An updated nomenclatural conspectus of infrageneric names in *Pinguicula*

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Abstract: A revision of the infrageneric (but supraspecific) names published for *Pinguicula* is performed, including the reference to the protologue and type for every validly published name, as well as the nomenclatural status and nomenclatural notes to explain certain cases, especially for those names that were not validly published or are illegitimate. In addition to discussing the underlying taxonomy from previous publications, we performed an updated phylogenetic analysis using representative ITS, *trnK*, *matK*, and *rpl32* + *rpl32-trnL* sequences available in the GenBank database, as internal reference. As a result of the study, the name *Brandonia* Rchb. is typified with the type of *Pinguicula lutea*, *P.* sect. *Brandonia* is recognised due to priority as the correct name for the clade previously known as *P.* sect. *Isoloba*. Finally, some author citations that were often incorrectly cited in the literature are corrected. *Pinguicula* sect. *Nana* and *P.* sect. *Micranthus* are proposed as *incertae sedis* instead of forming part of *P.* subg. *Temnoceras*, and at least *P.* sect. *Nana* might be probably better included in *P.* subg. *Pinguicula*. This new placement is supported by morphological and chorological data, and partly by our molecular phylogenetic reconstructions. Chromosome numbers from the literature were also taken into account and confirmed to be useful to delineate certain infrageneric taxa.

Introduction

The infrageneric classification of the genus *Pinguicula* L. (Lentibulariaceae, Lamiales), understood as the taxa that are subdivisions of the genus but above the specific rank, has been addressed by many authors, starting from De Candolle (1844), who divided the genus in three sections, viz., *P.* sect. *Orcheosanthus*, "*P.* sect. *Pionophyllum*" (nom. inval.), and *P.* sect. *Brandonia*. Afterwards, Barnhart (1916) recognised four subgenera, viz., *P.* subg. *Pionophyllum* and *P.* subg. *Orcheosanthus* for De Candolle's homonymous sections, plus *P.* subg. *Isoloba* (based on the genus *Isoloba* Raf.) and the new, monotypic *P.* subg. *Temnoceras*. Ernst (1961) accepted three sections by adopting De Candolle's *P.* sect. *Orcheosanthus* and "*P.* sect. *Pionophyllum*" (including *P.* sect. *Brandonia* and implicitly *Isoloba*), and by treating Barnhart's *P.* subg. *Temnoceras* as a section.

Nevertheless, the largest contribution to classify *Pinguicula* species into infrageneric taxa has been done by Casper (1962, 1963, 1966). However, the rules of nomenclature then in force were not always strictly followed when those taxa were named, especially concerning the indication or

designation of types, resulting in the creation of some not validly published names. This happened most notably in Casper (1962), where all infrageneric names for which a type was not indicated, following either the current International Code of Nomenclature for algae, fungi, and plants (ICN) Art. 10.8 (Turland *et al.* 2018; epithets of a subdivision of a genus identical with or derived from the epithet in one of the included species names) or the current ICN Art. 40.3 (reference to a single species name or citation of the type of a previously or simultaneously published species name), were invalidly published. This also occurred occasionally for infrageneric names coined in Casper (1963) and Casper (1966) for the same reasons. It should be noted that the inclusion of the type of a validly published species name can be effected by the citation or reference to such a name, even if it is just listed as a synonym (ICN Art. 10.3). As a result, there were some cases in which a single species was accepted in a subdivision of a genus, but the types of more than one species name were nevertheless included (e.g., *P. lusitanica* for the intended "*P.* subsect. *Pumiliformis* Casper" in 1966, since *P. subaequalis* Stokes was listed as a synonym). In some other cases, either later homonyms (i.e., names that are spelled identically but that are based on different types) or superfluous names (names for which another name or epithet ought to have been adopted) were created, resulting in illegitimate names that should not be used under the rules of the International Code of Nomenclature for algae, fungi and plants (ICN, Turland *et al.* 2018).

Nowadays, infrageneric taxa are, however, still often named not by choosing the validly published or the correct legitimate names, but the ones first mentioned in the literature, regardless of their nomenclatural status. In fact, the accumulation of infrageneric names in *Pinguicula* has reached a point where it is not easy to decide, even for specialists, which correct name should be used for a particular species group, whether at the level of subgenera, sections, or lower taxonomic ranks. The most recent publications dealing with a rather complete infrageneric classification of the genus (Fleischmann & Roccia 2018; Fleischmann 2021) have aimed at providing nomenclatural stability by adopting a revised taxonomy and already sorting out some nomenclatural problems (e.g., the invalidly published status of names proposed by Shimai 2017, because this PhD thesis is not effectively published according to ICN Art. 30.9), as well as creating new names for thus far unnamed clades. Nevertheless, we still have noted a few persisting mistakes that shall be corrected here. For example, the infrageneric taxon currently including only *P. elongata* has been named as *P.* ser. *Elongatae* (Casper 1963), later invalidly published as "*P.* subsect. *Heterophylliformis*" (Casper 1966) and "*P.* sect. *Elongatae*" (Shimai 2017), and finally accepted and validly published by Fleischmann & Roccia (2018) as *P.* sect. *Heterophylliformis* but with the incorrect author citation "(Casper) A. Fleischmann & Roccia" due to the assumption that the intended basionym in Casper (1966) was validly published. This name is now correctly cited in this study as *P.* sect. *Heterophylliformis* A. Fleischmann & Roccia.

Therefore, the aim of this contribution is to gather all validly published infrageneric names in *Pinguicula* (in addition to at least some invalidly published ones or later isonyms without nomenclatural status that are considered useful), check their nomenclatural status and types, and adopt the correct names for the most usual taxonomic assemblages, according to the ICN.

The background taxonomy largely follows Fleischmann & Roccia (2018), Shimai (2017), Shimai *et al.* (2021), and Fleischmann (2021). We have also performed updated phylogenetic analyses as an internal reference, trying to include most taxa for which DNA sequence data were available, to be as precise as possible in our decisions for the appropriate rank and synonyms of the accepted taxa. However, it should be noted that this publication is primarily focused on nomenclature and not on taxonomy, and therefore, future taxonomists should adapt their respective classifications

and choose the appropriate name (the oldest, legitimate name within the same rank) for each of the accepted taxa.

Material and methods

To explore the phylogenetic relationships in *Pinguicula* we used all available DNA sequence data from NCBI GenBank (search date: 2022-12-01), and selected one sequence per taxon of the ITS, *trnK-matK*, and *rpl32* + *rpl32-trnL* ("*rpl32*" thereafter) nucleotide regions, whenever possible from the same voucher specimen. These regions were targeted since they were the ones available for the largest number of taxa, the majority having been generated by Shimai *et al.* (2021). We also retrieved from NCBI GenBank the mentioned chloroplast loci from the chloroplast genomes of *P. alpina*, *P. casperiana*, *P. dertosensis*, *P. ehlersiae*, *P. mundi*, *P. saetabensis*, *P. submediterranea*, *P. tejedensis*, *P. vallisneriifolia* (from two populations, as they displayed considerable sequence variation compared to other taxa in the same group), and an unidentified *Pinguicula* accessioned as *P. jackii*. GenBank accession numbers are summarised in Table 1.

Table 1. GenBank sequences used for phylogenetic reconstructions.

Taxon	**ITS**	***trnK-matK***	***rpl32-trnL***
Pinguicula acuminata	AB199751	DQ010652	LC348618
Pinguicula agnata	AB199752	AF531782	
Pinguicula albida	AB212095	LC348432	LC348619
Pinguicula alpina	AB198341	MT740255	MT740255
Pinguicula antarctica	AB212096	DQ010653	LC348621
Pinguicula apuana	LN887909	OM161131	
Pinguicula balcanica subsp. *balcanica*	AB198342		
Pinguicula balcanica subsp. *pontica*	LC348695		LC348622
Pinguicula benedicta	AB212097	LC348433	LC348623
Pinguicula bissei	AB212098	LC348434	LC348624
Pinguicula bohemica	AB198343	LC348435	LC348625
Pinguicula caerulea	AB212099		LC348626
Pinguicula calderoniae	MG310271		
Pinguicula calyptrata	AB212100	FM200225	LC348627
Pinguicula casperiana		OL470666	OL470666
Pinguicula caussensis	AB198350	AF531794	LC348657
Pinguicula chilensis	AB212101		LC348628
Pinguicula christinae	LN887915	OM161129	
Pinguicula colimensis	AB199753	LC348436	LC348629
Pinguicula conzatii	AB199754	LC348437	LC348630
Pinguicula corsica	AB198344	AF531784	LC348631
Pinguicula crassifolia	AB199755	LC348438	LC348632
Pinguicula crenatiloba	LC348696		LC348633
Pinguicula crystallina	AB198363		LC348634
Pinguicula cubensis	AB212102	LC348439	LC348635
Pinguicula cyclosecta	AB199756	LC348440	LC348636

Table 1. Continued.			
Pinguicula debbertiana	AB199757	LC348441	
Pinguicula dertosensis	AB198345	OL470670	OL470670
Pinguicula ehlersiae	AB199758	HG803178	HG803178
Pinguicula elizabethiae	MG310274		
Pinguicula elongata	AB212103	FM200224	LC348639
Pinguicula emarginata	AB199759	AF531785	LC348640
Pinguicula esseriana	AB199760	DQ010656	LC348641
Pinguicula filifolia	AB212104	AF531786	LC348642
Pinguicula fiorii	AB198346	AF531787	LC348643
Pinguicula gigantea	AB199761	AF531789	LC348644
Pinguicula gracilis	AB199762	AF531790	LC348645
Pinguicula grandiflora subsp. *grandiflora*	AB198347	AF531791	LC348646
Pinguicula grandiflora subsp. *rosea*	AB198348		
Pinguicula gypsicola	AB199763	LC348444	
Pinguicula hemiepiphytica	AB199764	LC348445	LC348647
Pinguicula heterophylla	AB199765		LC348648
Pinguicula hirtiflora	AB198364	DQ010654	
Pinguicula ibarrae	AB251603	LC348446	LC348649
Pinguicula immaculata	AB199766	LC348447	LC348650
Pinguicula involuta		FM200226	
Pinguicula ionantha	AB212105	LC348448	LC348651
Pinguicula jackii	AB212106		
Pinguicula jaraguana	AB212107	LC348449	LC348652
Pinguicula jarmilae		FM200223	
Pinguicula kondoi	AB199781	LC348451	
Pinguicula laueana	AB199768	DQ010659	LC348654
Pinguicula leptoceras	AB198349	AF531792	LC348655
Pinguicula lignicola	AB300153		
Pinguicula lilacina	AB199769	LC348452	LC348656
Pinguicula longifolia	AB198351	OL470665	OL470665
Pinguicula lusitanica	AB198365	DQ010661	LC348660
Pinguicula lutea	AB212108	DQ010662	LC348661
Pinguicula macroceras subsp. *macroceras*	AB198353	AF531796	LC348662
Pinguicula macroceras subsp. *nortensis*	DQ222951	AF531795	
Pinguicula macrophylla	AB199770	LC348453	LC348663
Pinguicula mariae	LN887935		
Pinguicula martinezii	MG310278		
Pinguicula medusina	AB199771	LC348454	LC348664
Pinguicula mesophytica	AB251604		
Pinguicula mirandae	AB251605	LC348455	LC348665
Pinguicula moctezumae	AB199772	AF531797	LC348666
Pinguicula moranensis	AB199773	AF531798	LC348667
Pinguicula mundi	AB198354	OL470668	OL470668

Table 1. Continued.			
Pinguicula nevadensis	AB198355	DQ010664	LC348669
Pinguicula nivalis	AB199774	LC348456	LC348670
Pinguicula oblongiloba	AB199775	LC348457	LC348671
Pinguicula orchidioides	AB199776		
Pinguicula parvifolia	AB199777		
Pinguicula planifolia	AB212109	LC348458	LC348673
Pinguicula pilosa	AB199778		LC348672
Pinguicula poldinii	AB198356	AF531804	LC348674
Pinguicula potosiensis	AB199779	LC348459	LC348675
Pinguicula primuliflora	AB212110	DQ010666	LC348676
Pinguicula pumila	AB212111	LC348460	LC348677
Pinguicula ramosa	AB198357	DQ010667	LC348678
Pinguicula rectifolia	AB199780	AF531801	
Pinguicula reichenbachiana	AB198352	DQ010660	LC348659
Pinguicula rotundiflora	AB199782	AF531802	LC348679
Pinguicula saetabensis	MH022744	OL470673	OL470673
Pinguicula sharpii	AB199783	AF531803	LC348680
Pinguicula submediterranea		OL470671	OL470671
Pinguicula tejedensis		OL470669	OL470669
Pinguicula vallisneriifolia	AB198358	OL470672	OL470672
Pinguicula cf. *vallisneriifolia*	MH022735 & MH022736	OL470674	OL470674
Pinguicula vallis-regiae	LN887941		LC348682
Pinguicula variegata	AB198359	DQ010668	LC348683
Pinguicula villosa	AB198360	DQ010669	LC348684
Pinguicula vulgaris	AB198361	AF531806	LC348685
Pinguicula zecheri	AB199784	LC348461	LC348686
Pinguicula sp. (as *P. jackii*)		OM460823	OM460823
Genlisea margaretae	PP925598	HG530134	HG530134
Genlisea repens	AB212115	MF593124	MF593124
Genlisea violacea	MG027713	MF593126	MF593126
Utricularia amethystina	MH036219	MN223720	MN223720
Utricularia foliosa	MG027750	KY025562	KY025562
Utricularia gibba	MT248957	KC997777	KC997777
Utricularia macrorhiza	MG027747	HG803177	HG803177
Utricularia reniformis	MG027776	KT336489	KT336489

We used as outgroup taxa three *Genlisea* and five *Utricularia* species to root the phylogenies, but the addition of these sequences increased the number of ambiguously aligned positions very substantially, particularly for the ITS dataset. Therefore, sequences were aligned in two steps: i) alignment of the ingroup, ii) addition of the outgroup sequences with MAFFT-add (L-INS-I, Katoh *et al.* 2019), to keep consistent the alignment structure in the ingroup as much as possible. Ingroup sequences were auto-aligned with PASTA v1.9 (Mirarab *et al.* 2015) with the following

parameters: 10 iterations, keeping the best alignment, MAFFT (L-INS-i) as the aligner, OPAL as the merger, RAxML as the tree estimator, and a GTR + Γ model of DNA sequence evolution. The resulting sequence alignments were barely edited manually: only obvious misplacements concentrated at the beginning and the end of the sequences, some of them possibly from sequencing errors along the 5' or 3' ends of the sequences, one inversion of 42 bp in the *trnK-matK* dataset, and duplications in the *rpl32* dataset.

Shimai *et al.* (2021) reported incongruent phylogenetic signal among loci in the chloroplast datasets (like others reported incongruent topologies between nuclear and chloroplast data before, see Cieslak *et al.* 2005, Degtjareva *et al.* 2006, and Beck *et al.* 2008), so all selected DNA regions were first analysed independently using maximum likelihood (ML); the *trnK* intron was analysed separately from the *matK* exon since also an incongruent signal between them was found (see below). ML analyses were run in IQ-TREE v2.1.3 (Minh *et al.* 2020). ITS was originally partitioned in three potential subsets: ITS1, 5.8, and ITS2; the *matK* exon was also partitioned in three potential subsets corresponding to codon positions, while the *trnK* intron and *rpl32* were not partitioned. For the partitioned datasets, the final partitioning scheme and models were calculated with Model Finder (Kalyaanmoorthy *et al.* 2017) and the partition merging option of IQ-TREE. Congruence was investigated by assessing branch supports with 1000 replicates of ultrafast bootstrap (UFB, Hoang *et al.* 2018) and 1000 replicates of the SH-like approximate likelihood ratio test (SH-aLRT, Guindon *et al.* 2010). We considered that incongruences existed when a supported position (≥ 95% UFB and ≥ 85% SH-aLRT) in one phylogeny from a given locus was contradicted by another supported position in the phylogeny obtained from a different locus.

Given that the phylogenetic position of some species at sectional level was incongruent across some loci, we performed combined analyses by using the "multilabelling" approach indicated by Blanco-Pastor *et al.* (2012). The species and loci affected were as follows: *Pinguicula alpina* (*matK vs*. ITS+*trnK*+*rpl32*), *P. macrophylla* (ITS+*trnK vs. matK*+*rpl32*), *P. ramosa*, *P. variegata*, and *P. villosa* (ITS+*trnK vs. matK vs. rpl32*). We provided different labels to allow the analysis to treat them as potentially different taxa, then simultaneously showing their position in the tree according to each DNA locus or combination of loci. We used ML analyses following the procedure and partitions indicated above for single-locus trees, performing five replicates, keeping the tree with the best likelihood score. In this combined tree, branch support was more thoroughly assessed through the standard non-parametric bootstrap (BS, Felsenstein 1985), performing 500 replicates, as well as 1000 replicates of SH-aLRT. To consider the effect of rogue taxa, we also estimated the transfer bootstrap (TBE, Lemoine *et al.* 2018) through the online service of BOOSTER (https://booster.pasteur.fr/), using the previously generated standard bootstrap replicates.

Phylogenetic trees were drawn in FigTree v1.4.3 (Rambaut 2016) and the ML tree from the best replicate is shown in Fig. 1, with the following support values and significance thresholds: SH-aLRT (≥ 85%), BS (≥ 75%), TBE (≥ 85%). Results and discussion will focus on the combined analysis with notes to single-locus analyses when relevant.

Results

Phylogenetic analyses (Fig. 1) showed three well-supported major clades that roughly correspond to *Pinguicula* subg. *Isoloba* (including *P.* sect. *Ampullipalatum*, *P.* sect. *Brandonia* ["*P.* sect. *Isoloba*" of previous studies], *P.* sect. *Cardiophyllum*, and *P.* sect. *Pumiliformis*), *P.* subg. *Temnoceras* (including *P.* sect. *Agnata*, *P.* sect. *Heterophylliformis*, *P.* sect. *Homophyllum*, *P.* sect.

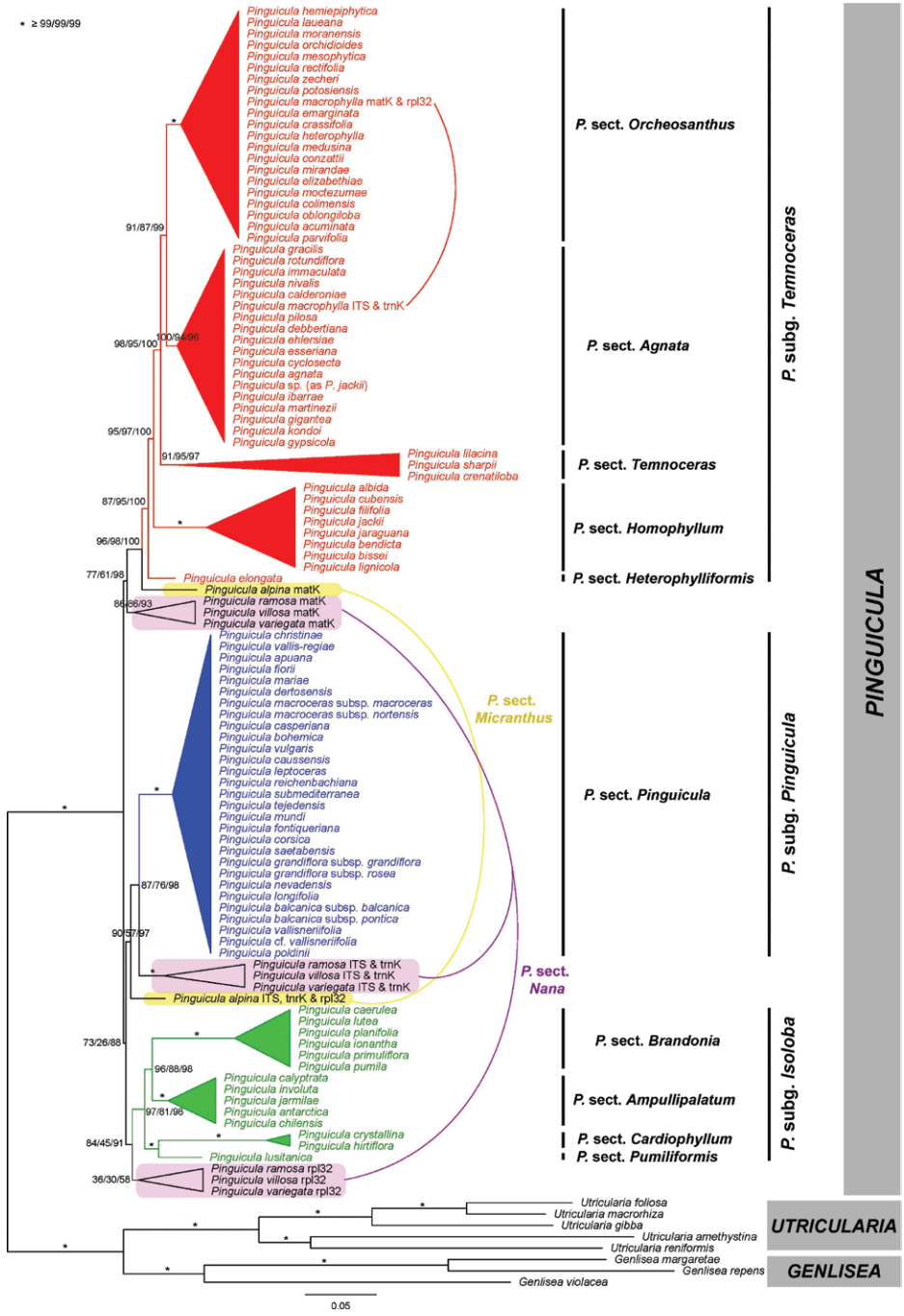

Figure 1: Maximum likelihood phylogram of *Pinguicula* based on *ITS*, *trnK*, *matK*, and *rpl32* DNA sequence data. Numbers on branches denote SH-aLRT/BS/TBE support values. Scale bar represents the average number of substitutions per site.

Orcheosanthus, and *P.* sect. *Temnoceras*), and *P.* subg. *Pinguicula* (including only *P.* sect. *Pinguicula*).

The position of *P.* sect. *Micranthus* and *P.* sect. *Nana* greatly varied across analyses. ITS and *trnK* data for *P.* sect. *Nana*, and ITS, *trnK* and *rpl32* data of *P.* sect. *Micranthus*, suggested that these two sections form a monophyletic group together with *P.* sect. *Pinguicula*, but this relationship was only supported by SH-aLRT (90%) and TBE (97%) in the combined analysis. The relationship of *P.* sect. *Nana* (ITS and *trnK* data) + *P.* sect. *Pinguicula* was supported in the combined dataset by all analyses.

With *matK*, both *P.* sect. *Micranthus* and *P.* sect. *Nana* formed a monophyletic group with *P.* subg. *Temnoceras*, being the relationship of *P.* sect. *Micranthus* + *P.* subg. *Temnoceras* highly supported by all analyses, while the relationship of *P.* sect. *Nana* + *P.* sect. *Micranthus* + *P.* subg. *Temnoceras* was only supported by TBE (98%).

Rpl32 data placed *P.* sect. *Nana* as sister to *P.* subg. *Isoloba*, a relationship supported by only TBE (91%), but the clade of *P.* sect. *Nana* comprising only *rpl32* data was itself unsupported. These deviating positions are highlighted in the combined analysis (Fig. 1).

Finally, the position of *P. macrophylla* varied between *P.* sect. *Agnata* (ITS and *trnK*) and *P.* sect. *Orcheosanthus* (*matK* & *rpl32*), and both alternative positions received good support.

Conspectus

The following information is provided: (i) accepted correct infrageneric names, with the citation of their place of publication; (ii) homotypic synonyms (preceded by "≡", first always the basionym and then names of the same of lower ranks if not included elsewhere); and (iii) type and reason or place of designation. Nomenclatural notes are also sometimes added to explain certain situations or choices. The accepted names are listed in alphabetical order following the adopted taxonomy (sections are listed within subgenera) and are frequently accompanied also by heterotypic synonyms (preceded by "=", sometimes with their own homotypic synonyms in a second level). Invalidly published names or later isonyms (preceded by "–") are added as well. Types and nomenclatural notes are also intercalated for heterotypic synonyms and for not validly published names when considered informative. For each lowest-ranked accepted name, a non-exhaustive list of included species is also provided as a guidance of the taxonomic coverage of the infrageneric name. Finally, taxonomic notes are included in cases where a justification of the adopted taxonomy is deemed necessary.

***Pinguicula* L. Sp. Pl. [Linnaeus] 1**: **17. 1753**

Typus: *Pinguicula vulgaris* L. [designated by A.S. Hitchcock in Hitchcock A.S. & Green M.L. (1929) Nom. Prop. Brit. Bot.: 116]

= *Isoloba* Raf., Fl. Tellur. 4: 58. 1838

Typus: *Pinguicula pumila* [designated by Casper 1963: 329]

= *Brandonia* Rchb., Consp. Regn. Veg. [H.G.L. Reichenbach]: 127. 1828

Typus: *Pinguicula lutea* Walter, Fl. Carol. [Walter]: 63. 1788 [**designated here**]

Nomenclatural notes: No species names were included in the generic name *Brandonia* by Reichenbach (1828), although the types of both *Pinguicula lutea* and *P. edentula* were included by citation of Edward's (1828) Botanical Register no. 126 and Hooker's (1828) Exotic Flora 1 p. 16, respectively. To our knowledge, neither this name nor any combination based on it has been typified until now.

Subgenus 1: *Pinguicula* subg. *Isoloba* (Raf.) Barnhart, Mem. New York Bot. Gard. 6: **47. 1916**
≡ *Isoloba* Raf., Fl. Tellur. 4: 58. 1838 [basionym]

Typus: *Pinguicula pumila* [designated by Casper 1963: 329]

Nomenclatural notes: Barnhart (1916: 47) provided an indirect reference to Rafinesque (1838: 58) by indicating "Isoloba (Raf. pro gen.)", which is acceptable for new combinations before 1 January 1953 (ICN Art. 41.3). However, this subgeneric name has thus far persistently been cited in the literature as "*P.* subg. *Isoloba* Barnhart", without the reference to the basionym author.

Section 1.1: *Pinguicula* sect. *Ampullipalatum* Casper, Bot. Jahrb. Syst. 82: 334. 1963
≡ *Pinguicula* subsect. *Alpiniformis* Casper, Biblioth. Bot. 31(127–128): 114. 1966
≡ *Pinguicula* ser. *Andinae* Casper, Biblioth. Bot. 31(127–128): 114. 1966

– "*Pinguicula* ser. *Andinae* Casper", Bot. Jahrb. Syst. 82: 334. 1963, nom. inval. [Arts. 40.1 and 40.3]

– "*Pinguicula* sect. *Andinae* (Casper) Shimai", Taxon. Conservation Ecol. Pinguicula 238 (2017), nom. inval. [Arts. 30.9 and 41.5]

Typus: *Pinguicula calyptrata* Kunth [designated by Casper 1963: 334 for *P.* sect. *Ampullipalatum* and by Casper 1966: 114 for *P.* subsect. *Alpiniformis* and *P.* ser. *Andinae*]

Nomenclatural notes: Authorships given for not validly published names here and elsewhere in the current publication are simply indicative of the way they were intended to be published but have no nomenclatural relevance. When Casper (1963: 334) intended to publish "*P.* ser. *Andinae*", he included more than one species name and did not indicate any as type, so the name cannot be considered validly published (ICN Arts. 40.1 and 40.3).

= *Pinguicula* ser. *Antarcticae* Casper, Bot. Jahrb. Syst. 82: 334. 1963

Typus: *Pinguicula antarctica* Vahl. [ICN Art. 10.8, and single species name cited for ICN Art. 40.3]

Species included: *Pinguicula antarctica*, *P. australandina*, *P. calyptrata*, *P. involuta*, *P. jarmilae*, *P. jimburensis*, *P. nahuelbutensis*, *P. ombrophila*, *P. rosmarieae*.

Section 1.2: *Pinguicula* sect. *Brandonia* (Rchb.) DC., Prodr. [A. P. de Candolle] 8: 32. 1844
≡ *Brandonia* Rchb., Consp. Regn. Veg. [H.G.L. Reichenbach]: 127. 1828 [basionym]
≡ *Pinguicula* subsect. *Primuliformis* Casper, Biblioth. Bot. 31(127–128): 80. 1966
≡ *Pinguicula* ser. *Emarginatae* Casper, Biblioth. Bot. 31(127–128): 82. 1966

– "*Pinguicula* ser. *Emarginatae* Casper", Bot. Jahrb. Syst. 82: 330. 1963, nom. inval. [ICN Arts. 40.1 and 40.3]

Typus: *Pinguicula lutea* Walter [designated by Casper 1966: 80 for *P.* subsect. *Primuliformis* and by Casper 1966: 82 for *P.* ser. *Emarginatae*; designated above in the present publication for *Brandonia*]

Nomenclatural notes: When Casper (1963: 330) intended to publish "*P.* ser. *Emarginatae*", he included more than one species name and did not indicate any as type, so the name cannot be considered validly published (ICN Arts. 40.1 and 40.3). The name *P. emarginata* Zamudio & Rzed. (Zamudio & Rzedowski 1986) had not been published at that date, and therefore ICN Art. 10.8 does not apply. *Pinguicula* sect. *Brandonia* has priority by more than 100 years over *P.* sect. *Isoloba*, and it is

therefore the correct name to be used for the section including *P. lutea*. While the former has never been used after its publication, the current ICN Art. 14 does not provide the means to conserve a name in the rank of subdivision of a genus, unless it is to change its type when the subgeneric name is the basionym of a generic name that cannot be used in its current sense without conservation (ICN Art. 14.1, final sentence). Fortunately, the impact of reinstating an unused name of a subdivision of a genus is small compared to names of families, genera, or species, and specifically the use of *P.* sect. *Isoloba* in its current sense is restricted to few recent scientific publications.

= *Pinguicula* sect. *Isoloba* Casper, Bot. Jahrb. Syst. 82: 330. 1963

≡ *Isoloba* Raf., Fl. Tellur. 4: 58. 1838

– "*Pinguicula* sect. *Isoloba* Casper", Feddes Repert. 66: 29. 1962, nom. inval. [ICN Arts. 40.1 and 40.3]

≡ *Pinguicula* ser. *Amphiatlanticae* Casper, Bot. Jahrb. Syst. 82: 330. 1963 [as "*Amphi-Atlanticae*"]

≡ *Pinguicula* subsect. *Agnatiformis* Casper, Biblioth. Bot. 31(127–128): 75. 1966

Typus: *Pinguicula pumila* Michx. [designated by Casper 1963: 329 for *Isoloba* (as "Subgenus II: *Isoloba* Barnhart") and *P.* sect. *Isoloba*, by Casper 1963: 330 for *P.* ser. *Amphiatlanticae*, and by Casper 1966: 75 for *P.* subsect. *Agnatiformis*]

Nomenclatural notes: *Pinguicula* sect. *Isoloba* was published by Casper (1963: 330) without a full and direct reference to the basionym (the generic name *Isoloba* Raf.) or to other names that may be treated as errors, e.g., *P.* subg. *Isoloba* (Raf.) Barnhart. The reference provided for *P.* subg. *Isoloba* (Raf.) Barnhart (as "Subgenus II: *Isoloba* Barnhart in Mem. N. York Bot. Gard. VI (1916)") lacks the page, which is an omission not acceptable under ICN Art. 41.6 and impedes considering it as a new combination under Art. 41.8(d). The same intended sectional name in Casper (1962: 29) did not fulfil ICN Arts. 40.1 and 40.3 (indication of a type), and it was therefore not validly published.

= *Pinguicula* ser. *Primuliflorae* Casper Bot. Jahrb. Syst. 82: 331. 1963

Typus: *Pinguicula primuliflora* C.E. Wood & R.K. Godfrey [ICN Art. 10.8]

= *Pinguicula* ser. *Pumilioideae* Casper, Biblioth. Bot. 31(127–128): 80. 1966

Typus: *Pinguicula ionantha* R.K. Godfrey [only the type of this species name was included, ICN Art. 40.3]

Species included: *Pinguicula caerulea*, *P. ionantha*, *P. lutea*, *P. planifolia*, *P. primuliflora*, *P. pumila*.

Section 1.3: *Pinguicula* sect. *Cardiophyllum* Casper, Bot. Jahrb. Syst. 82: 331. 1963

– "*Pinguicula* sect. *Cardiophyllum* Casper", Feddes Repert. 66: 34. 1962, nom. inval. [ICN Arts. 40.1 and 40.3]

Typus: *Pinguicula hirtiflora* Ten. [designated by Casper 1963: 331]

Nomenclatural notes: When Casper (1962: 34) intended to publish "*P.* sect. *Cardiophyllum*", he included more than one species name and did not indicate any as type, so the name cannot be considered validly published (ICN Art. 40.1 and 40.3).

Species included: *Pinguicula crystallina*, *P. hirtiflora*, *P. habilii* (correct name at species rank for the species usually known as *P. megaspilaea*).

Section 1.4: *Pinguicula* sect. *Pumiliformis* Roccia & A. Fleischm. in Ellison & Adamec, Carnivorous Plants: Physiology, Ecology, and Evolution. Oxford University Press: 75. 2018

– "*Pinguicula* subsect. *Pumiliformis* Casper", Biblioth. Bot. 31(127–128): 71. 1966, nom. inval. [ICN Arts. 40.1 and 40.3]

– "*Pinguicula* sect. *Pumiliformis* (Casper) Shimai", Taxon. Conservation Ecol. Pinguicula: 620. 2017, nom. inval. [ICN Arts. 30.9 and 41.5]

Typus: *Pinguicula lusitanica* L. [designated by Fleischmann & Roccia 2018: 75]

Nomenclatural notes: When Casper (1966: 71) intended to publish "*P.* subsect. *Pumiliformis*", he included more than one species name and did not indicate any as type, so the name cannot be considered validly published (ICN Art. 40.1 and 40.3). The name was validly published by Fleischmann & Roccia (2018) by providing both a reference to a previously and effectively published diagnosis (that of Casper 1966: 71) and a correct type designation.

Species included: *Pinguicula lusitanica*.

Subgenus 2: *Pinguicula* subg. *Temnoceras* Barnhart, Mem. New York Bot. Gard. 6: **47. 1916**

Typus: *Pinguicula crenatiloba* DC. [single species name included in Barnhart (1916)]

= *Pinguicula* subg. *Orcheosanthus* (DC.) Barnhart, Mem. New York Bot. Gard. 6: 47. 1916

≡ *Pinguicula* sect. *Orcheosanthus* DC., Prodr. [A. P. de Candolle] 8: 27. 1844 [basionym]

Typus: *Pinguicula moranensis* Kunth [designated by Casper 1963: 327]

Nomenclatural notes: The priority of *P.* subg. *Temnoceras* over *P.* subg. *Orcheosanthus* has been established by Fleischmann & Roccia (2018), who adopted *P.* subg. *Temnoceras* including *P.* sect. *Orcheosanthus* within it (ICN Art. 11.5). Although these authors indicated that "Barnhart's *P.* subg. *Temnoceras* has nomenclatural priority on subgenus rank", this was actually not true before their choice because names have no priority outside their rank (ICN Art. 11.2) and both subgeneric names were simultaneously published, therefore having equal priority.

Section 2.1: *Pinguicula* sect. *Agnata* Casper, Bot. Jahrb. Syst. 82: 331. 1963

≡ *Pinguicula* ser. *Agnatae* Casper, Bot. Jahrb. Syst. 82: 332. 1963

Typus: *Pinguicula agnata* Casper [ICN Art. 10.8]

= *Pinguicula* ser. *Cyclosectae* Casper, Biblioth. Bot. 31(127–128): 136. 1966

Typus: *Pinguicula cyclosecta* Casper [ICN Art. 10.8 and designated by Casper 1966: 136]

= *Pinguicula* subsect. *Violiformis* Casper, Biblioth. Bot. 31(127–128): 133. 1966

Typus: *Pinguicula gypsicola* Brandegee [single species name cited, ICN Art. 40.3]

= *Pinguicula* sect. *Crassifolia* Speta & F. Fuchs, Stapfia 10: 113. 1982

Typus: *Pinguicula ehlersiae* Speta & F. Fuchs [designated by Speta & Fuchs 1982: 113]

= *Pinguicula* sect. *Microphyllum* Luhrs in Luhrs & Lampard, Carniv. Pl. Newslett. 35: 9. 2006

Typus: *Pinguicula immaculata* Zamudio & Lux

Species included: *Pinguicula agnata*, *P. cyclosecta*, *P. debbertiana*, *P. ehlersiae*, *P. esseriana*, *P. gigantea*, *P. gracilis*, *P. gypsicola*, *P. ibarrae*, *P. immaculata*, *P. kondoi*, *P. martinezii*, *P. nivalis*, *P. pilosa*, *P. rotundiflora*, *P. simulans*, *P. tlahuica*.

Taxonomic and nomenclatural notes: The boundaries between *P.* sect. *Agnata* and *P.* sect. *Orcheosanthus* are not sharp with the available data, so some taxonomic and nomenclatural changes can be expected in the future. Fleischmann (2021) has provisionally been followed here. In case these two sections are treated as synonyms, the correct name has to be *P.* sect. *Orcheosanthus* due to priority.

Section 2.2: *Pinguicula* sect. *Heterophylliformis* A. Fleischm. & Roccia in Ellison & Adamec, Carnivorous Plants: Physiology, Ecology, and Evolution. Oxford University Press: 76. 2018

– "*Pinguicula* subsect. *Heterophylliformis* Casper", Biblioth. Bot. 31(127–128): 113. 1966, nom. inval. [ICN Arts. 40.1 and 40.3]

≡ *Pinguicula* ser. *Elongatae* Casper, Bot. Jahrb. Syst. 82: 334. 1963

– "*Pinguicula* sect. *Elongatae* (Casper) Shimai", Taxon. Conservation Ecol. Pinguicula: 304. 2017, nom. inval. [ICN Arts. 30.9 and 41.5]

Typus: *Pinguicula elongata* Benj. [ICN Art. 10.8, and single species name cited for ICN Art. 40.3 for *P.* ser. *Elongatae*; designated by Fleischmann & Roccia 2018: 76 for *P.* sect. *Heterophylliformis*]

Nomenclatural notes: When Casper (1966: 113) intended to publish "*P.* subsect. *Heterophylliformis*", he included more than one species name and did not indicate any as type, so the name cannot be considered validly published (ICN Art. 40.1 and 40.3). The name was validly published by Fleischmann & Roccia (2018) by providing both a reference to a previously and effectively published diagnosis (that of Casper 1966: 113) and a correct type designation.

Species included: *Pinguicula elongata*.

Section 2.3: *Pinguicula* sect. *Homophyllum* Casper, Bot. Jahrb. Syst. 82: 325. 1963

Typus: *Pinguicula jackii* [designated by Casper 1963: 325]

= *Pinguicula* sect. *Discoradix* Casper, Bot. Jahrb. Syst. 82: 332. 1963

Typus: *Pinguicula lignicola* Barnhart [designated by Casper 1963: 332]

Nomenclatural notes: The priority of *P.* sect. *Homophyllum* over *P.* sect. *Discoradix* has been established by Fleischmann (2021), who adopted *P.* sect. *Homophyllum* and included *P.* sect. *Discoradix* as a synonym (ICN Art. 11.5). Although in that publication it was indicated that "The name *P.* section *Homophyllum* is chosen here for the Cuban evolutionary lineage, as it is the oldest available one for that lineage at the rank of section", both names had equal priority before that choice (ICN Art. 11.5).

= *Pinguicula* ser. *Albidae* Casper, Bot. Jahrb. Syst. 82: 332. 1963

≡ *Pinguicula* subsect. *Agnata* Casper, Biblioth. Bot. 31(127–128): 92. 1966, nom. illeg. [ICN Art. 53.3]

Typus: *Pinguicula albida* Griseb. [ICN Art. 10.8 for *P.* ser. *Albidae*; designated by Casper 1966: 92 for *P.* subsect. *Agnata*]

= *Pinguicula* ser. *Intermediae* Casper, Bot. Jahrb. Syst. 82: 332. 1963

≡ *Pinguicula* subsect. *Homophylliformis* Casper, Biblioth. Bot. 31(127–128): 96. 1966

Typus: *Pinguicula benedicta* Barnhart [single species name cited in both cases, Art. 40.3]

– "*Pinguicula* sect. *Caribensis* Shimai", Taxon. Conservation Ecol. Pinguicula: 268. 2017 [nom. inval., ICN Art. 30.9]

Intended type: *Pinguicula albida* Griseb.

Species included: *Pinguicula albida*, *P. benedicta*, *P. bissei* (including *P. baezensis*), *P. caryophyllacea* (including *P. toldensis*), *P. casabitoana*, *P. cubensis*, *P. filifolia*, *P. infundibuliformis*, *P. jackii*, *P. jaraguana*, *P. lignicola*, *P. lippoldii* (including *P. moanensis*), *P. lithophytica*, *P. orthoceras*.

Section 2.4: *Pinguicula* sect. *Orcheosanthus* DC., Prodr. [A. P. de Candolle] 8: 27. 1844
≡ *Pinguicula* subsect. *Orchidopsis* Casper, Biblioth. Bot. 31(127–128): 136. 1966
≡ *Pinguicula* ser. *Caudatae* Casper, Biblioth. Bot. 31(127–128): 139. 1966
Typus: *Pinguicula moranensis* Kuhnt [designated by Casper 1963: 327 for *P.* sect. *Orcheosanthus*, by Casper 1966: 136 for *P.* subsect. *Orchidopsis*, and by Casper 1966: 139 for *P.* ser. *Caudatae*]
= *Pinguicula* sect. *Heterophyllum* Casper, Bot. Jahrb. Syst. 82: 332. 1963
≡ *Pinguicula* subsect. *Isolobopsis* Casper, Biblioth. Bot. 31(127–128): 99. 1966
Typus: *Pinguicula heterophylla* Benth. [ICN Art. 10.8 and designated by Casper 1963: 332 for *P.* sect. *Heterophyllum*; designated by Casper 1966: 99 for *P.* subsect. *Isolobopsis*]
= *Pinguicula* sect. *Longitubus* Zamudio & Rzed., Acta Bot. Mex. 14: 30. 1991
≡ *Pinguicula* subsect. *Infundibulares* Zamudio & Rzed., Acta Bot. Mex. 14: 31. 1991
Typus: *Pinguicula crassifolia* Zamudio
= *Pinguicula* subsect. *Utriculariopsis* Zamudio & Rzed., Acta Bot. Mex. 14: 31. 1991
Typus: *Pinguicula utricularioides* Zamudio & Rzed.
– "*Pinguicula* sect. *Mesoamericana* Shimai", Taxon. Conservation Ecol. Pinguicula: 350. 2017 [nom. inval., ICN Art. 30.9]
Intended type: *Pinguicula moranensis* Kunth

Species included: *Pinguicula acuminata*, *P. casperi*, *P. colimensis*, *P. conzatii*, *P. crassifolia*, *P. elizabethiae*, *P. emarginata*, *P. hemiepiphytica*, *P. heterophylla* (including *P. medusina*), *P. hondurensis*, *P. laueana*, *P. mesophytica*, *P. mirandae*, *P. moctezumae*, *P. moranensis* s.l., *P. oblongiloba* (including *P. michoacana*), *P. olmeca*, *P. orchidioides*, *P. parvifolia*, *P. potosiensis*, *P. rectifolia*, *P. robertiana*, *P. rzedowskiana*, *P. utricularioides*, *P. warijia*, *P. zamudioana*, *P. zecheri*. See comments under "Taxa *incertae sedis* in *P.* subg. *Temnoceras*" regarding the placement of *P. calderoniae*, *P. macrophylla*, and morphologically close species.

Section 2.5: *Pinguicula* sect. *Temnoceras* (Barnhart) Casper, Bot. Jahrb. Syst. 82: 333. 1963
≡ *Pinguicula* subg. *Temnoceras* Barnhart, Mem. New York Bot. Gard. 6: 47. 1916 [basionym]
– "*Pinguicula* sect. *Temnoceras* (Barnhart) Ernst", Bot. Jahrb. Syst. 80: 153. 1961, nom. inval. [ICN Art. 41.5]
Typus: *Pinguicula crenatiloba* DC. [single species name cited, ICN Art. 40.3]
– "*Pinguicula* sect. *Membraniformis* Shimai", Taxon. Conservation Ecol. Pinguicula 332 (2017) [nom. inval., ICN Art. 30.9]
Intended type: *Pinguicula lilacina* Schltdl. & Cham.

Species included: *Pinguicula bustamanta*, *P. crenatiloba*, *P. lilacina* (including *P. sharpii*), *P. pygmaea*, *P. takakii*.

Taxonomic and nomenclatural notes: If *P.* sect. *Temnoceras* and *P.* sect. *Orcheosanthus* are considered synonyms (as in Fleischmann & Roccia 2018), the correct name should be *P.* sect. *Orcheosanthus* due to priority. The phylogenetic position of the single DNA-sequenced specimen of *P. crenatiloba* (*Shimai s.n.* in herbarium TNS) is not certain in previous studies (see Shimai 2017 and Shimai *et al.* 2021), and so, there is also uncertainty regarding the correct placement and extent of both *P.* sect. *Temnoceras* and *P.* subg. *Temnoceras*. The analysis of DNA data from additional samples of *P. crenatiloba* is urgent to assess this problem, and further taxonomic and nomenclatural rearrangements of the homophyllous species are discouraged until then. In our analyses, *P. crenatiloba*

is sister to *P. lilacina*/*P. sharpii*, forming a well-supported group (Fig. 1), seconding the recognition of *P.* sect. *Temnoceras* as defined here.

Taxa *incertae sedis* in *P.* subg. *Temnoceras*:
Pinguicula subsect. *Caudatopsis* Casper, Biblioth. Bot. 31(127–128): 144. 1966
Typus: *Pinguicula macrophylla* Kunth [designated by Casper 1966: 144]
Pinguicula subsect. *Orcheosanthopsis* Casper, Biblioth. Bot. 31(127–128): 102. 1966
Typus: *Pinguicula imitatrix* Casper [single species name cited, ICN Art. 40.3]
Pinguicula sect. *Orchidioides* Luhrs, Phytologia 79: 118. 1996
Typus: *Pinguicula laxifolia* Luhrs
Pinguicula calderoniae Zamudio, Bol. Soc. Bot. México 68: 85. 2001
Taxonomic notes: Available DNA data from the ITS region place both *P. calderoniae* and *P. macrophylla* as sister species in *P.* sect. *Agnata* (Fig. 1). However, these two species are morphologically more similar to those of *P.* sect. *Orcheosanthus*, and indeed both *matK* and *rpl32* support this alternative placement for *P. macrophylla* (chloroplast data lacking for *P. calderoniae*). For caution and until having additional data, both species are regarded as *incertae sedis*, and the inclusion in *P.* sect. *Orcheosanthus* of some species sharing some morphological traits (e.g., *P. robertiana*, *P. rzedowskiana*) should be taken with caution (see above).
Pinguicula greenwoodii Cheek, Kew Bull. 49: 812. 1994
Taxonomic notes: This homophyllous species was originally placed in the Caribbean *P.* sect. *Homophyllum*, but its occurrence in Mexico and the colour of the corolla suggest that it belongs to *P.* sect. *Temnoceras*. Additional specimens are needed to clarify its taxonomic placement.

Subgenus 3: *Pinguicula* L. Sp. Pl. [Linnaeus] 1: 17. 1753 subg. *Pinguicula*
≡ *Pinguicula* L. Sp. Pl. [Linnaeus] 1: 17. 1753 sect. *Pinguicula*
≡ *Pinguicula* L. Sp. Pl. [Linnaeus] 1: 17. 1753 subsect. *Pinguicula*
≡ *Pinguicula* L. Sp. Pl. [Linnaeus] 1: 17. 1753 ser. *Pinguicula*
≡ *Pinguicula* subg. *Pionophyllum* Barnhart, Mem. New York Bot. Gard. 6: 47. 1916
– "*Pinguicula* sect. *Pionophyllum* DC.", Prodr. [A. P. de Candolle] 8: 28. 1844, nom inval. [ICN Art. 22.2]
Nomenclatural notes: De Candolle (1844) included all elements eligible as types for the corresponding autonyms of *Pinguicula* L. (ICN Art. 22.2), so "*P.* sect. *Pionophyllum*" was not validly published. In Barnhart (1916), however, *P. lusitanica* was excluded because it was treated in *P.* subg. *Isoloba*, and therefore Barnhart's subgeneric name is validly published because a type for *Pinguicula* was not designated until 1929 (see "Typus" below). To our knowledge, Barnhart's name has not been typified until now, so to avoid future confusions with this name, we explicitly designate *P. vulgaris* L. as the type, making the name homotypic to the autonym.
– "*Pinguicula* ser. *Septentrionales* Casper", Feddes Repert. 66: 114. 1962, nom inval. [ICN Art. 22.2]
– "*Pinguicula* ser. *Septentrionales* Casper", Bot. Jahrb. Syst. 82: 329. 1963, nom. inval. [ICN Art. 22.2]
– "*Pinguicula* ser. *Septentrionales* Casper", Biblioth. Bot. 31(127–128): 171. 1966, nom. inval. [ICN Art. 22.2]

Nomenclatural notes: Casper (1962: 114; 1963: 329; 1966: 171) included *P. vulgaris* L., which had previously been designated as type of *Pinguicula* L. by Hitchcock (in Hitchcock & Green, 1929: 116) (Art. 22.2).

Typus: *Pinguicula vulgaris* L. [designated by A.S. Hitchcock in Hitchcock A.S. & Green M.L. (1929) Nom. Prop. Brit. Bot.: 116 for *Pinguicula*; **designated here** for *P.* subg. *Pionophyllum*]

= *Pinguicula* ser. *Balcanicae* Casper, Feddes Repert. 66: 105. 1962

Typus: *Pinguicula balcanica* Casper [ICN Arts. 10.8 and 40.3]

= *Pinguicula* ser. *Grandiflorae* Casper, Feddes Repert. 66: 74. 1962 [as "*grandiflora*"]

Typus: *Pinguicula grandiflora* Lam. [ICN Art. 10.8]

= *Pinguicula* ser. *Hispanicae* Casper, Feddes Repert. 66: 112. 1962

Typus: *Pinguicula nevadensis* (H. Lindb.) Casper [only the type of this species name was included, ICN Art. 40.3]

= *Pinguicula* ser. *Longifoliae* Casper, Feddes Repert. 66: 61. 1962 [as '*Longifolia*']

≡ *Pinguicula* sect. *Longifoliae* (Casper) Blanca, Ruíz Rejón & Reg. Zamora, Folia Geobot. 34: 347. 1999 [as '*Longifolia*']

Typus: *Pinguicula longifolia* DC. [ICN Art. 10.8]

= *Pinguicula* ser. *Longifoliae* Casper, Biblioth. Bot. 31(127–128): 150. 1966, nom. illeg. [ICN Art. 53.3]

Typus: *Pinguicula vallisneriifolia* Webb [designated by Casper 1966: 150]

= *Pinguicula* ser. *Montanae* Casper, Biblioth. Bot. 31(127–128): 157. 1966

Typus: *Pinguicula leptoceras* Rchb. [designated by Casper 1966: 157]

= *Pinguicula* ser. *Prealpicae* Casper in Ansaldi & Casper, Wulfenia 16: 13. 2009

Typus: *Pinguicula poldinii* J. Steiger & Casper

– "*Pinguicula* ser. *Montanae* Casper", Feddes Repert. 66: 88. 1962, nom inval. [ICN Arts. 40.1 and 40.3]

– "*Pinguicula* ser. *Montanae* Casper", Bot. Jahrb. Syst. 82: 32. 1963, nom inval. [ICN Arts. 40.1 and 40.3]

Nomenclatural notes: When Casper (1962: 88 and 1963: 328) intended to publish "*P.* ser. *Montanae*", he included more than one species name and did not indicate any as type, so the name cannot be considered validly published in any of the two publications (ICN Arts. 40.1 and 40.3).

Species included: *Pinguicula apuana*, *P. arvetii*, *P. balcanica*, *P. bohemica*, *P. caussensis*, *P. casperiana*, *P. christinae*, *P. corsica*, *P. dertosensis*, *P. fiorii*, *P. fontiqueriana*, *P. grandiflora*, *P. leptoceras*, *P. longifolia*, *P. macroceras*, *P. mariae*, *P. mundi*, *P. nevadensis*, *P. poldinii*, *P. reichenbachiana*, *P. saetabensis*, *P. sehuensis*, *P. submediterranea*, *P. tejedensis*, *P. vallisneriifolia*, *P. vallis-regiae*, *P. vulgaris*.

Sections *incertae sedis*

Pinguicula sect. *Nana* Casper, Bot. Jahrb. Syst. 82: 329. 1963

– "*Pinguicula* sect. *Nana* Casper", Feddes Repert. 66: 41. 1962, nom. inval. [ICN Arts. 40.1 and 40.3]

Typus: *Pinguicula villosa* L. [designated by Casper 1963: 329]

Nomenclatural notes: When Casper (1962: 41) intended to publish "*P.* sect. *Nana*", he included more than one species name and did not indicate any as type, so the name cannot be considered validly published (ICN Art. 40.1 and 40.3).

= *Pinguicula* ser. *Variegatae* Casper, Bot. Jahrb. Syst. 82: 335. 1963

Typus: *Pinguicula variegata* Turcz. [ICN Art. 10.8]

Species included: *Pinguicula algida*, *P. ramosa*, *P. spathulata*, *P. villosa*.

Taxonomic notes: The group formed by these species is morphologically homogeneous and easy to diagnose on account of the temperate-heterophyllous growth form, the ± densely glandular scapes and sepals (the sepals in *P. algida* are more sparsely glandular than those of the other species), the scapes being also comparatively large and ± succulent, sometimes bearing more than one flower in two of the species, the comparatively small, usually lilaceous to violet flowers with a yellow palate, the ± distinctly petiolate and comparatively small leaves, and the habitat and distribution, with an apparent low tolerance to heat. Although this group has been considered a section within *P.* subg. *Temnoceras* by Fleischmann & Roccia (2018) and Fleischmann (2021), both its morphology and the phylogenetic reconstructions by Shimai (2017) and Shimai *et al.* (2021) suggest a placement elsewhere. The phylogenetic position is far from being resolved. In the phylogenetic reconstructions of Cieslak *et al.* (2005), based on the *trnK-matK* chloroplastic DNA region, the relationship of this group with the clade formed by *P. alpina* and the Mexican/Central American/Caribbean species is totally unsupported, while in Beck *et al.* (2008), who also used only *trnK-matK*, it is solely supported by the Bayesian analysis. Most phylogenies inferred from ITS data in Degtjareva *et al.* (2006) showed a closer but unsupported relationship to *P.* subg. *Pinguicula*, which might make sense taking into account the growth form and usual coloration of the corolla (except for the yellow palate) and especially the similar distribution. In Shimai (2017) and Shimai *et al.* (2021) the phylogenies based on the nuclear ITS region placed this group closer to *P.* subg. *Pinguicula* once more, while reconstructions based on DNA data from the chloroplast (*trnK-matK*, *rpl32-trnL*) placed this group closer to *P.* subg. *Isoloba*; this last option would be supported by, e.g., the colour of the corolla and the distribution. Nonetheless, none of these relationships received strong support, and ancient reticulation may have led to this lineage, which would explain conflicting tree topologies. Our phylogenetic analyses (Fig. 1) also point to similar results: *Pinguicula* sect. *Nana* is sister to *P.* subg. *Pinguicula* in the ITS and *trnK* trees (supported by SH-aLRT, BS, and TBE), sister to *P.* subg. *Temnoceras* in the *matK* tree (supported by TBE), and closer to *P.* subg. *Isoloba* in the *rpl32* tree (supported by TBE). The placement most in agreement with the morphological and chorological data is that of the ITS and *trnK* data, and also this placement is the one that received the highest support. Therefore, we have relegated this group as *incertae sedis* within the infrageneric classification of *Pinguicula*, while considering a placement within *P.* subg. *Pinguicula* as possibly most appropriate, according to morphology and distribution data.

Pinguicula sect. *Micranthus* Casper, Bot. Jahrb. Syst. 82: 335. 1963

≡ *Pinguicula* subg. *Micranthus* Casper, Bot. Jahrb. Syst. 82: 333. 1963, nom. illeg. [ICN Art. 52.1]

– "*Pinguicula* subg. *Micranthus* Casper", Feddes Repert. 66: 41. 1962, nom. inval. [ICN Arts. 40.1 and 40.3]

– "*Pinguicula* sect. *Micranthus* Casper", Feddes Repert. 66: 45. 1962, nom. inval. [ICN Arts. 40.1 and 40.3]

≡ *Pinguicula* ser. *Alpinae* Casper, Bot. Jahrb. Syst. 82: 335. 1963

– "*Pinguicula* sect. *Alpinae* (Casper) Shimai", Taxon. Conservation Ecol. Pinguicula: 231. 2017, nom. inval. [ICN Arts. 30.9 and 41.5]

Typus: *Pinguicula alpina* L., Sp. Pl. 1: 17. 1753. [designated by Casper 1963: 333 for *P.* subg. *Micranthus*, and by Casper 1963: 335 for *P.* sect. *Micranthus* and *P.* ser. *Alpinae*]

Species included: *Pinguicula alpina* (including *P. gongshanensis*).

Nomenclatural notes: When Casper (1962: 41 and 1962: 45) intended to publish "*P.* subg. *Micranthus"* and "*P.* sect. *Micranthus*", respectively, he included more than one species name and did not indicate any as type, so the names cannot be considered validly published (ICN Art. 40.1 and 40.3). *Pinguicula* subg. *Micranthus* (Casper 1963: 333) is illegitimate due to the inclusion of *P. crenatiloba*, type of *P.* subg. *Temnoceras*, the name that ought to have been adopted (ICN Art. 52.1). *Pinguicula* sect. *Micranthus* is, however, legitimate because *P. alpina* was designated as type, there was no competing synonym at that rank, and it was validly published in the same study (ICN Art. 53.1, Note 1).

Taxonomic notes: *Pinguicula alpina* is a morphologically and phylogenetically rather isolated species. It is the only species with temperate-heterophyllous growth form (i.e., forming hibernacula in winter and morphologically similar carnivorous leaves throughout the growing period) that has consistently white to yellow-white flowers and well-developed roots that persist year-round. Although the phylogenetic reconstructions from Cieslak *et al.* (2005), Beck *et al.* (2008), Shimai (2017), and Shimai *et al.* (2021) place *P. alpina* as sister to the clade comprising most of the Neotropical species (except the Andean ones in *P.* sect. *Ampullipalatum*), its inclusion as the only temperate-heterophyllous species in *P.* subg. *Temnoceras* makes this subgenus highly heterogeneous and, thus, difficult to diagnose. Furthermore, the statistical support of the clade including both *P. alpina* and *P.* subg. *Temnoceras* greatly varied depending of the study and the analyzed locus. In fact, the position inferred from the *rpl32-trnL* dataset in Shimai (2017) was discordant, sister to the clade representing *P.* subg. *Pinguicula*, which would make sense considering the growth form and distribution. In our analyses, *P. alpina* is sister to *P.* subg. *Pinguicula* (in broad sense, not necessarily excluding *P.* sect. *Nana*) with ITS, *rpl32*, and *trnK* data (supported by SH-aLRT and TBE), and it is sister to *P.* subg. *Temnoceras* using *matK* data (strongly supported in all analyses). The strong signal of the *matK* region seems to dominate the placement in combined analyses (e.g., Shimai 2017). However, given that all other DNA regions suggest a closer placement to *P.* subg. *Pinguicula* (despite the lower statistical support), and both the morphology and chorology would be in full agreement with this last option, we should not reject this alternative placement with the available information. We hope that additional DNA data, especially from nuclear regions, will help to elucidate the phylogenetic relationships of this highly distinct species.

Discussion

As explained in detail by Fleischmann (2021), the infrageneric classification of *Pinguicula* has undergone major changes since Casper (1962, 1963, 1966) to the present days. A stable and usable classification would preferably be the result of recognizing naturally evolving groups (i.e., monophyletic) that are at the same time diagnosable based on a series of observable traits (Christenhusz *et al.* 2015). These traits should ideally be synapomorphic (i.e., present in all species of a same group) and non-homoplastic (absent in species of any other group), although synapomorphic combinations of characters may be of diagnostic value when isolated characters lack it. The failure in following monophyly or diagnosability criteria would make a classification unnatural or impractical. Nevertheless, the criterion of monophyly may not always be achievable when evolution is reticulate, and therefore better represented as species networks rather than species trees. Groups where reticulation plays a significative role in the evolutionary process represent a challenge for strictly hierarchical classifications (Bremer & Wanntorp 1979, Sosef 1997), where a same lower-ranked taxon cannot be simultaneously placed in more than one higher-ranked taxon. The recognition of nothotaxa with

hybrid names (ICN, Chapter H) might help to alleviate this situation, but it is not developed above the rank of genus and seldom used for names of subdivisions of genera.

Morphology, distribution, and their meaning for infrageneric delimitations

It is becoming clearer that the growth forms and the distribution of *Pinguicula* species are rather well correlated to several monophyletic groups, and thus those characters, in combination with others, can be used to support diagnosable phylogenetically natural units (Fleischmann 2021). Of the three major growth forms (strictly homophyllous, temperate-heterophyllous forming a hibernaculum, and tropical-heterophyllous forming a rosette of non-carnivorous leaves ―sometimes facultatively, as in *P. moctezumae* or *P. emarginata*; Fig. 2), there are very few exceptions within each of the sections recognised by Fleischmann (2021).

Species with a strictly homophyllous growth form (Fig. 2) are distributed in *P.* subg. *Isoloba* (all sections), *P.* sect. *Homophyllum*, and *P.* sect. *Temnoceras*. Species in these groups may be annuals (rare, only few species) or perennials, traits that are sometimes synapomorphic at the sectional level. These sections, however, do not form a single monophyletic group, and therefore it is not possible to define a subgenus whose diagnostic character is "homophylly" alone. On the other hand, the addition of the geographical distribution allows the distinction of *P.* subg. *Isoloba* (temperate and Andean region) from the sections of *P.* subg. *Temnoceras* containing homophyllous species (tropical America, as other species in that subgenus). The few usually homophyllous species in *P.* sect. *Orcheosanthus* (e.g., *P. emarginata*) and *P.* sect. *Agnata* (e.g., *P. gigantea*) are able to form non-carnivorous leaves under exceptional circumstances such as adverse, very dry conditions, and are otherwise morphologically similar and obviously related to other species with a tropical-heterophyllous growth form.

Species with a temperate-heterophyllous growth form (forming a hibernaculum, Fig. 2) belong to *P.* subg. *Pinguicula*, *P.* sect. *Nana*, and *P.* sect. *Micranthus*. These three sections, which additionally contain species with overlapping ranges in the temperate Northern Hemisphere, all perennial, do not clearly form a monophyletic group in the available DNA-based phylogenetic analyses. The positions of *P.* sect. *Nana* and *P.* sect. *Micranthus* varied depending on the locus analysed (see Fig. 1 and "Taxonomic notes" under these names). If either *P.* sect. *Micranthus* or *P.* sect. *Nana* (or both) are included within *P.* subg. *Temnoceras* (following Fleischmann & Roccia 2018 and Fleischmann 2021), then this last subgenus cannot be characterised either by the growth form, the geography, or the combination of both, and not even by the addition of other characters. The diagnosability of *P.* subg. *Temnoceras* would then be challenging or impossible, making the name unpractical. On the other hand, the three groups with temperate-heterophyllous growth form, which also have additional characters that make them easily diagnosable, might be recognised as one subgenus, but further data are needed to confirm this hypothesis.

Pinguicula elongata is a very peculiar species with a growth form in between of the temperate-heterophyllous and the tropical-heterophyllous ones, with two flowering seasons and phylogenetically clearly related to the group of Mexican/Central American/Caribbean taxa (Beck *et al.* 2008; Shimai 2017; Shimai *et al.* 2021), which is not totally discordant with its distribution; it is recognised in its own *P.* sect. *Heterophylliformis*. Finally, the tropical-heterophyllous growth form (Fig. 2) is present in the immense majority of species of *P.* sect. *Agnata* and *P.* sect. *Orcheosanthus*, two groups that are also very closely related and form a higher-level monophyletic group. All these species are distributed in Mexico, Central America and the Caribbean, are ± perennial, and tend to

Figure 2: Morphology of selected examples of *Pinguicula* showing the different growth forms and associated flowers for each subgenus. Left: *Pinguicula* subg. *Pinguicula*, flower of *P. vallisneriifolia* and hibernacula of *P. casperiana* (temperate heterophyllous growth form). Center: *Pinguicula* subg. *Temnoceras*, flower of *P. hemiepiphytica* and rosette of non-carnivorous leaves of *P. laueana* with carnivorous leaves just sprouting (tropical heterophyllous growth form). Right: *Pinguicula* subg. *Isoloba*, flower of *P. hirtiflora* and rosette of carnivorous leaves of *P. habilii* (homophyllous growth form). Photos: J. C. Zamora.

have a single flowering period (with exceptions, as in the facultatively heterophyllous species). This distribution is, precisely, what best unites homophyllous and heterophyllous species in *P.* subg. *Temnoceras* as recognised here and can be considered diagnostic for the group.

Karyology

Besides morphology, karyological data have been used to characterise some infrageneric taxa in *Pinguicula* (Shimai *et al.* 2021). Casper & Stimper (2009) summarised and uniformised many chromosome counts from various studies and also provided novel counts; their results are synthetised here (Table 2).

The lowest reported chromosome number is $2n = 12$, unique of *P. lusitanica* (*P.* sect. *Pumiliformis*), while the highest is $2n = 128$ for hexadecaploid specimens of *P. apuana* and *P.* cf. *vulgaris* (s.l.) in *P.* sect. *Pinguicula*. The basic number $n = 8$ is very widespread in the genus, being characteristic of all studied species in *P.* sect. *Ampullipalatum* ($2n = 16$) and *P.* sect. *Temnoceras* ($2n = 16$), and apparently also of *P.* sect. *Pinguicula* and *P.* sect. *Micranthus*, where multiples, usually $2n = 32$ (tetraploids) and $2n = 64$ (octoploids), but up to $2n = 128$ in hexadecaploids, are the rule. $2n = 16$

chromosomes was also reported for *P. albida* (*P.* sect. *Homophyllum*) and *P. villosa* (*P.* sect. *Nana*), 2*n* = 32 for some species in *P.* sect. *Brandonia* and for *P. esseriana* (*P.* sect. *Agnata*), and 2*n* = 64 for *P. variegata* (*P.* sect. *Nana*).

Table 2. Chromosome numbers from Casper & Stimper (2009) within the currently accepted taxonomy.

Subgenus	**Section**	**Basic chromosome number**	**Total chromosome counts**
P. subg. *Isoloba*	*P.* sect. *Ampullipalatum*	*n* = 8	2*n* = 16 (all species)
	P. sect. *Brandonia*	*n* = 11 *n* = 8	2*n* = 22 (*P. ionantha*, *P. primuliflora*, *P. pumila*) 2*n* = 32 (*P. caerulea*, *P. lutea*, *P. planifolia*)
	P. sect. *Cardiophyllum*	*n* = 14	2*n* = 28 (*P. crystallina*, *P. hirtiflora*) 2*n* = 56 (*P. habilii*, *P. hirtiflora*)
	P. sect. *Pumiliformis*	*n* = 6	2*n* = 12 (*P. lusitanica*)
P. subg. *Temnoceras*	*P.* sect. *Agnata*	*n* = 11 *n* = 8	2*n* = 22 (most species) 2*n* = 44 (*P. ehlersiae*) 2*n* = 32 (*P. esseriana*)
	P. sect. *Heterophylliformis*		unknown
	P. sect. *Homophyllum*	*n* = 8 *n* = 9 *n* = 11	2*n* = 16 (*P. albida*) 2*n* = 18 (*P. bissei*, *P. filifolia*) 2*n* = 22 (*P. caryophyllacea*)
	P. sect. *Orcheosanthus*	*n* = 11	2*n* = 22 (most species) 2*n* = 44 (*P. moranensis*)
	P. sect. *Temnoceras*	*n* = 8	2*n* = 16 (all species)
	Incertae sedis	*n* = 11	2*n* = 22 (*P. calderoniae*, *P. macrophylla*)
P. subg. *Pinguicula*	*P.* sect. *Pinguicula*	*n* = 8	2*n* = 16 (*P. corsica*) 2*n* = 32 (many species) 2*n* = 64 (many species) 2*n* = 128 (*P. apuana*, *P.* cf. *vulgaris* [s.l.])
Incertae sedis	*P.* sect. *Micranthus*	*n* = 8	2*n* = 32 (*P. alpina*)
	P. sect. *Nana*	*n* = 8 *n* = 9	2n = 16 (*P. villosa*) 2n = 64 (*P. variegata*) 2n = 18 (*P. ramosa*)

The immense majority of species in the closely related *P.* sect. *Agnata* and *P.* sect. *Orcheosanthus* have the basic number $n = 11$ chromosomes (usually as diploids with $2n = 22$, but rarely $2n = 44$ for tetraploids in *P. ehlersiae* and *P. moranensis*), with the exception of *P. esseriana* ($2n = 32$) as indicated above. $2n = 22$ is also present in some species of *P.* sect. *Brandonia*.

On the other hand, $n = 9$ ($2n = 18$) chromosomes is an uncommon number only reported in a couple species of *P.* sect. *Homophyllum* and in *P. ramosa* (*P.* sect. *Nana*), while all species of *P.* sect. *Cardiophyllum* have a basic number of $n = 14$ chromosomes, either as diploids ($2n = 28$) or tetraploids ($2n = 56$), counts that are unique to this last section and presumably diagnostic (but see Casper & Stimper 2009 for comments on other numbers reported in the literature). Finally, the chromosome number of *P. elongata* (*P.* sect. *Heterophylliformis*) is not yet known.

To help with the identification and justification of the main groups accepted here, the following dichotomous key to *Pinguicula* subgenera and sections is provided:

1. Species developing a well-defined hibernaculum of non-carnivorous leaves in winter (temperate-heterophyllous growth form); perennial; flowering once per year; Holarctic……2
1. Species not forming a (proper) hibernaculum (either homophyllus or tropical-heterophyllous or anisophyllous growth form; non-carnivorous rosettes sometimes bulb-like) or exceptionally so (then tropical-anisophyllous, with two flowering periods per year, and Neotropical); perennial or annual; flowering once to several times per year (sometimes ± continuously); widely distributed……4

2. Palate not yellow (except for a small yellowish spot or area in some populations of *P. corsica*, *P. vallisneriifolia*, and *P. vulgaris*); ± broadly distributed across the Holarctic realm……***P.* subg. *Pinguicula* (*P.* sect. *Pinguicula*)**
2. Palate ± yellow; arctic-boreal and alpine species…….....……..…3

3. Corolla consistently white with yellow marks to almost entirely yellow; scapes and sepals subglabrous to sparsely glandular; roots persistent in winter……...……***P.* sect. *Micranthus***
3. Corolla ± lilac or violaceous (except in anthocyan-free forms); scapes and sepals ± densely glandular; roots not persistent in winter……...……***P.* sect. *Nana***

4. Species with a homophyllous to (rarely) anisophyllous growth form (continuously forming carnivorous leaves throughout the year); distributed in the Holarctic and in the Andean region……..……...……5 – ***P.* subg. *Isoloba***
4. Species with homophyllous, anisophyllous or heterophyllous (with a period in which non-carnivorous leaves are formed) growth forms; distributed in Mexico, Central America and the Caribbean region……...……8 – ***P.* subg. *Temnoceras***

5. Distributed in the Andean Region; corolla often with a broadly conical to ± broadly saccate spur, not always clearly delimited from the tube; scapes, in anthesis, often shorter to slightly longer than the leaves (rarely up to twice as long), subglabrous, sparsely, or moderately glandular……***P.* sect. *Ampullipalatum***
5. Distributed in the Holarctic; corolla with a narrowly conical to ± saccate spur, always clearly (and often, sharply) delimited from the tube; scapes, in anthesis, often much longer than the leaves (rarely of roughly equal length), moderately to densely glandular-pubescent…….....……6

6. Nearctic species; corolla with a strongly protruding palate densely covered by long hairs……***P.* sect. *Brandonia***
6. Palearctic species; corolla without or with a protruding palate, in the last case, papillose to shortly pubescent……7

7. Corolla distinctly bilabiate, with the two upper petals smaller than the three lower ones; lobes often notched; palate yellow, not conspicuously protruding; leaf margin involute or not, but never concealing most of the leaf upper surface; perennials……***P.* sect. *Cardiophyllum***
7. Corolla subactinomorphic, with roughly equal petals; palate not yellow, clearly protruding; lobes with entire, rounded margin; leaf margin conspicuously involute and frequently concealing an important part of the leaf upper surface, sometimes most of it; annuals to short-lived perennials……***P.* sect. *Pumiliformis***

8. Heterophyllous species typically with two periods in which carnivorous leaves are produced, alternating with two periods in which non-carnivorous leaves are formed, in one of them forming a loose hibernaculum but retaining its roots; typically with two different flowering periods; leaves thread-like, upright……***P.* sect. *Heterophylliformis***
8. Either homophyllous/anisophyllous growth form, or heterophyllous with a single period of production of carnivorous leaves and a single period of production of non-carnivorous leaves; roots typically dying in the non-carnivorous state; with a single (but sometimes extended) flowering period or flowering ± continuously; leaves in a flat rosette or upright, of various shapes……9

9. Homophyllous to (rarely) anisophyllous growth form……10
9. Frequently tropical-heterophyllous growth form, sometimes facultative and non-carnivorous leaves only produced under very unfavorable (dry) conditions……11

10. Leaves thin, often semi-transparent, with a conspicuously involute margin in the distal 1/2–2/3, usually not involute at all in the cuneate base; corolla pale lilac to whitish; distributed in Mexico……***P.* sect. *Temnoceras***
10. Leaves, in general, not particularly thin, rarely semi-transparent, with a straight to slightly revolute or involute margin, rarely conspicuously involute but then without a clear distinction between the distal and basal parts; corolla white, pink, or blue; distributed in the Caribbean region……***P.* sect. *Homophyllum***

11. Carnivorous leaves thin, ± membranous, not succulent (particularly thin and papery in *P. emarginata*); non-carnivorous rosettes rather variable, ± flat, concave or bulb-like (if leaves are thread-like, then winter rosettes not flat)……***P.* sect. *Orcheosanthus***
11. Carnivorous leaves often ± thick and fleshy, subsucculent; non-carnivorous rosettes frequently flat (always if leaves are thread-like)……***P.* sect. *Agnata***

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