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On the biology, biogeography, and taxonomy of *Arachnitis* Phil. nom. cons. (*Corsiaceae*) in respect to a new record from Bolivia

Abstract

Ibisch, P. L., Neinhuis, Ch. & Rojas N., P.: On the biology, biogeography, and taxonomy of *Arachnitis* Phil. nom. cons. (*Corsiaceae*) in respect to a new record from Bolivia. – Willdenowia 26: 321–332. 1996. – ISSN 0511–9618.

A new locality of *Arachnitis uniflora* from a forest in the central Andes of Bolivia is described. Thus, the species, hitherto well known only from Patagonia, shows a remarkable disjunction probably caused by climatic changes at least 10–11 000 years BP. The different habitat conditions of the two populations are characterised. A first complete description, including micromorphological characters, of Bolivian specimens is given. *A. uniflora* has protandric bisexual flowers which show a considerable growth during anthesis. The morphological plasticity of *A. uniflora* is discussed in respect of the second species *A. quetihuensis*, and attention is drawn to the position of *Arachnitis* within the *Corsiaceae*. A neotype of *A. uniflora* is designated.

Introduction

Achlorophyllous mycotrophic plant species have evolved convergently in at least seven angiosperm families. Although it is well known that achlorophyllous vascular plants are no real saprophytes decomposing dead organic material (like bacteria or fungi) but parasite on destruent/heterotrophic fungi, the term “saprophytes” generally is maintained (see Maas & al. 1986) and will be used in the present paper as well. Within the *Monocotyledoneae*, saprophytes are found in the *Orchidaceae*, *Burmanniaceae*, and some small families such as *Triuridaceae*, *Petrosaviaceae*, *Geosiridaceae*, and *Corsiaceae* including *Arachnitis*.

The genus *Arachnitis* was established by Philippi (1864) who first suggested the plant to be an orchid. Later, he recognised it as distinct from the *Orchidaceae* and proposed to place *Arachnitis* within a separate, new family (Philippi 1865a,b). In his remarks on Philippi’s article, Fenzl (1865) first drew a connection to the *Burmanniaceae*. The family *Corsiaceae* was established by Beccari (1878). However, Bentham (1883) only accepted a tribe *Corsieae* within the *Burmanniaceae*, a taxonomic concept that had been adopted also by Engler (1888). Later, Jonker (1938) separated the *Corsiaceae* from the *Burmanniaceae*, at least because of the strongly zygomorphic flowers of *Corsia* and *Arachnitis*. RübSamen (1986) in her extensive study of the *Burmanniaceae* and *Corsiaceae* clearly showed the separation of the *Corsiaceae* to be justified. Alone Muñoz (1966, 1971) followed Philippi (1865a,b) and considered the establishment of a new monogeneric family *Arachnitaceae* necessary.

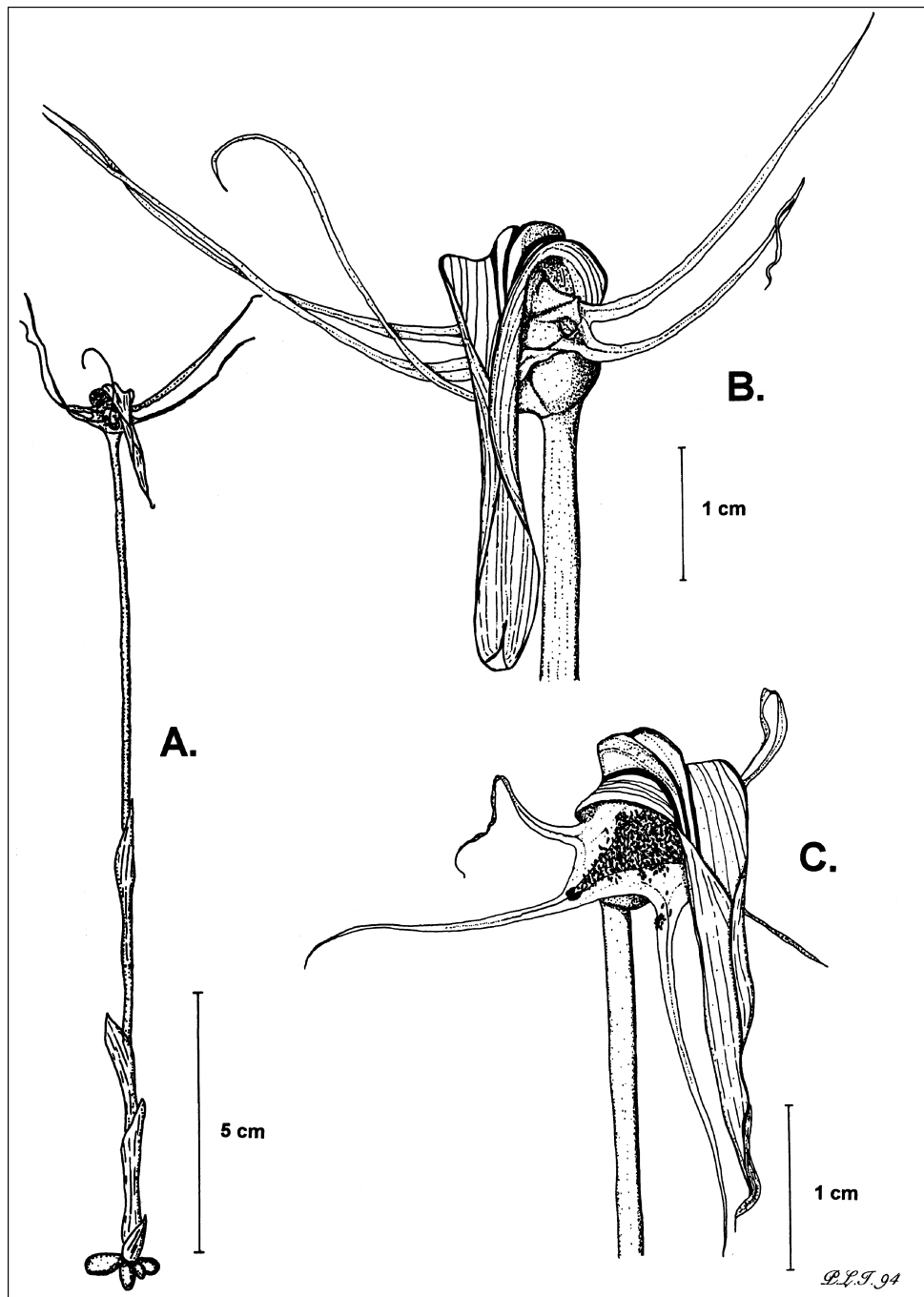


Fig. 1. *Arachnitis uniflora* from Bolivia (drawn after *Ibisch & al. 284, pl 1 (= 94, 0444)*) – A: habitus; B: flower in female stage of anthesis after dropping of anthers; C: flower in fruiting stage, tepals not withered.

The *Corsiaceae* are a family of the southern hemisphere: *Corsia* is restricted to the Australian-Pacific region, and *Arachnitis* to the southern part of South America (Cribb 1985, Dahlgren & al. 1985, Mabberley 1987).

Until 1972, when Dimitri described *Arachnitis quetrihuensis* (Dimitri 1972), the genus was monotypic consisting of *Arachnitis uniflora* Phil. only. Even modern literature (Dahlgren & al. 1985, Mabberley 1987) does not mention the second species. *A. quetrihuensis* and *A. uniflora* are known to occur (partially sympatric) in Patagonian *Nothofagus* forests of Chile and Argentina.

In the framework of a small German-Bolivian project of botanical investigations in the archaeological sites of “El Fuerte”, Samaipata, Bolivia, organised by the first author, it was possible to collect and document a population of *Arachnitis* which turned out to belong to *A. uniflora*. Prior to this record, *Arachnitis* was collected only two times during the 1970s in the tropics of Bolivia. Nevertheless, it was not recognised as a neotropical genus (see Maas 1979, Maas & al. 1986). A first description of Bolivian specimens of *Arachnitis uniflora* is realised. Furthermore, new data on biology and habitat conditions are presented, drawing the attention to the remarkable biogeographic pattern of this exceptional genus.

Methods

For scanning electron microscopy (SEM) flowers fixed in FAA (formalin, 70% alcohol, acetic acid, 90:5:5) were dried after the Critical-Point-Method, fixed to aluminum stubs by double sided adhesive tape, coated with gold (Balzers Union SCD 040) and investigated in a Cambridge Stereoscan 200. Epicuticular waxes were studied on shoots of airdried herbarium specimens. Small pieces of the shoot were fixed to aluminium stubs like the cp-dried specimens.

Arachnitis uniflora

Arachnitis uniflora Phil. in Bot. Zeitung (Berlin) 22: 217. 1864. – Type: Chile, Prov. Valdivia, Farm San Juan, 11.1863, *F. Philippi s.n.* (not extant). – Neotype (designated here): Ibid., 11.1864, *F. Philippi* (B!).

The name *Arachnitis* Phil. (1864) is conserved (see Greuter & al. 1994: 208) against the earlier, confusingly similar name *Arachnites* F.W. Schmidt (1793) for an orchid (type not designated), since they are to be treated as homonyms. As an invalid and to be corrected orthographic variant of the original “*Arachnitis*”, also the spelling “*Arachnites*” was later used by Philippi (1865a,b), and is also found in recent literature (e.g. Dahlgren & al. 1985).

The name *Arachnitis uniflora* was based on a few remaining plants of a larger collection made by Philippi’s son Frederic in November 1863, which otherwise was destroyed when Philippi’s house burnt down on 2.11.1865 (Philippi 1864, 1865a). These specimens, however, were in a bad stage (“remojándose en espíritu de vino, pero no me fué posible conocer bien ni el número i conformacion de los estambres, ni el estilo porqué todas estas partes así como el perigonio se pusieron demasiado blandas, casi como una jalea”, Philippi 1865b: 639), and were apparently not preserved after his son had recollected plants from the type location in November 1864 (“... hat mein Sohn, trotz der vielen Arbeiten, welche die Wirthschaft und das Wiederaufbauen der nöthigen Gebäude mit sich brachten, diese Pflanze wiederum aufgefunden, untersucht und gezeichnet, und ich erlaube mir hiermit, Ihnen seine Zeichnung und seine Beschreibung mitzuthellen ...”, Philippi 1865a: 517). The herbarium in Santiago de Chile (SGO) does neither house specimens of the collection of 1863 nor of 1864 (M. Muñoz, pers. comm.), but together with the extended description, the drawing, and his letter to Fenzl (Philippi 1865a) Philippi obviously sent a herbarium specimen of the second collection to Berlin. This specimen is still preserved in the Berlin herbarium (B); since it apparently is the only extant material collected at the type location and studied by Philippi, we propose to regard this specimen as neotype of the name *Arachnitis uniflora*.

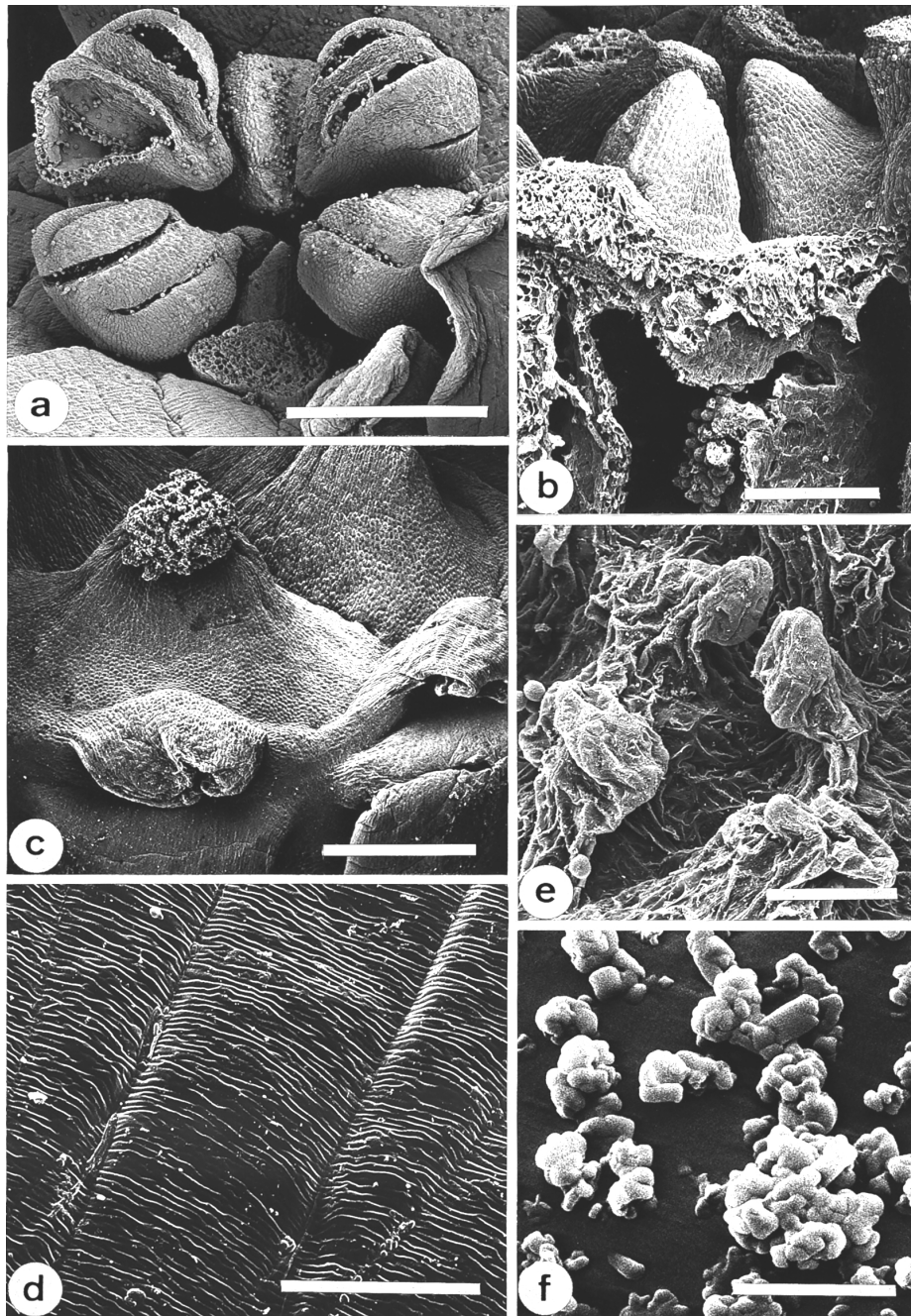


Fig. 2. SEM-micrographs of flower details (from *Ibisch & al. 284.pi1 (= 94.0444)*) – a: flower in male stage of anthesis, anthers covering the carpels; b: flower in male stage of anthesis, anthers removed and ovary opened, stigmas are not yet developed, ovules visible; c: flower in female stage of anthesis, anthers dropped, filaments reflexed, stigmas developed; d: cuticular foldings on the surface of the median tepal; e: warty swellings on the adaxial side of the reflexed median tepal; f: epicuticular wax crystals on the shoot, in part forming stout tubules.

Earlier, the drawing published by Philippi (1865a) and based on the collection of November 1864 was proposed by Dimitri (1972) to serve as a substitute of the type, who erroneously regarded another, then destroyed specimen as type material, which had been annotated as such by C. Muñoz P. in 1945 but which, however, was not collected before 1886.

Morphology

Chilean specimens were studied several times (e.g., Philippi 1865, Muñoz 1966, Correa 1969); the most recent work provides a morphological and anatomical analysis (Minoletti 1986).

In the following a description of the specimens from the new site in Bolivia (Fig. 1) is provided:

Achlorophyllous geophyte. Roots 4–8, short, tuberous, up to 15 mm long and 8 mm wide, brownish. Shoot erect, about 30 cm high and 6–7 mm in diameter, pale red at base, flesh-coloured toward apex. Leaves 5–8, scaly at the base and amplexicaul towards apex of the shoot, alternate, approximately distichous, up to 5 cm long, 1 cm wide, with 5–7 parallel nerves, in fruiting stage not exceeding half the length of the shoot, translucent. Flower solitary, terminal, inclined, bisexual, protandric, zygomorphic, with two whirls of three tepals each, not withering until seeds are dispersed, pale rose to flesh coloured. Tepals unequal, the inner three and the two lateral outer awl shaped, spreading, with one violet nerve, up to 5 cm long and 2–2.5 mm wide, the median outer tepal broad, acuminate, in most cases ending with a filiform tip, reflexed, concave, 4–5 cm long, 13–17 mm wide towards base, with 11–13 violet nerves, forming a helmetlike structure covering the reproductive parts of the flower, the median part involute, inner side characterised by two rows of bullate structures, becoming more prominent within the helmet (Fig. 2e). All tepals with regular parallel cuticular folds perpendicular to the length direction (Fig. 2d). Stamen six, during male flowering stage covering the carpels (Fig. 2a), filaments short, anthers opening with longitudinal slits. Pollen monocolpate, tectum reticulate. Ovary inferior, syncarp, with three carpels, each carpel terminated by a papillose stigma, stigma papillae developing after dropping of anthers (Fig. 2b, c). Although the growth of the flower continues considerably during anthesis, the hypanthium in all stages is shorter than wide. Fruit a loculicid capsule terminally splitting into a triangular opening. Seeds small, 0.8–1 mm long, 0.1–0.2 mm wide, testa cells oblong, anticlinal walls prominent, outer periclinal wall collapsed, anticlinal and inner periclinal walls with secondary sculpturing forming a reticulate pattern. Shoot and carpels covered by epicuticular wax crystals, most of them granulelike, in some cases forming stout tubules (Fig. 2f).

Taxonomy

Considering the published descriptions and comparing the Bolivian material with specimens of *Arachnitis uniflora* from Chile, morphological characters allow no differentiation between Bolivian and Chilean specimens. Analysing plants from Chile alone, a great morphological plasticity becomes obvious. In particular the flower proportions vary considerably, partially caused by growth during anthesis (see below). Other characters such as the colour of the plant (from white to yellow, reddish/flesh-coloured or grey/brown), the length of the shoot, and its covering by leaves are extremely variable, too.

Dimitri (1972) justifies the establishment of the second species, *Arachnitis quetrihuensis*, by the flower proportions: in contrast to *A. uniflora*, the narrow inner and lateral outer tepals of *A. quetrihuensis* are said to be shorter than or subequalling the broad median outer tepal, which is, moreover, even or hardly involute only; the hypanthium of *A. quetrihuensis* is stated to be more inflated. While *A. uniflora* s.str. occurs in the northern range of the genus, specimens regarded as *A. quetrihuensis* occur only in S Patagonia; therefore a climatic dependence of the flower proportions can not be excluded. The great variability of *Arachnitis* and the considerable growth during anthesis in mind, a close study of living plants from sites where both taxa occur symp-

trically may lead to the conclusion that *A. quetrihuensis* is conspecific to *A. uniflora*. Therefore we have considered all cited specimens to belong to *A. uniflora* in the present paper.

The characters of *Arachnitis* in comparison to *Corsia* give reason to think over its systematic position: *Arachnitis* shares the saprophytism, asymmetric flowers and six stamens with *Corsia* but differs considerably in important characters, e.g., the single shoot with tuberous roots versus a rhizome with several shoots, the gynoeceum (three separate stigmas versus one stigma), the fruit (capsule with one terminal opening versus capsule with three lateral valves), the seeds (“Staubsamen”, very similar to those of orchids, e.g., *Ophrys* (Rauh & al. 1975) versus “Feilspsamen”), the embryo (three-cellular versus multicellular), and the endosperm (lipids versus starch). The complete set of data is presented by RübSamen (1986). These features in connection with biogeographic data and a comparative analysis of all saprophytic monocotyledonous families may support a closer relationship of *Arachnitis* to the *Orchidaceae* than to *Corsia* or the *Burmanniaceae*, and the reestablishment of the family *Arachnitaceae*.

The remarkable disjunction of *Arachnitis uniflora*

Long distance disjunctions of saprophytic plants are quite common (P. & H. Maas pers. comm., Maas & al. 1986) but usually the disjunctions appear in genera not restricted to one continent or subcontinent but with a wide distribution (e.g. *Thismia*). The now documented distribution pattern of the exclusively South American genus *Arachnitis* is remarkable: published maps consider the traditionally known sites in Patagonia (Ugarte & Arriagada 1983, Minoletti 1986) where *Arachnitis* occurs between 33°45' and 50°25' S and up to 1000 m above sea level (Fig. 3). *A. uniflora* and *A. quetrihuensis* are found sympatrically in N Patagonia; the latter only is distributed also in *Nothofagus* forests of S Patagonia (Dimitri 1972) and has recently been recorded from the Falkland Islands (Cribb & al. 1995).

In the first preliminary checklist of the rich but insufficiently known flora of Bolivia (Foster 1958) neither the genus *Arachnitis* nor the family *Corsiaceae* are mentioned. Until now the existence of *Arachnitis* in Bolivia was generally not known (e.g., the national herbarium of La Paz (LPB) did not house *Arachnitis* material, S. G. Beck, pers. comm.). Maas & al. (1986) are the first and only to mention the occurrence of *Arachnitis* in Bolivia without giving detailed information about localities or specimens. To us, only two previous collections from Bolivia, i.e. Luer & al. 3598 and Davidson 3791 (see specimens seen, below), are known.

Considering all records, the distribution of the genus *Arachnitis* extends over 32 degrees of latitude (c. 18°S–50°S) which would correspond to the distance from Canada to Jamaica in the northern hemisphere. This large area may be nothing special for a genus but it is quite remarkable for a (non-cosmopolitan) species. Probably, there are no other vascular plant species existing in both Bolivia and Patagonia. Even at the genus level there are but a few examples (e.g., *Asplenium*, *Blechnum*, *Polypodium*, *Azara*, *Escallonia*, *Lithraea*, *Chusquea* – all of them evolved different species in the sub regions). The two disjunct areas of *Arachnitis* are separated by a broad belt of vegetation types which can be clearly predicted as unsuitable habitat for *Arachnitis* (Fig. 3): the Atacama desert, high mountain deserts and grasslands of the Andes, dry forests, the shrubby “monte”-vegetation and the Patagonian grasslands.

New records filling the distributional gap could only be expected in the Tucumanian-Bolivian forests of S Bolivia and N Argentina. It is most unlikely that seeds of *Arachnitis* are dispersed via long distant dispersal (see reproductive biology, below); it is probable that once a continuous area existed, and the disjunction may be due to the shift of vegetation zones during climatic changes. 18 000–19 000 years BP today's Patagonian *Nothofagus* forests were almost completely covered with glaciers (Graf 1992). It is most probable that in those times *Arachnitis* had a smaller but coherent range in N Patagonia. Many species had to migrate north in the W Andes (Baumann 1988, Graf 1992, W. Lauer, pers. comm.). The dry gap between Patagonia and the Tucumanian-Bolivian forest probably is quite young and, in glacial times, was bridged along the Andes by (at least) islands of montane forest (Baumann 1988, W. Lauer, pers. comm.).

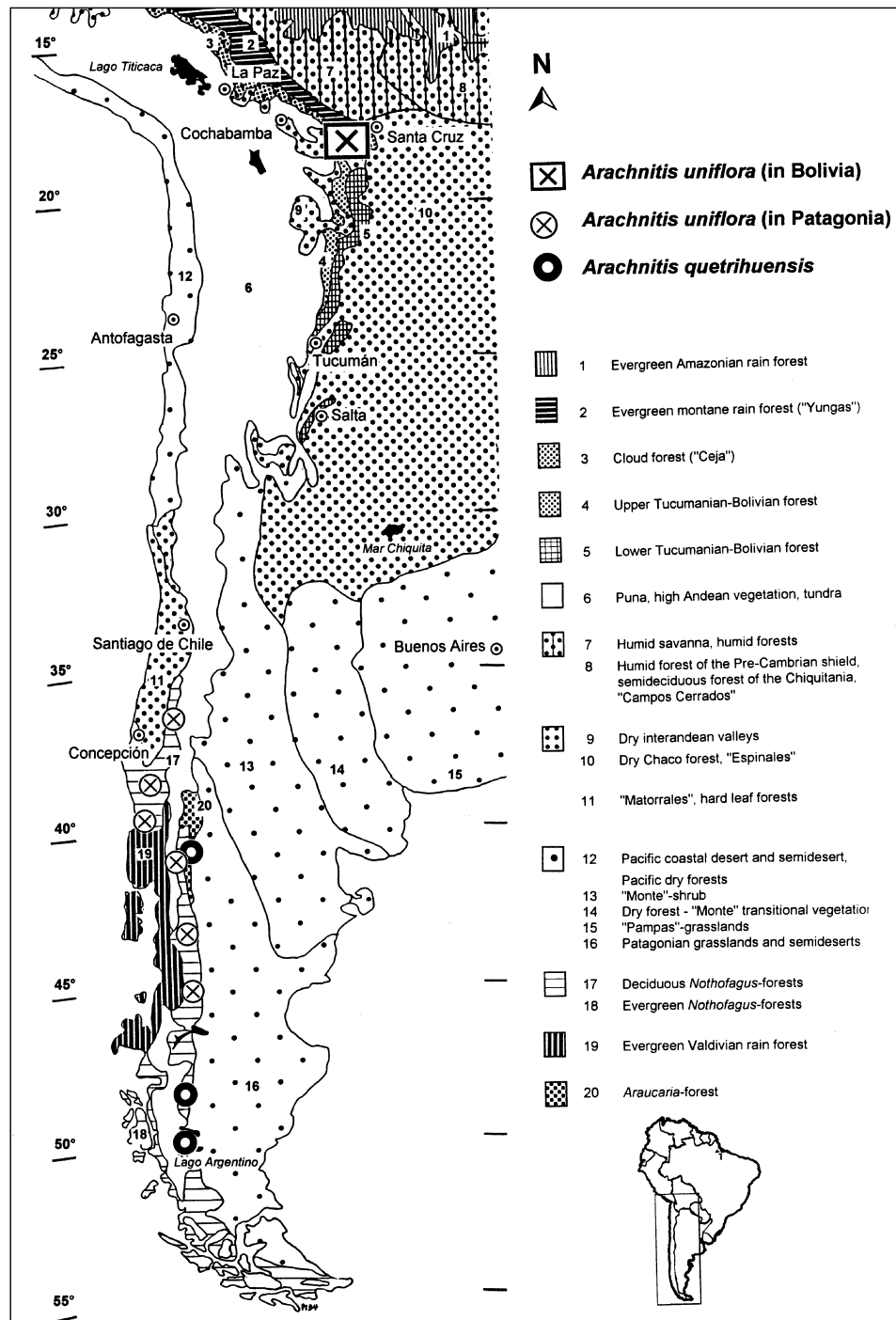


Fig. 3. Distribution of *Arachnitis* in South America (based on the vegetation map of Hueck & Seibert 1981, and considering Ugarte & Arriagada 1983).

About 10 000–11 000 years BP, with the post glacial era, the actual situation was created, and the populations of *Arachnitis* could have been separated efficiently. At the latest in this period a process of allopatric speciation could have begun like in other cases of today's Patagonian-Andean distributed genera. The two populations of *Arachnitis uniflora*, however, did not evolve morphologically differentiable taxa.

Specimens studied

BOLIVIA: Dep. Cochabamba, 70.3 km E of Epizana, Carretera Fundamental 4, Province of Carrasco, 5. 12. 1975, *C. Davidson 3791* (MO); Dep. Santa Cruz, above Comarapa, terrestrial in moist mossy hummock in cloud forest below Siberia, 2500 m, 1. 12. 1978, *Luer & al. 3598* (SEL); Dep. Santa Cruz, valley of "El Fuerte", Samaipata, Province of Florida, 1900 m, c. 63°51'W, 18°12'S, 28. 4. 1994, *P.L. Ibisch, P. Rojas, N. De la Barra, E. Fernández, M. Mercado, L. Ovando, G. Vargas 284.pi1 (= 94.0444)* (B, BOLV, LPB, UCZ, herb. R. Vásquez, herb. Ibisch – preserved in alcohol).

CHILE: Below Baños de Chillan, only found once in woods, 4-5000 ft, 24. 12. 1901, *H.J. Elwes s.n.* (K); Petrohué, aan bergwand, 150 m, 23. 12. 1937, *Andreas 287* (B); VIII. Región, Concepción, Inmediaciones del Parque Hualpén, 36°47'S, 73°10'W, 50 m, 16. 10. 1981, *J. Arrigada 52011* (B); near Temuco, forest dominated by *Aextoxicon punctatum*, 10. 1994, *E. Fischer C127* (herb. Fischer – preserved in alcohol); Fundo Wagner, Lago Villarica, 11. 1962, *K. Kubitzki 351* (M); VIII Región de Bío Bío, Prov. de Concepción, Valle Nonguén, 11. 1981, *E. Bayer 212* (M); Prov. Valdivia, San Juan, 11. 1864, *F. Philippi s.n.* (B); Prov. Valdivia, Panguipulli, 11. 1924, *A. Hollermayer 1939* (B, MO).

ARGENTINA: PROV. Río Negro, Lago Traful, shaded virgin woods, in humus, 18. 12. 1972, *C.A. Luer 53* (SEL); Prov. Neuquén, Halbinsel Quetrihué am Lago Nahuel Huapi, im Wald mit *Myrceugenella apiculata*, 16. 1. 1966, *H. & E. Walter 724* (B); Prov. Neuquén, Villa Puerto Manzano am Lago Nahuel Huapi im *Nothofagus dombeyi*-Wald, 16. 1. 1966, *H. & E. Walter 701* (B); Prov. Santa Cruz, Dep. Lago Argentino, Lago Argentino, Península Magallanes, 8 km al E del las Glaciar Moreno, bosque de *Nothofagus pumilo* y *N. betuloides*, suelo rico en humus, con *Gavilea lutea*, *Viola magellanica*, 14. 1. 1987, *B. Leuenberger & S.C. Arroyo 3681* (B); Río Negro, Barilloche, Cerro Otto, 22. 12. 1946, *Teague s.n.* (K).

FALKLAND ISLANDS / ISLAS MALVINAS: East Falkland, Cape Pembroke, E of Port Stanley, low ridges N of Whalebone Cove, few plants in sand amongst eroded sand stone ridge, 26. 2. 1964, *D.M. Moore 926* (K).

Habitat conditions

All sites of *Arachnitis* are characterised by similar microclimatic conditions: humose, deep soils, below dense vegetation with high humidity during the growing season (see Ugarte & Arriagada 1983, Minoletti 1986). However, the different sites are embedded in totally different macroclimatic situations.

Bolivia

The habitat of the Bolivian populations is characterised by a typical tropical mountain climate with daily temperature amplitudes substantially greater than the annual temperature amplitudes.

There are no meteorological observatories in these sites but in the case of Samaipata the climate can be extrapolated from data of Samaipata village (Nuñez 1992 cited by Saravia 1993): mean annual temperature about 17–18°C, with an annual variation of 4–5°C, annual precipitation about 800–1000 mm, dry season between May/June and September/October. The vegetation of the Samaipata region is a tropical semihumid, mostly deciduous forest with floristic elements originating from the humid montane forests of the Yungas, dry valleys and the Tucumanian-Bolivian forest. Typical trees are, e.g., *Erythrina falcata*, *Tecoma stans*, *Piper elongatum*, *Luehea*

species, *Cedrela lilloi*, and species of *Myrtaceae* and *Lauraceae*; there are several epiphytes, e.g., species of *Epidendrum*, *Oncidium*, *Pleurothallis*, *Tillandsia* and *Rhizalis* (a detailed description of the flora and the vegetation of the valley of “El Fuerte” will be provided by Ibisch & al. in prep.). Several local endemics occur in the region (e.g., *Samaipaticereus corroanus*, *Cleistocactus samaipatanus*, *Epidendrum samaipatanense*, *Pleurothallis yupankii*, *Puya nana*).

The collections *Luer & al. 3598* and *Davidson 3791* were both made in a tropical evergreen cloud forest near Siberia, c. 2500 m above sea level, with an estimated annual precipitation of 2000 mm and no clear separation between rain and dry season.

Patagonia

The climate is typical for moderate latitudes with summer and winter seasons, and annual temperature amplitudes exceeding the daily amplitudes.

The northern zone is dominated by mostly deciduous forests composed of trees such as *Nothofagus obliqua*, *N. procera*, *Cryptocarya alba*, *Aextoxicon punctatum* and *Peumus boldus*. Annual precipitation ranges from 1000–3000 (4000) mm and the mean annual temperature from 12–13°C ($\pm 7^\circ\text{C}$) (Hueck & Seibert 1981, Ugarte & Arriagada 1983).

In the southern zone with evergreen *Nothofagus* forests (of, e.g., *N. dombeyi*, *N. betuloides*) the precipitation ranges from 600–4300 mm and the mean annual temperature from 5–8°C ($\pm 7^\circ\text{C}$). In the southern *Nothofagus* forests (of *N. pumilio*, *N. antarctica*), where *A. quetrichuenensis* only occurs, the mean annual temperature is 5–8°C ($\pm 7^\circ\text{C}$) and the precipitation ranges from 500–1500 mm. (Hueck & Seibert 1981).

On the East Falkland islands, where forests are naturally lacking, the plants grow in “sand amongst rocks on an eroded sandstone ridge” (Cribb & al. 1995).

Reproductive biology

The flowering season of *Arachnitis* is the only period in which the plants appear. The flowering period lasts several months: in N Patagonia flowers were collected from August to November, in S Patagonia from November to February (see Dimitri 1972, Minoletti 1986, Muñoz 1971 and cited specimens). The Bolivian *Arachnitis uniflora* specimens were collected at the end of the Central-Andean rainy season (April/May). The period from beginning of anthesis to the release of the seeds in *Arachnitis uniflora* lasts about 15 days (Minoletti 1986). It is possible that the plants do not flower every year (P. & H. Maas, pers. comm.). Up to now, no pollination was observed. Fungal gnats are predicted to be the pollinators (Vogel 1978); the whole flower syndrome does not support alternatives, e.g., microstructural characters show that the plant even might deceive the pollinators by resemblance of fungal structures as it is known from other fungus-imitating flowers as well (Vogel 1978, Neinhuis & al. 1994). The long-spreading tepals may serve as osmophores; scent, however, has not been recognised.

Arachnitis has been regarded as unisexual or bisexual with male, female and hermaphrodite flowers until Minoletti (1986) pointed out and illustrated that it has bisexual protandric flowers. For the observed Bolivian specimens the same is valid: during male flowering stage the carpels are covered by the anthers, and stigma papillae are not yet developed. The stigmas become visible not until anthers are dropped. It seems that Minoletti did not recognise that this floral development is connected with a rather unique phenomenon: the flower grows considerably during anthesis, e.g., the length of the tepals increases and also the whole flower becomes larger.

Yet Vogel (1978) mentioned that the tepals do not wither after pollination. In the Bolivian population studied, the tepals maintained their form until seeds were dispersed. It seems possible that the plant continues attracting the pollinator using it as disperser as well which would be an unique case. In contrast, anemochory has been supposed by Minoletti (1986). The small orchidlike seeds surely seem to be adapted to wind dispersal but the plants are growing in a habitat with very low wind speeds, few centimetres above the ground covered by dense vegeta-

tion – factors that limit the efficiency of anemochory. However, it may be a case of polychory. From most saprophytes their dispersal is not exactly known (Maas 1979).

Conservation status of *Arachnitis uniflora* in Bolivia

Minoletti (1986) underlines that *Arachnitis uniflora* depends on intact primary forests. In Patagonia the plant is occurring regularly but only in a few and limited sites.

The population of *Arachnitis uniflora* found in Samaipata, Bolivia, does not exist anymore because of deforestation during archaeological excavations. The plants grew near stonewalls of ruins of an ancient Incan village covered by a dense secondary forest of about five to eight meters in height. During this century there have been cultivated fields in this area (probably until the 1960s). So it is obvious that *Arachnitis*, though a very vulnerable and ambitious species with regard to the site conditions, does colonise secondary vegetation if this reaches a certain stage of recovery. Furthermore, the fact that *Arachnitis* in Bolivia is found in different types of vegetation, ranging from semihumid montane forest to cloud forest, shows that it cannot be considered as endangered yet.

Acknowledgements

The present paper is a result of botanical studies in the valley of “El Fuerte” Samaipata during archaeological excavations. The first author is indebted to the authorities of Samaipata and in particular to Dr Albert Meyers (P.I.A.S. – financed by the German Research Association – DFG) for having a large interdisciplinary interest and making possible the studies during the topographical exploitation work. The publication is dedicated to Erika, Galia, Lourdes, Magaly and Nelly from Cochabamba in place of all Bolivian students and botanists – they will take over the responsibility for exploring and saving the great treasure, which is the extraordinary nature of Bolivia. Furthermore we are indebted to Prof. Dr W. Lauer, Bonn, Dr S. G. Beck, La Paz, T. Borsch, Bonn, and A. Gröger, Bonn, for providing valuable information. Prof. Dr P. Maas and Dr H. Maas, Utrecht, drew our attention to the Bolivian specimens in SEL, Lic. Mélica Muñoz, Santiago de Chile, sent us information about the destroyed type specimens in Santiago de Chile. We are grateful to the curators and directors of the following herbaria for providing us their specimens: B, K, M, MO, SEG, SEL; Dr E. Fischer, Bonn, provided a specimen of *Arachnitis uniflora* preserved in alcohol. Last but not least we want to thank Prof. Dr W. Barthlott, Dr W. Lobin, and Dr H. Edelmann, Bonn, for critically revising the manuscript.

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