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Pinguicula chuquisacensis (Lentibulariaceae), a new species from the Bolivian Andes, and first insights on phylogenetic relationships among South American *Pinguicula*

Abstract

Beck, S. G., Fleischmann, A., Huaylla, H., Müller, K. F. & Borsch, T.: *Pinguicula chuquisacensis (Lentibulariaceae),* a new species from the Bolivian Andes, and first insights on phylogenetic relationships among South American *Pinguicula.* – Willdenowia 38: 201-212. – ISSN 0511-9618; © 2008 BGBM Berlin-Dahlem.
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Pinguicula chuquisacensis is described and illustrated as a new species from the department of Chuquisaca of Bolivia. Data on distribution, ecology and a key for identification among other central Andean species are given. DNA sequence data are presented for this new taxon and related Andean species of *Pinguicula* for the first time. The plastid tree reveals a lineage of central Andean species (within the clade of tropical growth type species), whereas the northern Andean (Colombia, Venezuela) *P. elongata* appears distantly related and sister to all remaining taxa of the Mexican-Central American-Caribbean clade of *Pinguicula.*

Resumen

Se describe y se ilustra una nueva especie de *Pinguicula* de Chuquisaca, Bolivia, *P. chuquisacensis.* Se discuten la distribución, el hábitat y la ecologías y se presenta una clave de identificación entre las especies de las Andes Centrales. Se presentan una filogenia obtenida sobre la base de secuencias de ADN incluyendo este nuevo taxón y de las especies Andinas relacionadas por la primera vez. *P. chuquisacensis* pertenece a un grupo monofilético de las especies de las Andes Centrales pero *P. elongata* de las Andes del Norte (Colombia, Venezuela) es una línea hermana de todos los otras especies de *Pinguicula* que representan un clado distribuido en Mexico, Centro America y en el Caribe.

Additional key words: carnivorous plants, Andean biogeography, taxonomy, phylogenetics, *matK/trnK*

Introduction

The genus *Pinguicula* L. belongs to the carnivorous angiosperm family *Lentibulariaceae,* and is the sister group of the *Genlisea-Utricularia* clade (Jobson & al. 2003; Müller & al. 2004). *Pin-*

guicula is well supported as monophyletic by both molecular and morphological characters (Müller & al. 2004). Characteristic are flypaper traps with a special type of mucilage glands that loose turgor upon stimulation. To the contrary, the other two genera possess morphologically complex eel or bladder traps. Casper monographed *Pinguicula* in 1966, thereby recognizing 48 species. In a more recent synopsis Legendre (2000) already lists 85 species, and this number is still growing. Zamudio (2001, 2003, 2005) described several new taxa from Mexico; Casper & Urquiola Cruz (2003) and Casper (2003, 2004, 2007) from Cuba; and even in the European Alps a well isolated and easily distinguishable new species was discovered (Steiger & Casper 2001). Therefore, *Pinguicula* can be estimated to contain an approximated 100 species.

The first comprehensive phylogenetic analysis of *Pinguicula* used plastid *trnK/matK* sequence data (Cieslack & al. 2005). Rather than supporting a previous subgeneric and sectional classification system that had largely been based on floral morphology (Casper 1966), several geographically distinct radiations were unravelled. The most speciose of these radiations is a Mexican-Central American-Caribbean clade (*P. filifolia* Griseb., *P. moranensis* Kunth and relatives) with *P. alpina* L. as sister group. A Eurasian radiation with shallow branches probably resulting from rapid speciation comprises north temperate and sub-boreal taxa (*P. leptoceras* Rchb., *P. vulgaris* L. and relatives), whereas East Asian (*P. villosa* L. and relatives) and Mediterranean (*P. lusitanica* L. and relatives) appear as distinct lineages (Cieslack & al. 2005). From the South American butterworts *P. antarctica* Vahl (Patagonia, Tierra del Fuego) was resolved as the sister group to a clade of species from the southeastern United States (*P. lutea* Walter and relatives). So far, *P. antarctica* was the only South American *Pinguicula* included in any phylogenetic analysis. Degtarajeva & al. (2006) generated nrITS trees for *Pinguicula,* focussing on the Eurasian clade with particularly dense taxon sampling. Several major clades were congruently discovered with high bootstrap support such as the Eurasian clade *(P.* sect. *Pinguicula)* or the clade of species with tropical growth type from the southeastern United States (*P. lutea* and relatives), whereas deeper nodes only received confidence in Bayesian analysis of the data. Incongruent placements of *P. lusitanica* and *P. vulgaris* in the chloroplast and nuclear gene trees may point to the presence of ancient hybridisation in the evolution of *Pinguicula* but with the currently available data no conclusive assessment of reticulate evolution or other modes of speciation is possible. Using ITS sequences Shimai & al. (2007) recently analysed relationships among Cuban species of *Pinguicula*. These authors were also able to show that most of these narrow endemic species are distinguishable by their ITS ribotypes.

South American species of *Pinguicula* are known to grow in high Andean Paramo, Puna and Tierra Fria habitats (*P. calyptrata* Kunth, *P. elongata* Benj., *P. involuta* Ruiz & Pav.) or in Antarctic rain forests (*P. antarctica*, *P. chilensis* Clos; Casper 1966). All five South American species of *Pinguicula* were considered as closely related by Casper (1966) and classified as *P.* sect. *Ampullipalatum* Casper. In Bolivia the only known *Pinguicula* species was *P. involuta,* occurring in the Yungas of the La Paz departamento.

During preparation of the treatment of *Lentibulariaceae* for the Catalogo de las Plantas Vasculares de Bolivia morphologically and ecologically deviating plants of a new species of *Pinguicula* were encountered. Aims of this study were to evaluate their relationships among the South American taxa of *Pinguicula* using molecular and morphological data, to describe them as a new species, *P. chuquisacensis,* and to provide a key for identification of the currently accepted Andean species.

Material and methods

Plants were studied in their natural habitat by Hibert Huaylla at the type locality in Chuquisaca, Bolivia, and as herbarium specimens (see specimens citations). The validating description was provided by the authors of the new species. Measurements were taken from herbarium specimens and corollas were dissected using a binocular for detailed morphological analysis. Since herbar-

Table 1. List of the *Pinguicula* species and sources of the plant material from which *matK/trnK* sequences were generated and added to the *Pinguicula* alignment of Cieslack & al. (2005).

Species	Source	GenBank number	Geographic distribution
P. calyptrata	Peru, Depto. Amazonas, Prov. Chachapoyas, Balsas road to Leymebabamba, just below Abra Callacalla, 3559 m, *M. Weigend, E. Rodriguez, H. Förther & N. Dosert 2000/867* (M)	FM200225	central Andes (Colombia, Ecuador, Peru)
P. chuquisacensis	Bolivia, *C. E. Hinchliff, W. B. Warrington & A. Lliully 595* (without voucher but of same population as *Lliully & al. 587*, see specimens, below)	FM200223	central Andes (Bolivia)
P. elongata	Colombia, from tissue culture (no voucher)	FM200224	northern Andes (Colombia, Venezuela)
P. involuta	Peru, Dept. Huanuco, Weg von Laguna Copra zur Negro Coche, c. 3800 m, *T. Hofreiter & T. Franke 1/38* (M)	FM200226	central Andes (Bolivia, Peru)

ium material did not yield genomic DNAs in a quality that could be used for amplification of *matK/trnK* or ITS (T. Borsch, unpublished data), an additional specimen had to be recollected *(A. Lliully 895)* with some leaves preserved on silica gel.

For molecular phylogenetic analysis, *matK/trnK* sequences of *P. elongata, P. involuta, P. calyptrata* and of the new species were generated and added to the already existing *Pinguicula* alignment of Cieslack & al. (2005). Laboratory and alignment methods basically followed those described in Cieslack & al. (2005). The *trnK* intron including the *matK* gene was amplified and sequenced in two halves using primers trnK3914Fdi (GGGGTTGCTAACTCAACGG) and Le1 (ATAGAAATAGATTCGTTC) as well as ACmatK500F (TTCTTCTTTGCATTTATTACG) and trnK2R (AACTAGTCGGATGGAGTAG). The four new sequences generated for this study can be downloaded from EMBL/GenBank (Table 1). The alignment is available from the senior author upon request.

PAUP* (Swofford 2002) was used to execute parsimony ratchet command files generated by PRAP (Müller 2004). 10 random addition cycles with 200 ratchet iterations each were employed. During bootstrapping, searches for the optimal trees were far less intense, with only one tree swapped upon via TBR branch swapping in each replicate (Müller 2005). To minimize standard errors of bootstrap proportions, 10 000 replicates were run.

MrBayes v3.1.2 (Ronquist & Huelsenbeck 2003) was used for Bayesian analyses under the GTR+Γ model. Default priors were used, i.e. flat dirichlets (1.0,…,1.0) for state frequencies and instantaneous substitution rates, a uniform prior (0.0, 50.0) for the shape parameter of the gamma distribution, a uniform prior (0.0, 1.0) for the proportion of invariable sites, a uniform topological prior, an exponential prior Exp(10.0) for branch lengths. Four categories were used to approximate the gamma distribution. Two runs with 2 million generations each were run, and four chains were run in parallel for each run, with the temperature set to 0.2. The chains were sampled every 100th generation. To check for convergence of the independent runs under a given model, we ensured that plots of both runs indicate that stationary phase was reached in both runs, the potential scale reduction factor approached 1 for all parameters, and no significantly conflicting nodes were found among the consensus trees from the individual runs.

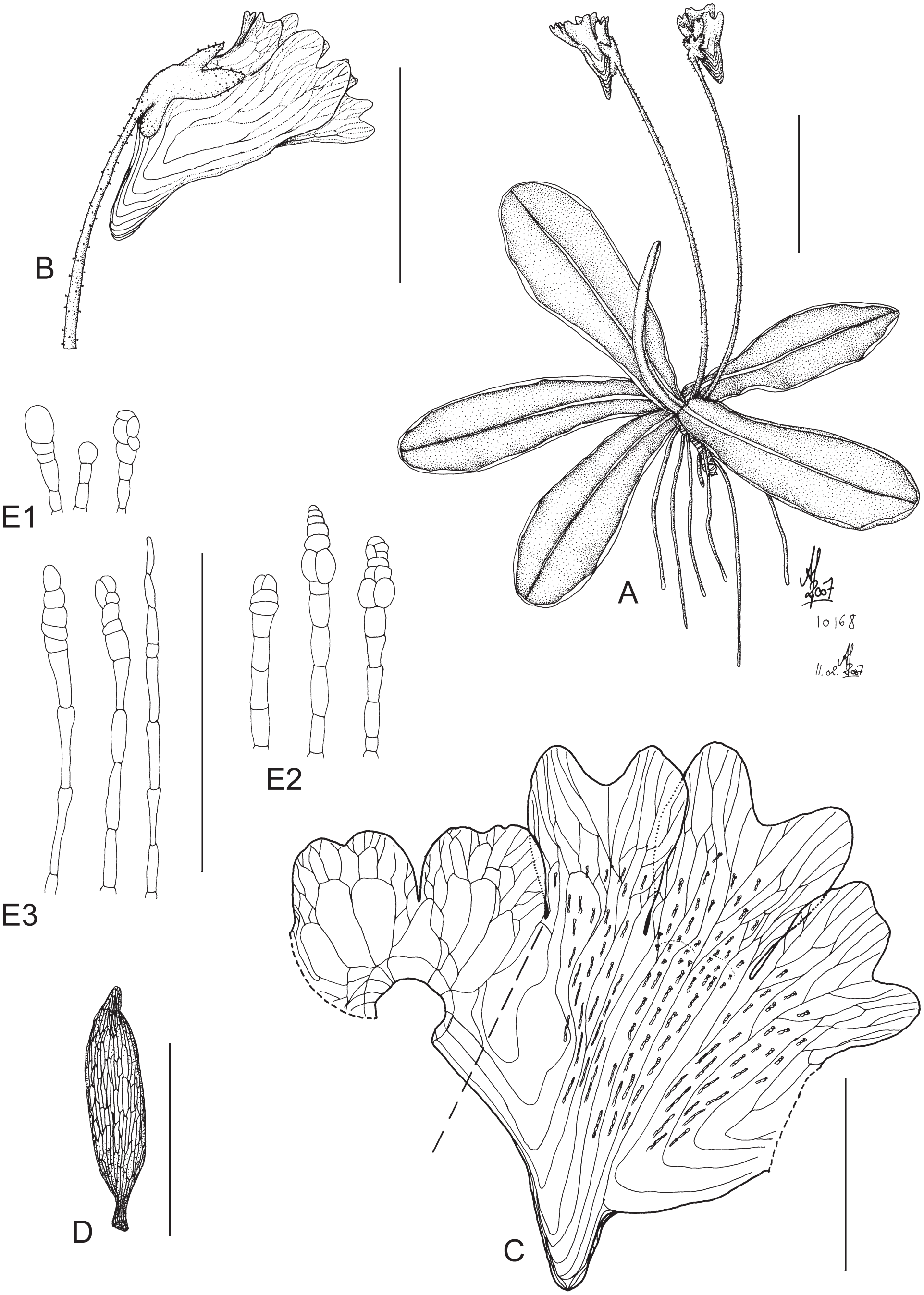

Fig. 1. *Pinguicula chuquisacensis* – A: habit of flowering plant; B: lateral view of the flower; C: corolla, opened; D: seed; E: hairs of the corolla tube, E1: hairs of the palate region, E2: hairs of the base of the lobes of the lower lip, E3: hairs of the three rows in the corolla tube interior. – Scale bars: A = 20 mm, B = 10 mm, C = 5 mm, D = 50 μm, E = 100 μm; drawn from the type collection by Andreas Fleischmann.

Results

Pinguicula chuquisacensis S. Beck, A. Fleischm. & Borsch, **sp. nov.**
Holotype: Bolivia, Depto. Chuquisaca, Prov. Belisario Boeto, 1 km de Nuevo Mundo a Padilla, 2250 m, 5.7.1995, *M. Kessler 5149 & J. Gonzales & K. Bach* (LPB; isotype: B).

Paratypes. – BOLIVIA: CHUQUISACA: Boeto, Nuevo Mundo, NE of Villa Serrano, steep base hills with wooded valleys and rough grazing, 2400 m, 23.11.1995, *J. R. I. Wood 10168* (HSB, K, LPB); Boeto, 1 km de la comunidad de Nuevo Mundo, camino a Serrano, 2518 m, 14.5.2004, *H. Huaylla 1121* (HSB, MO); Boeto, Nuevo Mundo, Quebrada Nuevo Mundo, cañón húmedo al sudoeste del pueblo, 2145 m, 30.11.2005, *J. Villalobos con M. Paredes & D. Villalobos 501* (B, HSB, LPB); same locality, 2.7.2007, *C. E. Hinchliff* with *W. B. Warrington & A. Lliully 587* (HSB, LPB, M, WS).

Pinguicula calyptrata Kunth affinis sed foliis 4-6 (non 5-10), valde majoribus (4-11 cm non 1-4.5 cm), oblongis ad ovato-oblongis (non obovatis ad rotundato-obtusis), corolla albida (non purpurea ad pallide lilacina), lobis labii superioris lobis labii inferioris distincte brevioribus (non similibus), subrectangulis et subemarginatis vel integerrimis (non profunde emarginatis) differt.

Herba perennis. *Rhizoma* simplex, ca. 15 mm longum, radicibus adventitiosis filiformibus numerosis. *Folia* 4-6 radicalia rosulata, solum adpressa vel suberecta, succulenta (sicco membranacea), (3-)4-6(-11) cm longa et (1-)2-3 cm lata, oblonga vel ovato-oblonga, apice rotundata, basin versus abrupte angustata, margine leviter involuta, laete viridia, superne glandulis obsita. *Hibernacula* nulla. *Scapi* 1-4(-5), erecti, teretes, glandulis stipitatis disperse obsiti, 5-7(-11) cm alti. *Flores* parvi, 13-15 mm longi (calcari incluso). *Calyx* bilabiatus, extus glandulis stipitatis modice dense obsitus; labium superum usque ad $^1/_3$ longitudinis trilobum, lobis subtriangulis vel ovatis; labium inferum usque ad $^1/_3$ longitudinis, bilobum, lobis ovato. *Corolla* bilabiata, albida, venis obscuris, extus glandulis stipitatis disperse obsita; labium superiorum bilobum, lobis subrectangulis angulis rotundatis, ca. 5 mm longis 2-3.5 mm latis, subemarginatis vel integerrimis; labium inferior paulo longius, trilobum, lobis obovato-oblongis vel subrectangulis angulis rotundatis, longioribus quam latis, 4.5-5 mm longis, 4-5 mm latis, perspicue emarginatis, basi pilis multicellularibus cylindricis vel subcapitatis obsitis. *Tubus* subcylindricus, venis obscuris, intus pilosus, parte inferiore pilis multicellularibus longis (ad 100 μm) subulatis, subclavatis vel subcapitatis in triabus lineis ordinatis cum palato; palatum bivesiculatum sparse pilosum pilis multicellularibus cylindricis vel capitatis, brevibus; tubus ad faucem ca. 3 mm diametro, in calcar conicum obtusum vel acutiusculum 2-3 mm longum gradatim transiens. *Stamina* 2, ca. 2 mm longa, basi ovarii adnata, filamenta brevia, incurvata. *Ovarium* subglobosum, glabrescens, in stylum brevissimum productum, stigma bilobum. *Capsula* subglobosa, ca. 3 mm longa, glabrescens. *Semina* numerosa, 0.5-0.65 mm longa, 0.15-0.25 mm lata, ellipsoidea, superficie reticulata.

Perennial herb, rosette forming, scapose. *Rhizome* c. 15 mm long, with numerous adventitious fibrous roots. *Leaves* 4-6, rosetted, flat on the ground or somewhat erect, succulent (drying membranous), (3-)4-6(-11) cm long, (1-)2-3 cm wide, oblong to ovate-oblong in outline, rounded at the tip and attenuated to the base into a short petiole c. 5 mm wide, with margins more or less uprolled, yellowish green, upper surface of lamina glandular, covered with carnivorous glands. *Hibernacula* (dormant buds) absent. *Scapes* 1-4(-5), erect, 5-7(-11) cm long, terete, 0.5-1 mm tick, 1-flowered, sparsely glandular. *Flowers* small, 13-15 mm long, including spur. *Calyx* two-lobed, upper surface of sepal tips sparsely covered with stipitate glands; upper lip divided to $^1/_3$ of its length into 3 lobes, the lobes ovate to subtriangular, each 2-3 mm long, outer lobes 1 mm wide at the base, central lobe 2 mm wide at the base; lower lip divided to $^1/_3$ of its length into 2 ovate lobes c. 2 mm long and 1 mm wide. *Corolla* two-lipped, whitish, lobes and tube striated by veins; upper lip two-lobed, lobes obovate c. 5 mm long and 2-3.5 mm wide, subemarginate at the apex; lower lip little larger than the upper lip, with 3 oblong to obovate-oblong lobes of nearly equal size, 4.5-5 mm long and 4-5 mm wide, each with emarginate apex, at the base near the throat with long multicellular uniseriate hairs. *Tube* funnel-shaped, at the entrance to the throat c. 3 mm wide,

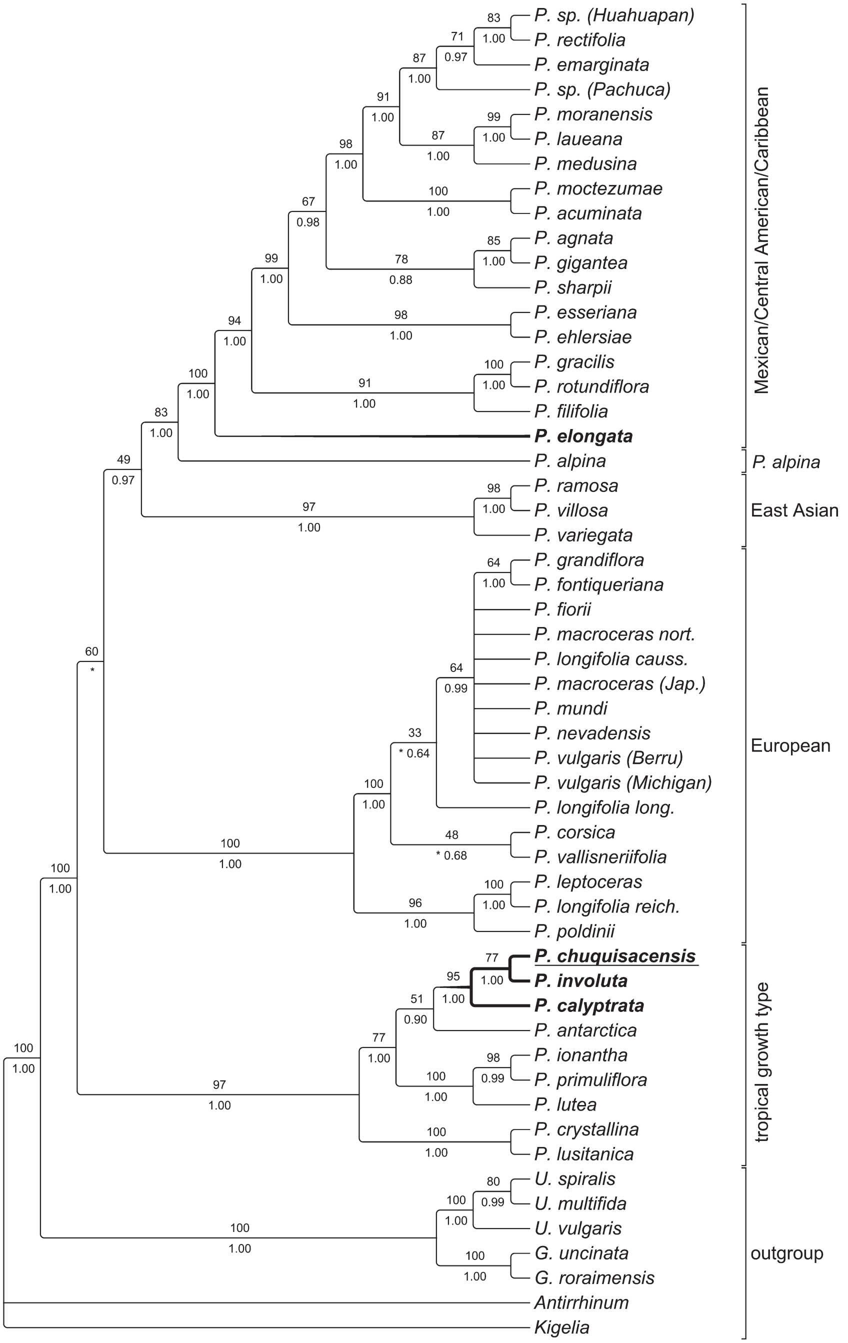

Fig. 2. Phylogenetic relationships in *Pinguicula* based on *trnK* sequences. Above nodes are bootstrap proportions from maximum parsimony analysis; below branches are posterior probabilities from the Bayesian MCMC analysis. An asterisk (*) marks nodes that collapse in the strict consensus tree from the nine most parsimonious trees found. Species not already analysed by Cieslack & al. 2005 (newly added in this study) are in bold; *P. chuquisacensis* described here as a new species is underlined.

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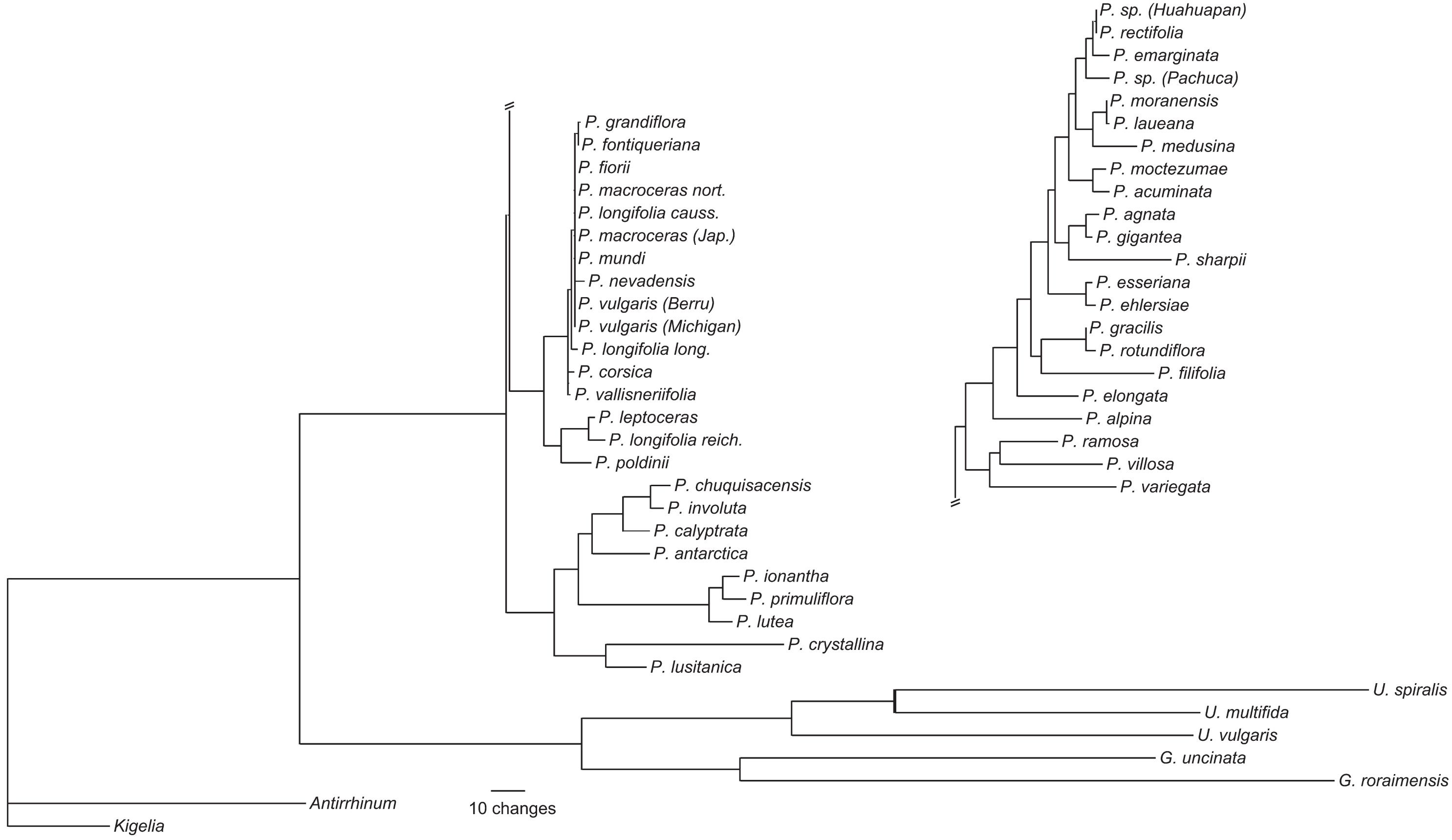

Fig. 3. Bayesian phylogram based on the *matK/trnK* dataset. Note the longer branch of *Pinguicula chuquisacensis* relative to its sister group *P. involuta,* caused by autapomorphies. The branches of the species of *Genlisea* and *Utricularia* are distinctly longer, caused by their distinctly higher mutation rates.

without palate. Spur short, 2-3 mm long, straight, grading into the tube, tapering into the blunt apex. *Stamens* with filaments incurved, c. 2 mm long, anthers c. 1.2 mm long. *Ovary* subglobose, subsessile, glabrous. *Capsule* subglobose, c. 3 mm in diameter. *Seed* fusiform, 0.5-0.65 mm long and 0.15-0.25 mm wide, with appendages on micropylar and chalazal end, brownish, seed coat surface with rectangular ornamentation.

Ic. – Fig. 1; see also colour photograph (leaf rosettes at the type locality) in the electronic supplement at www.bgbm.org/willdenowia/willd38/beck+al.htm.

Distribution. – *Pinguicula chuquisacensis* is endemic to the department Chuquisaca of Bolivia and so far only confirmed from the valley of Nuevo Mundo. It is the only species of *Pinguicula* known from the Bolivian-Tucuman biogeographic province (Arbo 1999; Navarro 2002; Wood 2005). Its altitudinal distribution ranges from about 2100 to 2500 m. According to field observation by Hibert Huaylla, the species can only be found in the area of one small cliff in the valley. The different altitudes possibly have to be explained by errors of GPS data.

Habitat and ecology. – *Pinguicula chuquisacensis* grows on steep, seasonally wet, dripping sandstone rock faces in the valleys of the seasonal forests of the Bolivian-Tucuman formation, in areas with frequent cloud covering. It is confined to the open upper parts of the acidic, wet sandstone cliffs, where it grows in small populations besides the road. It grows together with *Lycopodiella cernua* (L.) Pic. Serm. The evergreen seasonal *Myrtaceae* forest extends around with *Blepharocalyx salicifolia* O. Berg and *Myrcianthes pseudo-mato* (D. Legrand) McVaugh *(Myrtaceae)* and some *Lauraceae*. No hibernacula (dormant resting buds) have been observed in *P. chuquisacensis*, therefore this species can be assigned to the tropical homophyllous growth type, although it grows in seasonally wet habitats. All other known Andean species of *Pinguicula* are restricted to permanently wet soils. The plants have been collected in flower in July (*Kessler & al. 5149; Hinchliff & al. 587)* and in flower and fruit in November *(J. R. I. Wood 10168; Villalobos & al. 501*).

Conservation status. – *Pinguicula chuquisacensis* is a very rare local endemic species, known to exist only at a single location in the valley of Nuevo Mundo. Hibert Huaylla tried to find the species in other areas of the valley, but without success. Its area of occupancy is estimated to be less than 10 km² and with a significant decline projected in the area of occupancy by road construction. We therefore recommend to classify the new species in the Red List category "Critically Endangered (CR)" according to criteria B2a+b (IUCN 2001).

Molecular data. – Maximum parsimony analyses recovered 9 shortest trees with 1771 steps (CI = 0.761, RI = 0.803). The topology is shown in Fig. 2, with bootstrap proportions indicated above the branches, and posterior probabilities from the Bayesian analysis below the branches. Bayesian inference yielded a congruent tree that was slightly better resolved within the European clade. A Bayesian phylogram is shown in Fig. 3 indicating several autapomorphies in the *trnK/matK* sequence of the sample of *Pinguicula chuquisacensis* studied. Our new species belongs to a clade with the other two central Andean species *P. involuta* and *P. calyptrata* and the southern South American *P. antarctica,* whereas the northern South American *P. elongata* is resolved as sister to the remaining species of the Mexican/Central American/Caribbean Clade (Fig. 2-3). The second southern South American species, *P. chilensis* was not included in our analysis.

Delimitation. – Pinguicula chuquisacensis differs from the related *P. calyptrata* in having very long (up to 11 cm) oblong to ovate-oblong leaves, white flowers, less truncate corolla margins and short lobes of the upper lip, whereas in *P. calyptrata* the leaves are broad-ovate to rotundate-obtuse, the flowers are pale lilac to purple, have strongly truncate corolla lobes and relatively long lobes of the upper lip.

Key to the central Andean species of *Pinguicula*

1. Small plants; leaves obovate, leaf margins strongly incurved; upper lip of corolla much shorter than lower lip . . . . *P. involuta*

– Plants of medium size; leaves ovate-oblong, leaf margins poorly incurved; upper lip of corolla only slightly shorter than, or as long as lower lip 2

2\. Leaves 5-10, obovate to rotundate-obtuse, 10-35(-45) mm long and 7-20 mm wide; all corolla lobes deeply emarginate, lobes of upper lip equal in size to lobes of lower lip; flowers purple to pale lilac; plant of high altitudes (Paramos and cloud forest vegetation at > 3000 m altitude) . . . . *P. calyptrata*

– Leaves 4-6, oblong to ovate-oblong, 40-60(-110) mm long and 20-30 mm wide; lobes of upper corolla lip shorter than lobes of lower lip, lobes of upper corolla lip subemarginate; flowers white; plant of submontane to montane altitudes (Bolivian Tucumano Forest in 2000-2500 m altitude) . . . . *P. chuquisacensis*

Discussion

Species classification of Andean *Pinguicula*

Morphologically speaking the new species described here first appeared most closely allied to *Pinguicula calyptrata* but is clearly different (see above). Molecular data were thus elusive in further underscoring the difference to that species. As the *matK/trnK* trees indicates, the next relative may be *P. involuta* rather than *P. calyptrata.* Moreover, *P. chuquisacensis* has several autapomorphies in its *matK/trnK* sequence (see phylogram in Fig. 3) that seem rather many for within species variability. Nevertheless, the inclusion of further populations of *P. involuta, P. calyptrata* and *P. chuquisacensis* is needed, as is the use of nuclear markers to infer speciation patterns and better understand the origin of these species. At the species level, and sampling several geographically distinct populations per species, so far only the Eurasian *Pinguicula* clade (*P.* sect. *Pinguicula*) was analysed with molecular markers (Degtarajeva & al. 2006). These authors resolved different ITS ribotypes from the different populations of several respective taxa in as clades, and most likely, species-non monophyly (e.g. in *P. longifolia*) is caused by improper taxonomy rather than biological phenomena like reticulate evolution or incomplete lineage sorting. DNA sequences therefore appear to help recognizing groups of individual specimens, and are useful for species recognition.

The best known species in the central Andes of the high eastern Yungas slopes of Peru and Bolivia (as far south as Cochabamba) is *Pinguicula involuta* (Casper 1966; Brako & Zarucchi 1993). This species is a small plant growing on acid black soils in high elevations (up to 3500 m) that are rich in organic matter and permanently humid. Another species, *P. calyptrata*, grows in a similar habitat in wet Paramo soil (up to 4000 m) but has a more northern range from Peru through Ecuador to Colombia (Taylor 1975; Brako & Zarucchi 1993). *P. elongata* is very distinct and restricted to the Andes of Colombia and Venezuela (Luteyn 1999).

Relationships in South American *Pinguicula*

Pinguicula chuquisacensis belongs to a well supported clade of central Andean species within *P.* sect. *Ampullipalatum,* to which possibly also the southern Andean taxa represented here by *P. antarctica* belong. Although not sampled here, *P. chilensis* appears morphologically very closely allied to *P. antarctica* (Casper 1966) and may therefore be hypothesised as its closest relative. However, further sequence data are needed to corroborate the sister group relationship of these south Andean species to the central Andean *Pinguicula* clade, since there is only weak statistical support for this.

Our result that *Pinguicula elongata* is not related to the Andean species but to the Mexican-Carribean clade means that section *Ampullipalatum* of subgenus *Temnoceras* is polyphyletic in the circumscription of Casper (1966). All members of section *Ampullipalatum* are of the tropical growth type, and share a two-lobed corolla with conical tube, and a short, saccate spur which gradually widens into the corolla tube. However, *P. elongata* is of a tropical-heterophyllous growth type, while all other members of the section are homophyllous, i.e. they do not produce hibernacula or non-glandular “winter rosettes” but form rosettes of glandular carnivorous leaves instead all year round (Casper 1966). This difference from the other South American *Pinguicula* led Casper (1966) to differentiate a monotypic subsection *Heterophylliformis* for *P. elongata*. Although the position of *P. elongata* as sister lineage to all remaining species of the *Pinguicula* radiation in the Mexican-Central American-Caribbean region is a surprising result, it may mark a biogeographical pattern that can be explained by the proximity of continental South America. Further studies are needed to examine a possible convergent evolution of the tropical growth type in *P. elongata*.

Casper (1966) already hypothesized an origin of South American *Pinguicula* species in relation to the raise of the Andes based on the assumption that any of the high Andean elements were migrated from the North via Central America to South America in Pliocene (“Nordic Invasion”) including *Pinguicula* (Diels 1937). Ancestors of Andean *Pinguicula* were considered to have lived in the southern Caribbean area (south of the Isthmus of Tehuantepec) even considering *P. elongata,* which is the northernmost species of the extant South American *Pinguicula,* as a member of such an ancestral lineage (Casper 1966). The hypothesis that many of the high Andean species belong to north temperate genera and have migrated southwards via Mesoamerica with cooling climates after about the Mio-Pliocene have been confirmed by palaeobotanical evidence (Burnham & Graham 1999). A recent analysis using methods of molecular phylogeography and speciation in the genus *Lupinus* by Hughes & Eastwood (2006) indicated that there may have been several southward migration phases from North America with subsequent radiation in habitats offered by the uprising Andes as recently as late Pliocene or Pleistocene. According to our study, the origin of the Andean species of *Pinguicula* appears different from Casper's original assumption, because the clade of *P. lutea* and relatives from the southeastern United States is much more closely related than the Caribbean taxa. A further understanding of the origin of the central Andean *Pinguicula* will thus require a better understanding of speciation patterns in the tropical growth clade first recognized by Cieslack & al. (2005).

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