensu* Rafinesque (1836). This clade, here circumscribed as *P. section Temnoceras*, comprises all Central American and Caribbean taxa formerly assigned to *P. subg. Isoloba*.

*Pinguicula* subg. *Pinguicula* L. Type: *P. vulgaris* L.

In its new circumscription as a monophyletic entity it comprises only a single section:

- (5) *P. section Pinguicula* as circumscribed by Casper (1966), but excluding his *P. sect. Nana*. *Pinguicula* sects. *Crassifolia*, *Homophyllum*, *Longitubus*, *Orcheosanthus*, *Orchidioides*, previously assigned to *P. subg. Pinguicula* (Casper 1966), now are moved to *P. subg. Temnoceras*.

*Pinguicula* subg. *Temnoceras* Barnhart, Mem. N.Y. Bot. Gard. 6: 47 (1916), emend. Casper, Bibliotheca Botanica 127/128: 109 (1966). Type: *P. crenatiloba* DC.

Ironically, Barnhart's (1916) *P. subg. Temnoceras* initially comprised only *P. crenatiloba*, which displays a somewhat unusual corolla morphology, but now comprises the majority of species in the genus. De Candolle (1844) was the first to group all Central American species together (in *P. sect. Orcheosanthus*), but Barnhart's *P. subg. Temnoceras* has nomenclatural priority on subgenus rank. This subgenus includes:

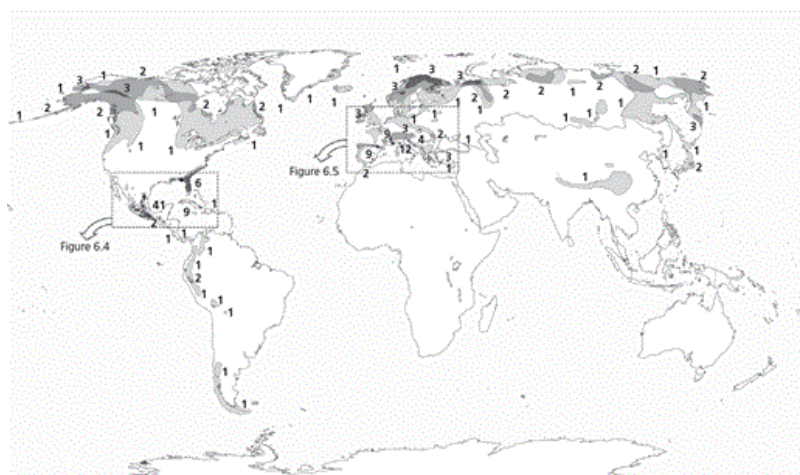
- (6) *P. sect. Temnoceras* Casper, Bot. Jb. 82: 333 (1963). (incl. *P. sects. Heterophyllum*, *Agnata*, *Discoradix*, *Homophyllum*, *Orcheosanthus*, *Crassifolia*, *Longitubus*, and *Orchidioides*).
- (7) *P. sect. Micranthus* Casper, Feddes Repert. 66: 45 (1962).
- (8) *P. sect. Nana* Casper, Feddes Repert. 66: 41 (1962).

- (9) *P. sect. Heterophylliformis* (Casper) A. Fleischm. & Rocchia stat. nov. Basionym: *P. subsection Heterophylliformis* Casper, *Bibliotheca Botanica* 127/128: 113 (1966). Type: *P. elongata* Benj.

## 6.4 Distribution

### 6.4.1 Global patterns of diversity

*Pinguicula* species grow on all continents except Australia and sub-Saharan Africa (Figure 6.3), although its occurrence in Africa is limited to only two species in a few scattered locations on the Mediterranean northern coast and in the Rif Mountains. The global range in Eurasia and the Americas is not evenly distributed (Figure 6.3), and the hygrophilous, monticolous genus *Pinguicula* is widely absent from large lowland areas (such as rainforests, savannas, grassland, and deserts). *Pinguicula* species have colonized a large variety of habitats, ranging from subarctic Greenland, Scandinavia, and northern Siberia in the Northern Hemisphere, the southernmost tip of the South American continent and Tierra del Fuego in South America, and in subtropical Central America and tropical Cuba. They grow from sea-level to mountainous regions up to 4200 m a.s.l. (*P. alpina* in the Himalayas and *P. calyptrata* in the Andes; Casper 1966). Some species grow in bogs, fens, marls, and swamps; others in grassy seepages; and still others on shallow soils, on wet, dripping walls or in crevices of bare or moss-covered rocks; and last (two species in the Caribbean), epiphytically on tree trunks or branches. The only common feature among these habitats is the presence of moist to wet soils (or wet air in the case of epiphytic species or the Japanese *P. ramosa*) during active growth phases. Soil and water acidity levels, and mineral contents, vary enormously among these habitats (Heslop-Harrison 2004). Adaptation to new habitats (and therefore to new geographic zones) appears to be one of the major forces driving evolution and diversification of *Pinguicula* (Cieslak et al. 2005, Zamudio 2005, Degtjareva et al. 2006, Shimai et al. 2007).



**Figure 6.3** Global distribution of *Pinguicula*, with species numbers indicated for a country or region (data from Meusel et al. 1965, Casper 1966, Zamudio 2001, Heslop-Harrison 2004, Fleischmann 2011b, 2015b, and additional information retrieved from herbarium records).

Map drawn by Andreas Fleischmann.

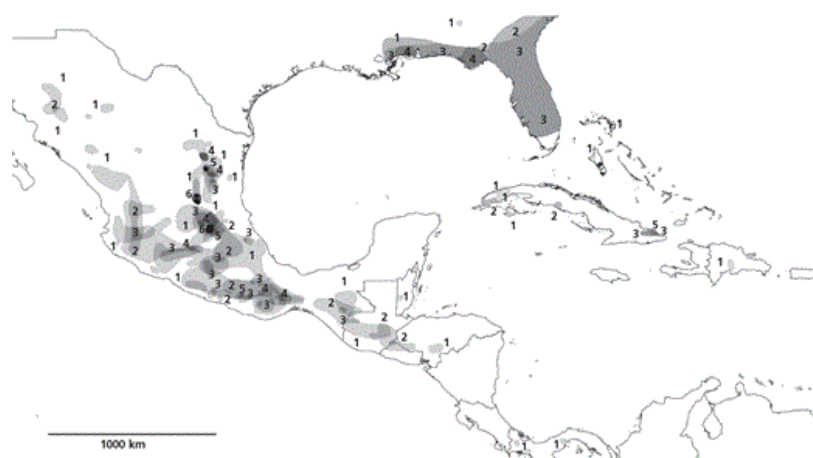
p. 77 Unlike most other carnivorous plant genera, the majority of *Pinguicula* species are calcicoles, and usually grow on alkaline substrates. Most European *Pinguicula* species grow on wet limestone outcrops, tufa dripping walls, humid pockets of soil on limestone cliffs, calcareous meadows, and along rivulets in alkaline wetlands. *Pinguicula grandiflora*, *P. alpina*, and *P. vulgaris* display wider edaphic tolerances, also



growing on decalcified substrate in limestone mountain ranges, on parapeaty soils under pine trees, on basaltic cliffs, along rivulets in heathlands, on bare peat, and among *Sphagnum* mosses in peat bogs. Only a handful of species are calcifuges that grow strictly to acidic substrates: *P. lusitanica*, *P. macroceras*, *P. nevadensis*, *P. ramosa*, *P. villosa*, *P. spathulata*, the six southeast USA species, several of the Cuban species from quarzitic sands or serpentine soils, and five of the six Andean species (the notable exception is *P. involuta*, which also can grow on limestone-based soils; Casper 1966). Some species are found occasionally or almost exclusively on serpentine rock, e.g., *P. balcanica*, *P. crystallina*, *P. christinae*, *P. cubensis*, *P. lusitanica*, *P. hirtiflora*, *P. macroceras*, and *P. megaspilaea*.

## 6.4.2 México: the center of diversity

The main center of *Pinguicula* biodiversity is in México, which has  $\approx 40$  species (equaling 38% of the total generic diversity), 37 (90%) of which are endemics, some of which are microendemics confined only to a single valley or mountain top (Zamudio 2001, 2005, Lampard et al. 2016, Rivadavia et al. 2017). Most Mexican species are confined to seasonally semiarid to arid climate of colline to montane altitudes, where they occur among xerophytic vegetation on exposed rock or in open, dry deciduous forests (Zamudio 2005). *Pinguicula* grow in all the Mexican mountain ranges (Figure 6.4), with the highest diversity being in the Sierra Madre Oriental (25 species, 22 endemics; Zamudio 2005, Lampard et al. 2016) and the Sierra Madre del Sur (15 species, ten endemics). Both mountain ranges are least seasonally arid, have bedrock ranging from limestone and gypsum to shale, granites, and basalts and a well-structured geological relief, all of which create many distinct habitats and abiotic factors favorable for *Pinguicula* (Zamudio 2001, 2005, Rivadavia et al. 2017).



**Figure 6.4** Distribution and number of species of *Pinguicula* in Central America, the Caribbean, and southeast USA (data from Casper 1966, Zamudio 2001, 2005, and additional information retrieved from herbarium records and *unpublished data* of Fernando Rivadavia).

Map drawn by Andreas Fleischmann.

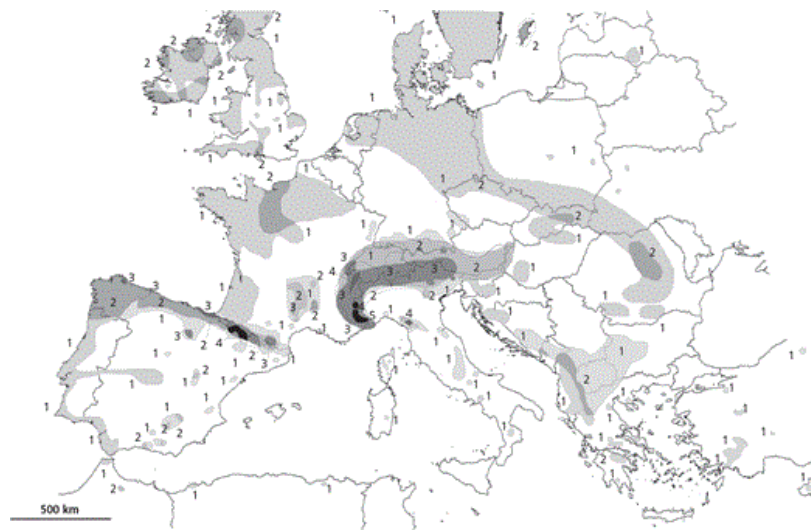
p. 78 The widespread and polymorphic *P. moranensis* tolerates almost any kind of substrate, including basalt (Zamudio 2001, 2005). Several Mexican *Pinguicula* species are found growing on decalcified soils in oak and pine forests, including the microendemics *P. moctezumae*, *P. elizabethiae*, *P. emarginata*, and *P. gigantea*. Seasonally wet ravines formed in the otherwise dry gypsum hills host the microendemics *P. gypsicola*, *P. takakii*, *P. colimensis*, *P. rotundiflora*, *P. pygmaea*, *P. nivalis*, and *P. immaculata*. The hemiepiphytes *P. hemiepiphytica* and *P. mesophytica* usually grow on moss-covered tree trunks.

### 6.4.3 Diversity of other regions

At least nine species grow on Cuba (Domínguez et al. 2014; Lampard et al. 2016), with substantial variation between its eastern and western sides. On the west side, the endemic annual *P. filifolia* grows in white quartz sand in damp open areas at very low altitude, whereas the narrow endemic *P. cubensis* is restricted to serpentine soil near a waterfall at intermediate altitude (Domínguez et al. 2014). The annual *P. albida* has a broader ecological tolerance and grows on both soil types, and on peaty sand in savannas. The two central Cuban species are found in montane tropical forests growing on seasonally wet limestone rock, whereas the eastern Cuban species usually grow in laterite or clay soils (Lampard et al. 2016). Finally, Cuba and the nearby Dominican Republic host two true epiphytic species that grow on bare or moss-covered tree stems and branches: *P. lignicola* and *P. casabitoana*.

Six widely scattered and mostly geographically disjunct species grow in the Andes (Figure 6.3). *Pinguicula elongata*, *P. calyptrata*, and *P. involuta* grow primarily in the high Andean *paramos*—low grasslands dominated by scattered *Espeletia* (Asteraceae) and that are ecologically similar to alpine heathlands—and *yungas*—wet tropical montane and cloud forests. *Pinguicula jarmilae* is known only from a single dripping wall of sandstone on a roadside at 2100–2500 m altitude (Beck et al. 2008). *Pinguicula chilensis* occurs in wet meadows and in wet places on volcanic gravels. At the very south of the continent, *P. antarctica* grows in peat bogs among *Sphagnum* and the cushion plant *Donatia fascicularis* (Stylidiaceae).

Other centers of high species richness are the European Alps, including the Apennines (12 species, nine [75%] endemics), the Baetic Mountains of the Iberian Peninsula (five species, four endemics; Roccia et al. 2016; Figure 6.5), and the southeast coast of the United States (six endemic species; Schnell 1976, Lampard et al. 2016, Roccia et al. 2016).



**Figure 6.5** Distribution and number of species of *Pinguicula* in Europe and Asia Minor (data from Meusel et al. 1965, Casper 1966, Heslop-Harrison 2004, Fleischmann 2015b, and additional information retrieved from herbarium records).

Map drawn by Andreas Fleischmann.

## 6.5 Carnivory and other plant–insect interactions

### 6.5.1 Prey

Carnivory in *Pinguicula* was first postulated and experimentally demonstrated by Darwin (1875), and enzymatic activity was studied by Heslop–Harrison (1975). Prey usually consists of small-to-very small arthropods, predominantly midges and mites (Heslop–Harrison 2004, Fleischmann 2016b). Prey probably are attracted by the combination of volatile musty, fungus-like scent emitted by *Pinguicula* leaves (Lloyd 1942, Heslop–Harrison 2004, Fleischmann 2016b), and the visual attraction of the glistening, wet mucilaginous lamina (Juniper et al. 1989). The open, exposed adhesive leaf rosettes also casually catch air-borne debris; >50% of the “prey” of *P. vulgaris* can be made up of pollen, largely from wind-pollinated plants (Karlsson et al. 1994).

### 6.5.2 Associated arthropods

A mutualistic plant–arthropod interaction has been documented between *P. longifolia* and the small symbiotic mite, *Oribatula tibialis* (Antor and García 1995). The butterwort offers food and protection to *O. tibialis* while *P. longifolia* benefits from scavenging activities of the mites, which eat fungal hyphae and insect remains, and prevent molds from damaging the leaves (Antor and García 1995).

Hemipteran kleptoparasites of the capsid bug family Miridae have been observed on *P. vallisneriifolia*, where they feed on trapped insects (Zamora 1995). Similar bugs have been observed on *P. dertosensis*, freely moving on the viscous adhesive leaves without being trapped (A. Roccia *personal observation*). Other species of Miridae are known to live on a large variety of sticky plants (including carnivorous *Drosera*, *Byblis*, and *Roridula*; Chapter 10). A second kleptoparasite has been documented from *P. vallisneriifolia*: the slug *Deroceras nitidum* can consume a large portion of the prey caught by the plant (Zamora and Gómez 1996). Ants may steal prey from a number of other *Pinguicula* species (Zamora 1990a).

## 6.6 Conservation

The most severe threats to *Pinguicula* populations are from human activities, especially when the hydrology of their often fragile, oligotrophic seepage habitats are disturbed by source channeling, roadside constructions, or eutrophication. Other threats include over-collection and poaching by plant collectors. Neither the majority of *Pinguicula* species nor their habitats are under any special protection, and no *Pinguicula* species is currently listed on CITES. The IUCN Red List only includes three species under the category “threatened:” *P. fontiqueriana* (vulnerable B1ab(iii) + 2ab(iii)), *P. mundi* (vulnerable D2), and *P. nevadensis* (Endangered B2ab(iii,v)). Two of these are native to Spain where they are listed on the Spanish Red List along with *P. dertosensis* and *P. vallisneriifolia*. But this listing does not offer any protection, only a recognition of their threatened status. However, most, if not all, populations of *P. nevadensis* occur within the Parque Nacional de la Sierra Nevada, many *P. vallisneriifolia* and *P. dertosensis* populations are found in various Natural Parks, and one of the two known *P. mundi* locations is included in the Parque Natural de los Calares del Río Mundo y de la Sima. Although not listed on the national red list, *P. longifolia* is also found in many places in the Parque Nacional de Ordesa y Monte Perdido and in its counterpart in France, Parc National des Pyrénées.

Similar situations apply elsewhere in the world. *Pinguicula crystallina* is considered endangered on Cyprus, the endemic lowland species *P. bohémica* is critically endangered in Czech Republic, the majority of the southeastern US species are threatened by habitat loss (the endemic and endangered *P. ionantha* is

protected by law), and many populations of widespread species are threatened on country level or local scale.

In several European countries (e.g., Great Britain, France, Germany, Switzerland), all naturally occurring species of *Pinguicula* are fully protected by law: it is forbidden to collect any plant parts, including seeds or roots. *Pinguicula arvetii*, *P. caussensis*, *P. grandiflora*, *P. longifolia*, *P. lusitanica*, *P. reichenbachiana*, and *P. vulgaris* benefit from this protection in France. Although this protection is effective only on a regional scale, for some taxa it does include their entire range (e.g., *P. grandiflora* subsp. *rosea* and *P. reichenbachiana*). Even *P. hirtiflora* benefits from some kind of protection from European and international directives, although it is considered as an alien invasive species in France.

Three species have not been relocated since their original discovery: *P. greenwoodii*, *P. imitatrix*, and *P. utricularioides*. All three are from México, and despite various attempts, they have not been observed again. Most of the Central American species grow in inaccessible habitats, although habitat loss by human activities sometimes happens on a very large scale. For example, the endemic *P. moctezumae* was thought to have gone extinct after much of its habitat in the Moctezuma valley was flooded after the construction of the Zimapán Hydroelectric Dam. The species was later found in a small side branch of the valley (F. Rivadavia unpublished data).

## 6.7 Future research

A well-resolved, comprehensive phylogenetic reconstruction based on large taxon sampling is still lacking for the genus. Incongruences between nuclear and plastid datasets, and low resolution of, or weak support for, some species groups in published phylogenies do not allow for subsectional evolutionary inferences or classifications. This is especially true for the species-rich but apparently young *P. sect. Temnoceras* from México and the Caribbean, which is morphologically and ecologically diverse, but for which existing classifications based on flower morphology and growth type seem to be rather artificial, and do not consider parallel evolution of morphological traits. The same holds true for the apparently young, polyploid species complexes of *P. subg. Pinguicula* from the Alps and Apennines (several of which might be the result of hybridogenesis). To reliably reconstruct the evolutionary history of these species-rich clades, and to overcome incongruences between plastid and nuclear DNA data, phylogenetic reconstructions considering reticulate evolution are needed, and will require sampling of many taxa, and large samples of geographically widespread and morphologically variable ones (e.g., *P. moranensis*, *P. ehlersiae*, *P. reichenbachiana*, and *P. vulgaris*).

Much less is known about the species interactions with other organisms, including their pollinators and the range of their prey. Field observations could fill this gap, and might shed light on whether different growth types and leaf shapes have evolved only as adaptations to certain habitats, or if they also mirror prey specialization. The diversity of corolla shapes and colors observed in the Central American species of *P. sect. Temnoceras* likely is related to different pollinator groups or pollination strategies, but the floral biology of Mexican and Caribbean species is unstudied. Successful conservation of these species demands a complete understanding of their biology and life history.

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