# Systematics and evolution of the genus *Deuterocohnia* Mez (Bromeliaceae)

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# 1 INTRODUCTION

## 1.1 Biology and systematics of the Bromeliaceae Juss.

In the course of their evolutionary history, the members of the Neotropical plant family of Bromeliaceae have conquered numerous ecological niches throughout the landscapes of Central and South America. Their spread was accompanied by a remarkable diversification in shape, size and structure. Bromeliads developed a set of adaptations which enabled them to grow in many kinds of habitats ranging from terrestrial and epilithic to epiphytic. Bromeliads can be found on various types of soil, in desert regions as well as in rainforests. The enormous variability of this plant group is perhaps best reflected by the contrast between the more than ten meter tall *Puya raimondii*, producing thousands of flowers and growing at altitudes of about 4000 m a.s.l., and the tiny single flowered *Tillandsia bryoides*, growing epiphytically on the eastern slopes of the Andes. Since the first formal taxonomic recognition of the Bromeliaceae by Jussieu (1789), the number of described species within the family has increased continuously, and nowadays amounts to almost 3200 (Luther 2008). Most of the species have in common the herbaceous rosulate shoot formed by slender, parallel-veined and often armed leaves. In so-called "tank" bromeliads, the leaf rosette forms a water reservoir which provides biotopes for small animals, mainly invertebrates and protozoa (Varga 1928, Pittendrigh 1948, Foissner et al. 2003, Ospina-Bautista et al. 2008, Alves-Silva and da Silva 2009). Some species, like *Brocchinia reducta*, even evolved adaptations which enable them to trap and digest animal prey in those cisterns (Givnish et al. 1984). While terrestrial bromeliads usually exhibit a well developed root system, this can be reduced in epiphytes, up to the point of completely rootless ramets as they occur in *Tillandsia usneoides*. The significant reduction of the root system in epiphytic bromeliads has become feasible due to the development of an outstanding water and nutrient uptake system by means of foliar trichomes (Benzing et al. 1976a, b, Martin 1994, Stefano et al. 2008).

The mostly terminal inflorescences of Bromeliaceae are often prominently bracteate. They are either located in the centre of the rosette or elevated by a peduncle. After having bloomed once, shoots either die or, more commonly, branches sprout from lateral buds. The typical bromeliad flower consists of three sepals, three petals, 3+3 stamens and three adnate carpels, but there are also exceptions. Ornithophily seems to be the main pollination syndrome as indicated by the often showy bracts and flowers, flowering during daytime and the absence of scent. However, pollination by bats, insects or wind has also been documented (Kessler and Krömer 2000). Fruits are either capsules or berries that produce many plumose, winged or glabrous seeds.

Besides the tank habit and the specialized trichomes, the crassulacean acid metabolism (CAM) is another key innovation that prompted the radiation of Bromeliaceae into habitats associated with drought stress. Many bromeliad species exhibit this type of photosynthetic pathway (Crayn et al. 2004). By mapping the character on a molecular tree based on the chloroplast *ndh*F gene, Givnish et al. (2007) showed that CAM photosynthesis arose at least four times independently from an ancestral $C_3$-metabolism.

The structure and function as well as the taxonomic and evolutionary relevance of a wide variety of morphological and anatomical characters of bromeliads have been studied intensively during the last two centuries, including characters of reproductive parts such as petal appendages (Brown and Terry 1992), floral nectaries (Budnowski 1922, Böhme 1988, Sajo et al. 2004), stigmata (Brown and Gilmartin 1984b, Schill et al. 1988, Brown and Gilmartin 1989a), pollen (Ehler and Schill 1973, Halbritter 1992) and seeds (Varadarajan and Gilmartin 1988a, Gross 1992, 1993a and b), as well as trichome morphology (Ehler 1977, Winkler 1986, Pierce et al. 2001), leaf anatomy (Robinson 1969, Horres and Zizka 1995) and karyology (Marchant 1967, Brown and Gilmartin 1986, Brown and Palací 1997, Ramírez-Morillo and Brown 2001, Gitaí et al. 2005). Furthermore numerous studies focused on various aspects of ecophysiology, reproduction and biogeography (e.g. Nyman et al. 1987, Medina et al. 1977, Scarano et al. 1999, Popp et al. 2003, Manetti et al. 2009, Jabiol et al. 2009, Vervaeke et al. 2001, Kessler and Krömer 2000, Wendt et al. 2002, Sgorbati et al. 2004, Ibisch et al. 1997, Schulte et al. 2005, Zizka et al. 2009).

As bromeliad fossils are only scarcely documented (Gómez 1972, Benzing 2000), the assessment of the family's age remains difficult. By calibrating a chloroplast DNA-based phylogeny of Bromeliaceae with the overall phylogeny of monocots and monocot fossils, Givnish et al. (2011) estimated that the stem group of bromeliads arose about 100 million years ago (mya), at the boundary of the Cretaceous and the Tertiary, whereas divergence within the crown group only began approximately 19 mya. While the Guayana Shield is supposed to be the provenance of Bromeliaceae (Medina 1974, Givnish 2004), the family is now distributed from the south of the USA to the south of Argentina. A single species, *Pitcairnia feliciana*, occurs in Guinea, western Africa (Porembski and Barthlott 1999), where it probably arrived through a long distance dispersal event (Givnish et al. 2004).

The closest relatives of the family have long been in discussion. Based on morphological and anatomical data bromeliads were traditionally assigned to the monotypic order Bromeliales (Engler 1924, Cronquist 1981, Dahlgren et al. 1985, Thorne 1992, Givnish et al. 1999, 2000). Whereas some authors suggested that Velloziaceae are sister to Bromeliaceae (e.g., Huber 1977, Gilmartin and Brown 1987), others assumed Rapateaceae to be the closest relatives

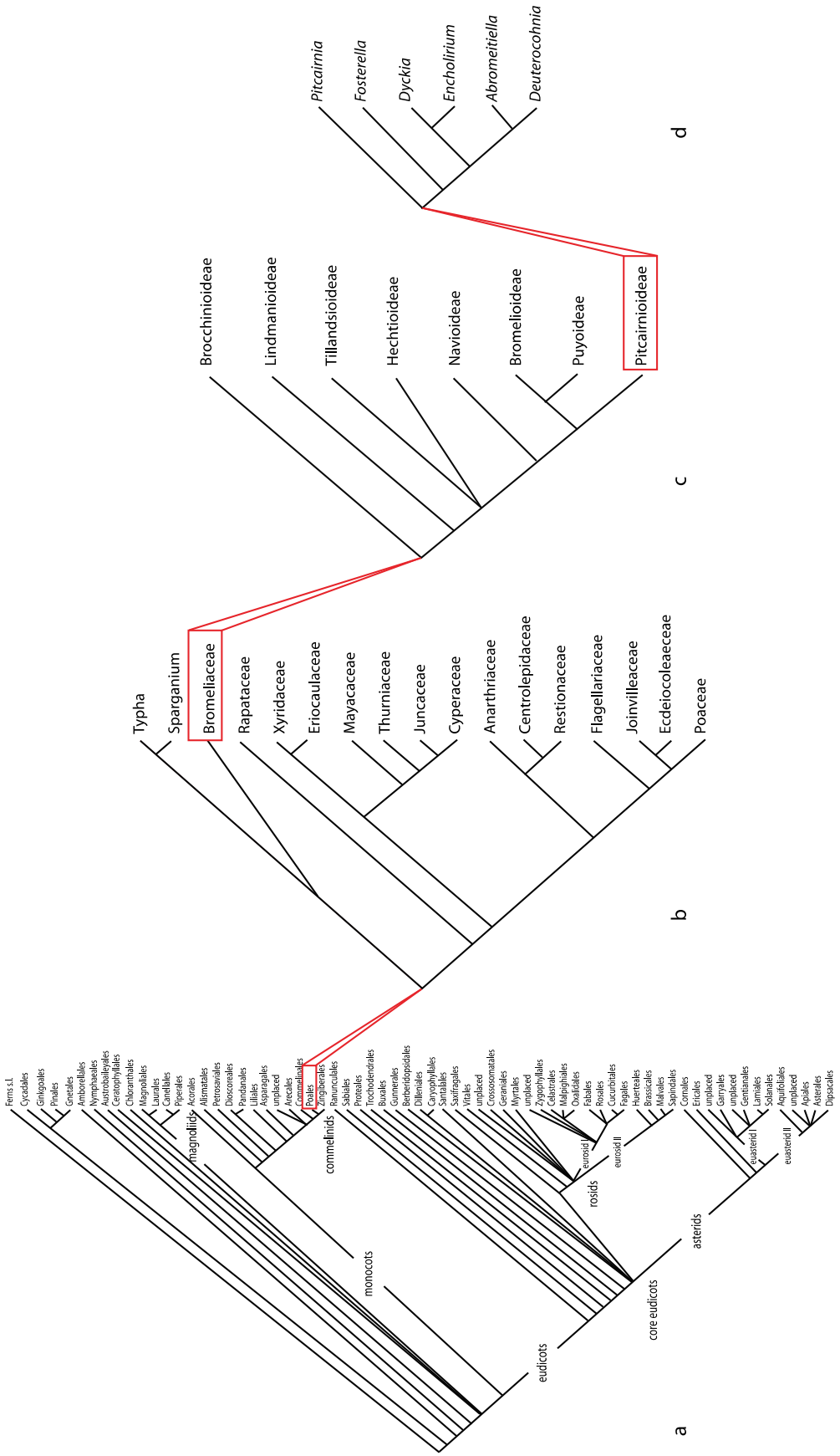


Fig. 1.1: Systematic relationships of Bromeliaceae. a: Position of Poales within vascular plants. b: Placement of Bromeliaceae within Poales. c: Intrafamiliar classification of Bromeliaceae. d: Relationships within subfamily Pitcairnioideae. a and b after APG III (2009); c and d modified after Givnish et al. (2007, 2011).

(Smith 1934, Clark 1993). Current molecular phylogenies revealed Bromeliaceae at the base of Poales sensu APG III (2009), where they occupy a sister position to Typhaceae and Sparganiaceae (Chase et al. 2006, Graham et al. 2006, Givnish et al. 2007, 2011, APG III 2009; Fig. 1.1 a, b).

Traditionally the bromeliad family has been divided into three subfamilies (Mez 1934, Smith and Downs 1974, 1977, 1979, Smith and Till 1998): (1) Tillandsioideae, with a superior ovary, capsular fruits and winged seeds; (2) Pitcairnioideae, likewise with a superior ovary and capsular fruits, but plumose seeds; and (3) Bromelioideae, with an inferior ovary, baccate fruits and unappendaged seeds. In the last 20 years, molecular data mainly based on chloroplast DNA sequence variation have increasingly been used to verify the monophyly of these subfamilies and to unravel the relationships between genera (Ranker et al. 1990, Terry et al. 1997a and b, Horres et al. 2000, Crayn 2000, Crayn et al. 2004, Givnish et al. 2004, Schulte et al. 2005, 2008, 2009, Barfuss et al. 2004, 2005b, Horres 2007). These studies generally supported the monophyly of Tillandsioideae and Bromelioideae. On the contrary, Pitcairnioideae in their traditional circumscription turned out to be highly paraphyletic, as had already been suspected by some earlier authors (Harms 1930, Smith 1934, Tomlinson 1969).
The chloroplast DNA trees led Givnish and coworkers to the suggestion of a new system of eight subfamilies (Givnish et al. 2007, 2008a and b, 2011; Fig. 1.1c). Following this classification the monophyletic Bromelioideae and Tillandsioideae remain as subfamilies while the paraphyletic Pitcairnioideae are split up into Pitcairnioideae s.str. and five new subfamilies: Brocchinioideae, Lindmanioideae, Puyoideae, Navioideae and Hechtioideae.

While the classification of Bromeliaceae at the subfamily level has become more and more approved, considerable uncertainty still exists regarding the monophyly of large genera, and relationships between and within genera, especially in Tillandsioideae (Barfuss et al. 2005b) and Bromelioideae (Sass and Specht 2010). Within Pitcairnioideae s.str., molecular studies so far indicate that *Pitcairnia* is sister to the remainder of the subfamily (Fig. 1.1d, Fig. 1.2) and that the three genera *Dyckia*, *Encholirium* and *Deuterocohnia* (including *Abromeitiella*) together form a monophyletic group – the so-called *Dyckia*-clade – which is sister to *Fosterella* (Crayn et al. 2004, Rex et al. 2009). Based on their chloroplast DNA tree, Givnish et al. (2007, 2011) dated the split of the *Dyckia* clade from *Fosterella* to about 11 mya, and the diversification of the extant *Deuterocohnia* species to about 2 mya (Fig. 1.2).

Several recent studies have addressed the taxonomy and phylogeny of *Fosterella* (Rex et al. 2007, 2009, Peters et al. 2008, Peters 2009), but few in-depth systematic investigations are yet available for the other genera of the Pitcairnioideae s. str. (Forzza 2005). It has not even been unambiguously clarified whether these genera are monophyletic. The research presented in this thesis aims to increase our knowledge of the genus *Deuterocohnia*, its taxonomy, biogeography, phylogeny and evolution.

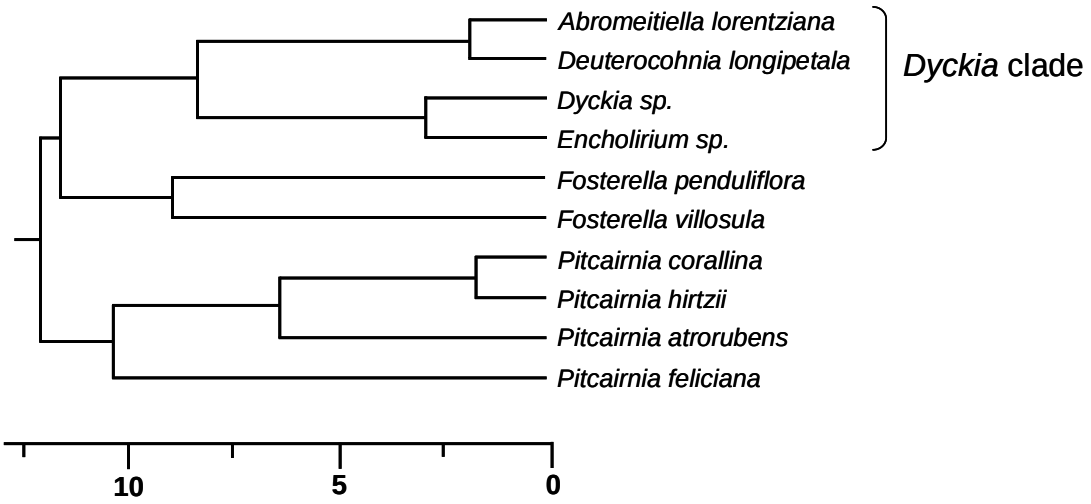


Fig. 1.2: Chronogram of Pitcairnioideae s.str. (after Givnish et al. 2007). Time scale in million years.

## 1.2 The genus *Deuterocohnia* Mez

Like all pitcairnioids, the species of *Deuterocohnia* show a terrestrial growth habit, generating dense rosettes with spiny leaves. Due to lateral branching, a single plant often comprises several to many ramets, which can form hemispherical groups, rings or extensive cushions (Fig. 1.3c, d, e). The main axis terminates with an inflorescence. In most *Deuterocohnia* species the axis of the inflorescence is perennial, becomes woody and is then able to flower for several years. With every anthesis, flowers are being formed along secondary branches. Perennial inflorescences are an exceptional character within Bromeliaceae, and are so far only known from *Deuterocohnia* and some species of *Hohenbergia* (Benzing 2000).

The flowers vary in size and colour, with a spectrum ranging from yellow to green, orange or red, either single- or bicoloured (Fig. 1.3a). In some species, petals are recurved. All *Deuterocohnia* species have petal appendages, a character that has been assigned taxonomic relevance (Brown and Terry 1992, Schulte 2007). The capsular fruits release many laterally alate seeds (Fig. 1.3b).


Fig. 1.3: Examples of morphology and habitat of *Deuterocohnia.* a-c: *Deuterocohnia meziana*, a: flower. b: fruit. c: flowering plant. FAN, Santa Cruz, Bolivia. d *Deuterocohnia strobilifera*, habitat, Bolivia. e *Deuterocohnia* (*Abromeitiella*) *lorentziana*, cushion, Bolivia.

*Deuterocohnia* species are distributed across central South America, with a centre of diversity in the Andes of southern Bolivia and northern Argentina (Fig. 1.4). *Deuterocohnia longipetala* shows a disjunct distribution pattern and is also known from the north of Peru, whereas *D. chrysantha* is endemic to northern Chile (Smith and Downs 1974, Ibisch 2003, Zizka 2003). Most of the species grow at altitudes between 1000 and 3000 m a.s.l. However, *D. meziana* also extends into the lowlands of western Brazil and northern Paraguay. Only one species occurs near the coast (*D. chrysantha* in Chile). Regardless of region and altitude, all *Deuterocohnia* species grow as terrestrial or epilithical plants on bare rocks, stony slopes and in dry valleys characterized by low precipitation and high insolation. In order to cope with their sun-exposed habitats the species generally developed xerophytic adaptations, such as evergreen, long-lived and slowly growing leaves with a spiny margin and pronounced water storage tissue, hairy indument and CAM photosynthesis (Crayn et al. 2004). *Deuterocohnia* is assigned to the ecophysiological type I after Pittendrigh (1948) and Benzing (2000).

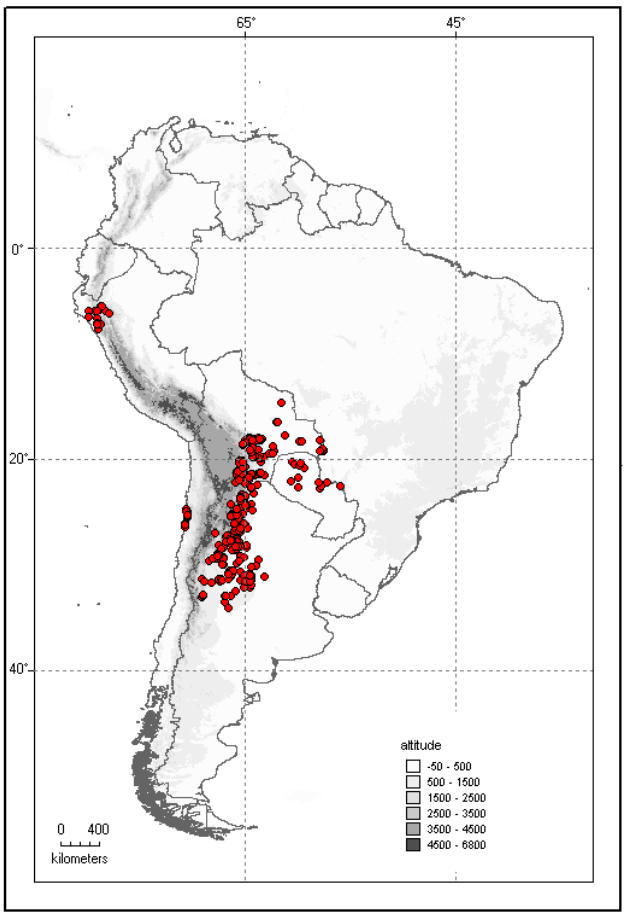


Fig. 1.4: Distribution of the genus *Deuterocohnia* Mez in South America according to the present study.

*Deuterocohnia* was first described in 1894 by the German botanist Christian Mez who characterized two species: *D. longipetala* and *D. chrysantha*. Eighty years later Smith and Downs (1974) listed seven *Deuterocohnia* species and two varieties in their extensive monograph of the Bromeliaceae (part I, Pitcairnioideae). Since this publication the number of recognized species within the genus has increased continuously (Rauh 1983, 1985, 1988a, Rauh and Hromadnik 1987, Gross 1990, 1991, Till and Hromadnik 1997, Vásquez et al. 2002, Ibisch and Vásquez 2003, Till 2004). At the onset of the present work, *Deuterocohnia* comprised 17 species, two subspecies and four varieties, including four species which had formerly been assigned to the genus *Abromeitiella*. *Deuterocohnia* and *Abromeitiella* were synonymized by Smith and Downs (1992), but many scientists still maintain the differentiation between the two genera (e.g. Crayn et al. 2000, Horres 2003, Givnish et al. 2007).

Apart from the discussion of the position of *Abromeitiella*, species delimitation within *Deuterocohnia* is not well clarified. While some species can be identified unambiguously (e.g. *D. brevispicata*), others are less well-defined. For example, *D. longipetala* is a widely distributed species showing a

broad morphological variability, but also high affinity to *D. meziana*. The difficulty of classifying the two cushion-forming species *D. brevifolia* and *D. lorentziana* is documented by their extensive nomenclatural history (Smith 1964b) which will be elucidated in the present study.

Up till now, only little molecular systematic data have been collected from *Deuterocohnia*. Molecular analyses of bromeliad relationships based on chloroplast DNA data usually included only a few *Deuterocohnia* accessions (Horres et al. 2000, 2007: *trn*L intron, *trn*T–*trn*L, *trn*T–*trn*F; Givnish et al. 2004, 2007: *ndh*F; Crayn et al. 2000, 2004: *mat*K, *rps*16 intron). In general, these studies suggested a close relationship of *Deuterocohnia* with *Dyckia* and *Encholirium*, which together form a sister clade to *Fosterella*. In some analyses, *Deuterocohnia meziana*, *D. brevispicata* or *D. scapigera* grouped together with *Dyckia* and *Encholirium* instead of forming a clade with the other *Deuterocohnia* samples, casting some doubt on the monophyly of *Deuterocohnia* (Horres et al. 2000, Crayn et al. 2000, 2004). In the only study so far where a broader set of *Deuterocohnia* accessions were included, Horres (2003) conducted an AFLP analysis of 14 *Deuterocohnia*, three *Dyckia* and four *Pitcairnia* species. The resulting tree supported a monophyletic *Deuterocohnia* clade, with *D. chrysantha* being sister to all other species of the genus. *D. longipetala* accessions were found at different branches of the tree, raising the possibility of the existence of cryptic species. However, branch resolution and statistical support of the AFLP tree generated by Horres (2003) were low, and infrageneric relationships remained ambiguous.
Considering that numerous new *Deuterocohnia* species have been described in the last two decades, that species and genus delimitations are somewhat ambiguous and infrageneric relationships unknown, a taxonomic revision of *Deuterocohnia* incl. *Abromeitiella* is overdue. Nowadays, such a revision should take into account morphological and anatomical characters as well as molecular data. Setting up a molecular phylogeny would not only greatly assist in unravelling infrageneric relationships, the monophyly of *Deuterocohnia,* and the position of *Abromeitiella*, it would also help to reconstruct the biogeographical history of the genus and its correlation with paleogeographic events like the uplift of the Andes.

## 1.3 Scope of the present study

This doctoral thesis provides

- A taxonomic revision of the genus *Deuterocohnia* Mez, including species descriptions, nomenclature, distribution and a key for the identification of currently accepted species, subspecies and varieties.

- A comprehensive overview of the genus' morphology, distribution and ecology.

- Analysis of phylogenetic relationships within *Deuterocohnia* as well as with the closely related genera *Dyckia* and *Encholirium* using chloroplast and nuclear DNA sequence data.

- A re-evaluation of the position of the former *Abromeitiella*-species.

- Hypotheses on the evolution of the genus and its species.

# 2 MATERIAL AND METHODS

## 2.1 Sources of plant material

### 2.1.1 Living plant material

Living plant material was collected and plants were assessed in their natural habitats in the course of two field trips to Bolivia and Argentina. These were carried out in 2006 and 2009 in close collaboration with the Herbario Nacional de Bolivia [LPB]. The trip in 2006 was funded by the DAAD. Localities of plant collections are shown in Figure 2.1.

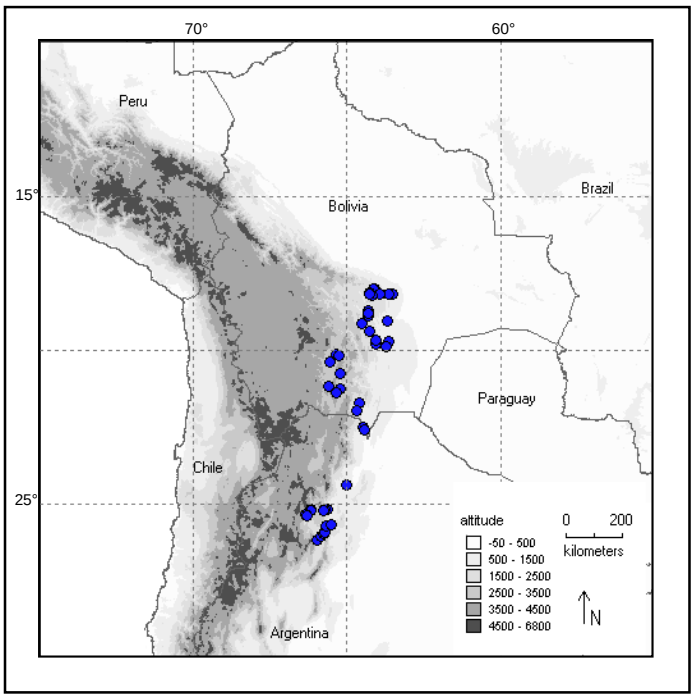


Fig. 2.1: Collection localities of *Deuterocohnia* from field trips to Bolivia and Argentina in 2006 and 2009.

Additional materials (plants, leaf samples or seeds) were obtained from the following Botanical Gardens and private living plant collections (in alphabetical order): Botanical Garden and Botanical Museum Berlin-Dahlem, Palmengarten Frankfurt/Main, Botanical Garden of the Georg-August-Universität Göttingen, Botanical Garden of the University of Hamburg, Botanical Garden of the Ruprecht-Karl-Universität Heidelberg (all Germany), Botanical Garden of the University of Vienna (Austria), Fundación Amigos de la Naturaleza (Santa Cruz, Bolivia), private brome-

liad collections of Roberto Vásquez (Santa Cruz, Bolivia) and Des. Elton M.C. Leme (Teresópolis, Río de Janeiro, Brazil).
By growing seeds either collected in the field or obtained from the above Botanical Gardens, a living plant collection was established at the greenhouse facilities of the Department of Botany at the University of Kassel. This collection presently (October 2011) comprises more than 60 accessions belonging to 13 *Deuterocohnia* species.
All species belonging to the genus *Deuterocohnia* were available for molecular analyses (DNA material Tab. 2.7).

### 2.1.2 Herbarium specimens

For the taxonomic studies, about 700 herbarium specimens from the following 39 Herbaria in South America, the USA and Europe were reviewed: A, B, BA, BAA, BM, C, CORD, F, FCQ, FR, G, GB, GOET, HB, HBG, HEID, HSB, HUH, HUT, K, LIL, LP, LPB, M, MCNS, MICH, MO, NY, R, RB, S, SI, U, UC, US, USM, USZ, WU, ZSS. Some specimens could be assessed on site, but most of them were obtained as loans, and studied at the Herbarium Senckenbergianum Frankfurt/Main [FR]. In a few cases vouchers had to be examined electronically as image files. Specimens collected during field trips were stored at LPB (Bolivian collections) and LIL (Argentinean collections). Duplicates were stored at FR. The Herbaria INPA, CUZ, and MOL were also contacted, but unfortunately no *Deuterocohnia* vouchers were available from these resources.

## 2.2 Taxonomic treatment

### 2.2.1 Abbreviations and terminology

The nomenclature of bromeliad species complies with Luther (2008), the intrafamiliar classification of Bromeliaceae follows Givnish et al. (2007). Species descriptions were performed in accordance with the International Code of Botanical Nomenclature (McNeill et al. 2006; (q.v.http://ibot.sav.sk/icbn/main.htm). Authors were abbreviated according to the International Plant Names Index (Croft et al. 1999; q.v. http://www.ipni.org). Acronyms of Herbaria refer to the Index Herbariorum (Holmgren et al. 1990; q.v.http://sciweb.nybg.org/science2/Index Herbariorum. asp). Book titles are abbreviated following Stafleu and Cowan (1976–1988; q.v. http://tl2.idcpublishers.info/), and abbreviations of periodicals follow the Botanico-Periodicum-Huntianum 2 (Bridson et al. 2004; q.v. http://fmhibd.library.cmu.edu/fmi/iwp/cgi?-db=BPH_Online&-loadframes). The terminology of taxonomic characters follows Stearn (2004)

and Simpson (2006). Despite the use of bromeliad specific terms in many morphological descriptions of bromeliads, the present study uses the original botanical terms as recommended by Scharf et al. (2007).

### 2.2.2 Assessment of morphological and anatomical characters

All character assessments refer to mature plants. Micromorphological and anatomical characters were investigated using a stereo microscope (Leica EZ4) and a light microscope (Leica DME), both equipped with digital cameras. For the generation of cross sections of peduncles, the tissue was boiled in water, cut with a rotation microtome (2035 Biocut, Leica), stained with safranine in 60% ethanol and finally embedded with Euparal (samples kindly processed by Jennifer Markwirth, Abt. Vor- und Frühgeschichte, Goethe-Universität Frankfurt). Cross sections of leaves were dewatered by ascending ethanol series, infiltrated and embedded with Technovit 7100 (Heraeus-Kulzer) according to manufacturer specifications. Cut sections (rotation microtome Leitz 1515) were stained with toluidine blue according to Trump et al. (1961) (samples kindly processed by Irene Diebel, University of Kassel). Flowering plants were usually used for taking measurements, except for some vouchers of cushion-forming plants where only vegetative parts were available. Plant parts were measured as defined in the following:

| | |
|---|---|
| Plant height: | The height of living plant material was defined as the distance from the ground of the green leaved part of the ramet up to the top of the fully developed inflorescence. |
| Leaves: | Wherever possible, measurements were taken from leaves derived from the middle part of the mature rosette. Herbarium specimen often exhibited few leaves only, which had been detached from the rosette. The former position of these leaves along the axis is indeterminate. |
| Leaf sheaths: | The lengths of the leaf sheaths were measured at the vertical median, their width at the broadest part, mostly just below the horizontal median. |
| Leaf blades: | The lengths of the leaf blades were measured at the vertical median, the width at the broadest part of the blade, at the transition to the sheath. |
| Peduncle: | The length of the peduncle was defined as the distance from its base at the top of the rosette to either the lowest floral bract in the case of a spike or a raceme, or to the lowest primary bract in the case of a compound inflorescence. The diameter of the peduncle was measured at its half height. |
| Peduncle bracts: | The measures of bracts were taken at half height of the peduncle. |

| | |
|---|---|
| Inflorescence: | The length of the inflorescence was defined as the distance from the top of the inflorescence to either the lowest floral bract in case of a spike or a raceme, or to the lowest primary bract in case of a compound inflorescence. |
| Primary bracts: | Primary bracts were measured at half height of the inflorescence. |
| Partial inflorescence: | The lengths of partial inflorescences were measured from their axile up to the top of the longest branch. |
| Flower parts: | Measurements of floral bracts and flower parts were generally taken from mature flowers occurring at half length of the branches and at half height of the inflorescence |
| Fruits: | Measurements generally refer to mature fruits before dehiscence. |

### 2.2.3 Biogeographical and ecological data

Biogeographical and ecological data such as geographical coordinates, altitude and habitat of each analysed sample were compiled from notations of herbarium vouchers as well as from own observations in the field. Sites only known from literature were not included, wherever species identities could not be confirmed. If coordinates of sampling sites were not specified on the voucher, degrees and minutes were roughly estimated by using other given information (like cities, rivers, roads etc. in the vicinity) and appropriate maps (Argentina and Peru: Freytag and Berndt, 2006; Bolivia: World mapping project, 2006), googleearth (http://earth.google.com) and geonames (http://www.geonames.org). Corresponding coordinates are marked with brackets. Distribution maps were drawn using the program DIVA-GIS (Hijmans et al. 2001) and ArcMap 9.2 (ESRI 2009) using WGS84. Allocated ecoregions refer to Olsen et al. (2001, "Ecoregion of the World/ Latin America") and Ibisch et al. (2004). Attendant numbers are listed in brackets according to Olsen et al. (2001).

## 2.3 Molecular methods

### 2.3.1 Equipment

Instruments utilized for laboratory work in the present study are summarized in Table 2.1.

Tab. 2.1: Instruments used for molecular analyses in the present study.

| Instrument | Company |
|---|---|
| Automated gel sequencer, IR² DNA Sequencer Long Readir 4200, incl. vertical rig for PA gels | LI-COR Biosciences, Lincoln |
| Automatic capillary sequencer, ABI 3730 DNA Analyzer | Applied Biosystems, Amsterdam |
| Electrophoresis microcomputer, consort E132 | Biozym, Oldendorf |
| Filtration plates, MultiScreen 96-well filter plates | Millipore, Billerica MA |
| Gel chambers for agarose gel electrophoresis | Home-made by facilities of the University of Kassel |
| Laboratory balance, BP3105 | Sartorius, Göttingen |
| Magnetic stirrer, KMO2 B | IKA®-Werke, Staufen |
| Microcentrifuges, 5804, 5804 R, 5415 D | Eppendorf, Hamburg |
| Mortar and pestle | Haldenwanger, Waldkraiburg, Berlin |
| Orbital shaker, 3017 | GFL, Burgwedel |
| pH meter, inoLab pH Level 1 | WTW, Weilheim |
| Pipettes, Rainin | Mettler-Toledo, Gießen |
| Thermocycler, T1 and TGradient | Biometra, Göttingen |
| Thermocycler, iCycler | Bio-Rad, Hercules, München |
| Thermomixer compact | Eppendorf, Hamburg |
| Tips, tubes, microtiter plates and other plastic consumables | Biozym, Oldendorf; Sarstedt, Nümbrecht |
| Gel documentation system (BioDocAnalyze) incl. UV-transilluminator (312nm) | Biometra, Göttingen |
| Vortex, Genie-2 | Scientific Industries, Bohemia |
| Vacuum concentrator, Savant SpeedVac® SPD101B | Thermo Fisher Scientific, Waltham |

### 2.3.2 Chemicals and solutions

Chemicals, enzymes and kits used in the present work are listed in Table 2.2. Buffers and solutions are summarized in Table 2.3.

Tab. 2.2: Chemicals, enzymes and kits used in the present study.

| Chemicals, Enzymes, Kits | Company |
|---|---|
| Agarose, NEEO Roti®agarose | Carl Roth, Karlsruhe |
| Ammonium persulfate, 98+% | Sigma®, St. Louis |

| **Chemicals, Enzymes, Kits** | **Company** |
|---|---|
| Boric acid | Carl Roth, Karlsruhe |
| Bovine serum albumin, 20 mg/ml | Fermentas, Burlington |
| Bromophenol blue | Carl Roth, Karlsruhe |
| Calf Intestine Alkaline Phosphatase | Fermentas, Burlington |
| Cetyltrimethylammoniuim bromide (CTAB) | Carl Roth, Karlsruhe |
| Chloroform | Acros Organics, Geel |
| Cycle Sequencing Kit, Thermo Sequenase™ Primer | GE Healthcare, Little Chalfont |
| Cycle Sequencing Kit, BigDye® Terminator v3.1 | Applied Biosystems, Amsterdam |
| Dimethylsulfoxide (DMSO) 100% | Sigma®, St. Louis |
| DNA ladder, 100 bp | Invitrogen, Carlsbad |
| EDTA | Carl Roth, Karlsruhe |
| Ethidium bromide | Carl Roth, Karlsruhe |
| Exonuclease I | Fermentas, Burlington |
| Formamide | Merck, Darmstadt |
| Glycerol | Merck, Darmstadt |
| Isoamyl alcohol | Carl Roth, Karlsruhe |
| Isopropanol | Carl Roth, Karlsruhe |
| β-Mercaptoethanol | Carl Roth, Karlsruhe |
| Lambda DNA | Fermentas, Burlington |
| Liquid nitrogen | Linde, München |
| Magnesium chloride 50 mM | Invitrogen, Carlsbad / Bioline, Taunton |
| Deoxyribonucleotides (dNTP) 100 mM | Carl Roth, Karlsruhe |
| Oligonucleotides (PCR primers), simple and fluorescent 100 µM | Metabion, Planegg-Martinsried |
| PCR buffer 10× (200 mM Tris-HCl pH 8.4, 500 mM KCl) | Invitrogen, Carlsbad / Bioline, Taunton |
| PCR Master Mix, 1.1× ReddyMix™ (2.5 mM $MgCl_2$) | ABgene® UK, Epsom |
| PCR purification Kit, PureLink™ / QIAquick® | Invitrogen, Carlsbad / QIAGEN, Hilden |
| PCR Gel extraction Kit, PureLink™ / QIAquick® | Invitrogen, Carlsbad / QIAGEN, Hilden |
| pGEM®-T Easy Vector System, cloning kit | Promega, Madison |
| Polyvinylpyrrolidon (PVP-40) | Sigma®, St. Louis |
| RNase A, 5 mg/ml | Invitrogen, Carlsbad |
| Sephadex® G-50 superfine or fine | GE Healthcare, Little Chalfont |
| Sodium chloride | Carl Roth, Karlsruhe |
| Sterile sea sand | Merck, Darmstadt |
| *Taq* DNA Polymerase, Mango *Taq*, 1 or 5 U/µl | Bioline, Taunton |
| *Taq* DNA Polymerase, 1U/µl | Invitrogen, Carlsbad |
| Tris-HCl | Carl Roth, Karlsruhe |
| Ultra Pure SequaGel® XR (incl. acrylamide) | National Diagnostics, Atlanta |
| Ultra Pure SequaGel® Complete Buffer Reagent | National Diagnostics, Atlanta |
| Xylene cyanol | Merck, Darmstadt |

Tab. 2.3: Composition of solutions used in the present study.

| **Stock solutions** | |
|---|---|
| Agarose gel solution | 0.8% or 1.5% agarose in 0.5× TBE buffer |
| Ammonium persulfate (APS) solution | 100 mg/ml in aqua bidest |
| CTAB-buffer | 2% CTAB (w/v), 1.4 M NaCl, 0.1 M Tris-HCl pH 8.0, 20 mM EDTA, 0.2% β-mercaptoethanol, 1% PVP-40 |
| Chloroform-isoamyl alcohol | Mixture of chloroform and isoamyl alcohol in a ratio of 24:1 (v/v) |
| DNA loading dye (DNA-extr. and PCR) | 40% (v/v) glycerol, 0.1% (w/v) bromophenol blue, 0.1% (w/v) xylene cyanol |
| DNA loading dye (sequencing) | 98% (v/v) formamide, 0.025% (v/v) basic fuchsine, 10 mM EDTA |
| Enzyme purification (ExoI / CIAP) | 6.66 u/µl ExonucleaseI, 0.66 U/µl Calf Intestine Alkaline Phosphatase |
| Ethidium bromide staining solution | 1 µg/ml in 0.5× TBE |
| Deoxyribonucleotide mix (dNTP) | 2.5 mM dATP, 2.5 mM dCTP, 2.5 mM dGTP, 2.5 mM dTTP in aqua bidest |
| Polyacrylamide gel solution 6% | SequaGel® solution, SequaGel® buffer, 10% APS solution in a ratio of 100:25:1 |
| Sephadex® solution | 75g/L Sephadex® in HPLC water mixed with 7% of 1× TE |
| TBE buffer 1× | 90 mM Tris-borate, 2 mM EDTA, pH 8.3 |
| TE buffer | 10 mM Tris-HCl, 1 mM EDTA, pH 8.0 |

### 2.3.3 DNA isolation

Due to the often poor quality of DNA isolated from herbarium material of Bromeliaceae, DNA was generally prepared from fresh or silica-dried plant material. As soon as possible after sampling, parts of fresh leaves were either dried in silica gel, or deep-frozen at -80°C. DNA was extracted using a modification of the standard CTAB (cetyltrimethylammonium bromide) method (Saghai-Maroof et al. 1984). The detergent CTAB destroys cellular and nuclear membranes. To protect the released DNA from degradation, the buffer contains EDTA that binds bivalent cations, necessary for nuclease activity. Beta-Mercaptoethanol is a strong reducing agent that prevents DNA from being damaged through oxidation processes. PVP-40 removes polyphenols, quinones und tannins and other secondary compounds through formation of insoluble complexes. Proteins, lipids and chlorophyll are removed via extraction with a chloroform/isoamyl alcohol mixture. Isopropanol is used for DNA precipitation.

**Procedure**

Fifty mg of silica-dried or 100 mg of fresh leaf tissue were grinded together with sterile sea sand and liquid nitrogen in a mortar. The powdered material was incubated in 500 µl CTAB buffer on

a thermomixer (30–60 min, 60°C, 1100 rpm). The sample was then mixed with an equal volume of chloroform/ isoamyl alcohol (24 : 1) and admixed by slight shaking for 10 min. It was then centrifuged at room temperature for 15 min at 9000 rpm to separate the phases. The upper, DNA-containing aqueous phase was transferred into a fresh reaction tube. For DNA precipitation 0.6 volumes of cold isopropanol were added. Samples were then mixed and incubated for 5–15 min at room temperature or for several hours at -20°C. After a short centrifugation in a table-top centrifuge (10°C, 13000 rpm, 15 min), the pellet was washed with 500 µl of 70% ethanol, centrifuged again (10°C, 13000 rpm, 15 min), dried at room temperature or in a speed vac and dissolved in 200 µl of 1 × TE buffer. To digest residual RNA present in the samples, 1 µl of an RNase A solution (10mg/ml) was added and samples were incubated over night at room temperature. DNA extracts were stored at -20°C at the laboratory of the Department of Botany, University of Kassel.

### 2.3.4 Gel electrophoresis

The quality and concentration of extracted plant DNA or PCR products were checked by electrophoresis on 0.8% or 1.5% agarose gels at 5 V per cm. Lambda DNA aliquots of different concentrations (2–50 ng/µl) were applied in parallel lanes for estimating the quantities of genomic DNA preparations. Before electrophoresis, samples were mixed with a small amount of DNA loading dye. A size standard (100 bp ladder) was used to determine the sizes of PCR products. Gels were stained in ethidium bromide solution and visualised under UV light with the help of an UV-transilluminator and a Biometra gel documentation system.
Denaturing polyacrylamide (PA) gels were applied for high-resolution electrophoresis. To prepare a 6% polyacrylamide gel, SequaGel® solution, SequaGel® buffer and APS were mixed in a ratio of 100 : 25 : 1. Before loading onto the gel, samples were mixed with formamide loading dye (see 2.3.5.2). DNA fragments were denatured and separated on 41 cm long, 0.2 mm thick gel matrices in an automated DNA sequencer (LI-COR; see 2.3.5.2)). Electrophoresis conditions were as follows: voltage 2000 V, current 25 mA, power 50 W, temperature 45°C, scanning-rate moderate, prerun 30 min.

### 2.3.5 PCR amplification and sequencing of chloroplast DNA fragments

Since the advent of molecular systematics, chloroplast DNA (cpDNA) sequences have remained the main source of data for elucidating relationships among plant taxa. The circular cpDNA molecule of about 120 to 160 kb comprises approx. 100 protein-coding regions as well as genes

for rRNA and tRNA (Borsch and Quandt 2009). The chloroplast genome combines several advantages for molecular phylogenetic analyses: (1) The conserved arrangement and sequence of cpDNA coding regions enable the design and use of so-called "universal" PCR primers that are functional across distantly related plant groups (Taberlet et al. 1991, Demesure et al. 1995, Dumolin-Lapegue et al. 1997, Weising and Gardner 1999, Shaw et al. 2007). (2) Given that cpDNA appears in many copies per chloroplast, and there are numerous chloroplasts per cell, tiny amounts of tissue often provide sufficient template for DNA amplification via PCR. (3) Because the chloroplast genome is haploid and recombination is rare, there is usually only a single version of a cpDNA molecule per individual plant. Exploiting nuclear DNA sequences for evolutionary studies is much more difficult due to the frequent occurrence of recombination, gene duplication and polyploidy in the nuclear genome, resulting in e.g. paralogues, pseudogenes, and gene families (Small et al. 2004).

Mitochondrial DNA (mtDNA) has been used a lot in phylogenetic studies of animals. However, the high sequence conservation and structural instability of plant mtDNA as well as frequent horizontal gene transfer events complicates the use of mtDNA sequence data in plants, especially of mtDNA intergenic regions (Palmer et al. 2000, Burger et al. 2003, Bergthorsson et al. 2003, Sugiyama et al. 2005).

When selecting suitable target regions for sequencing, the most relevant parameter is the extent of sequence variation among the taxa of interest. A sequence divergence of about 5–15% provides enough differences to resolve relationships on the one hand, and avoids the problem of mutational saturation on the other (Ritland and Clegg 1990). Studies at higher taxonomic levels, e.g. of relationships among families, typically utilize cpDNA coding regions (e.g., *atp*B, *rbc*L: Savolainen et al. 2000, Bremer 2002, *ndh*F: Givnish et al. 2000). To resolve relationships between more closely related taxa, noncoding sequence data from introns and intergenic spacers generally provide much more phylogenetically informative variation (e.g.: *trn*L–*trn*F, Taberlet et al. 1991, Schneider et al. 2006). In Bromeliaceae, studies at the family and subfamily level usually implemented cpDNA data from coding regions (e.g., *ndh*F: Terry and Brown 1996, Givnish et al. 2007, *mat*K: Crayn et al. 2000), whereas introns and intergenic regions were preferentially applied for investigations at the level of genera and species (e.g. Givnish et al. 2004, Barfuss et al. 2005a and b, Schulte et al. 2005, Rex et al. 2009).

#### 2.3.5.1 Selection and amplification of target fragments

As a single chloroplast locus scarcely provides enough variability to resolve phylogenetic relationships within genera, multi-locus studies are inevitable (Barfuss et al. 2008, Rex et al. 2009). How-

ever, the vast majority of current phylogenetic analyses based on chloroplast data rely on only a few markers, like e.g. *ndh*F, *matK, atp*B–*rbc*L, and *trn*L–*trn*F. Shaw et al. (2005) demonstrated that these commonly used markers do not exploit the full potential of cpDNA and presented a set of additional non-coding cpDNA loci that displayed more sequence variation. To further enlarge this set, Shaw et al. (2007) compared the fully sequenced chloroplast genomes from three pairs of closely related plant species and found 13 mutational hotspots, for which they designed flanking primers. Most of these newly discovered loci exhibited a higher variability than the 21 markers analysed in the previous study of Shaw et al. (2005). Two of the highly variable intergenic cpDNA spacers suggested by Shaw et al. (2007) were also used in the present investigation: *rpl*32–*trn*L and *rps*16–*trn*K. In the course of a parallel Diploma thesis (Wagner 2007), nine additional noncoding regions were tested for their phylogenetic utility within *Deuterocohnia*. Among these, the *trn*S–*ycf*3[1] intergenic spacer turned out to be the easiest to handle, showed appropriate variability and was also included in the present study. No bromeliad sequence for any of these three loci has been published in GenBank so far (as of June 2011), also Givnish et al. (2011) also used *rpl*32–*trn*L in their phylogenetic analysis of Bromeliaceae at the family level.

**Intergenic spacer *rpl*32–*trn*L**

The *rpl*32–*trn*L intergenic spacer is located in the small single copy region, between the coding sequences of the ribosomal protein 32 of the large subunit and a tRNA gene with specificity for leucine. This spacer proved to be the most variable cpDNA region in the publication of Shaw et al. (2007). Exhibiting a total length ranging from 543 to 1417 bp (average 1018 bp), the region shows large indels in different plant groups. Due to its length of about 1200 bp within *Deuterocohnia*, the region was sequenced in two parts. For that purpose, additional internal primers were designed (Tab. 2.4) using the program "Primer3" (Rozen and Skaletsky 2000).

**Intergenic spacer *rps*16–*trn*K**

The noncoding region between the ribosomal small subunit protein gene 16 (*rps*16) and a gene for a lysine-mediating tRNA (*trn*K) is part of the large single copy region of the chloroplast genome. Among the plant taxa included in the study of Shaw et al. (2007), the length of this region varied from 529 to 1008 bp (average 786 bp). Within *Deuterocohnia*, *rps*16–*trn*K was less than 1000 bp long and proved to be the most variable cpDNA region in pilot studies.

[1] The fragment *trn*S-*ycf*3 was published as *rps*4-*trn*T by Saltonstall et al. (2001). The comparison of this sequence with other cp genomes like that of *Triticum aestivum* reveald the target to be homolog to *trn*S-*ycf*3.

### Intergenic spacer *trn*S–*ycf*3

The intergenic spacer *trn*S–*ycf*3 is located in the large single copy region of the cpDNA. This locus was first used for molecular systematic analyses of Poaceae by Saltonstall (2001) who designed flanking PCR primers in the genes coding for the serine-mediating tRNA and the first intron of the ycf3-gene. The latter is an essential gene within the photosystem I complex. From the Diploma thesis of Wagner (2007), 46 *trn*S–*ycf*3 sequences were already at hand for *Deuterocohnia* and related taxa. This set was enlarged in the present study, to get a complete alignment of all investigated plant samples at three loci: *rpl*32–*trn*L, *rps*16–*trn*K and *trn*S–*ycf*3.

### PCR procedure

PCR assays were set up in total volumes of 15 or 25 µl, containing 1 × PCR reaction buffer, 1.5 mM $MgCl_2$, 0.2 mM of each dNTP, 0.25 µM each of forward and reverse primer, 0.1 U/µl *Taq* polymerase, 0.5 µg/µl BSA and ca 5 ng of DNA template (reagents and solutions listed in Tables 2.1, 2.2, 2.3). Amplifications were performed in a Biometra or Bio-Rad thermocycler under the following conditions: 5 min initial denaturation at 80°C followed by 30 cycles each of 1 min denaturation at 94°C, 1 min primer annealing at 52°C, and 2 min elongation at 65°C followed by a final elongation step of 5 min at 65°C, and cooling to 10°C. Product integrity and sizes were checked by agarose gel electrophoresis (see 2.3.4). Products aimed to being sent to a commercial facility for subsequent sequencing were purified using a PCR purification kit (Tab. 2.2) according to the manufacturer's instructions. All PCR primer sequences used in the present study are listed in Table 2.4. The 5´M13-tags served as targets for fluorescent M13-specific primers in subsequent sequencing reactions.

Tab. 2.4: Sequences of PCR primers used to amplify intergenic cpDNA regions of *Deuterocohnia* and related taxa. Concerning primers from Saltonstall et al. (2001) see footnote on page 19.

| Locus | Primer | Sequence | Reference |
|---|---|---|---|
| *rps*16–*trn*K | *rps*16 fwd | 5'-M13- AAA GTG GGT TTT TAT GAT CC -3' | Shaw et al. 2007 |
| | *trn*K rev | 5'-M13- TTA AAA GCC GAG TAC TCT ACC -3' | Shaw et al. 2007 |
| *rpl*32–*trn*L | *rpl*32 fwd | 5'-M13- CAG TTC CAA AAA AAC GTA CTT C -3' | Shaw et al. 2007 |
| | *rpl*32 internal rev | 5'-M13- TTT CAT ATC TAT CAC AAT TTC ATC A -3' | Schütz, present study |
| | *trn*L internal fwd | 5'-M13- GAG ATT GAA ACT CTT TTG TTA TAT GC -3' | Schütz, present study |
| | *trn*L rev | 5'-M13- CTA CTT CCT AAG AGC AGC GT -3' | Shaw et al. 2007 |
| *trn*S–*ycf*3 | *rps*4 (*trn*S) fwd | 5'-M13- TCS TAT TCC TGC AGT ACA GG -3' | Saltonstall et al. 2001 |
| | *trn*T (*ycf*3) rev | 5'-M13- CTG TAG GTG TAA CCT TTC GC -3' | Saltonstall et al. 2001 |

#### 2.3.5.2 Sequencing procedure

The sequences of appropriate PCR products were determined by cycle-sequencing-reactions (Sanger et al. 1977, Roemer et al. 1997, Sambrook and Russell 2001) using fluorescent primers. Bidirectional sequencing was enabled via labelling forward and reverse primers with separate fluorochromes that fluoresce at 700 nm and 800 nm, respectively. In the present study, the use of M13-tagged primers in preceding PCR reactions enabled the application of fluorescent M13 sequencing primers for each locus (Tab. 2.5; Fartmann et al. 1999).

Tab. 2.5: M13 sequencing primers.

| **Primer** | **Sequence** | **Reference** |
|---|---|---|
| M13-fwd-IRDye700 | 5'- TGT AAA ACG ACG GCC AGT -3' | Fartmann et al. 1999 |
| M13-rev-IRDye800 | 5'- CAG GAA ACA GCT ATG ACC -3' | Fartmann et al. 1999 |

Sequencing reactions were carried out in total volumes of 6 µl, containing 1.5 µl Thermo Sequenase™ Primer Cycle Sequencing Kit, 4 pmol of forward primer (M13-fwd-IRDye700), 6 pmol of reverse primer (M13-rev-IRDye800) and 10-50 ng of PCR product. All fragments were sequenced in both directions. The higher concentration of the IRDye800-labelled primer was needed due to lower signal intensities obtained with this primer. The sequencing program was as follows: 5 min initial denaturation at 95°C followed by 25 cycles each of 30 s denaturation at 95°C, 30 s primer annealing at 57°C and 1 min elongation at 72°C, followed by 10 min final elongation at 72°C and cooling to 10°C. Before loading the products onto the PA gel, samples were mixed with 6 µl formamide loading dye and denatured for 5 min at 80°C. The samples were run on an automated gel sequencer (LI-COR® Bioscience; see 2.3.4; reagents, solutions and supplementary material listed in Tables 2.1, 2.2, 2.3).

#### 2.3.5.3 Data processing

DNA sequences were edited using the e-seq™ software v2.0 (LI-COR® Bioscience). Consensus sequences and alignments were merged with the help of the program AlignIR v1.1 (LI-COR® Bioscience). To verify that the sequenced locus was the correct target, sequences were uploaded to GenBank and compared via BLAST search with available data.

### 2.3.6 PCR amplification and sequence analysis of nuclear DNA fragments

Nuclear DNA (ncDNA) exhibits advantages as well as disadvantages for comparative sequence analyses and molecular systematics as compared with cpDNA. On the positive side, the much larger nuclear genome provides an abundance of sequences for independent phylogenetic inferences of various unlinked loci, and the variable and often higher substitution rates ensure that nuclear loci can be used at all taxonomic levels. On the negative side, the nuclear genome is diploid or even polyploid, and gene duplication associated with recombination leads to the formation of gene families. Consequently, characterizing adequate markers often requires extensive efforts (Small et al. 2004). Given that only orthologous sequences are to be compared in phylogenetics, an appropriate nuclear locus should be either (1) a single copy marker with a minimum of allelic variation or (2) a low-copy marker, whose paralogues can be clearly distinguished from orthologues or (3) a high copy marker, which underlies concerted evolution (Zimmer et al. 1980).

Until recently, only one nuclear marker has been used as commonly as cpDNA for plant systematics: the nuclear ribosomal DNA (rDNA). The nuclear rDNA genes are organized in tandemly repeated units, each comprising the slowly evolving 18S and 28S rRNA genes (26S in plants) as well as internal and external transcribed spacers (ITS and ETS). Each unit is separated from the next by an intergenic spacer (IGS), which together with the ETS exhibits the highest mutation rates. The rDNA is subject to concerted evolution, i.e., the individual rDNA copies are usually homogenized in a fast and efficient manner via gene conversion-like processes (Baldwin et al. 1995). Consequently, only one or a few sequence variants usually occur in a given species, often enabling direct sequencing of PCR products (Baldwin 1992, Baldwin et al. 1995). In the early 1990s, ITS became a popular target for phylogenetic analyses because of the availability of universal flanking primers that are specific for the 18S and 26S-rDNA. ITS analyses proved to be mainly informative at the species level, and comparative sequencing of ITS is still widely used today (Soltis et al. 2008).

The use of protein-coding, low-copy nuclear markers for molecular systematic investigations began much more recently. Initial studies within plants focussed on a small number of loci, like PRK (phosporibulokinase, e.g. Norup et al. 2006), PHYC (phytochrome C, e.g. Samuel et al. 2005), GBSSI (granule-bound starch synthase, e.g. Evans et al. 2000), LFY (leafy, e.g. Bomblies and Doebley 2005) or RPB2 (RNA polymerase II subunit, e.g. Thomas et al. 2006). This list is however steadily growing (Steele et al. 2008, Levin et al. 2009).

#### 2.3.6.1 Selection and amplification of suitable ncDNA loci

In pilot experiments, PCR primer sequences of five ncDNA loci, i.e. ITS (internal transcribed spacer), MS (gene of malate synthase) intron2, PHYC (gene of phytochrome C) exon1, PRK (gene of phosporibulokinase) exon2 to exon5 and RPB2 (gene of RNA polymerase beta subunit 2) 23rd intron, were tested for their ability to amplify distinct PCR products in *Deuterocohnia* samples. These primer pairs were known to be functional in other plant species where they produced low-copy amplification products (e.g. Samuel et al. 2005, Grünstäudl et al. 2009, Schulte et al. 2009). Laboratory work on ncDNA was carried out at the Institute of Botany in Vienna, funded by a grant from SYNTHESYS, and at the Senckenberg Research Institute in Frankfurt. At the onset of the present project no nuclear DNA analyses for Bromeliaceae had been published. First molecular systematic analyses of Bromeliaceae based on ncDNA became available only recently, including Schulte et al. 2009 (PRK, Bromelioideae), Jabaily and Sytsma 2010 (PHYC, *Puya*), Sass and Specht 2010 (RPB2, Bromelioideae, *Aechmea*) and Chew et al. 2010 (rDNA/ITS, *Tillandsia*). The RPB2 and MS primers proved to be unsuitable for *Deuterocohnia* samples. The PCR of the ITS regions was successful, but sequencing revealed only the very homogeneous ITS 2 part to be legible. PHYC exon1 and PRK exon2–5 could be amplified and sequenced and provided more variability, thus these two loci were used for analyses within *Deuterocohnia* and related genera.

**PRK (gene coding for phosporibulokinase) exon2–5**

Phosphoribulokinase is an enzyme of the Calvin cycle. The PRK gene contains five exons and four introns and has an overall length of about 2000 bp in *Arabidopsis thaliana* (GenBank AT1G32060). Schulte et al. (2009) used the exon2–exon5 region of this locus for phylogenetic analyses of Bromelioideae and detected a five times higher number of informative characters as compared with any of the cpDNA loci analysed in the same plant material.

**PHYC (gene coding for phytochrome C) exon1**

Phytochrome C is a photoreceptor protein encoded by the PHYC gene. In *Arabidopsis thaliana*, the gene sequence is about 4000 bp long and contains three introns (GenBank, NC003076). Jabaily and Sytsma (2010) chose the first intron of this locus for their phylogenetic study of the bromeliad genus *Puya*, where they found an intrageneric variation of 5.6% (3% parsimony informative).

**PCR procedure**

PCR assays for all nuclear loci were carried out in total volumes of 20 µl, containing 18 µl PCR Master Mix (1.1x ReddyMix™), 20 pmol each of forward and reverse primer, 0.8 µl DMSO and 2–8 ng/µl of DNA template. Primer sequences are listed in Table 2.6. PCR programs for the amplification of the PHYC and PRK locus refer to Michael Barfuss, Botanical Institute of Vienna (unpublished data). The loci RPB2 and MS were amplified using the program of Denton et al. (1998), ITS amplification followed Grünstäudl et al. (2009). The reactions were carried out in a Biometra thermoblock. PCR products were purified using Exonuclease I and Calf Intestine Alkaline Phosphatase (Werle et al. 1994, reagents and solutions listed in Tables 2.1, 2.2, 2.3).

Tab. 2.6: Sequences of primers used to amplify (PCR) and subsequently sequence (SEQ) ncDNA regions. Unpublished primers were kindly provided by Michael Barfuss (Vienna) and will be published elsewhere.

| Locus | Primer | Reaction | Sequence | Reference |
|---|---|---|---|---|
| ITS | ITS18S F | PCR, SEQ | 5'- ACC GAT TGA ATG GTC CGG TGA AGT GTTCG -3' | Grünstäudl et al. 2009 |
| ITS | ITS5.8S F | SEQ | 5'- ACT CTC GGC AAC GGA TAT CTC GGC TC -3' | Grünstäudl et al. 2009 |
| ITS | ITS5.8S R | SEQ | 5'- ATG CGT GAC GCC CAG GCA GAC GTG -3' | Grünstäudl et al. 2009 |
| ITS | ITS26S R | PCR, SEQ | 5'- CTG AGG ACG CTT CTC CAG ACT ACA ATT CG -3' | Grünstäudl et al. 2009 |
| PHYC exon1 | phyc515f$_2$ | PCR | unpublished data | Barfuss, pers. comm. |
| PHYC exon1 | phyc524f | SEQ | unpublished data | Barfuss pers. comm. |
| PHYC exon1 | phyc974f$_2$ | SEQ | unpublished data | Barfuss pers. comm. |
| PHYC exon1 | phyc1145r | SEQ | unpublished data | Barfuss pers. comm. |
| PHYC exon1 | phyc1690r | SEQ | unpublished data | Barfuss pers. comm. |
| PHYC exon1 | phyc1699r$_2$ | PCR | unpublished data | Barfuss pers. comm. |
| PRK exon2–exon5 | prk621f | PCR | unpublished data | Barfuss pers. comm. |
| PRK exon2–exon5 | prk1069r$_2$ | PCR | unpublished data | Barfuss pers. comm. |
| PRK exon2–exon5 | prk630f | PCR, SEQ | unpublished data | Barfuss pers. comm. |
| PRK exon2–exon5 | prk735f | PCR, SEQ | 5'- CTG CAG ATC CGC AGA AGA AAT ATG C -3' | Schulte et al. 2009 |
| PRK exon2–exon5 | prk889r | PCR, SEQ | 5'- GGG TAT GAG CAT GTC AAT TTC CTC CC -3' | Schulte et al. 2009 |
| PRK exon2–exon5 | prk1057r | PCR, SEQ | unpublished data | Barfuss pers. comm. |

### 2.3.6.2 DNA sequencing and cloning of PCR-products

Using the primer pairs listed in Table 2.6, only few and inconsistent PCR products were obtained for MS and RPB2. These loci were therefore not included in further analyses. Sequencing of PCR products obtained from the ITS, PHYC and PRK loci was performed on an automated capillary sequencer (Applied Biosystems) using the Big Dye Terminator Kit vers. 3.1. with fluorescently labeled ddNTPs. PCR fragments were sequenced in both the forward and reverse direction, using

the sequencing primers shown in Table 2.6. Cycle sequencing reactions were set up in total volumes of 10 µl, containing 0.5–1 µl BigDye Terminator Kit, 1.5 µl reaction buffer (5x), 3.2 pmol primer and 250 ng PCR product. Cycling parameters were as follows: 1 min initial denaturation at 96°C followed by 35 cycles each of 10 s denaturation at 96°C, 5 s primer annealing at 50°C and 3 min elongation at 60°C, followed by cooling to 4°C. Reaction products were purified from unused fluorescent terminators on filtration plates filled with Sephadex® and mixed with formamide before loading onto the sequencer (reagents, solutions and materials listed in Tables 2.1, 2.2, 2.3). Due to heterozygous alleles or paralogues, several sequences of PRK exon2–5 obtained from direct sequencing showed polymorphic sites and/or sequence shift caused by indels. Especially the latter made it impossible to achieve the whole sequence length. In these cases, the PCR products were cloned using the pGEM-T Easy Vector System according to the manufacturer's protocol. Successfully cloned products for each sample were sequenced, and aligned, and ambiguous sites were exluded from further analyses.

#### 2.3.6.3 Data processing

Sequences were assembled using the program SeqMan Pro v7.1.0 (DNASTAR Lasergene). Alignments were generated with AlignIR v1.1 (LI-COR® Bioscience). To verify that the sequenced locus was the correct target, sequences were uploaded to GenBank and compared via BLAST searches with available data.

## 2.4 Phylogenetic analyses

### 2.4.1 Samples included in the molecular phylogenetic analyses

The molecular phylogenetic analyses were based on a complete taxon sampling, with at least one accession each of all known *Deuterocohnia* taxa included. Most of the species were represented by multiple specimens. Chloroplast DNA sequences of three loci were obtained from 103 *Deuterocohnia* accessions and 16 outgroup samples of the related genera *Dyckia* (8), *Encholirium* (2), *Fosterella* (4) and *Pitcairnia* (2) (dataset A). For a subset of the samples (dataset B, *Deuterocohnia*: 22, outgroup: 6), ncDNA sequences were additionally obtained. DNA preparations of *Deuterocohnia chrysantha* were kindly provided by the Department of Botany and Molecular Evolution at the Forschungsinstitut Senckenberg, Frankfurt. All samples for which DNA sequences were generated in the present study are compiled in Table 2.7.

Tab. 2.7: Plant material used for molecular phylogenetic analyses. Abbreviations of origins: BG: Botanical Garden. FAN: Fundacion Amigos de la Naturaleza, Santa Cruz, Bolivia. UG: Greenhouse of the University. [T] indicates plant material, were the type was collected from. Greyish taxa in brackets refer to the changes of the present study. cpDNA sequences were obtained from all accessions included in data set A, data set B was additionally analyzed with ncDNA sequences.

| Taxon | Collection number / Herbarium | Living plant | Locality of collection | DNA number | Data set |
|---|---|---|---|---|---|
| *Deuterocohnia brevifolia* (Griseb.) M.A. Spencer & L.B. Sm. | Unknown / KAS | UG Kassel 106 | Unknown | N 106 | A, B |
| | Balfanz 075 / HEID | BG Heidelberg 107170 | Bolivia / Tarija | N 138 | A, B |
| | Hromadnik 5124 / HEID | BG Heidelberg 107456 | Bolivia / Tarija | N 139 | A |
| | Schütz 06-061 / FR | Field collection | Bolivia / Tarija | N 173 | A |
| | Unknown / KAS | UG Kassel 222 | Unknown | N 222 | A |
| | Till, W. 59 / WU | BG Vienna s n | Bolivia / Tarija | N 277 | A |
| *Deuterocohnia brevispicata* Rauh & L. Hrom. | Hromadnik 5213 / B | BG Berlin 164-09-98-30 | Bolivia / Chuquisaca | N 112 | A, B |
| | Hromadnik 5213 / HEID [T] | BG Heidelberg 102379 | Bolivia / Chuquisaca | N 129 | A |
| | Schütz 06-022 / FR | Field collection | Bolivia / Santa Cruz | N 160 | A, B |
| | Schütz 06-037 / FR | Field collection | Bolivia / Chuquisaca | N 163 | A |
| | Schütz 06-041 / FR | Field collection | Bolivia / Chuquisaca | N 164 | A |
| *Deuterocohnia chrysantha* (Phil.) Mez | Zizka 8148 / FR | Field collection | Chile / Antofagasta | C 148 | A |
| | Zizka 8152 / FR | Field collection | Chile / Antofagasta | C 152 | A |
| | Zizka 8154 / FR | Field collection | Chile / Antofagasta | C 154 | A |
| | Zizka 8156 / FR | Field collection | Chile / Antofagasta | C 156 | A, B |
| | Zizka 8159 / FR | Field collection | Chile / Antofagasta | C 159 | A, B |
| | Katz s n / FR | BG Bochum s n | Chile / Antofagasta | H 196 | A |
| *Deuterocohnia digitata* L.B. Sm. | Rauh 64142 / HEID | BG Heidelberg 130000 | Argentina / Salta | N 141 | A, B |
| | Schütz 06-097 / LIL | Field collection | Argentina / Salta | N 191 | A |
| | Schütz 06-098 / LIL | Field collection | Argentina / Salta | N 192 | A, B |
| | Schütz 06-099 / LIL | Field collection | Argentina / Salta | N 193 | A |
| | Schütz 06-101 / LIL | Field collection | Argentina / Salta | N 195 | A |
| | Till, H. 88-151 / WU | BG Vienna 145-88 | Argentina / Salta | N 261 | A |
| *Deuterocohnia gableana* R. Vásquez & Ibisch | Vásquez 4253 / LPB [T] | Collection Roberto Vásquez | Bolivia / Santa Cruz | N 214 | A, B |
| *Deuterocohnia glandulosa* E. Gross | Hromadnik 5167 / HEID [T] | BG Heidelberg 103854 | Bolivia / Tarija | N 134 | A |
| | Schütz 06-021 / FR | Field collection | Bolivia / Santa Cruz | N 159 | A |
| | Schütz 06-025 / FR | Field collection | Bolivia / Chuquisaca | N 161 | A |
| *Deuterocohnia haumanii* A. Cast. | Rauh 64157 / HEID | BG Heidelberg 130119 | Argentina / Salta | N 143 | A |
| | Schütz 06-094 / LIL | Field collection | Argentina / Salta | N 189 | A |
| | Schütz 06-096 / LIL | Field collection | Argentina / Salta | N 190 | A |
| *Deuterocohnia longipetala* Mez | Unknown / B | BG Berlin 285-01-89-83 | Unknown | N 116 | A, B |
| | Till, W. s n / B | BG Berlin 167-02-98-63 | Argentina / unknown | N 127 | A |

| Taxon | Collection number / Herbarium | Living plant | Locality of collection | DNA number | Data set |
|---|---|---|---|---|---|
| *Deuterocohnia longipetala* Mez | Leuenberger 4478 a / HEID | BG Heidelberg 103725 | Argentina / La Rioja | N 131 | A |
| | Schütz 06-066 / FR | Field collection | Bolivia / Tarija | N 175 | A |
| | Schütz 06-067 / FR | Field collection | Bolivia / Tarija | N 176 | A, B |
| | Schütz 06-1182 / LIL | Field collection | Argentina / Salta | N 208 | A |
| | Schütz 06-124 / LIL | Field collection | Argentina / Salta | N 210 | A |
| | Till, W. s n / HEID | BG Heidelberg 104983 | Argentina / unknown | N 245 | A |
| | Till, W. 10045 / WU | BG Vienna B23-93 | Argentina / Tucumán | N 257 | A |
| | Till, W. 10050 / WU | BG Vienna B24-93 | Argentina / Tucumán | N 259 | A |
| | Till, W. 10082 / WU | BG Vienna 29-93 | Argentina / Jujuy | N 260 | A |
| | Till, W. 10126 / WU | BG Vienna B32-93 | Argentina / Jujuy | N 264 | A |
| | Till, W. 10249 / WU | BG Vienna B15-93 | Argentina / Tucumán | N 267 | A |
| | Till, W. 5038 / WU | BG Vienna B122-90 | Argentina / Córdoba | N 270 | A |
| | Till, W. 5089 / WU | BG Vienna 174-95 | Argentina / La Rioja | N 271 | A |
| | Till, W. 5131 / WU | BG Vienna 173-95 | Argentina / San Juan | N 272 | A |
| | Till, W. 5165 / WU | BG Vienna 65-90 | Argentina / La Rioja | N 273 | A |
| | Till, W. 79 / WU | BG Vienna s n | Bolivia / Tarija | N 276 | A |
| | Unknown / WU | BG Vienna B150-90 | Argentina / La Rioja | N 280 | A |
| | Till, W. 5068 / WU | BG Vienna AB21-90 | Argentina / La Rioja | N 284 | A |
| *Deuterocohnia lorentziana* (Mez) M.A. Spencer & L.B. Sm. [*Deuterocohnia abstrusa* (A. Cast.) N. Schütz] | Schütz 06-054 / FR | Field collection | Bolivia / Tarija | N 171 | A |
| | Schütz 06-056 / FR | Field collection | Bolivia / Tarija | N 172 | A |
| | Schütz 06-085 / LIL | Field collection | Argentina / Salta | N 183 | A |
| | Schütz 06-092 / LIL | Field collection | Argentina / Salta | N 187 | A |
| | Unknown / K | BG Kew 1996-2681 | Unknown | N 255 | A |
| [*Deuterocohnia brevifolia* (Griseb.) M.A. Spencer & L.B. Sm.] | Unknown / B | BG Berlin 118-02-74-83 | Unknown | N 120 | A |
| | Gouda 95-18 b / HEID | BG Heidelberg 105680 | Bolivia / Tarija | N 136 | A |
| | Till, W. 10156 / WU | BG Vienna 121-93 | Argentina / Salta | N 265 | A |
| | Till, W. 62a / WU | BG Vienna B178-95 | Bolivia / Tarija | N 275 | A |
| | Unknown / WU | BG Vienna 176-95 | Unknown | N 281 | A |
| *Deuterocohnia lotteae* (Rauh) M.A. Spencer & L.B. Sm. | Hromadnik 5175 / B | BG Berlin 226-02-85-33 | Bolivia / unknown | N 121 | A |
| | Hromadnik 5130 / HEID | BG Heidelberg 103817 | Bolivia / Tarija | N 133 | A |
| | Till, W. 62b / HEID | BG Heidelberg 105682 | Bolivia / Tarija | N 137 | A |
| | Hromadnik 9115 / HEID | BG Heidelberg 107467 | Bolivia / Tarija | N 140 | A |
| | Hromadnik 5131 / HEID [T] | BG Heidelberg 130005 | Unknown | N 247 | A |

| Taxon | Collection number / Herbarium | Living plant | Locality of collection | DNA number | Data set |
|---|---|---|---|---|---|
| *Deuterocohnia meziana* Kuntze ex Mez | Gouda 95-21 / HEID | BG Heidelberg 104977 | Bolivia / Santa Cruz | N 244 | A, B |
| *D. meziana* ssp. *carmineo-viridiflora* Rauh [*D.meziana* ssp. *carminea-viridiflora* (Rauh) N. Schütz] | Schütz 06-011 a / FR | Field collection | Bolivia / Santa Cruz | N 213 | A, B |
| | Schütz 06-011 e / FR | Field collection | Bolivia / Santa Cruz | N 224 | A |
| | Schütz 06-007 d / FR | Field collection | Bolivia / Santa Cruz | N 225 | A |
| | Rauh 40642 / HEID [T] | BG Heidelberg 103653 | Bolivia / Cochabamba | N 130 | A |
| | Rauh 46774 / HEID | BG Heidelberg 103808 | Bolivia / Cochabamba | N 132 | A |
| | Hromadnik 5030 / HEID | BG Heidelberg 130200 | Bolivia / Cochabamba | N 246 | A, B |
| | Hromadnik 5264 / HEID | BG Heidelberg 130181 | Bolivia / Cochabamba | N 254 | A |
| *Deuterocohnia pedicellata* W. Till [*D.meziana* ssp. *pedicellata* (W. Till) N. Schütz] | Schütz 09 / 009 | Field collection | Bolivia / Chuquisaca | N 293 | A |
| *D. meziana* ssp. indet. [*D.meziana* ssp. nov.] | Unknown / FR | Palmengarten Frankfurt 99192533 | Unknown | N 296 | A |
| *Deuterocohnia recurvipetala* E. Gross | Rauh 64236 / B | BG Berlin 281-02-97-33 | Argentina / unknown | N 111 | A |
| | Rauh 64236 / HEID [T] | BG Heidelberg 130120 | Argentina / unknown | N 144 | A, B |
| *Deuterocohnia scapigera* (Rauh & L. Hrom.) M.A. Spencer & L.B. Sm. | Hromadnik 5103 / HEID | BG Heidelberg 104591 | Bolivia / Potosí | N 135 | A |
| | Hromadnik 5275 / HEID [T] | BG Heidelberg 130020 | Bolivia / Potosí | N 142 | A |
| | Braun 701 / HEID | BG Heidelberg 130004 | Unknown | N 253 | A |
| | Till, W. 38 / WU | BG Vienna s n | Bolivia / Potosí | N 268 | A |
| [*D. scapigera.* var. nov.] | Hromadnik 5076 / HEID [T] | BG Heidelberg 130003 | Bolivia / Potosí | N 252 | A |
| | Hromadnik 5076 / B | BG Berlin 245-02-97-33 | Bolivia / Potosí | N 113 | A |
| *D. scapigera* ssp. *sanctae-crucis* R. Vásquez & Ibisch [*Deutero-cohnia sanctae-crucis* (R. Vásquez & Ibisch) N. Schütz] | Vásquez 3523 / LPB | Collection Roberto Vásquez | Bolivia / Santa Cruz | N 215 | A |
| | Balfanz 126 / HEID | BG Heidelberg 107165 | Bolivia / Santa Cruz | N 249 | A, B |
| | Schütz 09 / 014 | Field collection | Bolivia / Santa Cruz | N 295 | A |
| *Deuterocohnia schreiteri* A. Cast. | Unknown / HEID | BG Heidelberg 130148 | Unknown | N 145 | A |
| | Schütz 06-102 / LIL | Field collection | Argentina / Salta | N 196 | A |
| | Schütz 06-104 / LIL | Field collection | Argentina / Salta | N 197 | A, B |
| | Schütz 06-105 / LIL | Field collection | Argentina / Salta | N 198 | A |
| | Schütz 06-106 / LIL | Field collection | Argentina / Salta | N 199 | A, B |
| | Schütz 06-108 / LIL | Field collection | Argentina / Salta | N 201 | A, B |
| *Deuterocohnia seramisiana* R. Vásquez, Ibisch & E. Gross | Schütz 06-042 / FR | Field collection | Bolivia / Chuquisaca | N 165 | A |
| *Deuterocohnia strobilifera* Mez | Schütz 06-048 / FR | Field collection | Bolivia / Chuquisaca | N 168 | A |

| Taxon | Collection number / Herbarium | Living plant | Locality of collection | DNA number | Data set |
|---|---|---|---|---|---|
| *Deuterocohnia strobilifera* Mez | Schütz 06-049 / FR | Field collection | Bolivia / Chuquisaca | N 169 | A |
| | Schütz 06-051 / FR | Field collection | Bolivia / Tarija | N 170 | A |
| | Schütz 06-072 / FR | Field collection | Bolivia / Chuquisaca | N 177 | A, B |
| | Schütz 06-074 / FR | Field collection | Bolivia / Potosí | N 179 | A |
| | Hromadnik 5083 / HEID | BG Heidelberg 130015 | Bolivia / unknown | N 248 | A |
| *D. strobilifera* var. *inermis* L.B. Sm. | Hromadnik 5064 / HEID | BG Heidelberg 130001 | Bolivia / Chuquisaca | N 251 | A, B |
| | Unknown / WU | BG Vienna BRO 03805 | Unknown | N 279 | A |
| | Schütz 06-046 / FR | Field collection | Bolivia / Chuquisaca | N 167 | A, B |
| | Schütz 06-075 / FR | Field collection | Bolivia / Potosí | N 180 | A |
| *Dyckia estevesii* Rauh | Esteves-Pereira s n / HEID [T] | BG Heidelberg 105012 | Brazil / Goias | N 226 | A, B |
| *Dyckia ferox* Mez | Horst 375 / HEID | BG Heidelberg 130028 | Brazil / Bahia | N 242 | A, B |
| *Dyckia goehringii* E. Gross & Rauh | Rauh 67622 / HEID [T] | BG Heidelberg 105013 | Brazil / Minas Gerais | N 148 | A |
| *Dyckia granmogulensis* Rauh | Rauh 56484 / HEID [T] | BG Heidelberg 130019 | Brazil / Minas Gerais | N 241 | A |
| *Dyckia maritima* Baker | Unknown / WU | BG Vienna 514-96 | Unknown | N 286 | A |
| *Dyckia marnier-lapostollei* L.B. Sm. | Marnier-Lapostolle s n / KAS | UG Kassel 219 | Brazil / unknown | N 219 | A |
| *Dyckia spec.* | Laub s n / B | BG Berlin 108-08-02-10 | Argentina / unknown | N 126 | A |
| *Dyckia spec.* | Laub 17 / HEID | BG Heidelberg 107661 | Argentina / Catamarca | N 250 | A |
| *Encholirium horridum* L.B. Sm. | Schindhelm s n / HEID | BG Heidelberg 108213 | Brazil / Minas Gerais | N 223 | A, B |
| *Encholirium scrutor* (L.B. Sm.) Rauh | Horst 386 / HEID | BG Heidelberg 130035 | Brazil / Minas Gerais | N 243 | A, B |
| *Fosterella albicans* (Griseb.) L.B. Sm. | Peters 06-0005 / FR | Field collection | Bolivia / Santa Cruz | N 217 | A, B |
| *Fosterella penduliflora* (C.H.Wright) L.B. Sm. | Peters 06-0042 / FR | Field collection | Bolivia / Chuquisaca | N 216 | A |
| *Fosterella villosula* (Harms) L.B. Sm. | Peters 06-0105 / FR | Field collection | Bolivia / Cochabamba | N 218 | A |
| *Fosterella weddeliana* (Brongn. ex Baker) Mez | Vásquez 3636 / LPB | FAN | Bolivia / La Paz | 12 a | A, B |
| *Pitcairnia albiflora* Spreng. | Unknown / FRP | Palmengarten Frankfurt s n | Unknown | F15 a | A |
| *Pitcairnia loki-schmidtiae* Rauh & Barthlott | Schmidt s n / HEID | BG Heidelberg 104044 | Mexico / Jalisco | F47 a | A |

### 2.4.2 Alignment

The alignments generated by the AlignIR program were revised and if necessary, indels were manually readjusted according to the parsimony principle (minimal number of mutational steps). Regions with inversions and mononucleotide repeats (microsatellites) were excluded due to their potentially high extent of homoplasy (Borsch and Quandt 2009). Polymorphic sites occurring within the nuclear loci of the same accession are caused by heterozygous alleles and were also excluded. Indels were coded after Simmons and Ochoterena (simple indel coding, 2000) using the program Seqstate (Müller 2005). Gaps were treated as missing data. The alignments are shown in the electronic Appendix.

The assumption of a model for nucleotide changes, a substitution model, is possible for distance analyses as well as for Maximum Likelihood analyses and Bayesian inferences. The models applied for the various calculations are listed in the appropriate chapters. To test, if different datasets may be combined for further analyses, the incongruence length difference test (ILD-test, Farris et al. 1995) were conducted as implemented in PAUP v4.0 b10 (partition homogeneity test, Swofford 2001). This test analyses, if the phylogenetic signals of the single locus differ significantly from those of the combined loci.

### 2.4.3 Tree and network reconstruction

#### 2.4.3.1 Maximum Parsimony analysis

One of the oldest and most frequently used methods for phylogenetic reconstruction is the Maximum Parsimony (MP) approach (Edward and Cavalli-Sforza 1963). MP algorithms use discrete characters to reconstruct and compare potential trees under the optimality criterion of "maximum parsimony". Under this criterion, the most probable tree is the most parsimonious one, i.e., the tree that explains the data set with a minimal number of mutational steps. Only synapomorphic characters are parsimony informative. Originally developed for morphological data, this method has long been implemented in molecular systematic analyses based on DNA sequence data (Kitching et al. 1998). One of the main advantages of MP analysis is its relatively fast computational processing. The recently developed Ratchet Maximum Parsimony analysis (Nixon 1999) even further reduces calculation times and additionally facilitates the drop out of local optima while searching for the best tree. A drawback is that no evolutionary model can be integrated in MP analyses.

In the present study Ratchet MP analyses were performed by creating command files with the programs PRAP (Müller 2004) and executing them in PAUP v4.0 b10 (Swofford 2001). Twenty random addition cycles were run with 500 ratchet replicates each. Each ratchet replicate comprised 10 heuristic search replicates with TBR branch swapping and 25% randomly chosen positions upweighted to 2. One shortest tree was saved after each iteration. Most parsimonious trees were filtered and used for the reconstruction of consensus trees. To analyse the phylogenetic information content of indels, additional analyses were carried out, where indels were coded after the simple indel coding procedure (Simmons and Ochoterena 2000) using the program Seqstate (Müller 2005).

Statistical support was investigated via bootstrap analysis, which implies the calculation of phylogenies with modified character composition (Felsenstein 1985). Parsimony bootstrap analyses were carried out with 1000 replicates, each comprising 10 random taxon addition replicates and TBR branch swapping. To assess the degree of homoplasy within the dataset, the Consistency index (CI, Kluge and Farris 1969) and the Retention Index (RI, Farris 1989) were assessed for each dataset.

#### 2.4.3.2 Distance analysis

Distance analyses are phenetic methods, which transform discrete characters into a matrix of pairwise distances and use this distance matrix to deduce potential tree topologies. To calculate the genetic distance between two sequences, either uncorrected p-distances or nucleotide evolution models can be implemented. These models consider the fact that the observable mutation events within a data set are subject to saturation. Additionally, different probabilities can be assigned to different mutation types, e.g. transitions or transversions.

The most prevalent distance method used in phylogenetics is the Neighour-Joining analyses (NJ; Saitou and Nei 1987). Its main advantage is the fast calculation process. NJ does not require the assumption of a clock-like evolution as UPGMA does (Unweighted Pair Group Method with Arithmetic means; Sokal and Michener 1958). Since NJ is a cluster analysis, the output is a single tree.

In the present work NJ analyses were accomplished using PAUP v4.0 b10 (Swofford 2001). Not all substitution models included in the programm Modeltest v3.7 (Posada and Crandall 1998) can be implemented in NJ analyses in PAUP. To assess the influence of different evolutionary models on tree topology, all datasets were therefore analysed as uncorrected p-distances, as well as according to the Jukes-Cantor (JC; Jukes and Cantor 1969), Hasegawa-Kishino-Yano-85 (HKY;

Hasegawa et al. 1985) and General-Time-Reversible (GTR; Rodriguez el al. 1990) models of evolution. Analyses were run with and without coded indels (sic, see 2.4.2). Bootstrap analyses were carried out with 5000 replicates under the distance criterion.

#### 2.4.3.3 Maximum Likelihood analysis

The use of Maximum Likelihood (ML) methods for phylogenetic analyses of sequence data has been facilitated by Felsenstein (1981). The likelihood reflects the probability of the observed data (alignment) given a certain hypothesis (tree topology). The most probable tree is the one leading to a maximum likelihood value. ML uses discrete characters and allows the implementation of substitution models.

Because the ML approach is computationally intensive, it was often omitted in early molecular phylogenetic analyses of large data sets. In 2005 Stamatakis et al. presented RaxML, a faster algorithm for ML analyses. Together with the recently developed graphical front end raxmlGUI (Silvestro and Michalak 2010), RAxML has considerably facilitated the application of ML in phylogenetics.

In the present work ML analyses were conducted using the programms RAxML v7.2.6 (Stamatakis et al. 2005, Stamatakis 2006) and raxmlGUI v0.9 b2 (Silvestro and Michalak 2010). Partitions were set for each locus and branch lengths were saved for each partition. The analyses were carried out with indels either uncoded or coded (sic, see 2.4.2). RAxML implements the General-Time-Reversible (GTR) substitution model, thus GTR and gamma distribution for the among site rate variation were applied to DNA data, the coded indel partition was left uncorrected. Bootstrap analyses were conducted with 1000 replicates and partition related sampling.

#### 2.4.3.4 Bayesian analysis

First introduced into phylogenetics by Felsenstein (1968), Bayesian approaches of phylogenetic reconstruction obtained major attention only recently. Bayesian inferences aim to calculate posterior probabilities of each phylogenetic hypothesis (Huelsenbeck and Ronquist 2001). The best fitting tree exhibits the highest posterior probability which serves as the optimality criterion. Posterior probabilities of different topologies can be efficiently estimated using a Markov chain Monte Carlo (MCMC) approach, which is a heuristic search method. Each tree depends only on its immediate precursor in the chain. The Metropolis-coupled variant of MCMC involves the use of more than one chain per analysis to escape from local optima (MCMCMC; Altekar et al. 2004).

The Bayesian approach is relatively fast and incorporates statistical methods already during the analysis itself.

Bayesian inferences were carried out with the program MrBayes v3.1.2 (Ronquist and Huelsenbeck 2003). The dataset was partitioned into the three noncoding cpDNA loci *rpl*32–*trn*L, *rps*16–*trn*K, *trn*S–*ycf*3 and the indel coding section. Corresponding substitution models for each locus were ascertained using MrModeltest v2.3 (Nylander 2004) and the graphical front end ModelPie v1.01 (Nuin 2007). If the Akaike Information Criterion (AIC, Akaike 1974) and the hierarchical Likelihood Ratio Test (hLRT, Posada and Crandall 1998) supported different models, the AIC was chosen as recommended by Posada and Buckley (2004). The analyses were run with indels uncoded as well as coded (sic, see 2.4.2).

Analysis conditions were as follows: 2 independent MCMCMC runs, 4 chains with incremental heating, 5,000,000 generations, sampling every 100$^{th}$ generation, burn-in=200,000 generations (*trn*S–*ycf*3 500,000 generation). Indels were excluded, the parameter rate matrix, transition/transversion rates, base frequencies, shape of gamma distribution and invariable sites were unlinked between the partitions.

#### 2.4.3.5 Networks

Phylogenetic trees assume that evolutionary processes proceed dichotomously and hierarchically, thus one ancestor taxon splits into two (ore more) descendants. In contrast, phylogenetic networks allow the illustration of more complex relationships between organisms, which may be caused by e.g. hybridisation, recombination or horizontal gene transfer. Those events mainly occur at low taxonomic or population level (Posada and Crandall 2001). Furthermore, a network has the ability to display several alternative phylogenies simultaneously (Knoop and Müller 2006). In situations where trees are poorly resolved due to a limited number of phylogenetically informative characters, a network approach may still provide information of genealogical relationships (Posada and Crandall 2001).

Statistical parsimony network analyses were conducted using the programme TCS v1.21 (Clement et al. 2000). The connection limit was set to 95% and gaps were treated as missing data. Indels were coded with the simple indel coding scheme (sic, see 2.4.2).

# 3 RESULTS

## 3.1 Taxonomic history

***Deuterocohnia*. Beginning until 1992**

Carl Christian Mez (1866–1944) established the genus *Deuterocohnia* in 1894 after having examined the voucher *Humboldt and Bonpland 3595* from Peru and seven additional specimens from Argentina. The collection made by Humboldt and Bonpland had formerly been assigned to the genus *Dyckia* by John Gilbert Baker (1837–1920), who had described *Dyckia longipetala* in the "Handbook of Bromeliaceae" (1889). Mez recognized this specimen as being distinct from *Dyckia* mainly because of its longer petals, and the presence of appendages at the base of the adaxial petal side. He published the first description of *Deuterocohnia* in "Flora Brasiliensis", because he erroneously related the voucher collected by Humboldt and Bonpland to Brazil, although Peru was the real origin. In the same publication Mez also assigned *Pitcairnia chrysantha*, a species described in 1860 by Rudolph Amandus Philippi (1808–1904), to the new genus *Deuterocohnia*.
In 1896 Mez listed three species of *Deuterocohnia* in De Candolles "Monographiae Phanerogamarum". Beside *D. longipetala* and *D. chrysantha* he also constituted the Brazilian species *D. meziana* Kuntze ex Mez. In his classification of Bromeliaceae, *Deuterocohnia*, *Puya, Dyckia, Cottendorfia, Lindmania, Encholirion, Prionophyllum* and *Hechtia* formed the subtribe Puyinae within the tribe Pitcairnieae, based on a set of shared characters like superior ovary and alate seeds.
In 1906 Mez described *D. strobilifera* from Bolivia, and in 1919 *D. divaricata* from Paraguay. The latter was based on the collection of *Rojas* in herb. *Hassler 11098*. A voucher of the same collection located in the herbarium of Geneve was used to describe the species *D. paraguariensis* by Hassler (1919) six months earlier and therefore preceded the name *D. divaricata*, which was synonymized to *D. paraguariensis* by Harms in 1930.
The classification of subfamilies within Bromeliaceae was introduced by Harms (1930), with *Deuterocohnia* assigned to the Pitcairnioideae. Within *Deuterocohnia*, Harms distinguished between *Spiciformes*, bearing a laxly flowered inflorescence (*D. longipetala*, *D. meziana, D. paraguariensis*) and *Strobiliformes*, having densely arranged flowers (*D. chrysantha*, *D. strobilifera*). In 1934 Mez synonymized *D. paraguariensis* to *D. meziana*.
In the first part of their comprehensive monograph of Bromeliaceae, Smith and Downs (1974) recognized seven *Deuterocohnia* species. In addition to *D. longipetala*, *D. meziana, D. chrysantha*, and *D. strobilifera* already listed by Harms (1930), they also included *D. haumanii* A. Cast. (1929),

*D. schreiteri* A. Cast. (1929), *D. digitata* L.B. Sm. (1969) and the variety *D. strobilifera* var. *inermis* L.B. Sm. (1954).
The only attempt so far to sub-divide the widely distributed species *D. longipetala* was made by Castellanos (1933), who established *D. longipetala* forma *uberrima* due to their expanded partial inflorescences and larger flowers. This division was not maintained by Smith and Downs (1974). Subsequently, two more new species and one new variety were described until 1992: *D. meziana* var. *carmineo-viridiflora* Rauh (1985), *D. brevispicata* Rauh and L. Hrom. (Rauh 1988a) and *D. glandulosa* E. Gross (1990).

### *Abromeitiella*. Beginning until 1992

"If we were to hand out a prize to each genus of Bromeliaceae, we would be hard put to it to find an award for *Abromeitiella*, unless we had a contest for the most misunderstood genus."

Lyman B. Smith 1964b

For sure there would be additional awards for these exceptional plants. However, the taxonomic treatment of *Abromeitiella* and its synonyms has been quite confusing over the last 130 years and reflects the challenge in classifying these cushion forming plants.
Grisebach described in 1879 the taxon *Navia brevifolia*, without citing a specimen for typification. This taxon was assigned to the genus *Dyckia* in 1889 by Baker and named it *Dyckia grisebachii* because *Dyckia brevifolia* already existed (*Dyckia brevifolia* Baker, Ref. Bot. 1871). He cited the specimen *Lorentz and Hieronymus 947* [GOET] from the valley of Tambo, the area mentioned also in the protologue. This might be interpreted as leptotypification. The main problem in classifying this specimen was its sterility. Sixteen years later, in 1905, Fries made a new combination, *Pitcairnia brevifolia*, considering that the voucher would belong to the genus *Pitcairnia*.
Meanwhile Spegazzini (1899) described *Tillandsia chlorantha* based on the collection *Spegazzini s.n.* (LP 200). This species and *Navia brevifolia* were both assigned to the genus *Lindmania* by Hauman in 1917, *Lindmania chlorantha* and *Lindmania brevifolia*. The investigation of flowers, fruits and seeds revealed the differences to the genera *Dyckia*, *Navia* and *Tillandsia*. Hauman even constituted a new section for the two species within *Lindmania*, which he named *Azorellopsis*. However, this name had already been given to a genus of the Apiaceae, and is thus invalid. Nevertheless, Hauman (1917) did not take into account the concept of *Pitcairnia brevifolia* by Fries. In 1925 Castellanos reclassified *Lindmania chlorantha* to *Pitcairnia chlorantha* and resurrected *Pitcairnia brevifolia* (Griseb.) Fries.

In 1927 Mez was the first author, who assigned those cushion-forming bromeliads to a new genus. He named it *Abromeitiella*, in honour of the German botanist Johannes Abromeit (1857–1946) and established the species *Abromeitiella pulvinata* based on the collection *Fiebrig 3573*. The appendages at the base of the petals were considered as an important diagnostic character of the presumably monotypic genus.

Two years later Harms (1929) established a new genus, *Meziothamnus*. He synonymized *Pitcarnia brevifolia* and *P. lorentziana* under this genus to the species *Meziothamnus brevifolius* and proposed a synonymy of *P. chlorantha*. *P. lorentziana* had been described in 1896 by Mez referring to the type *Lorentz s.n.* (F, Berlin neg. 11386). The main difference between *P. lorentziana* and *P. brevifolia* was the size of the plants.

While Harms had ignored the description of *Abromeitiella*, Castellanos synonymized in 1931 *Meziothamnus* and *Abromeitiella*, so the nowadays well known combination *Abromeitiella brevifolia* was constituted. He also synonymized *Pitcairnia chlorantha* to *A. brevifolia* and mentioned that *A. pulvinata* would be a possible synonym. Castellanos (1931) published a third *Abromeitiella* species, *Abromeitiella abstrusa*, based on seven syntypes, all from Northern Argentina. This species was supposed to differ from *A. brevifolia* in having larger, more greyish leaves with only few spines.

In Englers "Pflanzenreich" (1934) Mez referred to three *Abromeitiella* species: *A. brevifolia*, *A. abstrusa* and the new combination *A. chlorantha* (Hauman) Mez. He based the latter on *Lindmania chlorantha* (Speg.) Hauman, and exclused the basionym, *Tillandsia chlorantha*. Nevertheless, Mez used the epitheton *chlorantha* to describe the small rosettes of *Fiebrig 3573* and others. Concerning *Pitcairnia lorentziana*, Mez did not cite it as a synonym of *A. brevifolia* as Castellanos did, but kept it as a distinct species.

In 1944 Castellanos assigned *A. chlorantha* to *A. brevifolia* and reestablished *A. pulvinata*. Furthermore, he established a new combination, *Abromeitiella lorentziana*, based on *Lorentz s.n.* (F, B neg. 11386) and synonymized *A. abstrusa* to it.

Smith (1967 b) simplified the previous classifications and cited two species: *A. brevifolia*, with leaves up to 22 mm, occurring in Bolivia, and *A. lorentziana*, comprising larger plants from Argentina. This same division was adopted in the Flora Neotropica by Smith and Downs (1974).

Schultze-Motel (1975) was not convinced of the synonymization of *A. brevifolia* and *A. chlorantha*. He therefore established the subspecies *A. brevifolia* ssp. *chlorantha*. However, this subspecies was ignored by all following authors. Until 1992 two new *Abromeitiella* species were described: *A. lotteae* (Rauh 1983) and *A. scapigera* (Rauh and Hromadnik 1987).

Types and the corresponding taxa according to selected authors are listed in Table 3.1.

Tab. 3.1: Type specimens related to the small, cushion-forming plants, similar to *D. brevifolia*, and the corresponding designation by different authors. #: Hauman constituted the (invalid) section *Azorellopsis* for this two *Lindmania* species. *: Typification ambiguous, see text 3.1.

| | | **Lorentz and Hieronymus 947** | **Spegazzini sn** | **Fiebrig 3573** | **Lorentz s.n.** | **Castellanos 29/60** |
|---|---|---|---|---|---|---|
| Grisebach | 1879 | *Navia brevifolia* | | | | |
| Baker | 1889 | *Dyckia grisebachii* | | | | |
| Mez | 1896 | | | | *Pitcairnia lorentziana* | |
| Spegazzini | 1899 | | *Tillandsia chlorantha* | | | |
| Fries | 1905 | *Pitcairnia brevifolia* | | | | |
| Haumann | 1917 | *Lindmania brevifolia* # | *Lindmania chlorantha* # | | | |
| Castellanos | 1925 | *Pitcairnia brevifolia* | *Pitcairnia chlorantha* | | | |
| Mez | 1927 | | | *Abromeitiella pulvinata* | | |
| Harms | 1929 | *Meziothamnus brevifolius* | (he assumed *Meziothamnus*) | | *Meziothamnus brevifolius* | |
| Castellanos | 1931 | *Abromeitiella brevifolia* | *Abromeitiella brevifolia* | *Abromeitiella pulvinata* | *Abromeitiella brevifolia* | *Abromeitiella abstrusa* |
| Mez | 1934 | *Abromeitiella brevifolia* | *Abromeitiella chlorantha** | *Abromeitiella chlorantha* | *Abromeitiella brevifolia* | *Abromeitiella abstrusa* |
| Castellanos | 1944 | *Abromeitiella brevifolia* | *Abromeitiella brevifolia* | *Abromeitiella pulvinata* | *Abromeitiella lorentziana* | *Abromeitiella lorentziana* |
| Castellanos | 1945 | *Abromeitiella brevifolia* | *Abromeitiella brevifolia* | *Abromeitiella pulvinata* | *Abromeitiella lorentziana* | *Abromeitiella lorentziana* |
| Smith | 1967 | *Abromeitiella brevifolia* | *Abromeitiella brevifolia* | *Abromeitiella brevifolia* | *Abromeitiella lorentziana* | *Abromeitiella lorentziana* |
| Smith and Downs | 1974 | *Abromeitiella brevifolia* | *Abromeitiella brevifolia* | *Abromeitiella brevifolia* | *Abromeitiella lorentziana* | *Abromeitiella lorentziana* |
| Schultze-Motel | 1975 | *A. brevifolia* ssp. *brevifolia* | *A. brevifolia* ssp. *chlorantha* | *A. brevifolia* ssp. *chlorantha* | | |
| Spencer and Smith | 1992 | *Deuterocohnia brevifolia* | *Deuterocohnia brevifolia* | *Deuterocohnia brevifolia* | *Deuterocohnia lorentziana* | *Deuterocohnia lorentziana* |
| Schütz | 2011 | *Deuterocohnia brevifolia* | *Deuterocohnia brevifolia* | *Deuterocohnia brevifolia* | *Deuterocohnia brevifolia* | *Deuterocohnia abstrusa* |

### *Deuterocohnia* and *Abromeitiella*. 1992

The comprehensive monograph of Bromeliaceae by Smith and Downs (1974, 1977, 1979) was followed by a series of supplementary generic revisions. One of these was the reevaluation of the generic delimitation of *Deuterocohnia* and *Abromeitiella* in 1992 by Spencer and Smith. The close relationship between the two genera, however, had already been highlighted by other authors. Harms mentioned in 1929 that the floral morphology of *Meziothamnus* (synonym of *Abromeitiella*) and *Deuterocohnia* was very similar, including the presence of petal appendages. Smith (1934) considered that *Abromeitiella* could have been derived from within *Deuterocohnia*, above all because the distributional range of *Abromeitiella* is located within that of *Deuterocohnia*. Consequently, the short inflorescence and the pulvinate habit in *Abromeitiella* were regarded as derived characters. In 1964, Smith stated again the similarity of both genera concerning flower and seed morphology. Varadarajan and Gilmartin (1987) mentioned the density of foliar trichomes as a link between *Deuterocohnia* and *Abromeitiella*. Additionally, the authors stated the monophyly of *Deuterocohnia* and *Abromeitiella* after conducting cladistic analyses of Pitcairnioideae (Varadarajan and Gilmartin 1988b). They described petal appendages and asymmetric sepals as synapomorphic characters, the short inflorescence of *Abromeitiella* as an autapomorphy.

Additional characters were also used to separate both genera, mainly related to habit, peduncle and flower number (Harms 1929, Smith 1934, Smith and Dows 1974). While *Deuterocohnia* was defined by having a ring-forming habit, a long peduncle and many flowers per inflorescence, *Abromeitiella* was characterized by a cushion-forming habit, no peduncle and only few flowers. Mez (1934) further differentiated the two genera by different types of seed appendages, *Abromeitiella* with "seminis ala utroque polo caudiformis" and *Deuterocohnia* with "seminis ala unica, dorsalis". The description of *A. scapigera* in 1987 (Rauh and Hromadnik) prompted a reevaluation of the delineation of the two genera. At that time *Abromeitiella* consisted of four species, and *A. scapigera* was the first *Abromeitiella* species exhibiting a short peduncle. Based on herbarium specimens, Spencer and Smith (1992) analysed the distinguishing characters of presence or absence of a peduncle, flower number and plant habit in some detail. They stated that the presence of a short scape was a character that could occur in *Abromeitiella* (*A. scapigera*) as well as in *Deuterocohnia* (*D. digitata* and *D. strobilifera*). Concerning flower number, they found that flower numbers of some *A. lorentziana* specimens were higher than those of some *D. strobilifera* individuals. In their opinion the habitual differences of the two genera were insufficient for generic delimitation, as those differences were minimal and had never been applied as diagnostic characters anywhere else in the bromeliad family.

Spencer and Smith (1992) also pointed out that numerous other characters were shared by both genera, like the presence of petal appendages, asymmetric sepals, wholly superior ovary, type of seed appendage, flavonoid profile, stigma type and type of pollen grains, which they took as supporting characters for the union. They therefore synonymized *Abromeitiella* with the earlier described *Deuterocohnia*.

***Deuterocohnia*. 1992 until 2011**

Since the lumping of *Deuterocohnia* and *Abromeitiella* the number of recognized species within the genus has increased continuously by the description of *D. recurvipetala* E. Gross (1991, described before the publication of Spencer and Smith, but they disregarded this species), *D. bracteosa* W. Till and L. Hrom. (1997), *D. seramisiana* R. Vásquez, Ibisch and E. Gross (2002), *D. scapigera* ssp. *sanctae-crucis* R. Vásquez and Ibisch (2003), *D. gableana* R. Vásquez and Ibisch (2003), and *D. pedicellata* W. Till (2004).

Notwithstanding the paper of Spencer and Smith (1992), many scientists apparently maintain the differentiation between *Deuterocohnia* and *Abromeitiella* (Benzing 2000, Crayn et al. 2000, Horres 2003, Givnish et al. 2007), probably because they have not been convinced by the arguments of these authors.

At the onset of the present study *Deuterocohnia* comprised 18 species, two subspecies and four varieties, including four species which were formerly assigned to the genus *Abromeitiella* (Luther 2008).

## 3.2 Morphology

The species names used in the following descriptions correspond to the present revision. The taxonomic treatment is presented at the end of this manuscript.

### 3.2.1 Life form, duration and habit

The species of *Deuterocohnia* are all perennial, xerophytic herbs, most of them exhibit a woody, perennial inflorescence. They grow terrestrial or saxicolous on stony soils, rocky slopes or crevices. In contrast to their epiphytic relatives they develop a water- and nutrient-absorbing root system, mainly consisting of adventitious roots. The evergreen, alternate leaves form a dense rosette along a compressed stem, which terminates with an inflorescence.

Mostly, the full-grown, flowering rosette is acaulescent. However, all species of *Deuterocohnia* possess the potential to generate axes, which may be multiple times longer than the corresponding

rosettes (Fig. 3.3c). In that case the green rosette retains about the same size at the distal end of the stem, while proximally the stem is covered by old, dry leaf sheaths. This habit has been also described for species of *Dyckia* (Foster 1945) and *Encholirium* (Forzza 2005). In the smaller species, green leaf blades cover a longer part of the stem. Different individuals of the same species may occur caulescent as well as acaulescent in the same locality. This is mainly due to the different ages of the individuals and their ramification mode.

With the exception of seedlings, a plant usually consists of a number of connected ramets (Fig. 3.3e, h). The sympodially branching plants produce derivatives at the upper region of the shoots (acrotonic growth; Fig. 3.3d, f). As the offshoots are tightly aggregated to the mother shoot, the formation is called "phalanx" (Fig. 3.1; Lovett Doust 1981, Sampaio et al. 2002), in contrast to the "guerilla" formation where the clones are produced at a distance from the mother shoot via stolons.

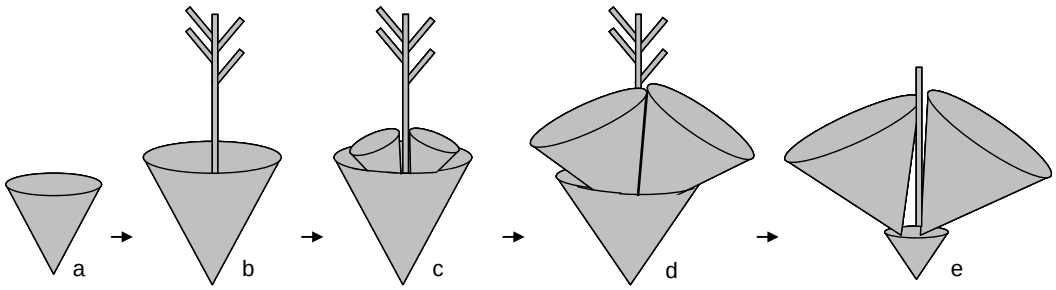


Fig. 3.1: Scheme of ramification (modified after Sampaio et al. 2002). a: Seedling. b: Mature plant with inflorescence. c: Two new ramets growing out of the upper part of the mother plant. d: Growing ramets, inflorescence of mother plant still in bloom; this might lead to the impression of a lateral inflorescence. e: Mother plant starting to decompose.

The number of ramets differs among different species of *Deuterocohnia*. Species with larger rosettes bear one to two (e.g. *D. meziana*), those with smaller rosettes three to four offshoots (e.g. *D. brevifolia*). The development of the plant's architecture starts with a seedling shoot and its subsequent inflorescence. If the mature plant produces just one ramet (Fig. 3.3b), a long stem may be generated after several generations, comprising the youngest, green-leaved ramet at the apex and the dry leaf sheaths of the older ones below (Fig. 3.3c). If the mature plant develops two offshoots (Fig. 3.3d), a dichotomous cluster of plants arises. This cluster may be dense, if the plants stay acaulescent or have only a short axis, but also lax if the ramets generate long axes (Fig. 3.3e). If three or more ramets are produced (Fig. 3.3f), the plant forms a more or less dense

cushion after several generations (Fig. 3.2). These cushions are persistent and may grow into large mats by a combination of vegetative and sexual reproduction (ramification and germination of seeds; Fig. 3.3g). The often cited circles formed by species of *Deuterocohnia* similar to the fairy rings of fungi (Smith 1964a) accrue from larger groups of ramets or cushions, in which the older, inner ramets decompose and leave the younger generations in a ring formation (Fig. 3.3h). Generally, the cushion habit is exhibited by those *Deuterocohnia* species that have small leaves, short internodes, regular ramification and uniform length growth (Rauh 1939). The smallest plants usually exhibit densest growth, like *D. brevifolia*, which form particularly rigid, compact cushions. The typical organisation of a cushion of *D. brevifolia* is shown schematically in Figure 3.2 (modified after Rauh 1988b). The inner ramets decompose with time, and provide a water storing mould.

Usually, ramification is associated with floral induction. However, branching without blooming has also been observed, notably for the cushion forming plants of *D. brevifolia*.

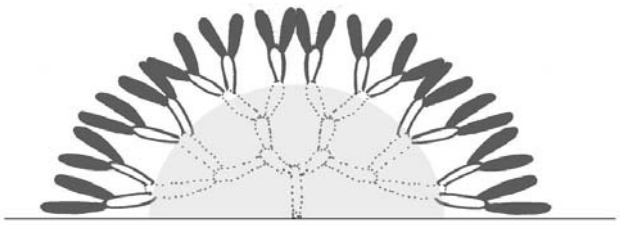

Fig. 3.2: Cushion organization of *Deuterocohnia brevifolia* (modified after Rauh 1988b). To simplify the illustration, only two ramets per generation are displayed. Whereas older, inner ramets (dotted lines) are starting to decompose, youngest ramets (black) form the surface of the cushion.


Fig. 3.3: Habits of *Deuterocohnia*. a: Dead stem of *D. meziana*, consisting of several generations with a single ramet each. b: Plant of *D. meziana* ssp. *pedicellata* producing a single ramet. c-e: *D. meziana* c: Plants hanging down a slope, with an elongated stem produced by several generations, youngest ramet not flowering yet. d: Plant generating two ramets. e: Lax, dichotomous cluster of ramets growing on the ground. f: *D. brevifolia* with three offshoots of a recent ramification. g: Large mats of dense cuhions of *D. abstrusa*. h: Ring-like growth of an older plant of *D. strobilifera*. Photo e: Ingo Michalak.

### 3.2.2 Foliage

**Sheaths**

The leaf sheaths of *Deuterocohnia* mostly are hard to see, because they overlap one another and are hidden by the more conspicuous leaf blades. The sheaths tightly surround the stem, but do not form a water storing cistern. In mature leaves the sheaths are ample, broadly ovate to reniform, with a coriaceous to succulent texture, which becomes membraneous towards the margin. Typically, the sheaths are glabrous and entire, however, at the transition zone between sheath and blade, peltate trichomes and a serrate margin may occur. Young leaf sheaths are whitish, older ones get abaxially brownish.

The leaf sheaths are relatively homogeneous within *Deuterocohnia* and do not bear any taxonomic relevance, except for their size.

**Blades**

The leaf blades of *Deuterocohnia* species are simple, narrowly triangular and never constricted at their base. They are rigid with a succulent texture, a pungent tip and a spinose margin with antrorsely or retrorsely curved, brownish spines, up to 0.5 cm long. The space between two adjacent spines usually is about 10–30 mm in the middle part of the leaf blades (Fig. 3.3a), but there are exceptions. Thus, some populations of *D. longipetala* in the southern part of the distribution area have more densely spined leaves, whereas *D. schreiteri* has more sparsely dispersed spines. Most *D. brevifolia* plants are regularly spinose, but some are completely devoid of spines (Fig.3.3e). The variety *D. strobilifera* var. *inermis* is diagnosed by its entire leaves in contrast to its spined sister variety (Fig. 3.3b, c). There are also intermediates between both varieties, which comprise just one or two spines.

Young leaves develop in the centre of the rosette. They are narrow, short and erect. While getting older, the leaves also get broader and longer, and eventually decline. The ascending or inclining leaf blades are typically recurved. *D. strobilifera* modifies this principle at high altitudes (up to 3900 m a.s.l.). In these areas, the blades are incurved and additionally curled longitudinally, which might be due to loss of water and concomitante shrinkage of water storage tissue. The abaxial, densely lepidote leaf sides turn upwards and the leaves form a closer, more sheltered rosette. A further interesting modification can be observed within *D. chrysantha*. Leaves growing horizontally in plagiotropous ramets curve upwards via unequal lateral growth (Fig.3.3d).

The leaf blade colour varies from greenish and greyish to reddish. While the basic colour is greenish, leaf blades may turn greyish due to the presence of dense layers of trichomes, as is the case

e.g. in *D. strobilifera*. The red pigmentation is caused by anthocyanins that are dissolved in vacuoles of parenchyma cells close to the surface. Partially or completely red-coloured leaves appear in several species, probably as a consequence of stress factors like the intense solar radiation at high altitudes (*D. strobilifera*) and at coastal areas (*D. chrysantha*). However, completely red-leaved plants have been observed side-by-side with green-leaved plants of *D. meziana* (Fig. 3.5). Another noticeable colouration pattern can be found in *D. brevispicata*, which shows a thin, reddish-brownish line along the leaf blade margin.

Whereas leaf blades provide important characters for species or genus delimitation in some bromeliad taxa (e.g. in *Cryptanthus*, *Fosterella*, *Neoregelia*) they are overall quite uniform in *Deuterocohnia*. Of taxonomical relevance are mainly their sizes (which vary from 1 cm in *D. brevifolia* to about 50 cm in *D. meziana*), their shape, and the size of the spines (Fig. 3.4).

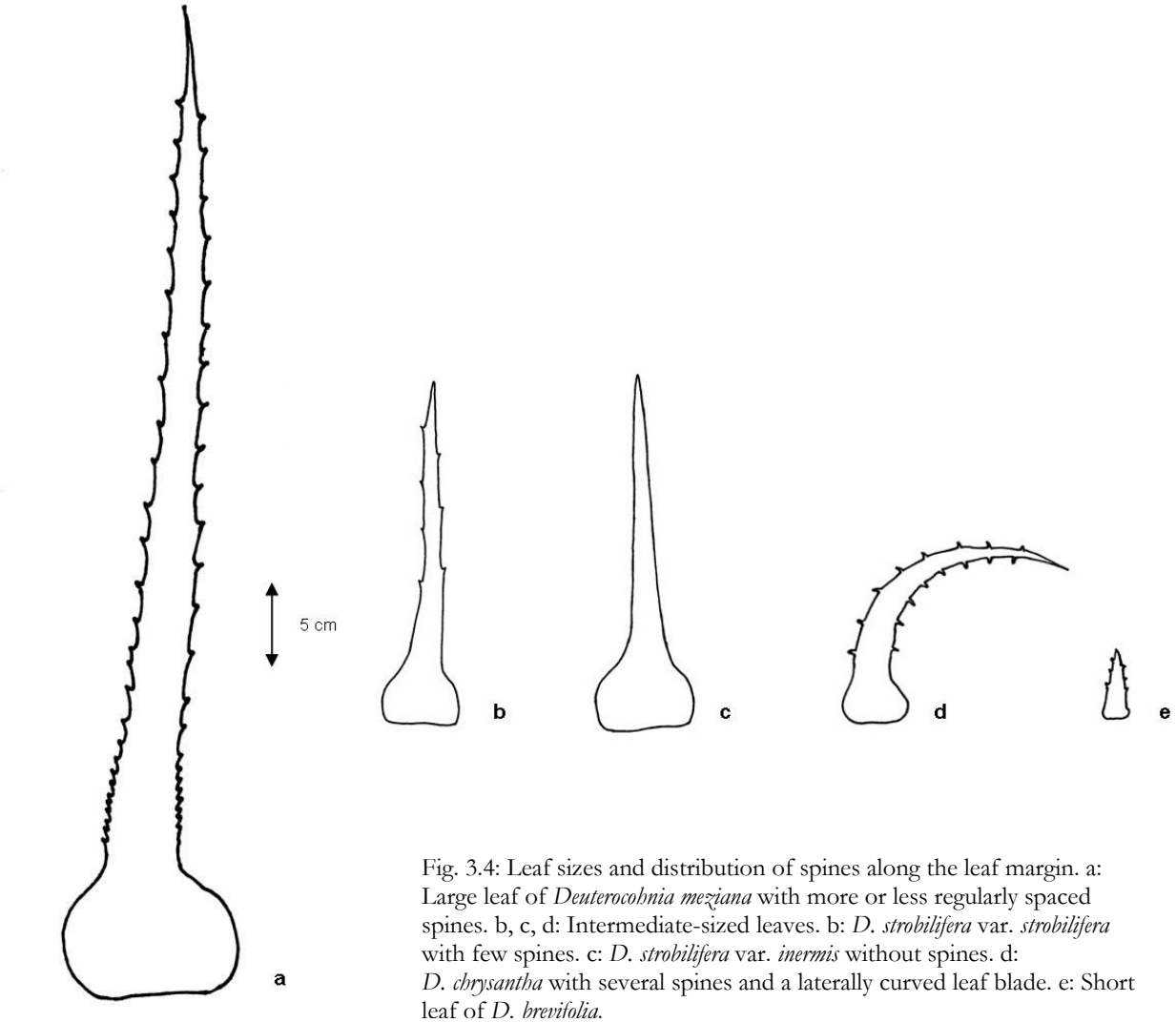


Fig. 3.4: Leaf sizes and distribution of spines along the leaf margin. a: Large leaf of *Deuterocohnia meziana* with more or less regularly spaced spines. b, c, d: Intermediate-sized leaves. b: *D. strobilifera* var. *strobilifera* with few spines. c: *D. strobilifera* var. *inermis* without spines. d: *D. chrysantha* with several spines and a laterally curved leaf blade. e: Short leaf of *D. brevifolia*.

**Indument**

The foliar indument presumably played an important role in conquering new habitats during bromeliad radiation (Benzing 2000). Within *Deuterocohnia* its most important functions are the reduction of transpiration and the protection from solar radiation. A dense layer of hydrophobic, peltate trichomes (Fig. 3.6) covers the surface of the leaf blades. The trichomes are arranged in parallel, longitudinal furrows and overlap one another. The furrows may be recognized by naked eye as stripes along the leaf. Usually, trichomes on the adaxial side are appressed to the epidermis and thus are less conspicuous than on the abaxial side. Varadarajan and Gilmartin (1987) noticed that *Deuterocohnia* (and *Abromeitiella*) exhibit the highest density of foliar trichomes among all Pitcairnioideae included in their study. The trichomes may vary in size, especially those from opposite leaf surfaces (Tomlinson 1969).

Bromeliad foliar trichomes, also called "scales" (Mez 1904), consist of a stalk and a shield, the latter being sectioned into a central disc, a concentric ring and marginal wing cells. While the stalk comprises living, cytoplasmatic cells, the shield consists of dead, inflated cells. The stalk of *Deuterocohnia* (and *Abromeitiella*) trichomes is made up of two cells (Tomlinson 1969), whereas the central disc consists of either a solitary cell (Varadarajan and Gilmartin 1987) or of four cells (Strehl and Winkler 1981). The peripheral cells of the shield show a more irregularly cell arrangement within *Deuterocohnia* and other Pitcairnioideae, than observed in Tillandsioideae. Winkler (1986) noted the relatively large size of *Abromeitiella* trichomes as compared with *Dyckia*, *Hechtia*, and *Puya*. *Deuterocohnia* samples were not included in his study. Ehler (1977) as well as Varadarajan and Gilmartin (1987) observed differences between foliar scales of *Deuterocohnia* and *Abromeitiella*. While the shields of the analysed *Abromeitiella* trichomes were differentiated into a ring region and a wing region (the latter containing smaller, more irregularly arranged cells), foliar scales of *Deuterocohnia* lacked such a structural distinction. Cells may be homologous to ring cells, with reduced wing cells, or conversely. Additionally, Varadarajan and Gilmartin (1987) found that the peripheral zone is more transparent and thinner in trichomes of *D. haumanii* (*D. schreiteri*) than in the corresponding region of *D. longipetala*. Rauh (1983) found fewer ring cells in trichomes of *D. lotteae* than in those of *D. abstrusa* (syn. *D. lorentziana*). Although the taxonomic relevance of foliar scale structure within *Deuterocohnia* is expected to be low, a thorough investigation of several individuals of all species would be necessary to clarify this aspect. The differences listed above rather seem to be a matter of intraspecific variability of the peltate trichomes within the same plant and among different localities. Some taxonomic value may however be associated with the overall density of the foliar scales on the adaxial leaf surface, which is typically high in *D. abstrusa* and *D. recurvipetala*, where it causes a greyish appearance.

Fig. 3.5: Differently coloured ramets of *Deuterocohnia longipetala* (*N. Schütz 06-068*) growing together at the same locality.

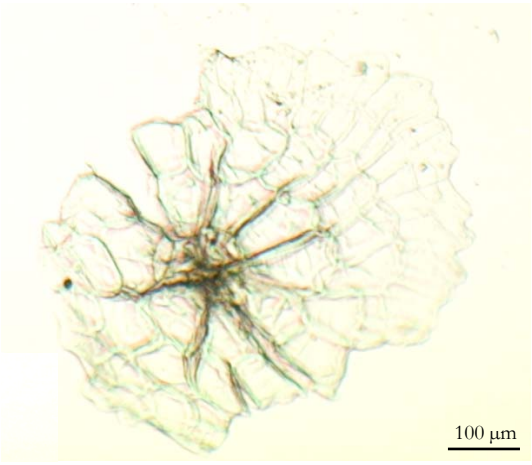


Fig. 3.6: Peltate trichome from the leaf blade of *Deuterocohnia meziana* ssp. *carmineo-viridiflora* (*N. Schütz 06-009*).

### 3.2.3 Peduncle and inflorescence

Peduncle and inflorescence provide important characters for species delimitation within *Deuterocohnia*. The inflorescence of all *Deuterocohnia* species is terminal, thereby limiting the apical growth of the plant and inducing vegetative ramification. The extremes of inflorescence and peduncle variability within the genus are best illustrated by *D. brevifolia* on the one hand and *D. meziana* on the other. *D. brevifolia* lacks a peduncle and generates just a single to few flowers in the centre of the rosette (Fig. 3.8). On the contrary, *D. meziana* gives rise to a many-flowered inflorescence, which is carried by a flowerless peduncle. Together, inflorescence and peduncle may reach a height of up to 2 m (Fig. 3.9).

Foster (1945) stated that lateral inflorescences occur in *Deuterocohnia*, *Encholirium* and *Dyckia*. While this is apparently true for species of *Dyckia*, it is not true for *Encholirium* (Forzza 2005) and *Deuterocohnia*. In *Deuterocohnia*, inflorescences may indeed give the impression of lateral growth at first glance, but this impression is caused by the appearance of new ramets that bend the inflorescence of the previous ramet aside. As the inflorescence is perennial, it still flowers when the new ramets are fully developed and this gives the impression of a lateral position (Fig. 3.9).

The perennial inflorescence is an extraordinary character of *Deuterocohnia*, occurring in most of its species. The axis lignifies and produces in every flowering period new lateral branches from buds of the main axis or branches. This enables the plant to flower for several years at the same inflorescence. This attribute is almost unique within Bromeliaceae, and has so far only been reported for some *Hohenbergia* species (Benzing 1980). While the length of peduncle and inflorescence is

determined in the first year, the proportion between both may vary during the lifetime of the plant. Branches occurring at peduncle nodes in the following years reduce the length of the flowerless part.

Bracts occurring at both the peduncle and the inflorescence are important diagnostic characters in many bromeliad taxa, e.g. in *Billbergia*, where they are colourful and attract pollinators. In *Deuterocohnia*, bracts are less conspicuous and their function is restricted to the protection of the buds. Bracts are leaf-like in the lower parts of the peduncle, but become continuously shorter and scale-like towards the apex. A taxonomic character used for differentiation between species of *Deuterocohnia* is the relative size of the primary bracts as compared with the corresponding primary branches (Fig. 3.7). Bracts can be longer or shorter than the partial inflorescence, or shorter than its sterile base. The base of the branches is covered with many small, imbricate bracts.

The inflorescences are spikes, racemes or panicles. A few sterile bracts with rudimentary floral buds occur at the apex. Within some species the inflorescence branches already in the first blooming period (e.g. *D. meziana*), while most species remain unbranched in the first year and start branching in the following year (e.g. *D. longipetala*). Branches occur up to the fourth order. They usually persist, but may also break off somehow over the years. All branches spread with an angle of about 45–75° to the preceding axis. Important for species delimitation is the branching as well as the position of the flowers along the branches (Fig. 3.7). Flowers may arise in dense clusters, e.g. in *D. brevispicata*, or laxly dispersed on a branch, as e.g. in *D. meziana*. Flowers accumulate towards the apex of the branches.

Very young branches infrequently exhibit a hairy cover, as observed in *D. meziana*. These hairs are similar to those on the sepals (see below).

The inflorescences of the cushion forming species comprise only one to a few flowers in the center of the rosette and never branch. *D. scapigera* has a small peduncle and is considered to be sort of a link between the peduncle-less groups and the species with a conspicuous peduncle.

Floral bracts are quite inconspicuous within *Deuterocohnia* compared to those of many other bromeliad taxa (e.g. *Tillandsia*). They are usually brownish, membranous to scarious and much smaller than the flowers. Across the genus, bracts vary in their absolute size as well as in their relation to the corresponding flowers. The largest floral bracts occur in *D. chrysantha* and *D. haumanii*, the smallest ones in *D. meziana*. Indument may be present on floral bracts as peltate or glandular trichomes.

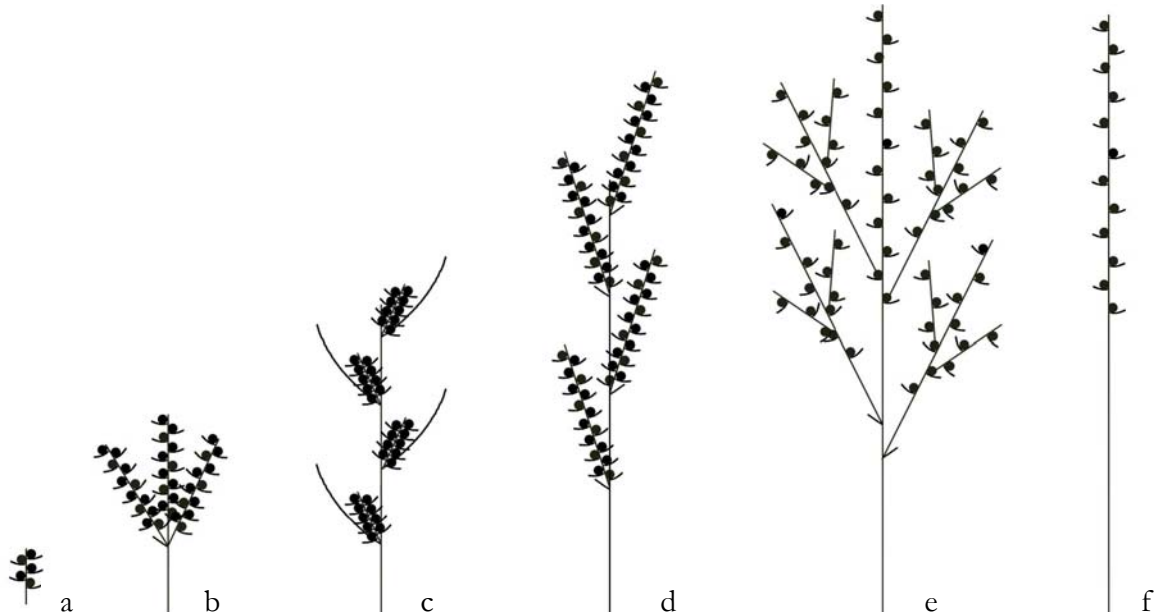


Fig. 3.7: Inflorescence (infl.) types within *Deuterocohnia*. a: Very short inflorescence, unbranched, few flowers. b: Short infl., primary bracts short, secondary branches subdigitate, densely flowered. c: Middle sized to large infl., primary bracts long, secondary branches separated by long internodes, very densely flowered. d: Large infl., primary bracts short, secondary branches separated by long internodes, densely flowered with several to many flowers. e: Large infl., primary bracts very short, secondary branches separated by long internodes, laxly flowered with many flowers. f: Infl. of former types may be unbranched in the first year. (Single flowered inflorescences and pedicellate flowers not shown.)


Fig. 3.8: Single flowered inflorescence of *Deuterocohnia brevifolia* (*coll. ign.* BGKS).


Fig. 3.9: Many flowered, elongated inflorescence of *Deuterocohnia meziana* ssp. *meziana*, cultivated in the "Fundación Amigos de la Naturaleza" (FAN), Santa Cruz, Bolivia.

### 3.2.4 Flowers

*Deuterocohnia* species have trimerous, dichlamydeous, perfect flowers with free sepals, petals, stamina and fused carpels. The flowers are actinomorphic and form a tubular perianth. In some species the petal apex rolls slightly outwards, in others the flower opens with recurved petals. At times, stamina and style emerge laterally out of the floral tube, giving the flower an asymmetric appearance. This has been observed in plants of *D. longipetala* and *D. chrysantha*.
Usually the flowers are sessile, but pedicels up to 15 mm long often occur in *D. meziana* (Fig. 3.11d). Flower sizes range from 10–40 mm. Flowers are odorless, but nectar is produced via septal nectaries and extrafloral nectaries (see below).

**Perianth**

The contort sepals are erect, slightly or distinctly asymmetric and broadly ovate in shape. The apex is rounded to acute and often mucronate. Due to the pressure of the axis in densely flowered branches, the adjacent sepals are carinate, others are ecarinate. The sepals' margin is entire and their texture is herbaceous. Small dots, which are caused by slightly exserted stomata, can be noticed on the abaxial side. Galetto and Bernardello (1992b) described extrafloral nectaries of the nonstructural and nonvascularized type for *Deuterocohnia longipetala* and eight species of *Dyckia* on the outer sepal side. These nectaries lack a differentiated tissue and their nectar is supposed to be released via the stomata. While the sepal stomata were distributed uniformly in the analysed *Dyckia* species, the authors found a higher density of stomata at the apex than at the rest of the sepal in *Deuterocohnia longipetala*. During the present study, droplets of nectar were observed also in plants of *D. meziana* (Fig. 3.11c), *D. recurvipetala*, *D. haumanii*, and *D. strobilifera* and might occur in other species as well.
Within *Deuterocohnia*, the sepals vary mainly in colour and indument. The colour ranges from greenish to yellowish, brownish, reddish, pink or orange. The indument may be glabrous, glandular or lepidote. While the peltate trichomes are sparsely dispersed, uniseriate capitate trichomes occur in a dense formation (Fig. 3.11e). The substances secreted by these capitate hairs (Fig. 3.10a, b) do not release any scent and no study of their function is available up to now. They may play a role in insect resistance (Peter and Shanower 1998).
The petals are 10–40 mm long, and about two to three times longer than the sepals. The aestivation is contort, with the right side above (sepals: left side above). All petals have a symmetric, narrowly oblong to oblanceolate shape, an acute and rounded apex and a membranous texture. Furthermore, they are ecarinate, glabrous and have an entire margin. An important character of

the petals of *Deuterocohnia* species is the presence of a single, parenchymatic appendage at the base of its adaxial side (also called petal scale, nectar scale, ligule or lateral fold; Benzing 2000). While the lower part of the appendage is adnate to the petal, the upper, fringed part is free. Petal scales may accumulate nectar secreted from septal nectaries (see below). Single appendages are typical for Pitcairnioideae and most Tillandsioideae, whereas two-parted ones occur in Bromelioideae. Within the family petal appendages occur in several groups and are often used to delimit taxa from each other. Brown and Terry (1992) argued that this character might have been overemphasized in early bromeliad taxonomy. Due to its late ontogenetic development it is probably more prone to homoplasy than other, early-developing characters. Interestingly, the sizes of the petal appendages are not correlated to the size of the flower, as they are smaller in the large flowers of *D. meziana* than in the small flowers of *D. strobilifera*. Rarely, petal appendages of *D. strobilifera* are covered with multicellular, branched trichomes (Fig. 3.10c, d, e), not mentioned for any bromeliad petal scale before. Potentially these trichomes produce additional substances to amend nectar composition.

Like the sepals, petals of *Deuterocohnia* exhibit various colours. Greenish, yellowish, reddish, pink or orange colour shades occur in different combinations with the sepals. The dominating colour is yellow, a colour most abundant in Pitcairnioideae. Tillandsioideae and Bromelioideae exhibit mainly scarlet, white or pale green perianths (Benzing 2000). Petals of most *Deuterocohnia* species have a more or less conspicuous green tip, which is completely absent only in *D. strobilifera*, *D. digitata* and *D. recurvipetala*.

Before and after anthesis the petals are usually erect. During anthesis they may either be erect, recurved (*D. strobilifera* and *D. recurvipetala*) or with the apex slightly rolled outwards. In *D. recurvipetala*, careful observation of flowers during anthesis showed that the petals recurve one after the other, and each petal takes just a few seconds to turn down (Fig. 3.11b). Given that *D. strobilifera* and *D. recurvipetala* are completely different in many other characters, their recurved petals have probably evolved in parallel and do not indicate a closer relationship. In some *Deuterocohnia* species, petals are spirally twisted after anthesis. This twisting is eminently compact in *D. meziana* (Fig. 3.11a, g), like in some species of *Puya* (Smith and Downs 1974). The perianth remains on the fruit while ripening.

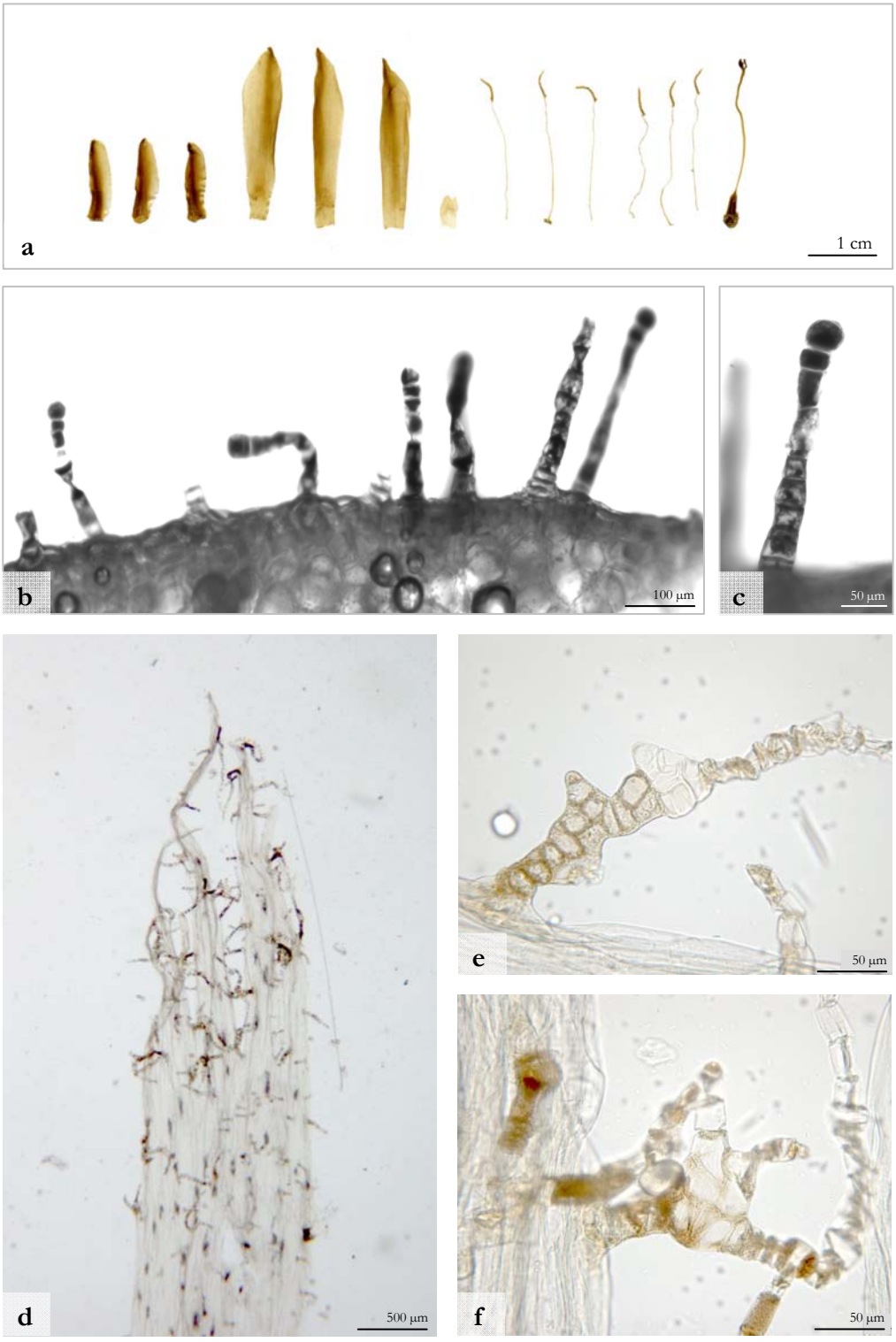


Fig. 3.10: Floral parts and related, non-peltate trichomes. a: *D. meziana*. From left to right: three sepals, three petals, one separated petal appendage, six stamina and the gynoecium. b-c: Capitate, uniseriate trichomes on the abaxial surface of the sepal of *Deuterocohnia haumanii*. d-f: Petal appendage of *D. strobilifera* with unusual capitate and filamentous hairs, which may be branched. d-e: hairs in detail.

**Androecium**

The six similar stamens are arranged in two whorls, the antipetalous ones are adnate to the base of the petals. Filaments may be undulated as it is described for filaments in *Tillandsia* (Benzing 2000). The stamens are erect, always shorter than the style and usually enclosed in the petal tube. In the recurved flower type they are exposed, and interestingly display recurved anthers as well (Fig. 3.11b). *D. chrysantha* also curves its exposed anthers, but keeps the petal tube more or less erect. The anthers are 3–5 mm long, linear and subbasifixed. After reaching maturity the greenish to yellowish anthers dehisce longitudinally and release pollen monads of about 40–48 × 23–30 µm (Ehler and Schill 1973). The pollen grains are oblate, sulcate and reticulate to foveolate. Halbritter (1992) noted an exine thickness ranging from 1.2–2.4 µm, muri thickness from 1.0–2.2 µm and brochi from 1.0–3.5 µm, but mentioned that these sizes are influenced by the swelling. Due to their gradual exine border towards the sulcus Halbritter (1992) classified the pollen of *Deuterocohnia* together with *Puya*, *Dyckia*, *Fosterella* and others as the *Puya*-type.

**Gynoecium**

The gynoecium comprises three fused carpels. The trilocular ovary is about 3–5 mm long, ovoid and wholly superior and bears numerous ovules in axile placentation. Septal nectaries are present in each septum (Böhme 1988). The style is about 7–40 mm long, terminal, filiform and whitish, greenish or reddish coloured. During anthesis the style exceeds the petal tube. The stigma is trilobed and conduplicate-spiral. According to Brown and Gilmartin (1989a) this stigma type is plesiomorphic within the family and widely distributed within Pitcairnioideae.

### 3.2.5 Fruits and seeds

Like all Pitcairnioideae, *Deuterocohnia* species produce capsules, exhibiting an ovoid shape with a cuspid apex and a glabrous, brownish surface (Fig. 3.11f, g). With the exception of size, capsules are very homogeneous within the genus. *D. recurvipetala* and *D. strobilifera* exhibit the smallest capsules with about 7 mm length, *D. meziana* the biggest ones (up to 12 mm long). At maturity the capsules dehisce septicidally and partially loculicidally (septa are reduced during maturation). This process starts apically, while the capsule remains connected at the base. The tiny seeds are 2–3 mm long and have a clavate to fusiform shape. Usually, the seeds of Pitcairnioideae are appendaged. This is caused by a bipartite testa, whose outer part forms a wing or tail-like escresence (Groß 1992). *Deuterocohnia* seeds carry a dorsal and apical outgrowth, which is quite slender in comparison to the broad seed wings of *Dyckia* species. While the appendage shows a fawn colour, whereas the remainder of the seed is brownish. *Deuterocohnia* seeds exhibit some interspecific


Fig. 3.11: Flowers, capsules and seeds of *Deuterocohnia*. a: Flowers of *D. meziana* ssp. *meziana* (BGBD 167-03-98-60) in different states of anthesis and post anthesis, showing the twisting of the petals. b: Flowers of *D. recurvipetala* (*Rauh 64236*) at anthesis with recurved petals and anthers. c: Nectar droplets of extrafloral nectaries on sepals of *D. meziana* ssp. *carmineo-viridiflora* (*Rauh 40642*). d: Pedicellate flowers of *D. meziana ssp. pedicellata* (*N. Schütz 09-009*) e: Glandular trichomes on sepals of *D. scapigera* (*L. Hromadnik 5275*). f: Capsular fruits of *D. meziana* ssp. *meziana*. g: Fruits of *D. meziana* ssp. *meziana* (*J. Anisits 2419*) with persistent, twisted petals. h: Seeds from left to right: *D. strobilifera* (*N. Schütz 06-071*), *D. meziana* ssp. *carmineo-viridiflora* (*N. Schütz 06-004*), *D. longipetala* (*A. Charpin 22942*) and *D. meziana* ssp. nov. (*T. Rojas 7515*). Photo e: Timm Stolten.

variation, e.g. very slender forms are generated in *D. meziana*, and thicker ones in *D. chrysantha* and *D. strobilifera* (Fig. 3.11h).

Varadarajan and Gilmartin (1988a) classified the seeds of *Deuterocohnia* as a variation of the *Fosterella* type since they have slightly thickened tails. However, in contrast to the symmetric seeds of *Fosterella*, those of *Deuterocohnia* have one acuminate and one broad end, which is also reminiscent of the *Puya ferruginea* type. The study of Varadarajan and Gilmartin (1988a) did not include seeds of *D. strobilifera* or *D. chrysantha*, which demonstrate this character more obviously. *Deuterocohnia* seeds contain a massive endosperm and relatively small embryos (Benzing 2000).

## 3.3 Anatomy

### 3.3.1 Leaf

The leaf anatomy of *Deuterocohnia* displays a set of remarkable adaptations to xerothermal habitats, in particular a prominent water storing tissue.

Leaf cross sections illustrate the pronounced growth of the abaxial leaf side (Fig. 3.12a, b). The adaxial side may be either plane or likewise concave. The epidermis cells have thick cell walls, and cells may contain silica grains (Ehler 1977). Hypodermal sclerenchyma supports the rigidity of the leaves (Fig.3.13b, e) which is less pronounced in small leaves of *D. brevifolia*. The adjacent hydrenchyma dominates the cross section conspicuously (Fig. 3.13a), as also noted by Horres and Zizka (1995) who found that adaxial water storing tissue comprised 32–48 % of the cross-section of *Deuterocohnia* species. On the abaxial side of the leaf, vascular bundles (Fig. 3.13d) are surrounded by a ring of sclerenchyma and embedded in assimilation parenchyma (Fig. 3.13c). Below, there is an abaxial layer of hydrenchyma that contains more chloroplasts than the adaxial one. The lower hypodermis and epidermis are composed in a similar way as the upper ones, but are regularly interrupted by the occurrence of stomata, which are arranged in parallel rows. According to Ehler (1977) *Deuterocohnia* stomata consist of two guard cells and four accessory cells, Tomlinson (1969) defined two guard cells, four subsidiary cells and 4 neighbouring cells. In some species, guard cells exhibit a conspicuous cuticular hood (Tomlinson 1969). Peltate trichomes are located both on the upper and lower surface of leaves, but are more pronounced abaxially.

The shared character of an abrupt boundary between adaxial water storage and assimilation parenchyma led several authors to assume a close relationship between the genera *Deuterocohnia*, *Dyckia*, *Encholirium* and *Hechtia* (Robinson 1969, Robinson and Taylor 1999). Current phylogenies based on molecular data however classify *Hechtia* as belonging to a separate subfamily

(Hechtioideae, Givnish et al. 2007, 2011) which indicates convergent evolution of these anatomical characters.

Within *Deuterocohnia*, leaf anatomy is quite uniform and lacks anytaxonomically relevant characters.

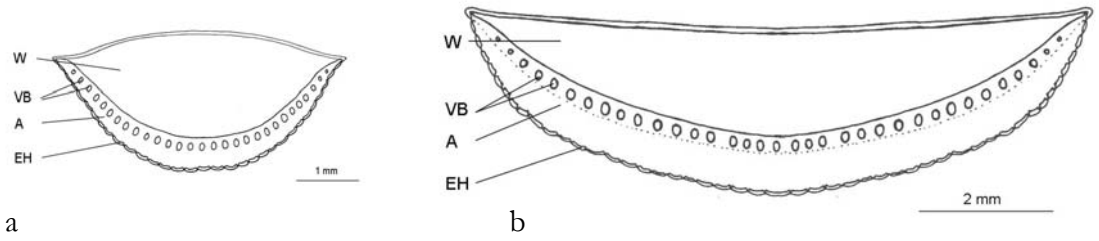


Fig. 3.12: Leaf blade cross sections, overview. a: *Deuterocohnia lotteae* (*L. Hromadnik 5131*). b: *D. meziana* (*N. Schütz 06-009*). A = Assimilation parenchyma. EH = Epidermis and hypodermal sclerenchyma. VB = Vascular bundles. W = Water storing tissue. Stomata distributed abaxially.

### 3.3.2 Peduncle

Up till now, only few studies have addressed the anatomy of inflorescence axes in bromeliads Tomlinson (1969). Peduncle cross sections of several *Deuterocohnia* species were made in the present study (Fig. 3.14a–h, 3.15), showing that the perennial peduncle axis is dominated by lignified tissue. A cortex and a central cylinder can be clearly distinguished (Fig. 3.14a, c). The cortex comprises a lignified epidermis, one or two rows of likewise lignified, hypodermal sklerenchymatic cells, and a conspicuous layer of periderm and adjacent parenchyma in which scattered vascular bundles are embedded (Fig. 3.14c). The periderm layer in *D. meziana* was previously analysed by Foster (1945), who assumed it to represent a cambium-like layer. On the contrary, Tomlinson (1969) identified this tissue to be a "well-developed 'etagen'-type periderm", whereas Fahn (1974) described this protective tissue as storied cork, occurring in thickened stems also of other monocotyledons. In contrast to the periderm of dicotyledons, this cork is not generated by a layer of phellogen. Instead, it is generated by parenchymatic cortex cells that convert into meristematic cells. They divide tangentially and form short cell rows containing up to ten cells. Figure 3.15 illustrates cells after several divisions as well as cells in the initial stage, after a single cell division.

The central cylinder contains isolated, scattered vascular bundles. The peripheral bundles are smaller and surrounded by more sclerenchymatic sheath cells than the inner ones.

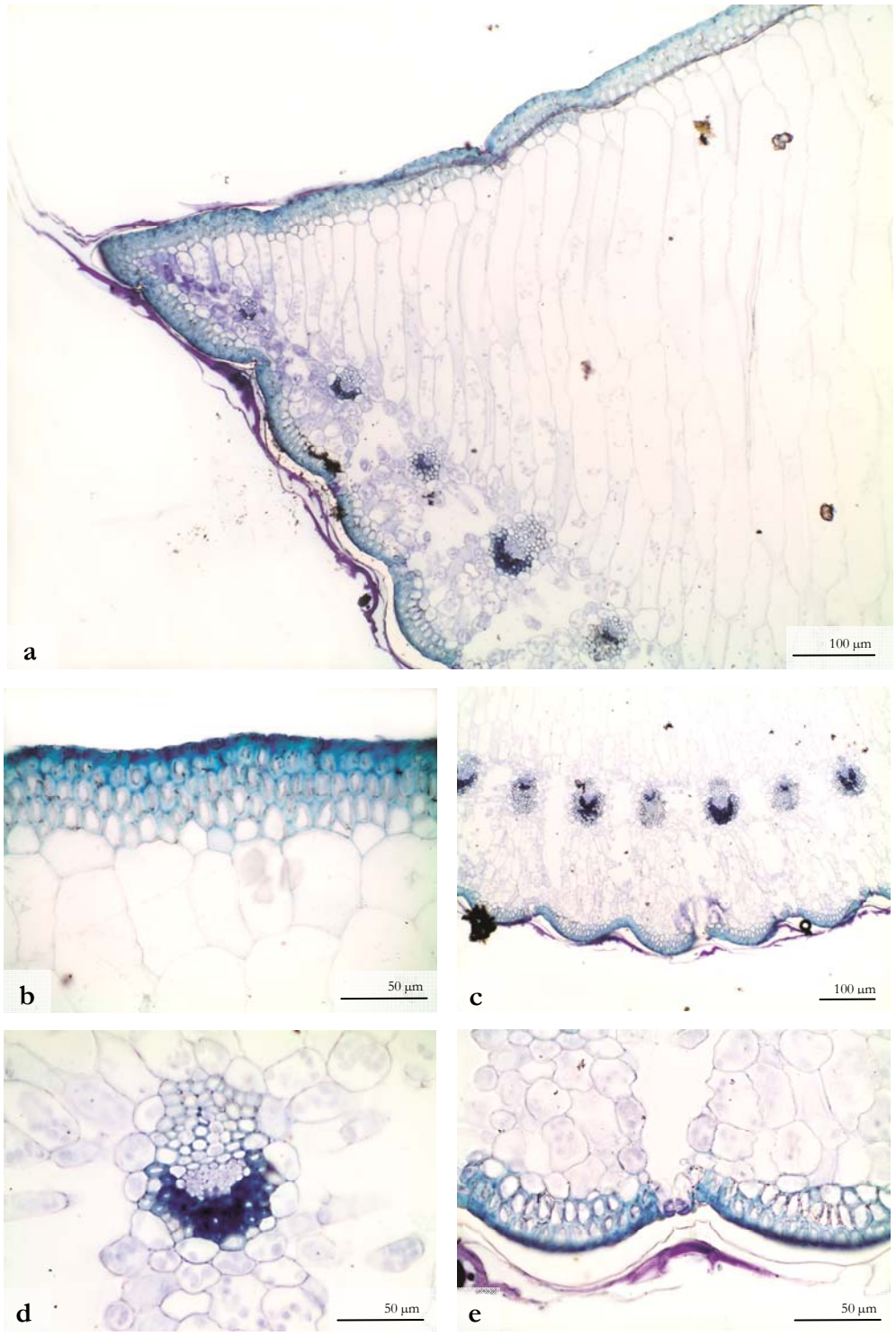


Fig. 3.13: Leaf blade cross sections, detail. a-e: *Deuterocohnia lotteae* (*L. Hromadnik 5131*). a: Lateral part of the leaf. b: Adaxial epidermis, sclerenchyma and water storing tissue. c: Part of the abaxial leaf side, with vascular bundles and assimilation parenchyma. d: Vascular bundle. e: Detail of the adaxial leaf side, comprising a peltate trichome, epidermis, stoma, hypodermal sclerenchyma and adjacent parenchyma. A = Assimilation parenchyma. EH = Epidermis and hypodermal sclerenchyma. VB = Vascular bundles. W = Water storing tissue.

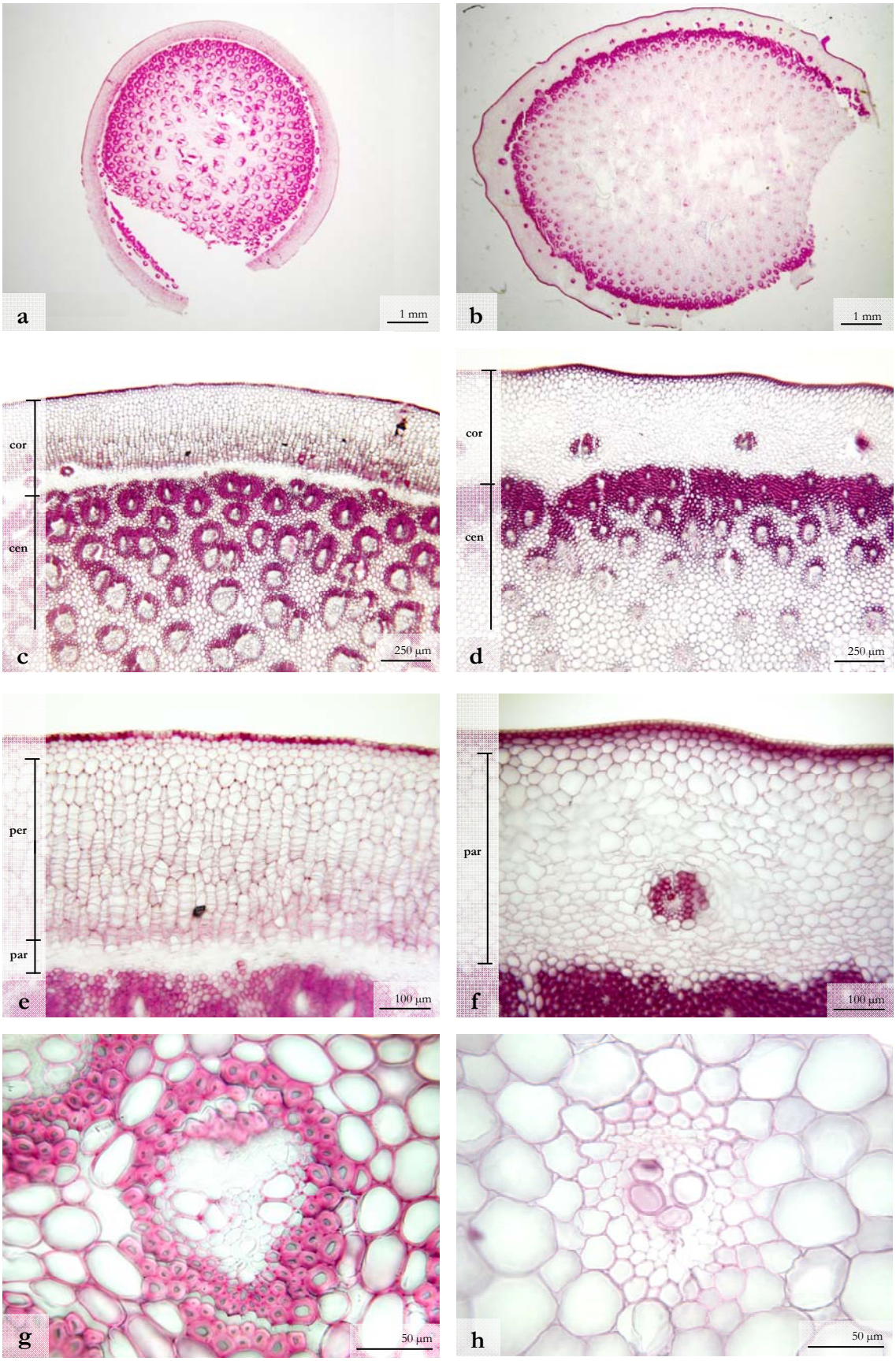


Fig. 3.14: Cross sections of peduncle axes. a, c, e, g: *Deuterocohnia glandulosa* (*N. Schütz 06-020*). b, d, f, h: *Dyckia brevifolia* (*coll. ign.*, BGKS). a, b: Overview. c, d: Part of cortex and central cylinder. e, f: Detail of cortex. g, h: Vascular bundles from the inner part of the axis. cen = central cylinder, cor = cortex, par = parenchyma, per = periderm.

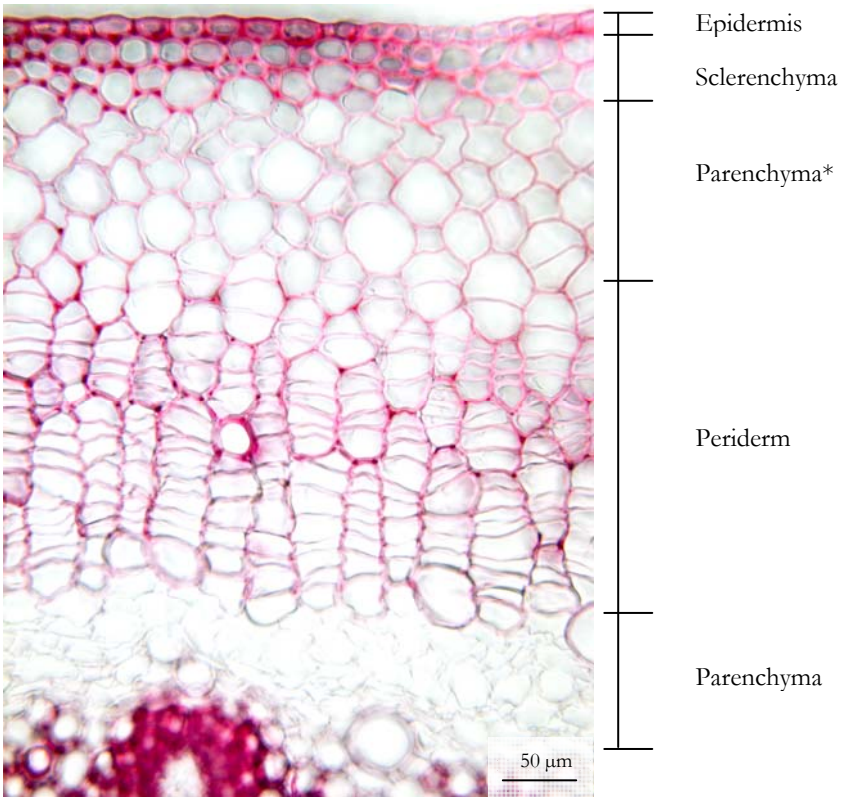


Fig. 3.15: Cross section of peduncle axis. Detail of the cortex (*Deuterocohnia longipetala*, *N. Schütz 06-067*). *Parenchyma with the potential to differentiate into periderm cells.

The parenchyma between the vascular bundles is also lignified (Fig. 3.14g).
Compared to the samples of *Deuterocohnia*, the cross sections of peduncles from *Dyckia brevifolia* show less lignification, less pronounced sclerenchyma sheaths around the inner vascular bundles and a cortex without peridermal cells (Fig. 3.14d, f). The periderm in the cortex of *Deuterocohnia* seems to be an important key innovation for maintaining the persistant inflorescence.

## 3.4 Karyology

The current data suggest that bromeliads exhibit a relatively small genome, e.g. 441–526 Mbp in *Ananas* (Arumuganathan and Earle 1991, Bennett and Leitch 1995), and also small chromosomes. There have been numerous chromosome studies in Bromeliaceae (e.g. Marchant 1967, Cotias de Oliveria et al. 2004, Gitai et al. 2005). The basic number is n=25. Exceptions occur e.g. in *Cryptanthus*, where n=34, 36 or 54 have been reported (Ramírez-Morilla and Brown 2001). There are only few reports of polyploidy and bimodal karyotypes (Benzing 2000). Chromosome numbers within *Deuterocohnia* were published for *D. longipetala* (McWilliams 1974, Brown and Gilmartin 1984a, 1989b), *D. haumanii* (Brown and Gilmartin 1989b) and *D. lorentziana* (Gitai et al. 2005).

They all counted 2n=50 chromosomes. A surprising anomaly was reported by Horres (2003), who found different chromosome numbers as well as differing morphology of two different individuals of *D. lorentziana* growing together in the same pot. One plant had the usual number of 25 chromosome pairs, with 19 large and 6 small pairs (2.29–1.14μm), whereas the other comprised 1 large and 49 small pairs (1.94–0.5 μm). Unfortunately, this plant is not cultivated in the BGHD anymore. Ebert and Till (1997) analysed genome sizes within Pitcairnioideae (sensu Smith and Downs 1974) and obtained C-values of 0.39 pg for *D. longipetala* and 0.37 pg for *D. schreiteri*. In species of the closely related genera *Dyckia* and *Encholirium* C-values were about twice as high as in *Deuterocohnia*.

Tab. 3.2: Chromosome numbers in *Deuterocohnia*.

| | Chromosome number (2n) | Reference |
|---|---|---|
| *D. haumanii* | 50 | Brown and Gilmartin 1989b |
| *D. longipetala* | 50 | McWilliams 1974, Brown and Gilmartin 1984a, 1989b |
| *D. lorentziana* | 50; 100 | Horres 2003, Gitai et al. 2005 |

## 3.5 Distribution and ecology

### 3.5.1 Distribution, habitat and ecology

The genus *Deuterocohnia* is distributed in the Andes and adjacent areas of S Bolivia and N Argentina. Some species occur apart from this area, like *D. chrysantha*, which is endemic to the north of Chile and *D. meziana*, which spreads from Bolivia into the lowlands of W Brazil and N Paraguay. *D. longipetala* has a disjunct distribution, occurring in Bolivia and Argentina as well as in an isolated area in the north of Peru. Sites of collection range from (5°30' ) 14°30'–35° S, and 55–80° W.

Most of the species are characterized by a narrow distribution range, some are only known from the type locality (e.g. *D. gableana*). *D. longipetala* has the widest distribution range, occurring in almost two thirds of the genus' distribution area. The actual distribution range of many species may in fact be larger than anticipated, since the present data may suffer from a lack of collection (Vásquez et al. 2002).

The genus can be found from sea level up to 4000 m a.s.l. However, every species has its own, more or less narrow elevation range (Fig. 3.16). *D. chrysantha* occurs from close to sea level to

about 400 m a.s.l. in the Atacama Desert. Cushion forming plants of *D. brevifolia* have the broadest altitudinal range, which is about 2000 m, from 1100–3000 m a.s.l. Only few species grow at even higher altitudes, including *D. strobilifera* that almost reaches 4000 m a.s.l. in Potosí, Bolivia. Within Bromeliaceae only species of *Puya* are able to survive at higher altitudes.

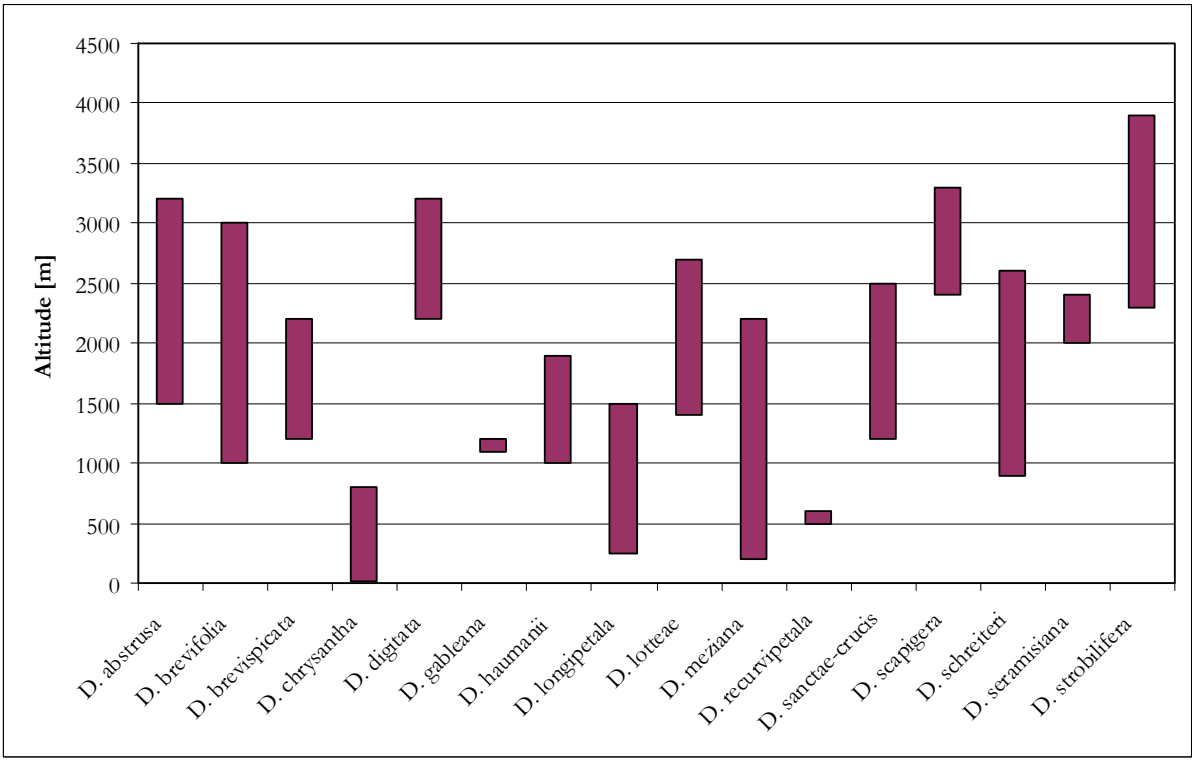


Fig. 3.16: Altitudinal range of *Deuterocohnia* species.

Within the genus some trends in relation to altitude can be recognized:

- In lowland areas woody peduncles and inflorescences are longest, like in *D. meziana* where they reach almost 2 m. Peduncles and inflorescences become successively shorter with increasing altitude and typically do not exceed 30 cm in *D. strobilifera* or *D. digitata*.
- Species with laxly flowered inflorescences usually are found at lower altitudinal level (e.g. *D. meziana*, *D. recurvipetala*), while more compact inflorescences become more abundant with increasing elevation (e.g. *D. schreiteri*). Somewhat exceptional in this respect are the compact partial inflorescences of Chilean *D. chrysantha*, which grows near the coast. This could perhaps be explained by a close relationship of this species to species from higher altitudes on the eastern slopes of the Andes, as for example *D. haumanii*.
  A similar pattern of increasing compactness of the inflorescence at higher altitudes was also described for Ecuadorian *Puya* species (Miller 1986). This author demonstrated that

the most compact and pubescent inflorescences maintain the flower buds significantly warmer than laxer and more glabrous inflorescences.

- With the exception of cushion-forming species, flowers tend to be longer at low elevation (up to 55 mm in *D. meziana*) than at high altitudes (10 mm in some populations of *D. strobilifera*). *D. recurvipetala* behaves against this trend, bearing small flowers at low elevation (Fig. 3.17).

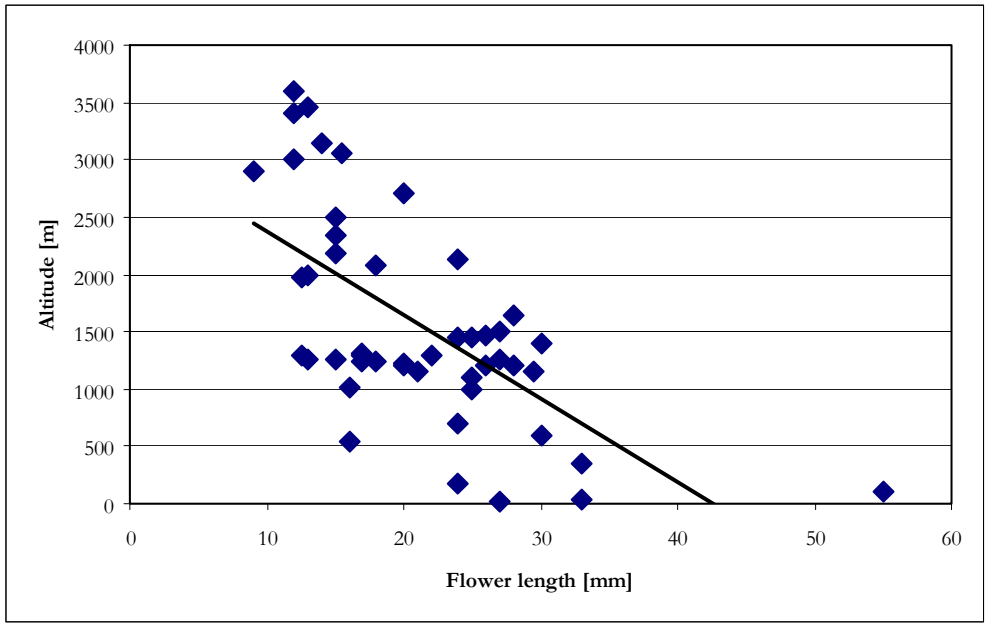


Fig. 3.17: Flower length in relation to altitude in species of *Deuterocohnia*. Cushion-forming species are excluded, because they roughly maintain their flower size in different altitudes.

Additionally, the following adapations of particular species seem to be related to increasing elevation:

- At high altitudes, *D. strobilifera* exhibits conspicuously incurved leaves. Increased leaf posture could be a consequence of loss of water and the related shrinkage of the water storage tissue. Another explanation was provided Lüttge et al. (1986) who presumed that leaves of *Pitcairnia integrifolia* roll inwards to expose the dense trichome layer on the abaxial surface to protect the leaves from solar radiation. However, Pierce et al. (2001) noted this phenomenon also in glabrous *Pitcairnia valerii* leaves.
- Light stress may cause the reddish coloured upper leaf sides in plants of *D. strobilifera*, growing at high altitudes.
- A dense layer of trichomes is developed also on the adaxial leaf surface in *D. abstrusa*.

Species of *Deuterocohnia* can be found in various ecoregions, all of which are related to the Andes. In Chile the endemic species *D. chrysantha* occurs in the Atacama Desert close to the Pacific coast and nearby mountains, at the border between the ecoregions Atacama Desert and Chilean Matorral. The Atacama Desert is one of the driest deserts in the world. On the coastal side of the Andean cordillera, the cold Humboldt Current prevents accumulation of clouds while at its western side the high Andean mountain range causes a lee position. Precipitation in this area is less than 50 mm per year, in some years it does not rain at all. Along the coastline, coastal fog complements water supply. This area allows only very drought-resistant plants to reside, and Cactaceae are the most common plants here (Fig. 3.18).

All other species of *Deuterocohnia* occur in areas having a dry season of 4–9 months in winter, moderate precipitation in summer and an annual rainfall between 300 and 1500 mm. With about 300–400 mm precipitation per year, the montane grassland of the Central Andean Puna (Prepuna and semihumid Puna) in Bolivia and Argentina reflects the drought and cold limit of the genus' distribution area. Frost occurs occasionally, and concerning *Deuterocohnia*, only *D. strobilifera* expands into this area (Fig. 3.19). Likewise dry, but much warmer conditions are typical for the Gran Chaco, with maximum temperatures of up to 48°C (Ibisch and Mérida 2004). In this area, populations of *D. meziana* grow in the understory of low deciduous dry forests. The highest precipitation within the distribution area of *Deuterocohnia* refers to the lowlands of eastern Bolivia and the adjacent border to Brazil, where the annual rainfall amounts to 1000–1500 mm per year. Within this region known as the Chiquitania dry forests, *D. meziana* grows mainly at azonal localities on outcrops.

Most of the *Deuterocohnia* species occur in the Interandean dry valleys and along the eastern slopes of the Andes, particularly in an area south of the so-called "Andean knee". Interandean dry deciduous forests (Bolivian montane dry forest) occur at elevations of 500–3300 m a.s.l. and exhibit an annual rainfall of 500–700 mm or less. While the average temperature is about 12–16°C, the maximum may exceed 30°C and the minimum fall below 0°C (Ibisch and Mérida 2004). In semiarid habitats of NW Argentina, where arboreal vegetation is scarce, populations of *D. haumanii* and *D. schreiteri* are an important floristic element and in some areas dominate the vegetation up to almost pure stand (Fig 3.20). This vegetation is one of the very few bromeliad-dominated formations that can easily be recognized from the air (Smith 1964a).

The eastern slopes of the Andes are considered as a hot spot of biodiversity (Mueller et al. 2002). They provide various ecological niches at different altitudes and moderate to high precipitation coming from the Amazon in the northeast. An area called the Tucuman-Bolivian forests or Andean Yungas (Fig. 3.21) are located at the eastern slopes below the Andean knee. This part exhib-

its less humidity and more seasonality than the one north of the Andean knee towards Peru (Bolivian-Peruvian forest, Peruvian Yungas; Ibisch and Mérida 2004). The Tucuman-Bolivian forests display a broad variation in altitude (800–3900 m a.s.l.), precipitation (700–2000 mm per year) and mean temperature (5–23°C). Southwards, they extend into Argentina down to about 29°S. Adjacent areas in the south are the Argentine Monte, the Cordoba montane savannas and the arid Chaco, where only *D. longipetala* occurs, in the Argentine Monte additionally *D. abstrusa*. Northwards, the distribution area of *Deuterocohnia* reaches its limit close to the Andean knee. However, some populations of *D. longipetala* have a disjunct occurrence in NW Peru, isolated from the main distributional range in Bolivia and Argentina by more than 2000 km. In Peru, the plants grow on the eastern as well as on the western slopes of the Andes. Given that the disjunct populations are morphologically similar, the distribution pattern seems to be a result of a long distance dispersal event.

Although distribution areas of different species may overlap, species growing sympatrically at the same locality have been observed during own field trips only in the case of *D. abstrusa* and *D. haumanii* in NW Argentina. However, hybrid zones may exist in this region for *D. haumanii* and *D. schreiteri* and in S Bolivia for *D. meziana* and *D. longipetala*.

The species of *Deuterocohnia* are terrestrial or saxicolous, with the ability to grow on plane ground as well as on vertical slopes. In regions with more precipitation such as the Chiquitania or Bolivian-Tucuman dry forests, the plants are often confined to azonal habitats, like rocky outcrops or steep slopes along roads. Little is known about soil preferences of *Deuterocohnia* species. It is however known that *D. longipetala* is able to grow on saline ground as documented for the area of Ischigualasto in Argentina (Márquez et al. 2005).

The adaptation of *Deuterocohnia* species to their arid environment is reflected by their slow growth, leaf persistance, xeromorphic leaf anatomy and CAM-photosynthesis. According to Benzing (2000) *Deuterocohnia* belongs to the ecophysiological type 1. The cushions of *D. brevifolia* and *D. abstrusa* exhibit additional adaptations, like the decomposing inner ramets that provide nutrients and also function as a water reservoir. Rauh (1978a) compared the architecture of these cushions with the anatomy of a globular cactus. The outer, greenish rosettes correspond to the assimilation parenchyma, the inner, decomposing ramets parallel the water storing tissue.

Fig. 3.18: *Deuterocohnia chrysantha* in a coastal region of the Atacama Desert, Chile. Photo: Georg Zizka.

Fig. 3.19: *Deuterocohnia strobilifera* in Prepuna region, between Otavi and Padcayo, Chuquisaca, Bolivia.

Fig. 3.20: Vegetation dominated by *Deuterocohnia haumanii* in northwestern Argentina.

Fig. 3.21: Landscape covered by Tucuman-Bolivian forest in S Bolivia.

Beside their relationship to pollinators (see below), animal-plant interactions have also been documented for *Deuterocohnia* species and ants. Galetto and Bernardello (1992b) found that eight *Dyckia* species and one *Deuterocohnia* (*D. longipetala*) species attracted ants with extrafloral nectar. The fact that a relatively high concentration of amino acids (121–975 µl/ml) was found in the nectar led them to the assumption that ants are the targeted fauna and not pollinators. This interaction might protect the plants against herbivory. During the present study, ants were observed on individuals of *D. digitata* in the field (Fig. 3.22) as well as on *D. recurvipetala* in the greenhouse.

Controverse results have been published concerning the presence of mycorrhiza in *Deuterocohnia*. Whereas Lugo et al. (2009) found arbuscular mycorrhiza as well as dark septate endophytes in samples of *Deuterocohnia longipetala* and *Dyckia* (but not in *Bromelia*), Fracchia et al. (2009) did not observe mycorrhiza in the same species, *D. longipetala*.


Fig. 3.22: Ants of the genus *Camponotus* (Formicinae) on immature flowers of *Deuterocohnia digitata* in its natural habitat (*N. Schütz 06-098*).

### 3.5.2 Phenology and pollination

The main flowering period of *Deuterocohnia* species is September to January. However, according to herbarium material, plants also show the potential to produce flowers in between. Anthesis is acropetally, i.e. flowers at the base of a partial inflorescence mature first. Life time of the diurnal flowers is about 2–6 days. Galetto and Bernardello (1992a) reported flower lifetime within the natural habitat of 2.5–3 days for *D. brevifolia*, 5–6 days for *D. abstrusa* and 2.5 days for *D. longipetala*. Blooming time of the overall inflorescence differs within the genus. In the greenhouse, *D. recurvipetala* flowered for about 2 months, whereas *D. longipetala* and *D. meziana* completed blooming after 3–4 weeks. After anthesis, the petals are compressed by the sepals and thus, the flower tube is closed.

Many assumptions about pollination systems in *Deuterocohnia* were published, but only few of these were based on studies in the field. The overall consensus is that the colourful flowers are zoophilous. Based on stigma morphology and other floral characters, Varadarajan and Brown (1988) concluded insect pollination to be widespread within *Deuterocohnia*. Benzing (2000) stated that due to floral pigmentation and structure, *Deuterocohnia* pollination depends on insects. However, Bernardello et al. (1991) also observed hummingbirds (*Chlorostilbon aureoventris*) feeding on *D. longipetala*, and also on species of *Dyckia*. The authors additionally predicted bird pollination for *Deuterocohnia haumanii*, having similar flowers. Böhme (1977) analysed the ratio of gland body to septal nectarium and concluded that a ratio > 2/3 (which was the case for *Deuterocohnia* samples) is an indicator of ornithophily (or chiropterophily).

Own field observations during the present study revealed that *D. brevispicata* and *D. meziana* are visited by hummingbirds. Both species have tubular flowers with reddish or orange colour shades and a conspicuously green tip. Red is often described as the typical colour of ornithophilous flowers (Forrest and Thomson 2009), whereas yellow is more allocated to entomophily. However, birds may also be attracted by yellow flowers. The tubular, scentless flowers of *D. longipetala* bearing yellow petals with a green tip are visited by hummigbirds (Bernardello et al. 1991), and the same is probably true for other *Deuterocohnia* species having similar flowers, like e.g. *D. haumanii*.

This situation is different in *D. strobilifera*, *D. digitata* and *D. recurvipetala*. These species bear single-coloured yellow flowers, which are small and open at anthesis (*D. digitata* remains closed). This leads to the assumption of entomophily in these species, although no observation has been documented to date. The cushion-forming plants of the former *Abromeitiella* species were predicted to be bird pollinated according to floral features and nectar composition (Galetto and Ber-

nardello 1992a), but likewise no field observation has yet been documented. The greenish tip of these flowers is not that distinct from the yellowish-greenish base as is the case in their relatives. An interesting finding is the appearance of nectar droplets at the apex of the flowers of *D. brevispicata* grown in the greenhouse. They appear in fading flowers, when the sepals compress the floral tube and thus excess nectar is released at the apex. Given that such droplets have not been observed in other species of the genus, this points to a particularly high production of nectar in *D. brevispicata*. The occurrence of nectar droplets on the abaxial sepal side in other species is caused by different structures (see 3.5.1).

*D. recurvipetala* and *D. brevispicata* set seeds in the greenhouse as well as (present study, Stolten 1999), whereas *D. brevifolia*, *D. meziana* and *D. longipetala* do not. This might be caused by different success of selfing or, in the case of *D. recurvipetala*, by the occurrence of an alternative pollinator that visited the open, anthers and stigma presenting flowers. Generelly the stigma is slightly or conspicuously exerted above the anthers and the petals to prevent autogamy.

Asexual reproduction may play an important role in cushion-forming plants of *D. brevifolia* and *D. abstrusa*, where ramification may occur independently from flowering. Especially in shady places, flower development seems to be suppressed in heliophilic bromeliads (Benzing 2000). A dense cushion of about one meter in size, growing on the ground in the greenhouse, did never bloom in its whole life span.

### 3.5.3 Seed dispersal and germination

In contrast to the hairy seeds of Tillandsioideae and the fleshy fruits of Bromelioideae, the fruits and seeds of *Deuterocohnia* bear – like in other Pitcairnioideae – no obvious facilities for dispersal. The capsules release small, inconspicuously appendaged seeds, which are either distributed by wind (boleochorous), water or accidently by animals (Gross 1993b).

The germination of all Pitcairnioideae is epigeic (Fig. 3.23). The growth of *Deuterocohnia* plants is slow. Large rosettes of e.g. *D. meziana* grow over many years before they reach their mature size.


Fig. 3.23: Seedlings of *Deuterocohnia meziana* ssp. *carmineo-viridiflora* (*N. Schütz 06-009*). a: Cotyledon. b: First rosulate leaves. c: Leaves have taken their characteristic triangular form and a lepidote surface (about five months old).

Fig. 3.24: Seedlings of *Deuterocohnia meziana* ssp. *meziana*, having germinated within the capsule on the inflorescence. Photo: Ingo Michalak.

After four years growing in the green house, the plants of *D. meziana* had reached about 15 cm in diameter. Small plants of *D. brevifolia* had already branched once or twice within the same period.
Accidentally, seeds may also germinate within the capsule on the inflorescence (Fig. 3.24).

### 3.5.4 Conservation, use and common names

The species of the genus *Deuterocohnia* do not seem to be highly endangered through direct damage or destruction of their habitat by humans as it is the case for example for species of *Fosterella* (own observations). Growing in very arid and sparsely populated areas (e.g. Atacama, Prepuna) or on steep slopes, bare rocks in more humid regions, *Deuterocohnia* does not compete much with men who are looking for suitable areas for agriculture or housing.
However, the plants may be negatively affected by adverse environmental conditions. Rundel and Dillon (1998) stated that extended drought conditions might have caused the extensive mortality of *Deuterocohnia chrysantha* in northern Chilean coastal areas. More recently, Zizka et al. (2009) classified *D. chrysantha* as being endangered, Squeo et al. (2008a, b, c) as "en peligro". The floristic components of the "Interandean *Prosopis ferox* thorn woodland" in Bolivia (Navarro 1997), comprising *D. strobilifera*, are considered to be vulnerable. Thus, climate change may play an important role in the continuity of *Deuterocohnia* populations especially in the mentioned areas, where increasing temperature and decreasing water supply may exceed the stress tolerance capabilities of the plants.
Also important to mention is the general endangerment of local endemics (e.g. *D. seramisiana*, *D. gableana*), which are restricted to small areas. Widespread species like *D. longipetala* or *D. meziana* are less vulnerable, as small-scale changes affect only a part of the populations.
The 1997 IUCN Red List of Threatened Plants (Walter and Gillett 1998) listed two species of *Abromeitiella* and five species of *Deuterocohnia* to be vulnerable (V) or rare (R): *A. brevifolia* (R), *A. lorentziana* (R), *D. chrysantha* (V), *D. digitata* (V), *D. haumanii* (R), *D. meziana* (R) and both varieties of *D. strobilifera* (V). In the most recent version (v.2010.4), no species of *Deuterocohnia* is regis-

tered. This is perhaps due to changing criteria rather than increasing populations, given that the slowly growing plants can not have increased much in number and area within only ten years. Little information is available about the use of *Deuterocohnia* plants. Vargas (voucher 6282, WU) noted on a herbarium specimen of *D. brevispicata* that the apical meristem has been utilized as medicine against liver diseases. Leaf fibers of *D. meziana* are used to produce hammocks and ropes (voucher Bourdy 2141, LPB). Novara (voucher 8339, MCNS) mentioned that cushions of *D. brevifolia* are planted on top of walls as a kind of barbed wire. Funes (2008) investigated the potential of *Deuterocohnia longipetala* for revegetation of degraded slopes caused by metal mining. Vernacular names for *Deuterocohnia* species are "chaguar" or "chaguar del jote". These names are widespread, used in Chile (Muñoz Pizarro 1960) and Argentina (De la Peña 1997), and are also given to other spinose bromeliads. In some areas of Argentina, *D. abstrusa*/*D. brevifolia* is named "chaguar violeta" (Femenia 2009), *D. haumanii* "chaguar blanco" (voucher Schreiter s.n., LIL 34593). Another local name is "caraguata" or "caraguata guasu" (voucher Bourdy 2141, LPB) for *D. meziana*. This term originates from Guaraní, an indigenous language of S Bolivia and Paraguay. In Potosí, Bolivia, the plants of *D. strobilifera* are called "Kayara" (voucher Cárdenas 3741, LIL).

## 3.6 Molecular phylogenetic analyses

### 3.6.1 Statistics of sequence data

Chloroplast-DNA (cpDNA) sequence data were generated from 119 accessions (103 *Deuterocohnia*/ 16 outgroup) and nuclear DNA sequence data from 28 accessions (22 *Deuterocohnia* / 6 outgroup). All *Deuterocohnia* species could be included in the analyses. Statistics of the analysed loci are described in the following sections, and are summarized in Tables 3.3 and 3.4 and Figures 3.25–3.28.

#### 3.6.1.1 Intergenic spacer *rpl*32–*trn*L

The sequence alignment of the chloroplast intergenic spacer *rpl*32–*trn*L revealed a set of 1018 characters. The shortest sequence had a length of 863 bp, the longest of 982 bp. The alignment begins inside the *rpl*32 gene and ends on the verge of the *trn*L gene. Two polymorphic poly-A regions ($A_8$–$A_{14}$ at pos. 648, and $A_6$–$A_{11}$ at pos. 733) as well as one inversion were excluded from the analyses. Additionally, two nested insertions specifically found in some *Pitcairnia* sequences were eliminated due to problematic homology assessment. The final alignment comprised 890 characters, of which 86 (9.66%) were variable, and 51 (5.73%) were parsimony informative among the full data set. Within *Deuterocohnia*, 35 characters (3.93%) were variable, and 23 characters (2.58%) were parsimony informative. For phylogenetic reconstruction, eleven indels were coded of which seven were parsimony informative. Maximal sequence divergence across all species and accessions was 3.90% (*Fosterella villosula* compared with *Dyckia ferox*, *Dy. granmogulensis*, or *Encholirium inerme*. Within *Deuterocohnia*, the highest sequence divergence (1.89%) was observed between *D. lotteae* on the one hand and *D. meziana* / *D. brevispicata* on the other.

#### 3.6.1.2 Intergenic spacer *rps*16–*trn*K

The lengths of the analysed *rps*16–*trn*K fragments varied from 683 to 713 bp, resulting in a sequence alignment of 730 characters. This alignment begins at the 3´ end of the *rps*16 gene and ends 5´ to the *trn*K gene. Three polymorphic mononucleotide repeat regions ($A_8$–$A_{19}$ at pos. 64, $T_8$–$T_{16}$ at pos. 263 and $T_7$–$T_{11}$ at pos. 467) were excluded from the analyses. Since only one of the two poly-T regions turned out to be present in *Pitcairnia* and *Fosterella*, the "birth" of the second repeat was probably triggered by a base mutation from C to T in the common ancestor of the *Dyckia* clade. Within *Deuterocohnia*, the poly-A repeat is restricted to group *j*, where it probably

evolved through a base substitution from T to A, combining three and four A positons that had previously been separated by the T. Interestingly this repeat also expanded in *Dyckia* and *Encholirium inerme*, probably through an independent, additional mutation from T to A. The large size of this poly-A repeat in *Dyckia* makes it difficult to sequence the *rps*16–*trn*K fragment precisely (present study and Krapp 2009), as the DNA-polymerase may "stutter" at this site (Weising et al. 2005).

Of the remaining 705 characters included in the final alignment, 79 (11.21%) were variable and 54 (7.66%) parsimony informative among the full data set. Within *Deuterocohnia*, 39 characters (5.53%) were variable, and 31 (4.40%) were parsimony-informative. Eleven indels were coded, of which nine were parsimony informative. Across the full data set, sequence divergence was highest between *Fosterella penduliflora* and *Dyckia estevesii* (4.35%). Within *Deuterocohnia*, maximal sequence divergence occurred between *D. longipetala* and *D. brevispicata* / *D. meziana* (3.15%).

#### 3.6.1.3 Intergenic spacer *trn*S–*ycf*3

The alignment of the chloroplast intergenic spacer *trn*S–*ycf*3 revealed a set of 679 characters. The shortest sequence had a length of 645 bp, the longest of 673 bp. The aligned sequence begins on the negative strand 3´ to the *trn*S gene and ends between exon1 and exon2 of the *ycf*3 gene. One poly-T region was found in the area ($T_9$–$T_{12}$ at pos. 586), and was excluded from the analyses. Of the remaining 654 characters, 35 (5.35%) were variable and 24 (3.67%) were parsimony informative among the full data set. Within *Deuterocohnia*, 21 characters (3.21%) were variable and 16 (2.45%) were parsimony informative. Four indels were coded, of which one was parsimony informative and three were autapomorphic. Taking all accessions into account, sequence divergence was highest between *Fosterella weddeliana* and *Deuterocohnia scapigera* / *D. longipetala* (2.05%). Within *Deuterocohnia*, maximal sequence divergence was observed between *D. longipetala* on the one hand and *D. meziana* / *D. scapigera* on the other (1.73%).

Tab. 3.3: Statistics of cpDNA sequence alignments of 119 accessions (103 *Deuterocohnia* / 16 outgroup), including all species of *Deuterocohnia*. Potentially homoplastic regions were excluded from the final analyses.

| **Statistics/ Region** | | ***rpβ*2–*trn*L** | ***rps*16–*trn*K** | ***trn*S–*ycf*3** | **combined** |
|---|---|---|---|---|---|
| Size range of sequenced fragments | | 863–982 | 683–713 | 645–673 | 2201–2317 |
| Length of raw alignment | | 1018 | 730 | 679 | 2427 |
| Start of sequence relative to base position in *Triticum aestivum* (NC_002762) | | 104298 | 4695 (complem.) | 44862 (complem.) | - |
| End of sequence relative to base position in *Triticum aestivum* (NC_002762) | | 105158 | 3985 (complem.) | 44167 (complem.) | - |
| Number of gap positions | | 165 | 67 | 44 | 276 |
| Number of microsatellites | | 2 poly-A | 2 poly-T, 1 poly-A | 1 poly-T | 3 poly-A, 3 poly-T |
| Number of inversions | | 1 | - | - | 1 |
| Number of coded indels | | 11 | 11 | 4 | 26 |
| Number of parsimony informative coded indels | | 7 | 9 | 1 | 17 |
| Length of final alignment used in analyses (incl. coded indels) | | 890 (901) | 705 (716) | 654 (658) | 2249 (2275) |
| Number of variable characters (%), without coded indels | *Deuterocohnia* | 35 (3.93) | 39 (5.53) | 21 (3.21) | 95 (4.22) |
| | incl. outgroups | 86 (9.66) | 79 (11.21) | 35 (5.35) | 200 (8.89) |
| Number of parsimony informative characters (%), without coded indels | *Deuterocohnia* | 23 (2.58) | 31 (4.40) | 16 (2.45) | 70 (3.11) |
| | incl. outgroups | 51 (5.73) | 54 (7.66) | 24 (3.67) | 129 (5.74) |
| Range of pairwise sequence divergence (%) | *Deuterocohnia* | 0–1.889 | 0–3.148 | 0–1.732 | 0–1.954 |
| | incl. outgroups | 0–3.896 | 0–4.349 | 0–2.047 | 0–3.211 |

### 3.6.1.4 Nuclear low copy marker: PRK exon2–5

The lengths of the analysed PRK exon2–5 fragments varied from 743 to 1009 bp, resulting in an alignment of 1043 characters. The aligned sequence begins within the intron2 and ends within the exon5 of the PRK gene. Two polymorphic mononucleotide repeats ($C_3$–$C_6$ at pos. 259, and $T_5$–$T_7$ at pos. 265) were found in the area and were excluded from the analyses. Polymorphic signals due to either allelic variation (heterozygosity) or paralogues occurred at 21 isolated base positions and on one larger contiguous stretch of 36 bases. All these regions were excluded from the alignment. Of the remaining 941 characters, 165 (17.54%) were variable and 120 (12.75%) were parsimony informative within the full data set. Within *Deuterocohnia*, 59 characters (6.27%) were variable and 33 (3.51%) were parsimony informative. In all, 42 indels were coded of which 32 were parsimony informative. Sequence divergence was highest between *Encholirium scrutor* and *Fosterella albicans* (11.56%). Within *Deuterocohnia*, the highest sequence divergence occurred between *D. meziana* and *D. brevispicata* (3.28%).

#### 3.6.1.5 Nuclear low copy marker: PHYC exon1

The sequence alignment of the nuclear low copy marker PHYC exon1 revealed 1064 characters. The length of the sequence was identical for all 28 samples, no indels or microsatellites were observed. Polymorphic signals due to either allelic variation (heterozygosity) or paralogues occurred at 4 positions, which were therefore excluded from the alignment. Of the remaining 1060 characters, 78 (7.36%) were variable and 39 (3.68%) were parsimony informative among the full data set. Within *Deuterocohnia*, 29 characters (2.74%) were variable and 11 (1.04%) were parsimony informative.

Maximal sequence divergence across the full dataset occurred between *Fosterella albicans* and *Dyckia estevesii* (3.48%). Within *Deuterocohnia*, the highest sequence divergence (1.32%) occurred between *D. chrysantha* and *D. meziana.*

Tab. 3.4: Statistics of ncDNA sequence alignments of 28 accessions (22 *Deuterocohnia* / 6 outgroup) from 11 species of *Deuterocohnia*. Potentially homoplastic regions were excluded from the analyses. For comparison, the data from combined chloroplast markers derived from the same 28 accessions are shown in the last column.

| **Statistics/ Region** | | **PRK exon2–5** | **PHYC exon1** | **Combined nuclear markers** | **Combined chloroplast markers** |
|---|---|---|---|---|---|
| Size range of sequenced fragments | | 743–1009 | 1064 | 1804–2070 | 2206–2247 |
| Length of raw alignment | | 1043 | 1064 | 2107 | 2270 |
| Start of sequence relative to base position in *Triticum aestivum* | | Between 1114 and 1200 (X57952) | 2693 (AJ295224) | - | - |
| End of sequence relative to base position in *Triticum aestivum* | | 1919 (X57952) | 3759 (AJ295224) | - | - |
| Number of gap positions | | 403 | 0 | 403 | 86 |
| Number of microsatellites | | 1 poly-C, 1 poly-T | 0 | 1 poly-C, 1 poly-T | 3 poly-A, 3 poly-T |
| Number of inversions | | 0 | 0 | 0 | 1 |
| Number of excluded polymorphic positions | | 22 | 4 | 26 | 0 |
| Number of coded indels | | 42 | 0 | 42 | 14 |
| Number of parsimony informative coded indels | | 32 | 0 | 32 | 12 |
| Length of final alignment used in analyses (incl. coded indels) | | 941 (983) | 1060 | 2001 (2047) | 2149 (2163) |
| Number of variable characters (%), without coded indels | *Deuterocohnia* | 59 (6.27) | 29 (2.74) | 88 (4.40) | 63 (2.93) |
| | incl. outgroups | 165 (17.54) | 78 (7.36) | 243 (12.13) | 127 (5.91) |
| Number of parsimony informative characters (%), without coded indels | *Deuterocohnia* | 33 (3.51) | 11 (1.04) | 44 (2.20) | 47 (2.19) |
| | incl. outgroups | 120 (12.75) | 39 (3.68) | 159 (7.95) | 80 (3.72) |
| Range of pairwise sequence divergence (%) | *Deuterocohnia* | 0–3.281 | 0–1.316 | 0–1.855 | 0–1.908 |
| | incl. outgroups | 0–11.493 | 0–3.479 | 0–6.463 | 0–3.074 |

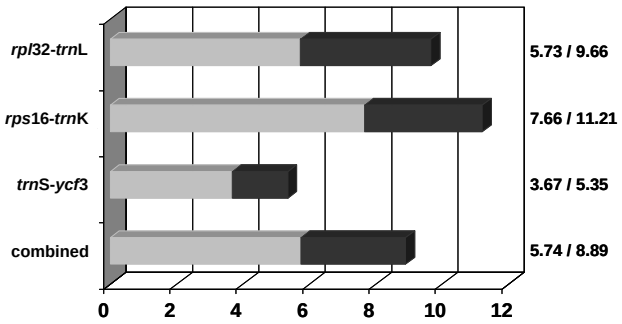


Fig. 3.25: Sequence variation at the *rpl*32-*trn*L, *rps*16-*trn*K, and *trn*S-*ycf*3 locus within *Deuterocohnia* plus outgroups of the Pitcairnioideae. Total length of bars = % total variability, grey parts = % parsimony informative characters.

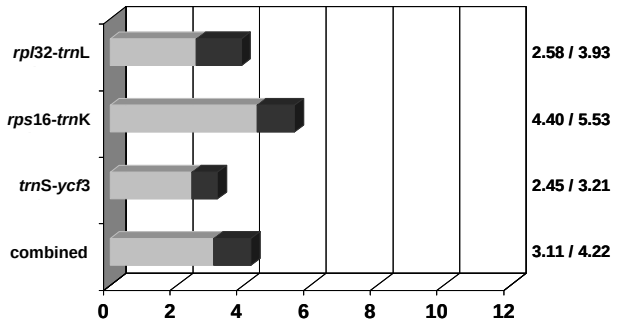


Fig. 3.26: Sequence variation at the *rpl*32-*trn*L, *rps*16-*trn*K, and *trn*S-*ycf*3 locus within *Deuterocohnia*. Total length of bars = % total variability, grey parts = % parsimony informative characters.

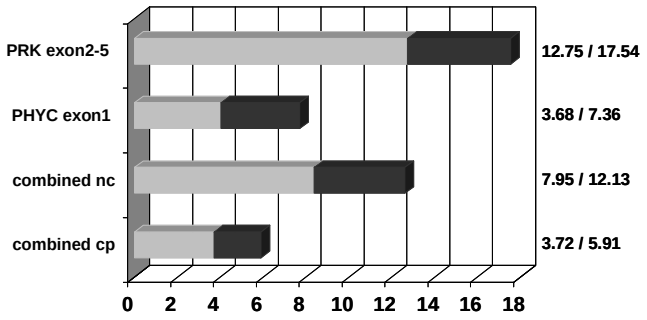


Fig. 3.27: Sequence variation at the nuclear PRK and PHYC loci within *Deuterocohnia* plus outgroups of the Pitcairnioideae. Total length of bars = % total variability, grey parts = % parsimony informative characters.

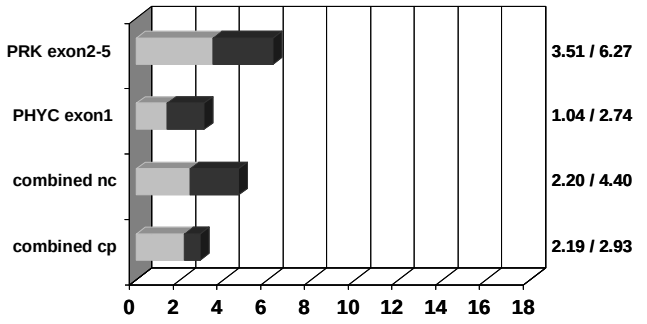


Fig. 3.28: Sequence variation at the nuclear PRK and PHYC loci within *Deuterocohnia*. Total length of bars = % total variability, grey parts = % parsimony informative characters.

### 3.6.2 Phylogenetic reconstructions

#### 3.6.2.1 Individual chloroplast loci

The plant material used for molecular phylogenetic analyses is compiled in Table 2.7. A total of 119 accessions (103 *Deuterocohnia* / 16 outgroup) were included in the cpDNA analyses, covering all species of *Deuterocohnia*. Phylogenetic trees resulting from the individual data sets showed different degrees of resolution and varying support values for the individual clades. As there where no conflicting data among topologies based on the individual loci and given that there is usually no recombination in the chloroplast genome (2.3.5), the alignments of the three loci were concatenated for a combined analysis. Trees resulting from analyses of each individual locus are shown in the Appendix. The results of the combined analyses set are specified in the following. Specimens refer to the former taxonomic delimitations, as used at the beginning of the study, see Table 2.7 for taxonomic changes.

#### 3.6.2.2 Combined chloroplast loci

The concatenated chloroplast data set, consisting of the three intergenic sequences *rpl*32–*trn*L, *rps*16–*trn*K and *trn*S–*ycf*3, altogether comprised 2275 characters, including coded indels (Tab. 3.3). Among the full data set, 8.89% of the characters were variable and 5.74% were parsimony informative. For all phylogenetic reconstructions except for the RAxML analyses, the two *Pitcairnia* samples were used as outgroups to root the trees. In RAxML, *P. albiflora* was chosen as a single outgroup since program settings allow only one sample to be defined as outgroup.

**Maximum likelihood analysis**

The best tree obtained from the RAxML analysis of the combined chloroplast data set exhibited a -log likelihood of 4729.9793024. The overall tree topology is depicted in Figure 3.29, a simplified tree showing the main clades only is shown in Figure 3.30. The tree can be described as follows:

- *Pitcairnia* is sister to a monophyletic group consisting of all ingroup taxa. The bootstrap support (BS) is 100.
- *Fosterella* is monophyletic and takes a sister position to the likewise monophyletic *Dyckia* clade which comprises all samples of *Deuterocohnia*, *Dyckia* and *Encholirium*.
- The monophyly of the *Dyckia* clade is corroborated with 99% bootstrap support. The clade splits up into two highly supported subclades (each with BS 100). One of these sub-

clades includes only accessions of *Deuterocohnia* (*Deuterocohnia* subgroup A). The other subclade comprises a monophyletic clade of *Deuterocohnia* samples (*Deuterocohnia* subgroup B, BS 86) which is sister to a monophyletic clade of samples of *Dyckia* and *Encholirium* (BS 88). This topology reveals *Deuterocohnia* to be paraphyletic.

- While the backbone of the tree is well-resolved and highly supported, the resolution within *Deuterocohnia* is rather low. By far the most part of the infrageneric sequence variation actually splits the genus into the two subclades A and B. Within these two groups, branch lengths are very short, reflecting that mutations accumulated only sparsely.

The extent of sequence variation within and among *Deuterocohnia* subgroups A and B is summarized in Tab. 3.5.

Tab. 3.5: Maximal sequence divergence within different sample sets of *Deuterocohnia* and outgroups accessions (*Dyckia* and *Encholirium*), based on the concatenated cpDNA data set of 2249 characters (see Tab. 3.3).

| **Sample set** | **Max. sequence divergence (%) within sample set** | **Polymorphic characters within sample set (%)** | **Parsimony informative characters within sample set (%)** |
|---|---|---|---|
| *Deuterocohnia* all samples | 1.954 | 4.22 | 3.11 |
| *Deuterocohnia* subgroup A | 0.698 | 2.19 | 1.35 |
| *Deuterocohnia* subgroup B | 0.558 | 1.40 | 0,61 |
| *Deuterocohnia* subgroup B & *Dyckia* and *Encholirium* | 1.117 | 2.56 | 1.40 |

Except for *D. scapigera*, the assignment of the *Deuterocohnia* samples to the two subclades A and B is strictly species-related. Thus, all investigated samples of *D. meziana*, *D. brevispicata*, *D. seramisiana*, *D. pedicellata* and *D. gableana* are confined to subclade B, whereas all samples from all other *Deuterocohnia* species (except *D. scapigera*) are restricted to subclade A. *Deuterocohnia scapigera* is present in both subclades, with one subspecies occurring in each subgroup. *Deuterocohnia* subgroup A is shown in higher magnification in Fig. 3.31. It is split into two moderately supported clades. One smaller clade (i, BS 64) comprises samples of *D. strobilifera*, *D. lotteae*, *D. longipetala*, *D. lorentziana* and *D. scapigera*. The second clade (BS 62) contains several moderately to well supported groups arising from an otherwise largely unresolved polytomy (*a–h* in Fig. 3.31). Some samples cannot be assigned to any obvious group. The groups a–i can be characterized as follows:


Fig. 3.29: Phylogenetic tree obtained from a Maximum likelihood (RAxML) analysis of the concatenated cpDNA data set (2275 characters), using GTR+G as substitution model. The negative log likelihood value is 4729.9793024. Bootstrap values (>50) from 1000 bootstrap replicates are shown above the branches. The tree was rooted with *Pitcairnia* (outgroup). Collection and DNA numbers are included for all samples.

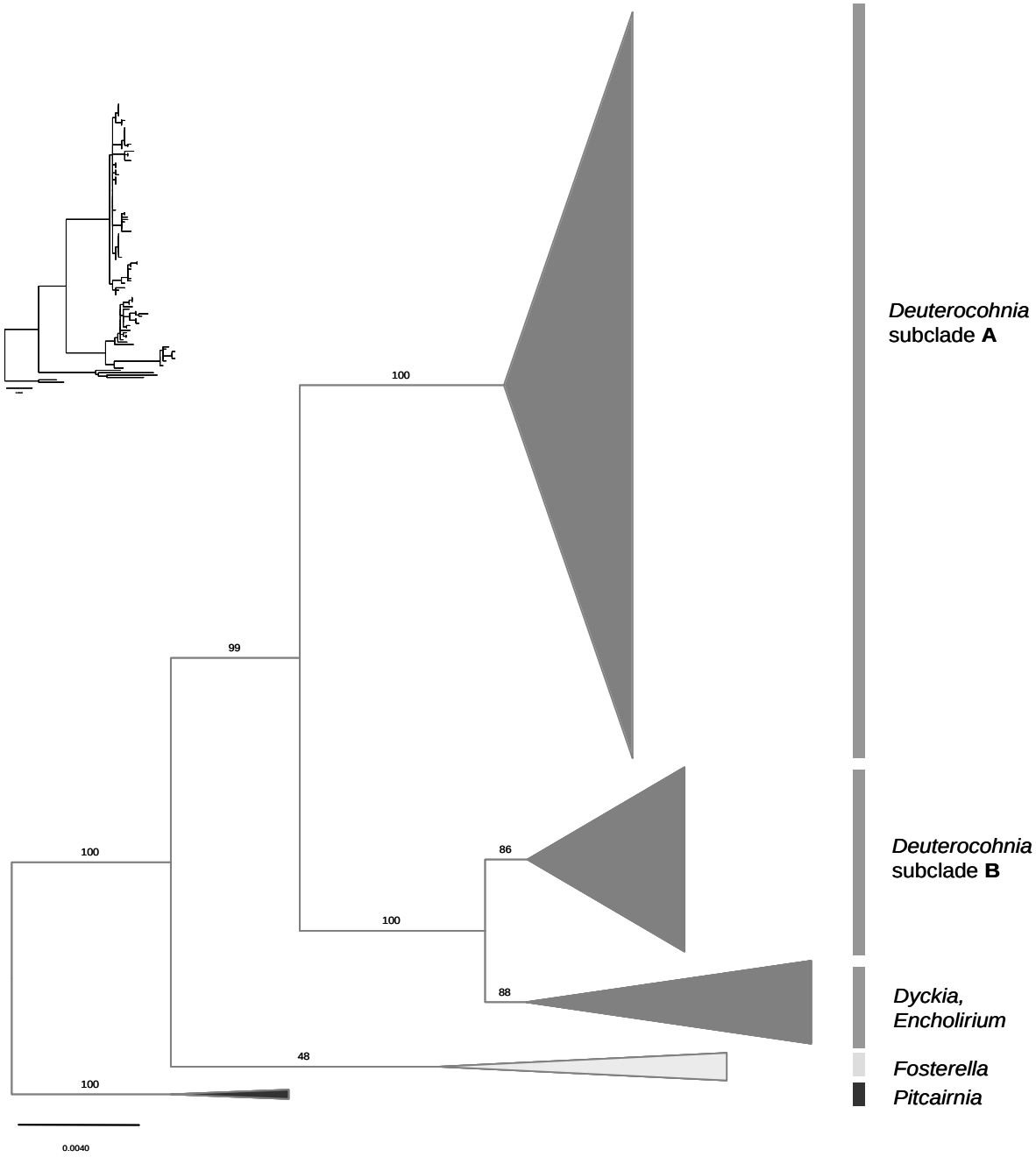


Fig. 3.30: Main clades of the phylogenetic tree resulting from the Maximum likelihood analysis shown in Fig. 3.29. Bootstrap values are depicted above the branches.

a Group *a* (BS 65) comprises two monophyletic clades: one with all samples of the Chilean species *D. chrysantha* (BS 75) and a second with *D. longipetala* samples from the Prov. La Rioja and Salta in Argentina (BV 86).

b Group *b* (BS 61) unites three samples of *D. longipetala* from Argentina.

c Group *c* (BS 92) contains all specimens of the Argentinean endemic species *D. haumanii*, together with two Argentinean samples of *D. longipetala*, originating from Prov. Salta and Jujuy, respectively.

d Group *d* (BS 88) comprises the two investigated specimens of the Argentinean endemic *D. recurvipetala*, together with seven *D. longipetala* samples, all originating from Argentina (Prov. La Rioja, San Juan and Córdoba).

e Group *e* (BS<50) unites three samples of *D. lorentziana* from Prov. Salta, Argentina.

f Group *f* (BS 64) includes samples of *D. digitata* and *D. schreiteri*, all from the Prov. Salta, Argentina.

g Group *g* (BS 61) comprises several accessions each of *D. brevifolia* and *D. lorentziana*, intermingled with each other. Apart from some unknown localities, these accessions were collected in the Dept. Tarija, Bolivia.

h Group *h* (BS 96) contains samples of *D. strobilifera* and *D. scapigera* from the Dept. Potosí and Chuquisaca in Bolivia.

i Group *i* (BS 64) is a mixed clade that includes samples of *D. strobilifera*, *D. lotteae*, *D. longipetala*, *D. lorentziana* and *D. scapigera*. Most of the accessions originate from the Provinces of Tarija and Chuquisaca, Bolivia.

*Deuterocohnia* subgroup B is shown in higher magnification in Fig. 3.32. It has only little internal resolution and is therefore described here as a single group (Group j):

j Group *j* (BS 86) includes all investigated accessions of *D. meziana*, *D. brevispicata*, *D. seramisiana*, *D. pedicellata*, *D. gableana* and *D. scapigera* var. *sanctae-crucis*. Species are not clearly separated from each other in the tree, but all species and samples of this group except one (*D.scapigera* from Potosí) originate from the same geographic region, i.e. the area of Santa Cruz and Cochabamba, Bolivia.

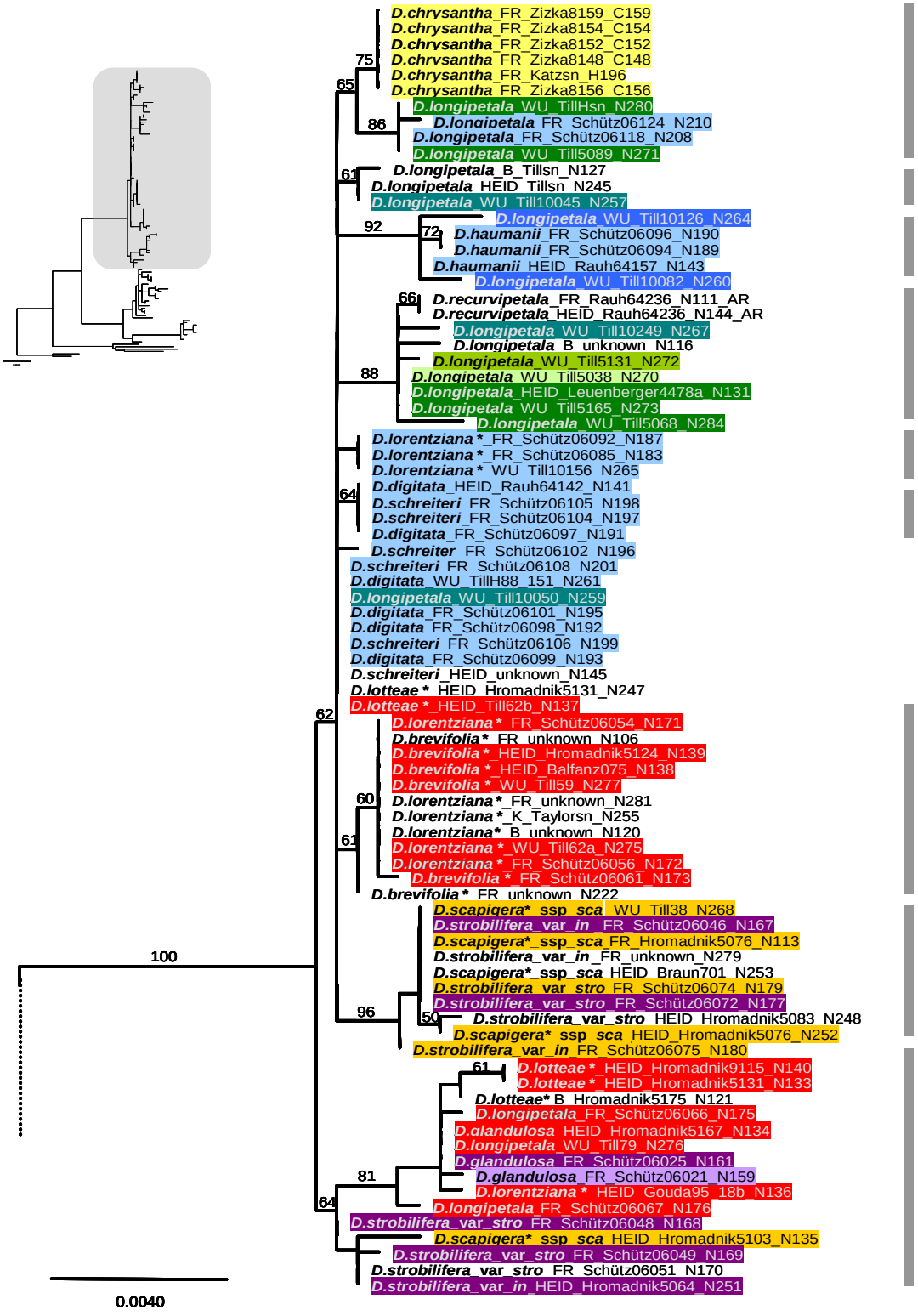


Fig. 3.31: *Deuterocohnia* subclade A of the phylogenetic tree resulting from the Maximum likelihood analysis shown in Fig. 3.29. Bootstrap values are depicted above the branches. See text for details on groups a to i that are numbered alphabetically from top to bottom. Collection and DNA numbers are included for all samples. Geographical origins of the samples are colour-coded, see legend of Fig. 3.32 and map of Fig. 3.36.

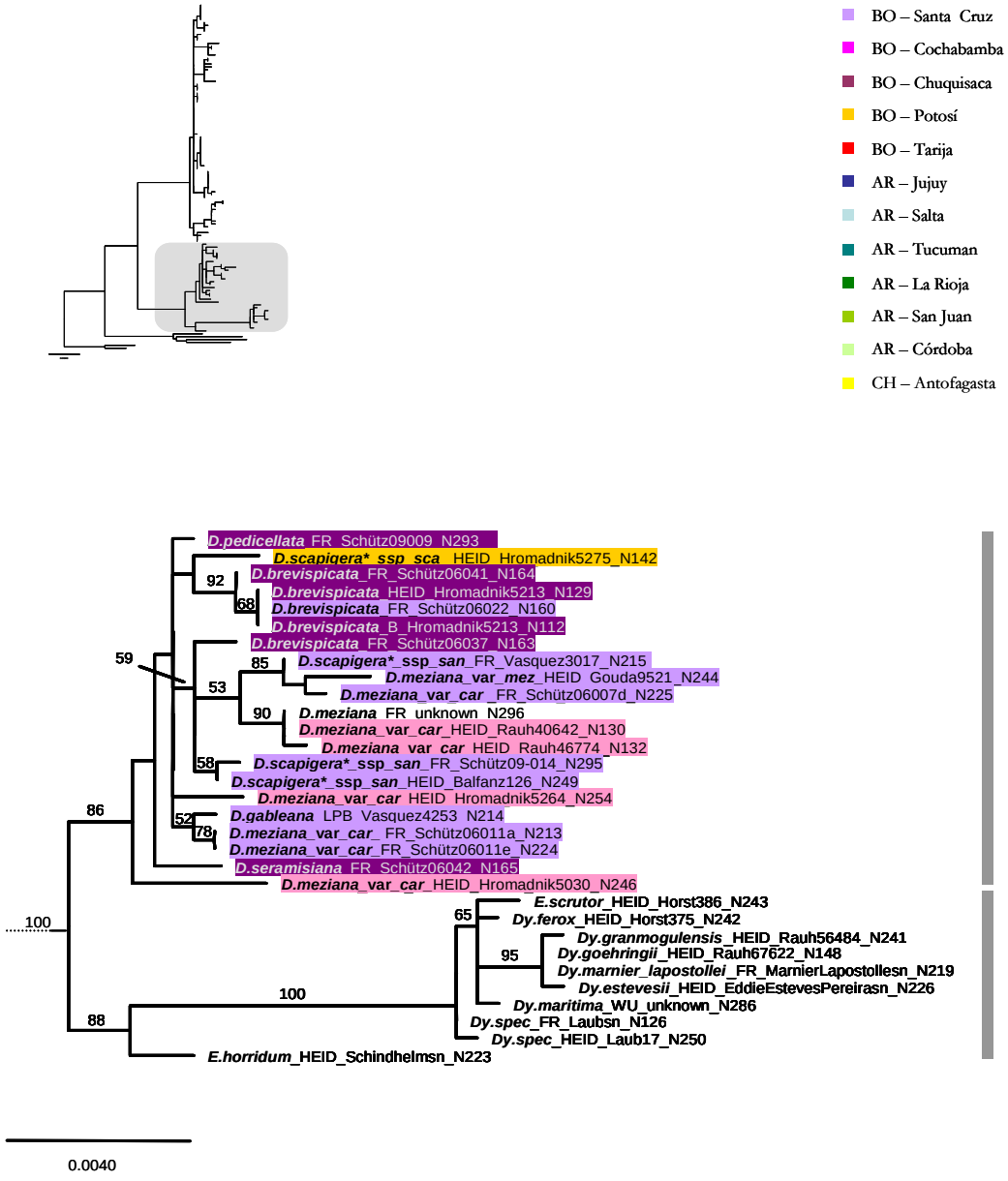


Fig. 3.32: *Deuterocohnia* subclade B (= group j) and the *Dyckia* group of the phylogenetic tree resulting from the Maximum likelihood analysis shown in Fig. 3.29. Bootstrap values are depicted above the branches. See text for details. Collection and DNA numbers are included for all samples. Geographical origins of the samples are colour-coded, see also map of Fig. 3.26.

Several alternative algorithms were applied for phylogenetic cpDNA tree reconstruction that all resulted in the same principal backbone topology as the ML tree shown in Fig. 3.29, and also provided a good overall support of the groups a to j defined above. However, internal branching patterns and relationships between groups a to j showed some variation, as outlined in the following and in Figs. 3.33–3.35.

**Maximum parsimony ratchet analysis**

The strict consensus tree of the MP ratchet analysis of the concatenated cpDNA alignment was calculated from 28 shortest trees of 292 steps length (CI = 0.801, RI = 0.964). It is shown in Fig. 3.33. The tree topology is mostly in congruence with that of the ML tree shown in Fig. 3.29. As in the ML tree, bootstrap values strongly support the backbone of the tree, whereas internal clades receive only low to moderate support. In contrast to the ML analysis, monophyly of *Fosterella* is corroborated with 100 % bootstrap value. Although *Deuterocohnia* subgroup A forms a large polytomy in the strict consensus MP tree, the same weakly to moderately supported *Deuterocohnia* groups can be recognized as found in the ML tree (*a–j*; Fig. 3.33).

**Neighbour joining analysis**

The phylogenetic tree obtained from a NJ analysis of the concatenated cpDNA alignment using the GTR substitution model is shown in Figure 3.34. The topology and the support values are largely conform to the above trees resulting from the ML and MP analyses. All groups of *Deuterocohnia* (*a–j*) are also present in the NJ tree, relationships between the groups vary among ML, MP and NJ analyses. As in the MP tree, *Fosterella* is a well supported monophyletic group (BS 100). NJ analyses using other substitution models (HKY and JK) or the uncorrected p-distance gave consistent results (not shown).

**Bayesian analysis**

Bayesian inferences were carried out using appropriate substitution models for each DNA partition, as suggested by MrModeltest: 2.3: GTR+G for *rpl*32–*trn*L and *rps*16–*trn*K and HKY+I for *trn*S–*ycf*3. The 50% majority rule consensus tree of 96,000 trees was obtained from two runs of 5,000,000 generations and a burn-in phase of 200,000 generations each. The resulting phylogeny (Fig. 3.35) shows a highly supported backbone which is identical to the analyses described above. All *Deuterocohnia* groups identified in ML, MP and NJ trees (*a–j*) can be found within the Bayesian tree, with moderate to good support by posterior probabilities (PP). At first glance, the Bayesian analysis also seems to provide a better differentiation between internal clades, as compared to the very low resolution provided by the other trees. However, only few nodes internal to groups a–j are statistically supported (PP < 0.05), and the uncertainty of the relationships between the groups is also reflected by the differing topology when the data set was analyzed without coded indels.

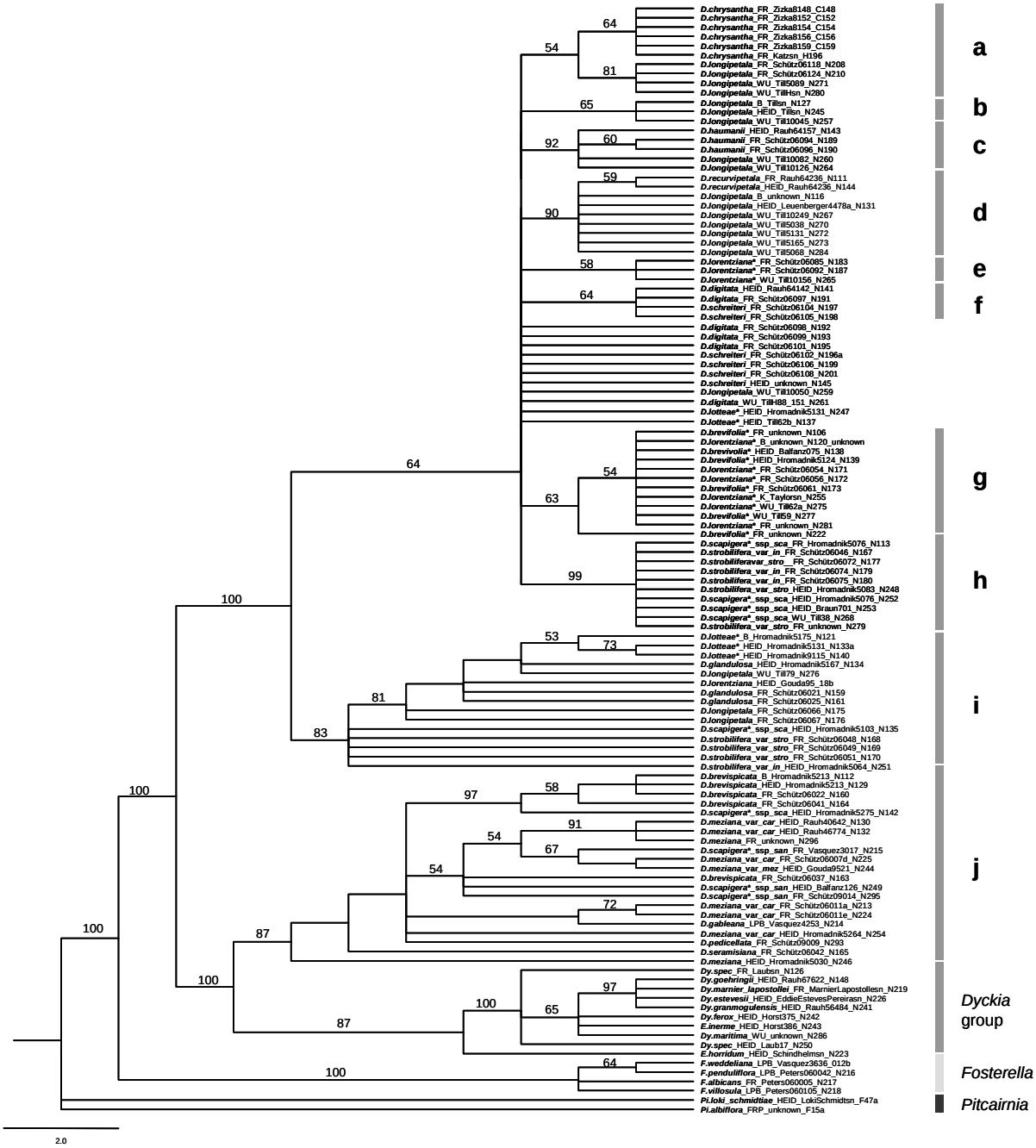


Fig. 3.33: Strict consensus tree of a maximum parsimony ratchet analysis of the concatenated cpDNA data set (2275 characters), calculated from 28 shortest trees with a length of 292 steps. Consistency index CI = 0.801, Retention index RI = 0.964. Bootstrap values (>50) from 1000 bootstrap replicates are shown above the branches. Vertical bars (a-j) indicate groups of outgroup genera and of *Deuterocohnia* samples as described in the ML tree (Figs. 3.31 and 3.32).

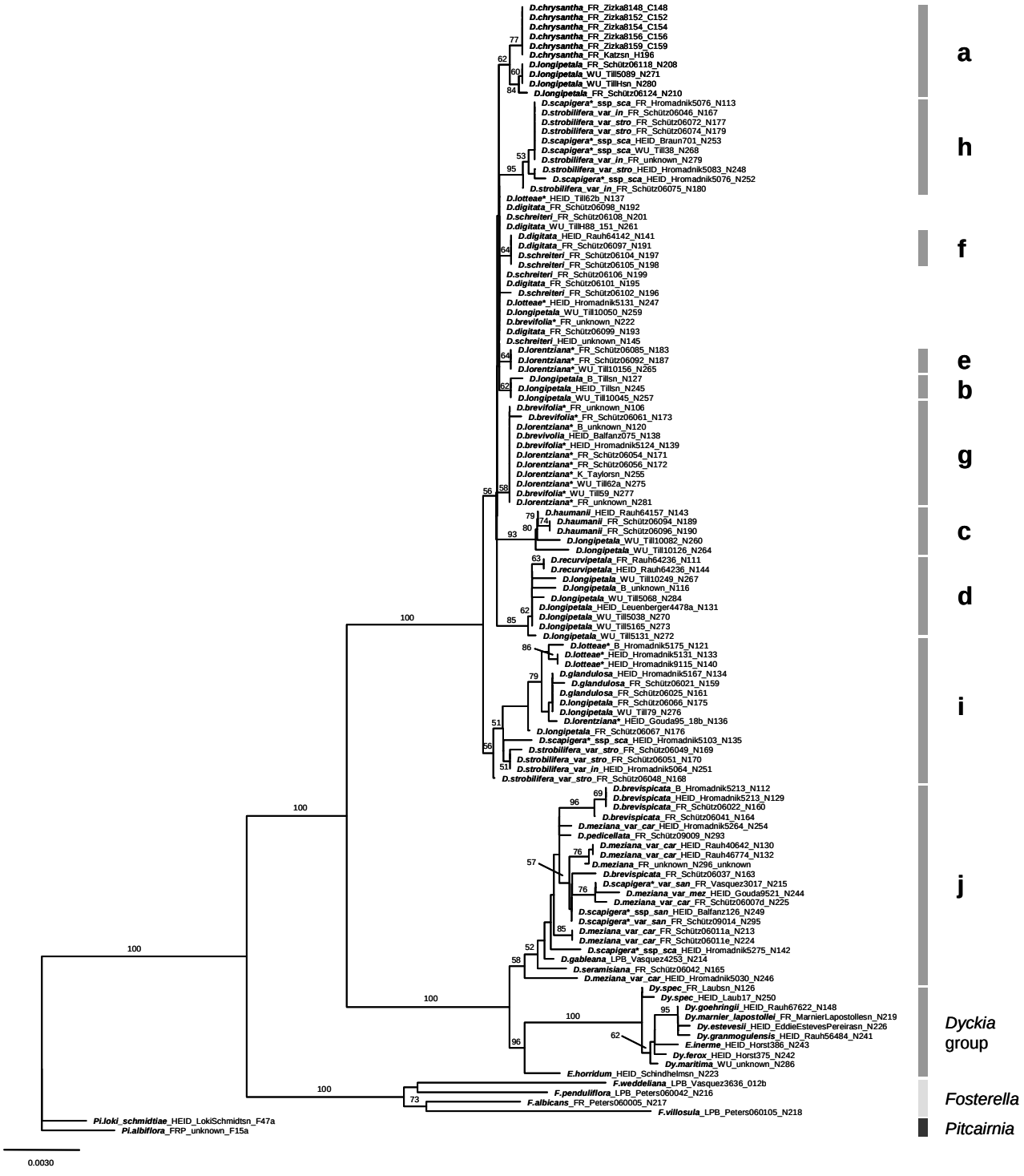


Fig. 3.34: Phylogenetic tree obtained from a Neighbour Joining analysis of the concatenated cpDNA data set (2275 characters) using GTR as substitution model. Bootstrap values (>50) from 5000 bootstrap replicates are shown above the branches. Vertical bars (a-j) indicate groups of outgroup genera and of *Deuterocohnia* samples as described in the ML tree (Figs. 3.31 and 3.32).

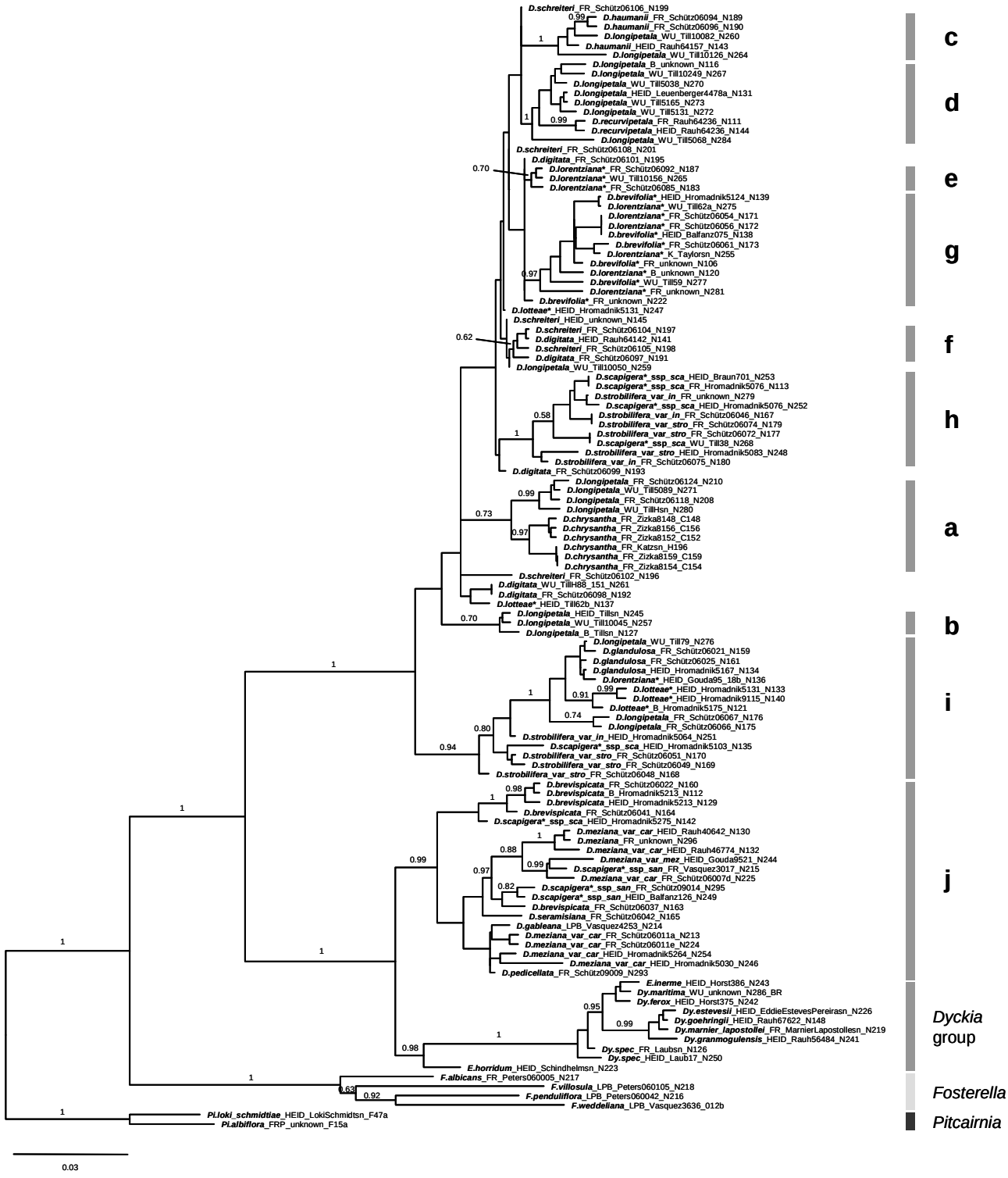


Fig. 3.35: The 50 % majority rule consensus tree of a Bayesian analysis of the concatenated cpDNA data set (2275 characters) using partition specific substitution models. The tree is a consensus from 96,000 trees out of two runs with 5,000,000 generations and a burn-in phase of 200,000 generations each. Posterior probabilities (>0.5) are shown above the branches. Vertical bars (a-j) indicate groups of outgroup genera and of *Deuterocohnia* samples as described in the ML tree (Figs. 3.31 and 3.32). The tree was rooted with *Pitcairnia* (outgroup).

Taken together, only very few *Deuterocohnia* species come out as monophyletic in the chloroplast trees shown in Figs. 3.29–3.35, and the accessions of most of the species are scattered across the tree. This is especially true for the most widely distributed species, *D. longipetala*. On the other hand, there is a striking correspondence between the individual clades and the geographic origin of the included accessions. The geographical distribution of the described groups is shown in Figure 3.36. The same colour-coding was used as in Figures 3.31 and 3.32.

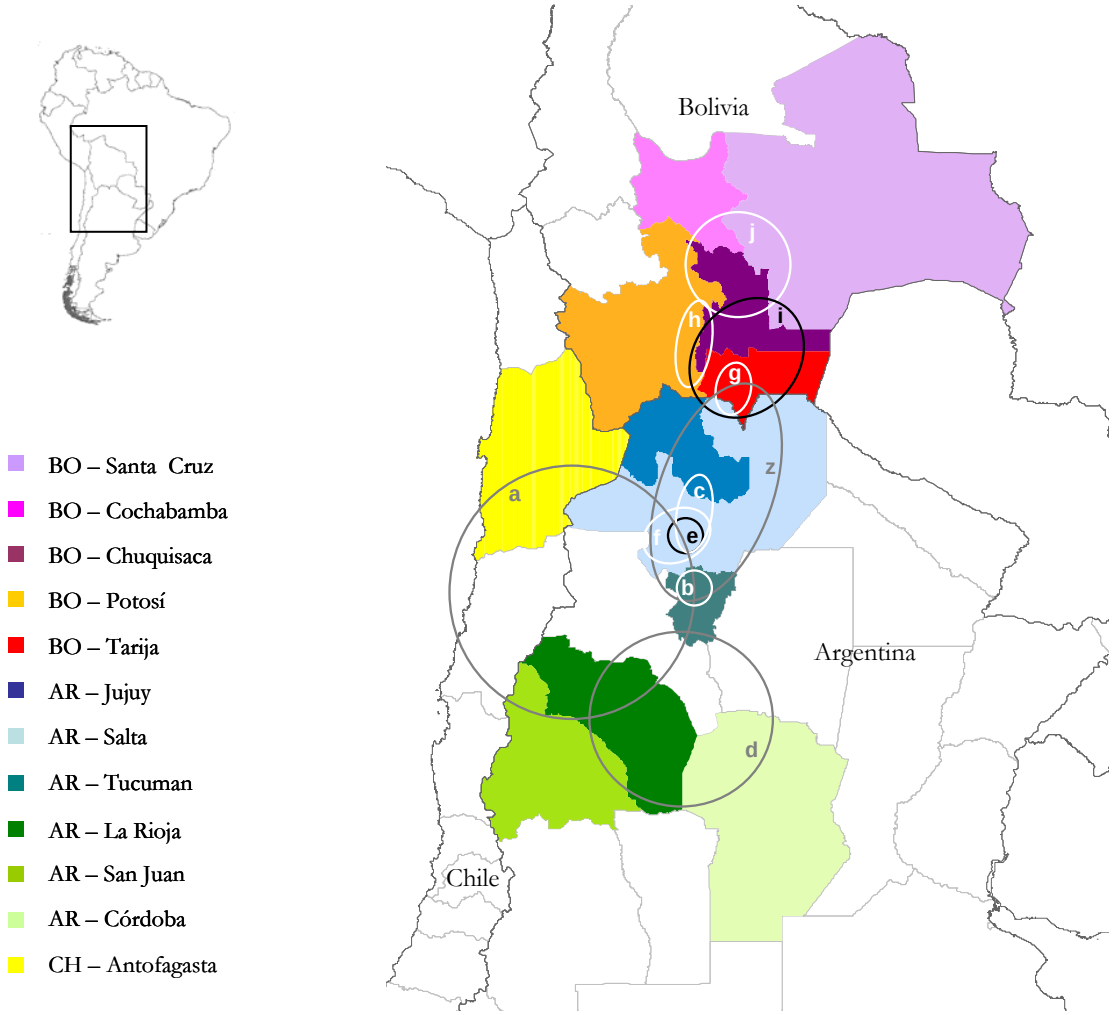


Fig. 3.36: Geographic distribution of the *Deuterocohnia* groups a-j and z found in tree and/or network topologies. Circles define the area from which samples were included. Circle colour differs only for a better differentiation.

**Network analysis**

Given that the sequence variation within each of the two *Deuterocohnia* subgroups was so low, it appeared appropriate to evaluate the genetic relationships between the different species and accessions also using a haplotype network approach. A statistical haplotype network was therefore calculated with the parsimony-based programme TCS (Clement et al. 2000), using the same alignment as for the tree reconstructions. The network is depicted in Figure 3.37. Each circle represents one particular cpDNA sequence variant (=haplotype), each connecting line between two circles refers to one mutational step. The sizes of the circles correspond to the number of accessions having this particular sequence variant. Samples are abbreviated with the first three letters of the appropriate species name. Colours refer to the geographical origin of the sample as illustrated in Figures 3.36.

Among 103 samples of *Deuterocohnia*, 51 different haplotypes were observed. Nine additional haplotypes occurred in the 10 investigated samples of *Dyckia* and *Encholirium*. Altogether, 71 missing haplotypes (MH) were included by the TCS program to connect the observed haplotypes, and to integrate *Dyckia* and *Encholirium* into the network. *Deuterocohnia* subgroup B (group j) was found to be separated from *Deuterocohnia* subgroup A (groups a–i) by no less than 32 mutational steps. On the contrary, only 11 and 18 mutational steps separated *Deuterocohnia* subgroup B (group *j*) from *Encholirium horridum,* and from the remainder of the *Dyckia* and *Encholirium* samples, respectively. Thirty-six mutational steps separated *Deuterocohnia* from the closest haplotype of the included *Fosterella* samples.

Within *Deuterocohnia*, haplotype *z* takes a central position and is radially connected with several other groups of haplotypes (Fig. 3.37). These groups generally correspond to those found in the phylogenetic trees (groups *a–j*). They have been described in detail in section 3.6.2.2. All haplotypes and the accessions where they occur are listed in the Appendix. Haplotypes that occur in accessions of group *a–j* were labelled according to "their" group letter, followed by a sequential number (for example a1, a2, a3). Haplotypes that do not belong to any of these groups (*z*, *s* and *y*) were named arbitrarily.

The central haplotype (*z*) contains 11 accessions, from five species (*D. brevifolia*, *D. digitata*, *D. longipetala*, *D. lotteae* and *D. schreiteri*). All these accessions are part of the major polytomy within subclade A of the cpDNA tree (Fig. 3.31) and all were collected from an area ranging from Tarija in Bolivia to Tucuman in Argentina. Except for the long branch, that leads to group *j*, all connections from the central haplotype to the different groups comprise only one to four mutational steps and form a star-like pattern. Within each of the groups, between 1 and seven mutational

Tab. 3.6: Number of accessions and chloroplast haplotypes per species occurring in the TCS network.

| Species | Abbr. | No. of haplotypes | No. of accessions |
|---|---|---|---|
| *D. brevifolia* | *brf* | 3 | 6 |
| *D. brevispicata* | *brs* | 3 | 5 |
| *D. chrysantha* | *chr* | 1 | 6 |
| *D. digitata* | *dig* | 2 | 6 |
| *D. gableana* | *gab* | 1 | 1 |
| *D glandulosa* | *gla* | 3 | 3 |
| *D. haumanii* | *hau* | 2 | 3 |
| *D. longipetala* | *lon* | 15 | 20 |
| *D. lorentziana* | *lor* | 3 | 10 |
| *D. lotteae* | *lot* | 3 | 5 |
| *D. meziana* | *mez* | 6 | 9 |
| *D. pedicellata* | *ped* | 1 | 1 |
| *D. recurvipetala* | *rec* | 1 | 2 |
| *D. scapigera* | *sca* | 6 | 9 |
| *D. schreiteri* | *sch* | 3 | 6 |
| *D. seramisiana* | *ser* | 1 | 1 |
| *D. strobilifera* | *str* | 6 | 10 |

steps were found except for group *j* which comprises 23 steps. Closed loops in the network are indicative of homoplasy in the data set, they occurred once in group *h*, twice in group *j* and once between the haplotypes *z*, *g* and *i*.
Within-group haplotype diversity differs among the different groups. For example, groups *a*, *g* and *h* comprise 10 to 11 accessions sharing 2 to 4 haplotypes and include a maximum of one MH, while groups *i*, *j* and *d* harbour between 9 and 21 accessions with 6 to 15 haplotypes and 2 to 22 MH. Haplotype diversity within species is lowest in *D. chrysantha* (with all 5 accessions sharing the same haplotype) and highest in *D. longipetala* (with 15 haplotypes in 20 accessions). The numbers of haplotypes per species are listed in Table 3.6.

As is the case in the phylogenetic trees, the distribution of cpDNA haplotypes among *Deuterocohnia* species does not reflect taxonomical expectations. On the one hand, most species have more than one haplotype (with a few exceptions, like *D. chrysantha*, Tab. 3.6). On the other hand, a given haplotype can be found in more than one species (Fig. 3.37). Rather obviously however, the various haplotypes found in *Deuterocohnia* form geographically defined groups. Thus, different accessions or species occurring in the same distribution area generally share the same haplotype or a closely related haplotype that belongs to the same group. This can for example be illustrated with the morphologically distinct species *D. strobilifera* and *D. scapigera*. Both species share haplotype *h2* in Chuquisaca and Potosí, but exhibit additional haplotypes (haplotypes *i1–4*) at other localities of Chuquisaca, Potosí and Tarija. Another example is provided by *D. scapigera* var. *sanctae-crucis* and *D. gableana*, which both belong to group *j* together with the two geographically closely related, but morphologically quite distinct species *D. meziana* and *D. brevispicata*.
From north to south the *Deuterocohnia* groups roughly occur in the order *j*, *i*, *h*, *g*, *z*, *c*, *e*, *f*, *b*, *a*, *d* (Fig. 3.36). Thus, the central haplotype *z* is found in samples that were collected in the centre of the distribution area of the genus, which is in Tarija, Jujuy and Salta. Haplotype diversity increases in groups at the periphery of the distribution area (groups *i* and *j* in the north, group *g* in the south).

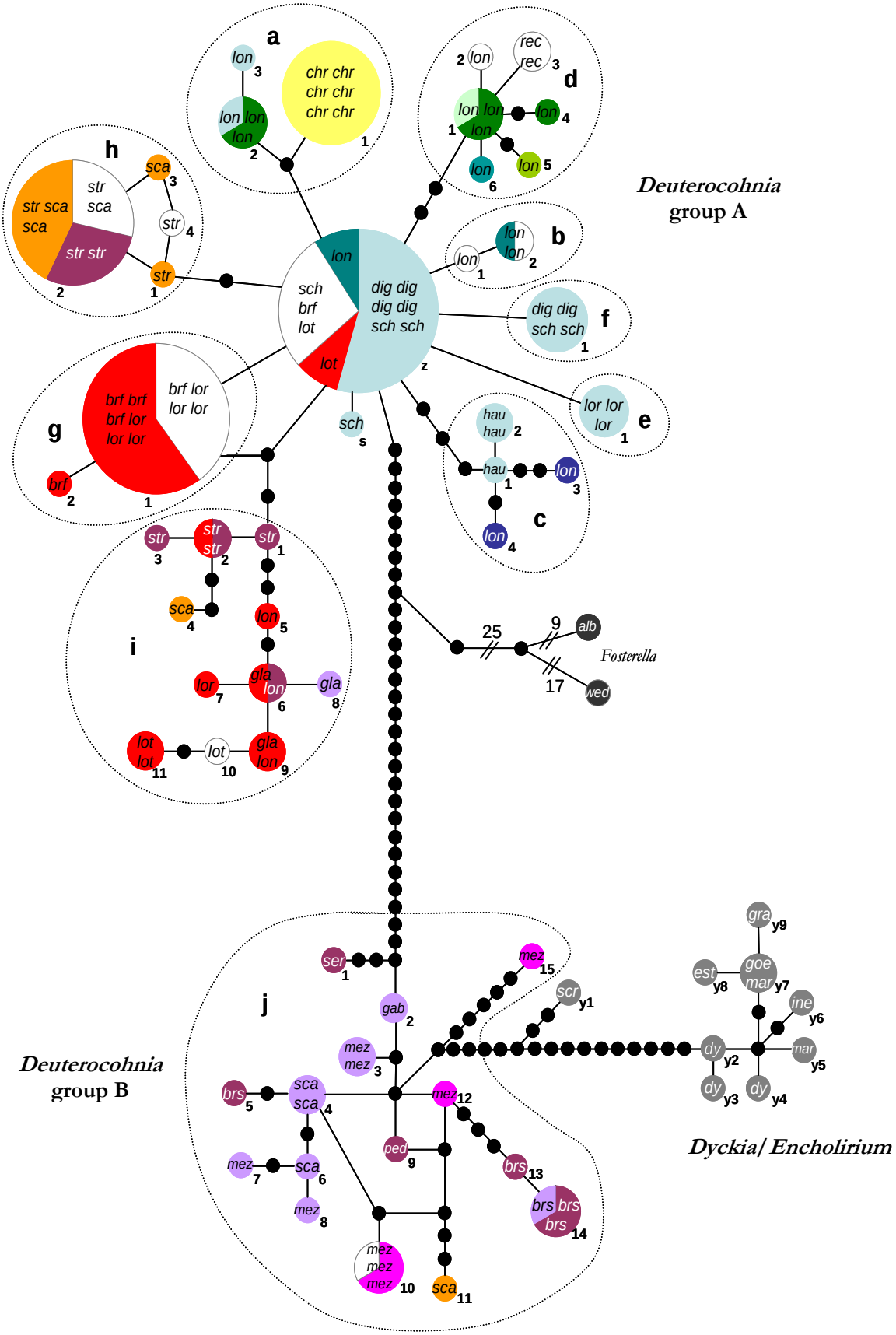


Fig. 3.37: Statistical haplotype network based on a TCS parsimony network analysis using the combined cpDNA data set (2275 characters). Each circle represents a distinct haplotype, sizes of the circles correspond to the number of samples having this particular sequence variant. Colours of the circles refer to the geographical origin of the haplotypes as described in Fig. 3.37. Grey circles and large black circles indicate haplotypes from outgroup species. White plots indicate samples with unknown sampling localities, small black circles indicate missing haplotypes. Species names are abbreviated by their first three letters (exceptions: *brs=brevispicata*, *brf=brevifolia*). Each connecting line refers to one mutational step. Numbers next to lines indicate number of missing haplotypes, which are not illustrated by circles.

#### 3.6.2.3 Individual nuclear loci

Because *Deuterocohnia* was paraphyletic in all analyses using chloroplast DNA data, nuclear loci were additionally examined with regard to the question of monophyly of this genus. To address this question, a reduced taxon set – sufficient for delimitation of genera – of 26 accessions of the genera *Deuterocohnia* (22, including specimens from subclade A and B), two of *Dyckia*, two of *Encholirium* and two of *Fosterella* were analysed.
Trees generated from sequence data at the two nuclear loci PHYC exon1 and PRK exon2–5 both highly supported the monophyly of *Deuterocohnia* in all conducted analyses (trees derived from individual loci are shown in the Appendix). The incongruence length test (ILD, Farris et al. 1995) revealed some incongruence between the two nuclear data sets ($p = 0.004$). However, given that the informative value of the ILD test has been contested by various authors (Barker and Lutzoni 2002, Givnish et al. 2011) and trees from separate analyses did not show conflicting topologies, the two loci were nevertheless also analysed in combination.

#### 3.6.2.4 Combined nuclear loci

The combined alignment of the PHYC exon1 and the PRK exon2–5 comprised 2047 characters (incl. indels; Tab. 3.4). Across the full data set, 12.13% characters were variable and 7.95% were parsimony informative. The trees were rooted with the two *Fosterella* species.

**Maximum parsimony ratchet analysis**

Figure 3.38 shows the strict consensus tree resulting from the MP ratchet analysis. The consensus tree was calculated from 174 shortest trees of 337 steps length. The main clades of the tree are as follows:

- *Fosterella* is sister to a monophyletic group of all ingroup taxa (BV 100, PP 1), together defining the so called *Dyckia* clade.
- All included *Deuterocohnia* samples form a monophyletic clade with high statistical support (BS99, PP 1).
- *Deuterocohnia* is sister to a monophyletic group of all included *Dyckia* and *Encholirium* samples (BS 100, PP 1).

- Within *Deuterocohnia* three clades are recognized. One basal group solely comprises the two samples of *D. chrysantha* (BV 100, PP 1) from Chile. Of two derived sister clades (BS<50, PP<0.5), one contains samples of *D. brevispicata*, *D. meziana*, *D. strobilifera* and *D. schreiteri,* whereas the other harbours accessions of *D. meziana*, *D. schreiteri* and all samples of all other analysed species.

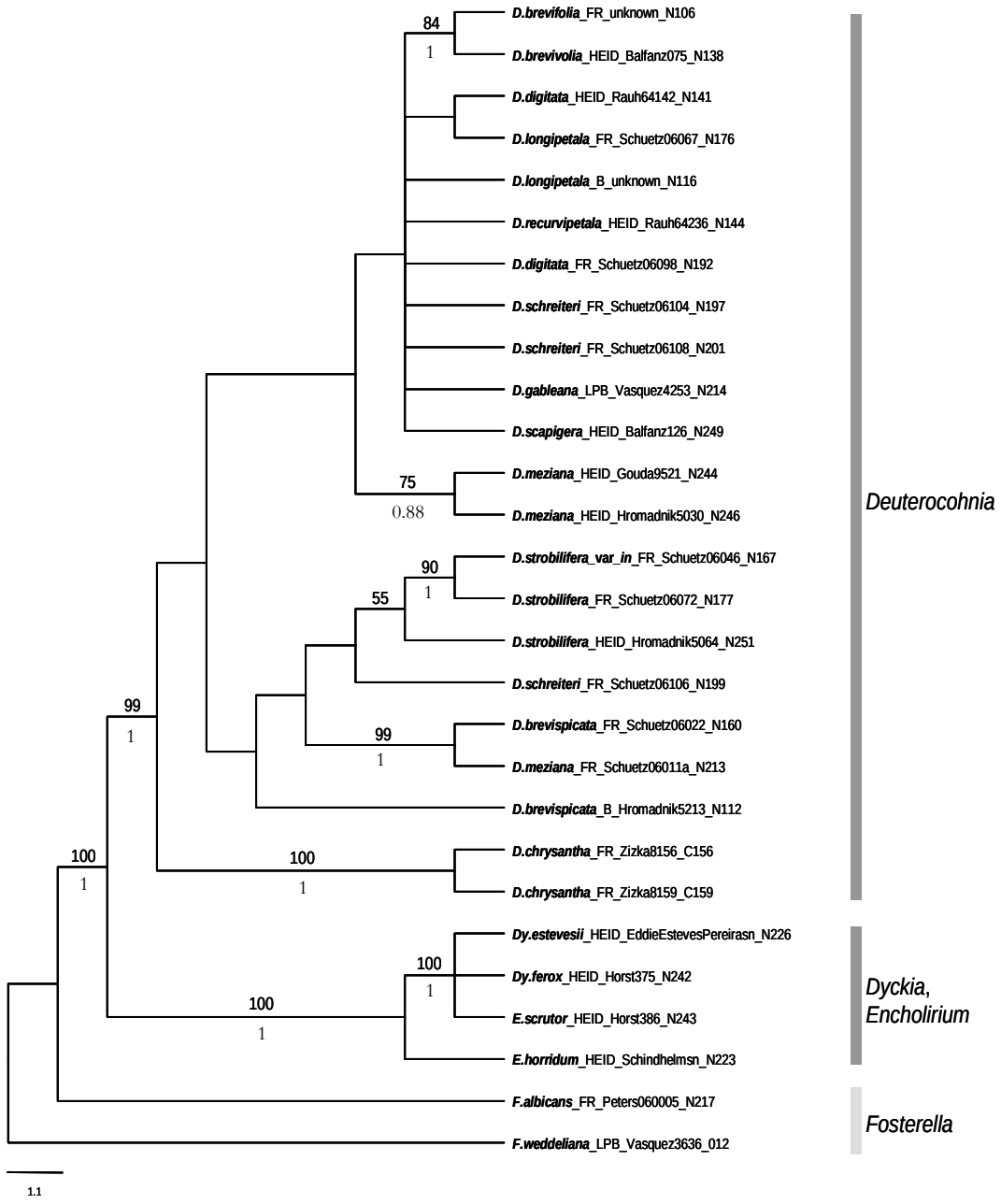


Fig. 3.38: Strict consensus tree obtained from the MP ratchet analysis of 2047 characters of the combined nuclear data set (PRK + PHYC), resulting from 174 shortest trees of 337 steps length. Consistency index CI = 0.795, Retention index RI = 0.826. Bootstrap values (>50) from 1000 bootstrap replicates are shown above the branches, posterior probabilities from Bayesian analyses (>0.5) are shown below. The tree is rooted with *Fosterella weddeliana.*

**Maximum likelihood analysis**

The best tree obtained from the RAxML analysis of the combined nuclear marker set exhibited a -log likelihood of 4832.682043 (see Appendix). The topology reveals *Deuterocohnia* to be monophyletic (BS 94). Like in the MP analysis, *D. chrysantha* appears at the base of the *Deuterocohnia* clade and all other species split into two groups.

**Neighbour joining analysis**

The phylogenetic tree obtained from the NJ analysis using the GTR substitution also strongly supports the monophyly of *Deuterocohnia* (BS 100). In contrast to the topologies of the MP and ML phylogenies, the neighbour joining tree resolves *D. meziana* accessions at a basal position of the *Deuterocohnia* clade (see Appendix). The other samples are split into one clade that contains the *D. chrysantha* accessions and a tritomy comprising all other *Deuterocohnia* samples.

**Bayesian analysis**

Bayesian inferences were carried out using appropriate substitution models for each partition: GTR+I for PRK and HKY+I+G for PHYC. The 50% majority rule consensus tree of 99,000 trees was obtained from two runs of 5,000,000 generations and a burn-in phase of 50,000 generations each. The resulting tree (see Appendix) has a high support value for the monophyly of *Deuterocohnia* (PP 1). Like in the NJ tree, two samples of *D. meziana* are placed at the base of the *Deuterocohnia* clade, followed by samples of *D. chrysantha* and a polytomy of all other samples.

**Network analysis**

The network analyses with TCS did not succeed in connecting all included samples in a single network (data not shown) although a high "connection limit" parameter was chosen. Instead, three independent, separate networks were formed by (1) the accessions of *Deuterocohnia*, (2) *Dyckia* incl. *Encholirium* and (3) *Fosterella*, respectively. Within the *Deuterocohnia* network numerous closed loop structures were observed, indicative of a large amount of homoplasy.

Altogether, each of the analyses based on the nuclear gene loci PRK exon2–5 and PHYC support the monophyly of *Deuterocohnia*. There is only little resolution within *Deuterocohnia*. Moreover, different analyses provide different topologies, each of which contains only few well-supported clades. Most trees however agree in the observation that *D. chrysantha* forms a separate and distinct group. This group is in all but one analyses sister to the remainder of the genus. In contrast to the cpDNA data, the nuclear marker does not obviously reflect a geographical pattern.

# 4 DISCUSSION

## 4.1 Methodical aspects

### 4.1.1 Herbarium work

Herbarium work is an essential part of taxonomic studies, providing a vast amount of morphological and biogeographical data. Altogether, more than 700 herbarium specimens were examined in the present work, providing a broad overview of the 17 species of *Deuterocohnia*. In addition, material from eleven *Deuterocohnia* species has been investigated and collected in the field. Herbarium vouchers of this newly collected material were prepared and stored in LPB, LIL and FR. Alcohol material of flowers were stored in FR.

A considerable problem concerning the work with herbarium specimens of capacious plants is the often fragmentary state of the vouchers. Beside the general problems associated with herbarium work, like colour loss, shrinking and other changes caused by the drying of the plants, the incompleteness of organisms makes it difficult to standardize data acquisition. In *Deuterocohnia*, there is no strict correlation between the sizes of single leaves or fragments of the inflorescence (on herbarium vouchers) on the one hand and original the sizes of the rosette or the whole inflorescence on the other. For this reason, measurements based on herbarium specimens should generally be considered as rough approximations rather than as absolute values. Additional problems concern the evaluation of some inflorescence characters: (1) The terminal (or lateral) position of the inflorescence cannot be verified, when separated from the rosette. (2) Some details of the branching system – e.g. the occurrence of secondary branches in the first or second year, the size relation of the peduncle to the flowering part – may not be recognized in fragmented vouchers and without any notes about the age of the inflorescence. (3) Older inflorescences may be truncated and thus show an irregular growth pattern.

Flower discolouration of herbarium material necessitates information about the original flower colour on the corresponding labels. The lack of flower colour description or the varying colour descriptions from different collectors hampers the classification of taxa, for which flower colour is an important delimiting character, e.g. in *D. meziana*. Flower colour descriptions are also missing in some protologues, e.g. in the case of *D. longipetala*.

An important part of herbarium work is the collection of biogeographical data provided on the labeled vouchers. Particularly on older specimens, geographical coordinates are listed only scarcely. When no explicit coordinates were listed, estimates of latitude and longitude were made with the information given on the labels (2.2.3). Coordinates estimated in this way are of course only approximations and do not reflect the exact localities. Nevertheless, they provide very important information for e.g. the preparation of distribution maps, or for monitoring the threat status of the investigated taxa (Willis et al. 2003).

### 4.1.2 Molecular analyses

#### Taxon sampling

A broad taxon sampling within the group of interest is important to avoid undesired phenomena such as long branch attraction in phylogenetic trees and to detect hidden paraphyletic groups (Lecointre et al. 1993, Graybeal 1998, Hedtke et al. 2006). Due to restricted sampling, e.g. Reinert et al. (2003) were not able to reveal the Pitcairnioideae s.l. as paraphyletic in their molecular analyses, and the cpDNA-based tree shown by Givnish et al. (2011) likewise did not detect the paraphyly of *Deuterocohnia*.

In the present study, all species of *Deuterocohnia* could be sampled for molecular analyses. The 103 included specimens provide an average of about six samples per species. Widely distributed species such as *D. longipetala* were represented by more individuals than narrow endemics. The samples cover the main geographic distribution range of the genus, except for the peripheral region in Brazil and Paraguay, and except for the disjunct occurrence of *D. longipetala* in Peru, from where no material was available.
In addition to the 103 *Deuterocohnia* samples several accessions of the four other genera belonging to the subfamily Pitcairnioideae s.str. (Givnish et al. 2007, 2011) were included in the analyses, especially to investigate the monophyly of *Deuterocohnia* and its relationships with *Dyckia* and *Encholirium*. The latter two genera proved to be closely related with *Deuterocohnia* in earlier studies (Crayn et al. 2004, Rex et al. 2009). *Pitcairnia* was chosen as outgroup, because *Pitcairnia* is the most basal lineage of Pitcairnioideae s.str., according to all current bromeliad phylogenies (Givnish et al. 2007, 2011).

Whereas all available accessions were sequenced at three cpDNA loci, the sampling set was reduced for the nuclear sequence analyses. As only the question of monophyly of the genus was to be addressed with nuclear markers, the taxon set comprised a representative selection of samples

of *Deuterocohnia* (both subclades), *Dyckia* and *Encholirium*, with *Fosterella* used as outgroup. To facilitate the comparison of nuclear and cpDNA trees, additional cpDNA analyses were also conducted with this reduced taxon set.

**DNA sequencing of cpDNA loci**

In the present study, three chloroplast loci and two nuclear low copy markers were used for phylogenetic analyses within *Deuterocohnia* and relatives. The loci were chosen according to their extent of sequence variation and their performance in PCR and sequencing in prior tests (part of this study and Wagner 2007).

The *rpl*32–*trn*L intergenic region was the most variable cpDNA region in the publication of Shaw et al. (2007). Following the recommendations of Shaw et al. (2007), the *rpl*32–*trn*L locus was hence included in several recent investigations. For example, Meimberg et al. (2009) revealed a variation of 5.1% in the grass genus *Aegilops* (including outgroup taxa), whereas Krapp (2009) found a low variation of only about 1.8% for this region in the bromeliad genus *Dyckia*. The intergenic spacer *rpl*32–*trn*L was also applied in population genetics (Reberning et al. 2010, *Melampodium*, Asteraceae). In the present study, *rpl*32–*trn*L comprised 3.93% variable characters within *Deuterocohnia* and 9.66% across the Pitcairnioideae s.str. The locus was easy to amplify in two portions, after developing internal primers.

The intergenic spacer *rps*16–*trn*K – also recommended by Shaw et al. (2007) – turned out to be the most variable cpDNA region for *Deuterocohnia*, exhibiting a variation of 5.53% within all *Deuterocohnia* samples (11.21% within Pitcairnioideae). Up to now, only a few publications included this locus in their analyses. Within monocots, studies with *rps*16–*trn*K focussed on grasses and orchids. For example, Grünstäudl et al. (2009) studied the intergeneric relationships of Barnadesioideae (Poaceae) and found 6.35% variation, only about half of that found in Pitcairnioideae. Investigations on the genus *Nolana* (Solanaceae, Tu et al. 2008) revealed 4.9% variable characters (including outgroup). Mononucleotide repeats occurred within the *rps*16–*trn*K region of *Deuterocohnia*, as was also documented by Pinheiro et al. (2009) for the genus *Epidendrum* (Orchidaceae). Although the mononucleotide repeats was excluded from the analyses due to the risk of homoplasy, their presence vs. absence in different clades nevertheless provided some phylogenetic information. Thus, one of the poly-T regions turned out to be a synapomorphy of the *Dyckia*-clade, whereas the poly-A repeat was present in both the *Deuterocohnia* group j and the *Dyckia* and *Encholirium* samples. Additionally, the extension of this repeat in *Dyckia* and *Encholirium* united these two genera. In *Dyckia* the copy number of this poly-A-region increases conspicuously and inter-

feres with the precise sequencing of the fragment (present study and Krapp 2011), as the DNA-polymerase may "stutter" at this site (Weising et al. 2005).

The intergenic spacer *trn*S–*ycf*3 was first used for molecular systematic analyses of Poaceae by Saltonstall (2001; published as *rps*4–*trn*T in that study). Merely a handful of studies included this locus in their work. Vilatersana et al. (2010) found 3.9% informative characters within sequences of *Ptilostemon* (Asteraceae) and related genera, Garcia-Jacas et al. (2009) found less than 1% variation among species of *Centaurea*. Within *Deuterocohnia* 3.21% characters were variable, 5.35% within Pitcairnioideae. This locus was quite easy to handle, but provided the lowest variation among the three selected cpDNA loci.

Taken together, the applied cpDNA regions, especially *rpl*32–*trn*L and *rps*16–*trn*K, proved to be suitable for molecular systematic analyses within Pitcairnioideae s.str. At first glance, the three loci also provide a reasonable amount of sequence variation within *Deuterocohnia*, but unfortunately this variation was for the most part responsible for the split of the genus into two groups. Within the two *Deuterocohnia*-subclades, variation and resolution proved to be disappointingly low. To achieve better-resolved trees, sequencing of several more cpDNA loci would probably be necessary, but the cost and benefits of such an approach would have to be weighed for two reasons. First, several earlier studies demonstrated that including additional cpDNA loci increased statistical support of individual clades, but provided only little supplemental information (Krapp unpublished data, Wagner unpublished data). As whole chloroplast genome sequencing for a broad sampling is still an expensive effort, it will therefore be difficult to unequivocally resolve the cpDNA phylogeny for the genus. Second, the cpDNA tree of *Deuterocohnia* does apparently not reflect the species tree (3.6.2.2, 4.2.4), and molecular systematic analyses of other genomic compartments seem to be more important than adding more cpDNA data. Thus, additional information and perhaps better-resolved trees could result from sequence analysis of appropriate nuclear low-copy loci, and/or from the application of alternative DNA-marker techniques like "amplified fragment-length polymorphism" (AFLP; Vos et al. 1995). However, it has to be taken into account that design and analyses of additional nuclear loci may be time and cost intensive.

**DNA sequencing of ncDNA loci**

Sequence data of the nuclear locus PRK exon2–5 were successfully applied in several phylogenetic analyses within several plant groups, most notably within tribes and subfamilies of Arecaceae (Lewis and Doyle 2002, Roncal et al. 2005, Thomas et al. 2006, Norup et al. 2006, Loo et al.

2006). Loo et al. (2006) recognized 30% variation in Arecinae, Roncal et al. (2005) more than 20% in Arecoideae. Schulte et al. (2009) used this locus for a study of Bromeliaceae, subfamily Bromelioideae, where it provided a variation of about 36%. These authors detected two paralogues in six of the investigated species. The clones of the target copy of PRK revealed some base substitutions in most of the taxa and a few indels were detected for several species.
No paralogues of PRK were found within the Pitcairnioideae samples analysed in the present study. Whereas 6 out of 28 analyzed plants were homozygous at all positions, others exhibited a few polymorphic sites (1–12 [–21]) and a small number of indels. While indels and most of the base substitutions are probably a consequence of heterozygosity, some point mutations may also have been caused by errors of the *Taq*-polymerase. All polymorphic sites were excluded from the analyses, even when they occurred in a single sample only. The variation within *Deuterocohnia* was about 6%, and raised to 17.5% when *Dyckia*, *Encholirium* and *Fosterella* were included. The molecular trees generated from the data set revealed a good support for the delimitation of the genera, the resolution within *Deuterocohnia*, however, was low. This might be a consequence of homoplasy within the data set (Hamilton et al. 2003). Different characters may provide different phylogenetic signals and thus produce a poorly resolved topology despite a moderate degree of variation. Schulte et al. (2009) appraised this region to be a valuable phylogenetic tool. They found higher variation and higher resolution for this locus than for the investigated cpDNA loci. However, the higher taxonomic level in their study might facilitate the use of this region, as divergence time between the taxa might have been longer and the proportion of homoplastic characters in the data set may be lower.

The nuclear locus PHYC exon1 is currently used more often than PRK exon2–5, mainly because sequences can often be obtained via direct sequencing without cloning (Helsen et al. 2009, Davis and Anderson 2010, Jabaily and Sytsma 2010). In studies of *Opuntia* (Cactaceae) Helsen et al. (2009) found 1.4% of variation for this locus. Jabaily and Sytsma (2010) used PHYC for phylogenetic investigations within the bromeliad genus *Puya* and revealed 5.6% variable characters. In the present work, PHYC proved to be easier to amplify and to sequence than PRK. Readable sequences were obtained from all investigated samples via direct sequencing of PCR products. No indels and only a few polymorphic sites (1–4) were observed within the data set, Jabaily and Sytsma (2010) found 1–15 polymorphic sites within the same sample. The variation within *Deuterocohnia* (2.7%) was lower than the one found in *Puya* (Jabaily and Sytsma 2010). The "Core *Puya*" were not resolved sufficiently within that study and thus it was not very surprising, that

PHYC proved to be useful for the delimitation of the genera *Dyckia* and *Deuterocohnia*, but was much less suitable for differentiating the species of *Deuterocohnia*.

Summarizing, the two nuclear low copy markers PRK exon2–5 and PHYC exon1 were well suitable for the generic delimitation, which was the scope of their use in the present study. However, for further purposes like infrageneric delimitation and relationships the two loci are not recommendable due to the low resolution in the resulting trees. Additionally, the necessity for cloning will increase the effort in the case of PRK. Other nuclear loci should therefore be screened for analyses at the infrageneric level.

**Phylogenetic analyses**

A thoroughly compiled alignment is the basis for subsequent phylogenetic analyses. Automatically generated alignments should be checked carefully by hand as indel setting with computer programmes might be insufficient and orthology may be improved considerably by reviewing the alignment. The present study treated gaps as missing data or coded the indels according to Simmons and Ochoterena (2000). Although indel coding sometimes improves the resolution of the tree (Simmons et al. 2001), it did not do so in the present study. Only the support values increased in some calculations.

Analyses were conducted using different mathematical approaches. Distance methods were applied as well as methods using discrete characters. While the Neighbour joining (NJ) method results in a single tree, Maximum parsimony (MP) analyses, Maximum likelihood (ML) analyses and Bayesian inferences (BI) exhibit optimality criteria to find the best tree topology. To further optimize the phylogenetic reconstructions, NJ, ML and BI additionally enable the implementation of substitution models (2.4.3). New algorithms and programmes (e.g. RAxML, Stamatakis et al. 2005; PRAP, Müller 2004) facilitate the use of ML and BI, which need more processing power than MP and NJ analyses. However, with these methods an exhaustive search is not possible for a larger taxon and data set. In nearly all cases a heuristic search has to be conducted, which may not find the optimal tree.

A robust data set is expected to result in similar topologies, no matter what algorithm is used. The results of the tree reconstruction methods used in the present study revealed only little differences. They all identified the same groups (a–j) of *Deuterocohnia* samples and also the deep paraphyletic split within the genus when using cpDNA data. All ncDNA analyses supported the monophyly of *Deuterocohnia*. One considerable difference occurred in the support values of the *Fosterella* clade in cpDNA analyses. In the RAxML analysis the *Fosterella* clade was only poorly sup-

ported (BS 48), while all other analyses provide a BS of 100 or PP of 1. This might be a consequence of the hypothetical data set used in bootstrap analyses. This data set could by chance include only some of the characters, which support the *Fosterella* clade. Beside this difference, results of the different algorithms are mainly congruent and support the same topology. Thus the obtained trees reflect well the given data.

Apart from the different assumptions about evolutionary processes, all tree-based methods provide a more or less dichotomous branching pattern. However, evolution might also be reticulate and especially between young taxa hybridization may occur. Networks are usually used to analyse infraspecific relationships, however, in taxa with low genetic diversity it may be helpful at the interspecific level as well. Alternative evolutionary scenarios may be displayed and haplotypes may occur at internal nodes. The network analyses of cp-haplotypes in the present study revealed the same groups (a–j) as found in the tree topologies. The deep split within *Deuterocohnia* is shown by 32 mutational steps between group j and the rest of the *Deuterocohnia* samples. All groups are connected to the central haplotypes *z*. Central haplotypes as well as frequent haplotypes are supposed to reflect ancestral conditions (Crandall and Templeton 1993). However, in the present study the haplotype *z* occurs in several species, of which some most probably do not reflect ancestral states, e.g. *D. lotteae*. Again the topology is more related to the biogeography, as the specimens carrying the central haplotype are found in the centre of the genus' distribution area.
No matter, whether it is expressed as a tree or a network, the hypothesized phylogeny of a data set might not necessarily reflect the phylogeny of the species (see below).

## 4.2 Systematics of *Deuterocohnia*

### 4.2.1 Synonymization of *Deuterocohnia* and *Abromeitiella*

The taxonomic treatment of the genera *Deuterocohnia* and *Abromeitiella* prior to the onset of the present revision has been described in detail in chapter 3.1. The similarity of the two genera was recognized by many authors (Harms 1929, Smith 1964b, Ehler and Schill 1973, Williams 1978, Varadarajan and Gilmartin 1987, 1988a and b, Böhme 1988, Brown and Gilmartin 1989a), but there are also a number of distinctive characters that were considered sufficient to keep the two genera separate until 1992 (Harms 1934, Smith 1934, Smith and Downs 1974). The description of *Abromeitiella scapigera* in 1987 (Rauh and Hromadnik) led Spencer and Smith (1992) to re-evaluate the taxonomic status of the two genera. As a result, they suggested to synonymize *Abromeitiella* under the earlier described genus *Deuterocohnia* (3.1).

With regard to the comprehensive revision performed in the frame of the present study, the following conclusions on the taxonomic treatment of the genera *Deuterocohnia* and *Abromeitiella* can be drawn:

(1) Delimitation of *Deuterocohnia* including *Abromeitiella* from other genera

The taxa belonging to *Deuterocohnia* including *Abromeitiella* (referred to as *Deuteroconia/Abromeitiella* in the following) share a set of diagnostic morphological characters, which together clearly distinguish them from the closely related genera *Dyckia*, *Encholirium*, *Fosterella* and *Pitcairnia*. The most important of these characters are the higher density of foliar trichomes, the usually longer floral tube, the slightly asymmetric sepals, the presence of petal appendages, a wholly superior ovary and comma-shaped, appendaged seeds. It is therefore beyond doubt that the two genera together form a morphologically distinct group.

Phylogenetic trees based on the nuclear single copy markers PHYC exon1 and PRK exon2–5 (present study) as well as earlier AFLP analyses by Horres (2003) likewise support that *Abromeitiella* and *Deuterocohnia* together form a monophylum. Phylogenetic trees based on cpDNA sequences, however, deeply split *Deuterocohnia/Abromeitiella* into two clades, with one of the two clades being more closely related to *Dyckia* and *Encholirium* than to the remainder of *Deuterocohnia/Abromeitiella* (4.2.1, Figs. 3.31, 3.32, 4.3). At first glance, this result seems to argue against the monophyly of the *Deuterocohnia/Abromeitiella* alliance. However, as outlined in more detail below, the cpDNA tree and network topology explicitly correspond to geographical patterns rather than to taxonomy and the apparent paraphyly of *Deuterocohnia/Abromeitiella* in the cpDNA trees is hence better explained by an early chloroplast capture event.

(2) Delimitation between *Deuterocohnia* and the former *Abromeitiella* taxa

Traditionally, those species of the *Deuterocohnia/Abromeitiella* group that grow in dense cushions and produce small, single- to few-flowered plants were included in *Abromeitiella*, and those that grow in groups or rings and form large, many-flowered plants were referred to as *Deuterocohnia.* The description of *D. scapigera* in 1987 demonstrated, however, that the two traditional genera were not that explicitly separated as hitherto thought. This led Spencer and Smith (1992) to synonymize the two genera, a concept which was supported by the later description of *D. gableana.* Vásquez and Ibisch (2003) actually interpreted *D. gableana* to be a missing link between the two genera. This may indeed be the case, if one consider *D. longipetala* to be the most ancient species in the *Deuterocohnia/Abromeitiella* alliance (4.2.4). Several lineages may have evolved from that ancestral form (4.2.4), one of which could have led to the taxa that were earlier united under *Ab-*

*romeitiella*. In this hypothetical evolutionary lineage, the plants became gradually smaller, and the peduncle and the inflorescence became shorter and less branched (like in *D. gableana*). Perhaps in conjunction with the colonization of higher altitudes of the Andes, plants eventually evolved that had only minute rosettes, a single flower and no peduncle at all, as is the case in *D. brevifolia*, *D. lotteae* and *D. abstrusa*. *Deuterocohnia scapigera* and *D. sanctae-crucis* may be considered as kind of intermediates, because their inflorescences are still able to branch.

Molecular data based on the single copy markers PHYC exon1 and PRK exon2–5 included three accessions of former *Abromeitiella* taxa, but their position in relation to *Deuterocohnia* remained ambiguous because of low tree resolution. In the AFLP tree presented by Horres (2003), the – at that time described – *Abromeitiella* species *A. brevifolia*, *A. lorentziana*, *A. lotteae* and *A. scapigera* together form a derived, monophyletic clade within *Deuterocohnia* supporting the above hypothesis that the former *Abromeitiella* taxa form a separate monophyletic lineage within *Deuterocohnia*. Unfortunately, *D. gableana* and *D. sanctae-crucis* from Bolivia were not included in the AFLP study of Horres (2003). As already mentioned above, no sound taxonomic conclusions on the distinction between *Abromeitiella* and *Deuterocohnia* can be drawn from the cpDNA data, because in these trees the former *Abromeitiella* taxa form clades with *Deuterocohnia* accessions from the same geographical areas.

Whereas the union of *Abromeitiella* and *Deuterocohnia* could be verified by the present work, the argumentation of Spencer and Smith (1992) is not completely convincing. The authors stated that the existence of intermediate species like *A. scapigera* would make it impossible to distinguish the two genera. It is certainly the case that some specimens of *D. abstrusa* (in part the former *A. lorentziana*) have a higher flower number than some of *D. strobilifera*, and some specimens of *D. scapigera* (formerly *A. scapigera*) have longer peduncles than some of *D. strobilifera* (unfortunately Spencer and Smith (1992) did not cite the voucher they investigated). However, there are clear lower and upper limits of the character states within each of these taxa, and there is only limited overlap. *Abromeitiella lorentziana* and *A. scapigera* form the largest plants within *Abromeitiella*, and *Deuterocohnia strobilifera* and *D. digitata* form the smallest plants within *Deuterocohnia*. On should add that Spencer and Smith (1992) compared atypical forms of each species with each other. Taken together, a slight overlap of one or more particular character states that occur between different taxa should not be taken as the sole argument for uniting these taxa, especially when extreme, atypical growth forms were looked at. Overlapping character states occur in many pairs of plant taxa that are otherwise very well distinguishable. For example, *D. brevispicata* and *D. seramisiana*

have overlapping leaf sizes, but are well distinguishable from each other by their different flower colour, floral bracts and altitudinal range.
Concerning the habitual differences of *Deuterocohnia* and *Abromeitiella*, Spencer and Smith (1992) noted that these are minimal and not used elsewhere in Bromeliaceae to differentiate genera. Indeed, large conglomerates of plants may also be observed within *Deuterocohnia*, but as the rosettes are larger, they do not form such compact cushions as in *Abromeitiella*.

To conclude, the synonymization of *Abromeitiella* and *Deuterocohnia* (Spencer and Smith 1992) is confirmed by the results of the present study, both with morphological and molecular data. The integration of *Abromeitiella* into *Deuterocohnia* keeps the latter genus monophyletic. However, it has not been shown unambiguously so far whether the former *Abromeitiella* taxa including *D. gableana* form a monophyletic lineage within *Deuterocohnia*. If this proves to be correct, *Abromeitiella* could well be retained at the sectional level.

### 4.2.2 Species classification

After a comprehensive examination of the taxonomy, morphology and biogeography of the belonging taxa, 17 species, 4 subspecies and 4 varieties of *Deuterocohnia* are accepted in the present revision. Taxonomic states were changed or newly described in the following cases:

- *A. abstrusa* is re-established and transferred to *D. abstrusa*
- *D. brevifolia* includes part of the former *D. lorentziana*
- *D. bracteosa* is synonymized to *D. strobilifera*
- A new subspecies of *D. meziana* is described
- *D. meziana* var. *carmineo-viridiflora* is classified as a subspecies of *D. meziana*
- *D. pedicellata* is classified as a subspecies of *D. meziana*
- *D. scapigera* ssp. *sanctae-crucis* is classified as a species
- A new variety of *D. scapigera* is described
- A new epitype is chosen for *D. longipetala*

All other species were kept as described by Spencer and Smith (1992) or – in the case of more recently described species – the respective protologue.

Important morphological characters for species delimitation proved to be:

- Size of the rosette
- Density of spines on the leaf margin
- Length of the inflorescence
- Branching order
- Density of flowers on partial inflorescence
- Relation of primary bracts to partial inflorescence
- Size of the floral bracts
- Flower length
- Flower colour
- Single- versus bicoloured flowers
- Presence versus absence of a pedicel
- Indument of the sepals
- Curving of the stamina during anthesis
- Curving of the petals during anthesis
- Twisting of the petals after anthesis

The genus includes several well distinguishable, individually recognizable species, as there are *D. brevispicata*, *D. chrysantha*, *D. digitata*, *D. lotteae*, *D. recurvipetala*, *D. seramisiana* and *D. strobilifera.* Other taxa are more difficult to delineate. These taxa and the taxonomic modifications applied to them are described in the following:

***Deuterocohnia meziana***

The populations of *D. meziana* comprise a broad overall morphological variation. Especially the flowers vary in numerous colour shades of rose, reddish, orange or yellow, whereas the petals always exhibit a greenish tip. Moreover, sepals and petals may have similar or different colours. Nevertheless, morphologically distinct groups can be recognized within the species, which occur in different geographical regions and habitats. Given that geographic distribution patterns are generally considered to be important for the recognition of infraspecific taxa (Stuessy 1990, Wendt et al. 2000), the following four subspecies of *D. meziana* were classified in the present study (distribution map Fig. 5.22): ssp. *meziana*, ssp. *carmineo-viridiflora*, ssp. *pedicellata* and ssp. nov. Hybrid zones between the subspecies may occur, e.g. in the border region of Chuquisaca, Santa Cruz and Cochabamba, where neighbouring populations showed gradual differences in certain

characters (e.g. pedicel length). Sometimes different characters states (e.g. flower colour) were even found in the same population.

(1) *Deuterocohnia meziana* ssp. *meziana* is mainly confined to the lowlands of SE Bolivia and adjacent areas in W Brazil, where it grows on outcrops in the Chiquitania dry forest. Along the Río Paraguay this taxon spreads into Paraguay. In the west of Santa Cruz de la Sierra, Bolivia, it also climbs up the eastern slopes of the Andes (200–1400 m a.s.l.). *Deuterocohnia meziana* ssp. *meziana* plants form the largest rosettes and inflorescences of the whole genus, the flowers have orange sepals and orange-yellowish petals.

(2) *Deuterocohnia meziana* ssp. *carmineo-viridiflora* had formerly been described as a variety by Rauh (1985). The subspecies is found in the mountain ranges of the central Bolivian departments of Cochabamba and Santa Cruz (1200–2200 m a.s.l.), at the north eastern border of the species' distribution area. The sepals are rose, magenta or carmine; the petals are always carmine.

(3) *Deuterocohnia meziana* ssp. *pedicellata* had formerly been described as a separate species (Till 2004). It is restricted to central Bolivian inter-Andean dry valleys, at 900–1400 m a.s.l. The conspicuously pedicellate flowers (10–15 mm) have greenish sepals and yellow petals.

(4) *Deuterocohnia meziana* ssp. nov. occurs on arenaceous soil in the understorey of lowland dry forests in N Paraguay (100–300 m a.s.l.). With up to 50 mm, it has the longest flowers within the genus, with rose sepals and rose-magenta petals. The leaves are smaller and the inflorescences bear fewer flowers than in the other subspecies.

The new subspecies were established in the present study due to their peculiar morphology, ecology and biogeography (s. a.). Whereas the cpDNA data revealed a close relationship between three of the subspecies (*D. meziana* ssp. nov. not included), no conclusions can be drawn yet on their genetic differentiation due to low sequence variation. Future studies on *D. meziana* should include gene flow analyses between populations (e.g. with microsatellites), as well as investigations on pollination biology. Both approaches are expected to give insights into speciation processes of this group.

### *Deuterocohnia longipetala* vs. *Deuterocohnia meziana*

The infraspecific morphological diversity of *D. longipetala* and *D. meziana* is considerable, and a certain overlap of some character states might render the correct species assignment sometimes difficult. In general, *D. longipetala* plants exhibit smaller rosettes, sparsely branched inflorescences, distinct floral bracts and comparatively short, sessile, yellow-greenish flowers. In contrast, *D. meziana* has larger rosettes, manifold branched inflorescences, short to minute floral bracts and longer, pedicellate flowers, with orange, yellow or reddish petals. Usually, the secondary branches

of *D. meziana* appear already in the first year of maturity, while *D. longipetala* starts branching in the second year.

*Deuterocohnia longipetala* and *D. meziana* both have wide distribution ranges. While *D. longipetala* is mainly distributed in N Argentina, *D. meziana* occurs in SE Bolivia, N Paraguay and W Brazil. Intermediate forms occur along the border between Bolivia and Argentina, where both distribution areas overlap. In this area the assignment of populations to one of the two species might be difficult, indicating possible hybrid formation. For example, in the Dept. of Tarija, Bolivia, plants can be found that possess typical character states of *D. meziana* (e.g. huge inflorescences and long leaves), intermingled with characters that resemble *D. longipetala* (sessile, yellowish flowers and distinct floral bracts).

Molecular analyses of cpDNA sequences separate the two species into two distinct subclades (*D. longipetala* subclade A, *D. meziana* subclade B, Figs. 3.31, 3.32).

***Deuterocohnia longipetala***

*Deuterocohnia longipetala* exhibits the largest distribution area among all species of *Deuterocohnia*. Within this area, a morphological gradient from N to S can be observed: southwards the inflorescences get laxer, more delicate, bear shorter flowers and sometimes display a greyish adaxial leaf surface. The *D. longipetala* vouchers *Stuckert 11041* and *Stuckert 12098* [G] from Córdoba both carry a label with the name *Deuterocohnia gracilis* Mez. This name was never published, however, probably Mez wanted to point out this difference between northern and southern populations of *D. longipetala*. Castellanos (1933) described *D. longipetala* f. *uberrima* from Tucumán, Argentina, having larger secondary branches and longer flowers than the type. This taxon was synonymized to *D. longipetala* by Smith and Downs (1974) without further comments.

Despite the considerable extent of morphological plasticity within *D. longipetala*, no variety or form of this species was described in the present study, because no clear line can be drawn between the gradually changing populations.

Phylogenetic investigations of cpDNA data in the present study placed *D. longipetala* within several different clades, which at first glance would indicate a paraphyletic species. However, the analyses of cpDNA data turned out to generally reflect the geographical distribution of chloroplast haplotypes rather than a taxonomical correlation. These data can therefore not be used for species delimitation, especially not in the case of a widely distributed taxon such as *D. longipetala*. Former AFLP-studies (Horres 2003) also indicated paraphyly of *D. longipetala*. This is an interesting result, since AFLP fragments are supposed to be derived from the whole genome and therefore should reflect the species tree better than cpDNA does. However, during the present revi-

sion the plants used in the work of Horres (2003) were revised, and two "*D. longipetala"* plants from Botanical Gardens turned out to belong to *D. meziana* (H173/HEID 130200, H174/HEID 130181). Thus, the putative paraphyly of *D. longipetala* shown in the AFLP study of Horres (2003) may simply have been caused by false plant identification.

### ***Deuterocohnia longipetala* vs. *D. haumanii* vs. *D. schreiteri* vs. *D. glandulosa***

*Deuterocohnia longipetala* is morphologically quite similar to *D. haumanii*, but differs in having laxer partial inflorescences, smaller floral bracts, usually glabrous floral parts and branches of 2nd order. *Deuterocohnia schreiteri* differs from both in having noticeably smaller floral bracts and smaller flowers. The sepals of *D. schreiteri* are glabrous as in *D. longipetala*, but the branches are mainly of 1st order as in *D. haumanii*.

Although the typical plants of each species are easily delimited, the occurrence of natural hybrids may complicate the determination and differentiation of populations. Hybridization between *D. longipetala*, *D. haumanii* and *D. schreiteri* seems to be common in the Argentinean provinces Salta and Tucuman, where intermediate character states or intermingled character state combinations occur.

*Deuterocohnia glandulosa* from Bolivia is delineated from *D. haumanii* by having larger rosettes, less robust axes and smaller floral bracts. Compared to *D. longipetala*, this species exhibits denser partial inflorescences and frequently carries glandular trichomes on the abaxial sepal surface.

The presence or absence of glandular trichomes on floral parts as species delimiting character should, however, be handled with care. On the one hand, there are some accessions of *D. longipetala*, with laxly flowered inflorescences and small floral bracts, which *do* have glandular trichomes on the floral parts (e.g. *Cantino 657*, CORD). On the other hand, there are specimens of *D. haumanii*, which have densely flowered partial inflorescences and large floral bracts, but which do not have glandular trichomes (e.g. *Castellanos 46630*, BA). The same can be the case in *D. glandulosa* (e.g. *Hromadnik 5167* with glandular trichomes*, Schütz 06-020* without glandular trichomes).

### ***Deuterocohnia gableana, D. scapigera, D. sanctae-crucis***

The Bolivian species *D. gableana*, *D. scapigera* and *D. sanctae-crucis* have in common a short peduncle, yellow-greenish flowers and glandular trichomes on the sepals. *D. gableana* differs in having a bigger rosette, a longer peduncle, which conspicuously exceeds the rosette, and distinctly pedicellate flowers. The peduncles of *D. scapigera* and *D. sanctae-crucis* are mostly concealed by the rosette, and the flowers are sessile or subsessile. *Deuterocohnia sanctae-crucis* exhibits the smallest rosettes of

Fig. 4.1: Herbarium voucher of *Deuterocohnia scapigera* (left, *Hromadnik 5076*) and *D. sanctae-crucis* (right, *Vargas 3185*), demonstrating the considerable differences in size and branching.

these three taxa and occurs like *D. gableana* in the Department Santa Cruz. In contrast, *D. scapigera* grows – close to *D. strobilifera* – in the Departments of Potosí and Chuquisaca.
In 2002, Vásquez and Ibisch mentioned a new locality of *D. scapigera*, which they found in the Bolivian Dept. Santa Cruz. Based on this and additional vouchers the authors decided one year later to establish a new subspecies: *D. scapigera* ssp. *sanctae-crucis*. They noted that this taxon might also turn out to be a separate species.
The present revision delineates *Deuterocohnia sanctae-crucis* as a separate species, because it differs from *D. scapigera* in forming smaller rosettes, and having more delicate inflorescences, shorter floral bracts and a higher ability to branch (Fig. 4.1). Additionally, *D. scapigera* and *D. sanctae-crucis* grow in different ecoregions (Andean Yungas vs. Central Andean Puna) and are strongly separated from each other in cpDNA trees (*D. scapigera* belongs to subclade A, *D. sanctae-crucis* to subclade B).
Furthermore, a new variety of *D. scapigera* is described in the present study. It varies from the type in having orange-greenish and glabrous petals.

### *Deuterocohnia brevifolia* vs. *D. abstrusa*

The taxonomic delimitation of *D. brevifolia* from its small-sized, cushion-forming relatives is quite challenging and outlined by the comprehensive classification history of this lineage (3.1). During the present revision it became obvious that there are diverse populations, varying in the size of the rosette, length of the ramets, density of spines, leaf colour, density of leaf indument and number of flowers. Observations in the field revealed that variation even occurs within the same population. It should therefore be pointed out that herbarium specimens cannot adequately represent this diverse morphology.
Mez (1934) distinguished *A. brevifolia*, *A. abstrusa* and *A. chlorantha* by the size of their leaves and the density of the spines on the leaf margin. He described *A. brevifolia* plants as having few spines

at the base, whereas *A. abstrusa* and *A. chlorantha* have many spines all over the margin. On the contrary, Rauh and Hromadnik (1987) described *A. brevifolia* to be spinose at the leaf margin, whereas *A. lorentziana* (which comprised the *A. abstrusa* from Mez in 1934) should have just few or no spines.

Smith (1967 b) adduced that he was only able to distinguish two of the polster forming *Abromeitiella* species – at that time *A. lotteae* and *A. scapigera* were not described yet – and classified them according to their size. Large plants he determined as *A. lorentziana*, smaller ones as *A. brevifolia*. Smith and Downs (1974) adopted this differentiation. Morphological investigations in the present study provide evidence that leaf sizes in *A. brevifolia* and *A. lorentziana* vary continuously and that there is no distinct, separating boundary in this character (Fig. 4.2).

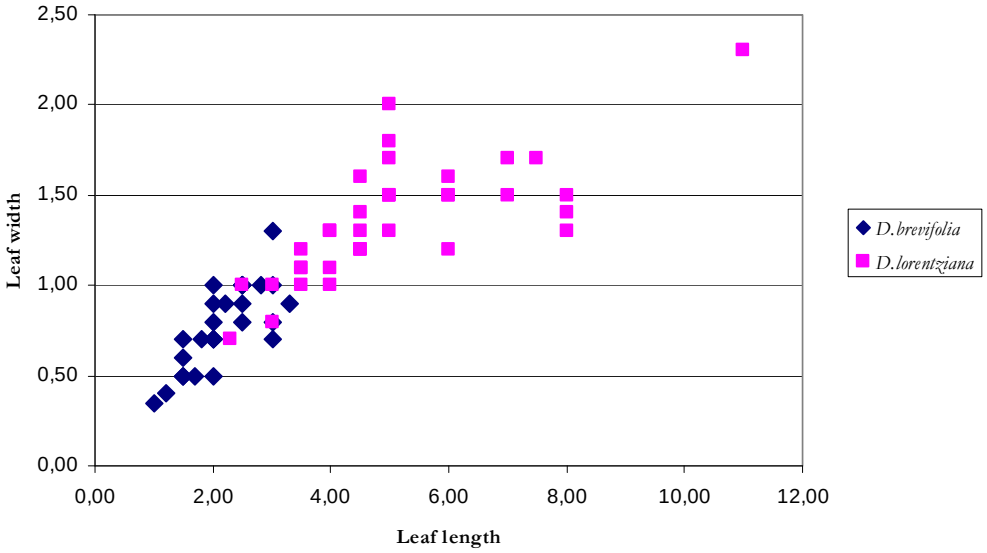


Fig. 4.2: Relation of leaf length (cm) to leaf width (cm) of randomly selected herbarium vouchers of *Deuterocohnia brevifolia* and *D. lorentziana*, 30 specimens for each species. Names were applied as indicated on the voucher. Blue rhombs: *D. brevifolia*. Pink squares: *D. lorentziana*.

Consequently, the two species could as well be united into a single taxon with a broad morphological variability. This option was already mentioned by Smith (1967 b), who stated that *A. brevifolia* and *A. lorentziana* might also form a monotypic species with several varieties. Until now, phylogenetic analyses could not resolve the relationships among these taxa, either as a consequence of limited taxon sampling or due to the geographic pattern within cpDNA based tree topologies in the present study.

Before uniting these taxa into one species, further investigations at the level of populations should be conducted – morphological studies in the field as well as molecular analyses. There-

fore, the present revision still differentiates two species: *D. abstrusa* and *D. brevifolia*. Larger plants with greyish leaf indument refer to the description of *D. abstrusa* (Castellanos 1931). Smaller plants with greenish leaf indument are sorted to *D. brevifolia*. The epithet "*abstrusa*" is re-established, as the type voucher of *D. lorentziana*, *Lorentz s.n.* (basionym *Pitcairnia lorentziana*), is assigned to *D. brevifolia*.

### 4.2.3 Generic relationships and the monophyletic status of *Deuterocohnia*

The morphological distinctness of *Deuterocohnia* has never been argued since the first description of the genus, and aside from the question of its relationship to *Abromeitiella* (4.2.2), its monophyletic status has never been questioned in pre-molecular times. The close association between *Deuterocohnia* and *Dyckia* is already reflected by the fact that the type specimen of *Deuterocohnia* (i.e. *Deuterocohnia longipetala*, Mez 1894) had formerly been assigned to *Dyckia* (*Dyckia longipetala*, Baker 1889). *Deuterocohnia* species mainly differ from those of *Dyckia* in having a terminal inflorescence, petal appendages, usually longer petals, and exposed stigmata (Smith and Downs 1974, Smith and Till 1998). Nevertheless, the two genera also have several characters in common, like the succulent, spinose leaves, a common type of leaf scales, some features of leaf anatomy, the CAM-photosynthesis pathway, the usually pedunculate inflorescence and a preference for yellowish or reddish flower colours (Smith and Downs 1974, Smith and Till 1998). All systematic investigations so far revealed *Dyckia* and *Deuterocohnia* (with or without *Abromeitiella*) to be closely related. Based on a set of shared characters relating foliar scales and leaf anatomy, Varadarajan and Gilmartin (1987) assumed that there is a close association of *Abromeitiella* and *Deuterocohnia* with *Dyckia*, *Encholirium*, *Hechtia* and *Puya*. Later the same authors formally grouped these genera together with the Venezuelan genus *Brewcaria* into the tribe Puyeae (Varadarajan and Gilmartin 1988a, b). This classification was, however, challenged by Robinson and Taylor (1999) who instead established the tribe Dyckieae, including *Dyckia*, *Encholirium*, *Deuterocohnia* (incl. *Abromeitiella*) and *Hechtia* (without *Puya*) based on leaf cross-sections.

Since the advent of comparative DNA sequence analyses in phylogenetic research, several cpDNA-based phylogenies of Bromeliaceae have been conducted. All these studies showed that *Deuterocohnia* is only distantly related with the likewise succulent genera *Hechtia* and *Puya* (Horres 2003, Crayn et al. 2004, Givnish et al. 2007, 2011, Rex et al. 2009). Apparently, the sharing of a set of xeromorphic characters between these genera had been caused by convergence in adaptation to arid habitats. The close relationship of *Deuterocohnia*, *Dyckia* and *Encholirium* was, however, supported by all molecular studies. Based on a broadly sampled cpDNA phylogeny of Bromeli-

aceae, Givnish et al. (2007) eventually established a new classification of bromeliad subfamilies, with the xerophytic genera *Deuterocohnia* (incl. *Abromeitiella*), *Dyckia*, *Encholirium* and the mesophytic *Fosterella* and *Pitcairnia* forming the monophyletic subfamily Pitcairnioideae s.str. A closer relationship of *Deuterocohnia* with the two mesophytic genera *Fosterella* and *Pitcairnia* had never been proposed in earlier morphological investigations.

Only one or a few species of *Deuterocohnia* were incorporated in previous molecular systematic studies of Bromeliaceae, and almost all of these were based on cpDNA sequence variation. *Deuterocohnia* (incl. *Abromeitiella*) either came out as monophyletic (Givnish et al. 2007, 2011) and in sister position to *Dyckia* and *Encholirium*, or (more often) as paraphyletic, with some *Deuterocohnia* specimens being closer related with *Dyckia* than with the other *Deuterocohnia* samples (e.g. Horres et al. 2000, Crayn et al. 2000, 2004, Reinert et al. 2003, Rex et al. 2009). The *Deuterocohnia* specimens showing this unexpected behaviour, i.e. a close affinity with *Dyckia*, all belonged to the Bolivian species *D. meziana*, *D. brevispicata* or *D. scapigera* (the sample of *D. scapigera* is now assigned to *D. sanctae-crucis*).

The present study aimed, among other scopes, to investigate these indications of paraphyly of *Deuterocohnia*. More than 100 specimens of *Deuterocohnia* covering all described species and additionally ten samples of *Dyckia* and *Encholirium* were included in a molecular phylogenetic analysis based on three cpDNA loci. All conducted analyses proved *Deuterocohnia* to be deeply paraphyletic with high statistical support values (BS 100 and PP 1 for each subclade, Fig. 4.3). One deep split separated twelve species of *Deuterocohnia* (subclade A) from the remaining five species (subclade B) that grouped with the accessions of *Dyckia* and *Encholirium*. Subclade B contained the Bolivian species *D. brevispicata*, *D. gableana*, *D. meziana*, *D. sanctae-crucis* and *D. seramisiana*, in correspondence with the earlier studies cited above.

Due to the apparent paraphyly of *Deuterocohnia* in studies using cpDNA data, the two nuclear loci PHYC exon1 and PRK exon2–5 were additionally examined with regard to the question of monophyly of this genus. These analyses were run with a reduced taxon set, which proved to be sufficient for genus delimitation. Accessions from both *Deuterocohnia* subclades were included and the same reduced taxon set was also used to construct a cpDNA tree for direct comparison. In contrast to the cpDNA based results, trees generated from nuclear sequence data at both loci corroborate the monophyly of *Deuterocohnia* (Fig. 4.3) with high statistical support (BS 94–100, PP 1) in all conducted analyses. AFLP studies of *Deuterocohnia*, *Dyckia* and *Pitcairnia* accessions conducted by Horres (2003) likewise revealed *Deuterocohnia* and *Dyckia* to be each monophyletic (BS 80–92).

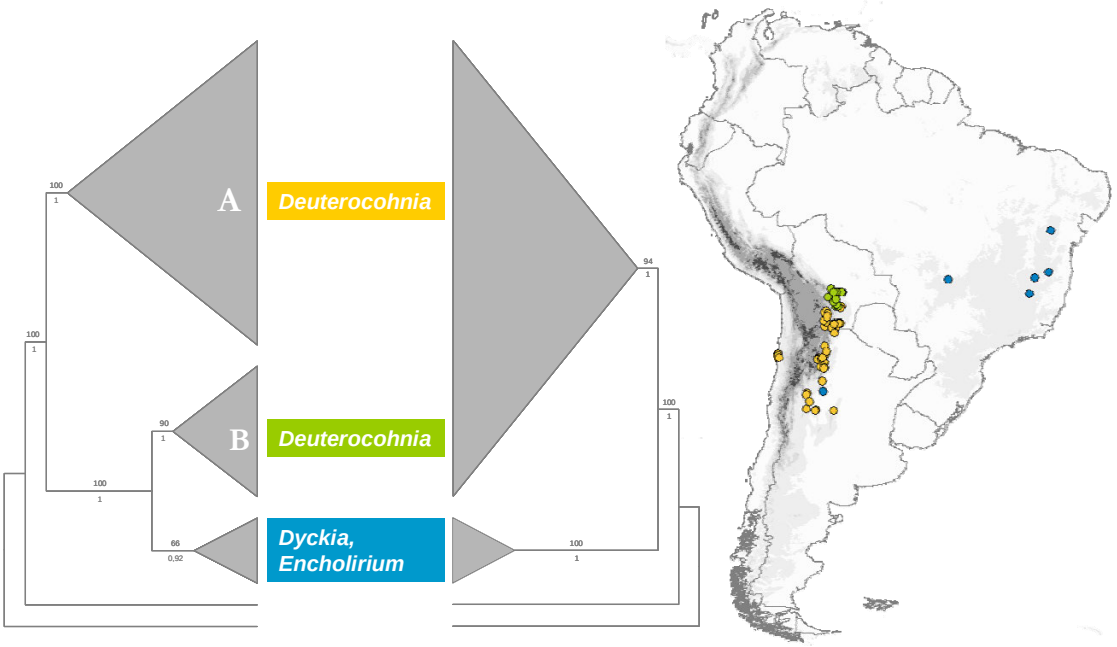


Fig. 4.3: Incongruence of the tree topologies obtained with chloroplast DNA data (left) and nuclear DNA data (right). Bootstrap values are depicted above the branches, posterior probabilities below. The map includes collection localities of all accessions of the large sample set (Tab. 2.7), for which coordinates were available. Green dots: accessions belonging to *Deuterocohnia* subclade B, orange dots: *Deuterocohnia* subclade A, blue dots: *Dyckia* and *Encholirium*.

Given that the monophyly of *Deuterocohnia* is suggested by molecular data from the nuclear genome as well as from morphological evidence, the question remains, how the deep split within *Deuterocohnia* and the relation of subclade B to *Dyckia* in cpDNA analyses might be explained. Two alternative interpretations may be envisaged:

(1) The paraphyly of *Deuterocohnia* suggested by the cpDNA data reflects a "real" **paraphyletic** genus, and *Dyckia* evolved from within *Deuterocohnia*, more precisely from the common ancestor of *Dyckia* and *Deuterocohnia* subclade B. Morphologically this would be conceivable – like the bird lineage that arose from within the reptile lineage – but then one should expect that this paraphyly should also be indicated by the nuclear data, at least by the AFLP-data that probably represent an average sample of the whole genome. Single gene trees might not reflect species trees (Doyle 1992), and the analyzed nuclear genes of *Deuterocohnia* subclade A and B could have experienced some exchange after the split of *Dyckia* and *Encholirium* from *Deuterocohnia* subclade B.
Another argument against the origin from *Dyckia* and *Encholirium* from within *Deuterocohnia* is the fact that the perennial inflorescence in *Deuterocohnia* is considered to be a derived, evolutionary

advantageous character, that enables the plants to produce flowers for several years without generating a new rosette and a full inflorescence in each flowering period. If the "paraphyly" hypothesis were correct, the perennial inflorescence would have been lost in the *Dyckia/Encholirium* lineage, which would have probably been a disadvantage. Alternatively, one may assume that the perennial inflorescence evolved two times independently in *Deuterocohnia* subclade A and B, which is even more unlikely under the parsimony criterion.

(2) The second – and more likely – explanation would assume that *Deuterocohnia* is in fact **monophyletic** and the paraphyly arose via introgression of the chloroplast genome from the *Dyckia* lineage into the ancestor of the *Deuterocohnia* subclade B.
According to Givnish et al. (2011; 4.2.4), the most recent common ancestor of *Deuterocohnia* and *Dyckia/Encholirium* lived in N Argentina and S Bolivia. The *Deuterocohnia* lineage later extended its distribution area into the Andes, climbing up to moderate or even high altitudes. The *Dyckia/Encholirium* lineage took the opposite direction and colonized the lowlands of Argentina, Bolivia and Brazil. After having diverged into the two lineages, hybridization between the ancestors of *Deuterocohnia* and *Dyckia/Encholirium* might still have been possible, but probably was a rare event, due to geographical, ecological, pre- or postmating barriers. In SE Bolivia hybridization might have occurred more frequently, perhaps triggered by the development of orange coloured flowers in these *Deuterocohnia* populations. Orange is the dominating flower colour in *Dyckia*, while most of the *Deuterocohnia* species exhibit yellow flowers. Fertilization of *Dyckia* populations by *Deuterocohnia* pollen would have led to a hybrid population containing the maternally inherited *Dyckia* chloroplast genome (chloroplast capture, Rieseberg and Soltis 1991, Wolfe and Elisens 1995, Tsitrone et al. 2003). Repeated back-crossing of these hybrid populations with the *Deuterocohnia* pollen parent would eventually result in plants that have a *Deuterocohnia* phenotype and contain the *Deuterocohnia* nuclear genome, but also carry the *Dyckia* chloroplast genome. In this way the common ancestor of the *Deuterocohnia* species/accessions in subclade B could have captured the chloroplast genome from the ancestor of the *Dyckia/Encholirium* lineage. Pollinators, which are mostly hummingbirds but also insects may have played an important role both in the hybridization event and the evolution of orange and reddish coloured flowers in *Deuterocohnia*. Hummingbird diversification (Bleiweiss 1998) occurred at about the same time as the diversification within the Pitcairnioideae s.str.
There is also the vague possibility, that the ancestor of the *Dyckia/Encholirium* lineage would have received the chloroplast genome from *Deuterocohnia* subclade B. If this were the case, the split of the two *Deuterocohnia* subclades must have been established well before the hybridization event,

producing very distinct chloroplast lineages within *Deuterocohnia*. This seems to be rather unlikely, because the diversification of the *Deuterocohnia* lineage and the *Dyckia/Encholirium* lineage might have taken place at about the same time according to cpDNA analyses (Givnish et al. 2011). At about the same time period when the cross-genus hybridization took place, the stream Río Pilcomayo might have started forming a geographical barrier between the *Deuterocohnia* populations in the north (subclade B) and those from the south (subclade A). This river presently rises in the high Andes at almost 6000 m a.s.l., between the Bolivian Departments of Potosí and Oruro, and flows southwards towards Paraguay and Argentina (Fig. 4.4). During the Pleistocene the high Andes were glaciated (Graham 2010) and in interglacial times the Río Pilcomayo might have been even much more spacious than it is today. If the Río Pilcomayo already existed during the time period when *Deuterocohnia* subclades A and B split from each other, it could well have served as a barrier for seed dispersal as well as for potential pollinators. This barrier would then have prevented further gene flow between the two *Deuterocohnia* subclades and preserved the close chloroplast relationship of *Deuterocohnia* subclade B with *Dyckia* and *Encholirium*.

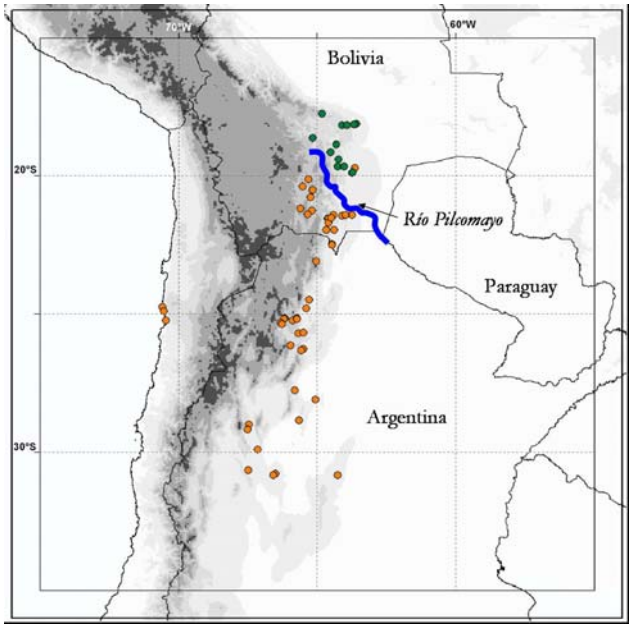


Fig. 4.4: Distribution of the *Deuterocohnia* samples used in chloroplast DNA analyses and their relation to the Río Pilcomayo. Green dots: accessions belonging to *Deuterocohnia* subclade B, orange dots: *Deuterocohnia* subclade A. Blue line: upper Río Pilcomayo.

Incomplete lineage sorting might also be an explanation for this pattern. Different copies of the chloroplast genome might have co-existed in the ancestor of *Deuterocohnia* and *Dyckia/Encholirium*. One copy could have established in *Deuterocohnia* subclade A, another in *Dyckia* and *Deuterocohnia* subclade B. Distinguishing lineage sorting from introgression might be difficult as they may both result in similar patterns of allele sharing (Small et al. 2004). Plants of *Deuterocohnia* and *Dyckia* have been successfully crossed in garden experiments and these "*Dyckcohnia*" samples (Grant and Zijlstra 1998) prove the ability of the two genera to produce hybrids.

Incongruence between chloroplast and nuclear based phylogenies has been reported for several other plant groups (e.g. Petit et al. 2004, Kim 2008, Guggisberg et al. 2009, Willyard et al. 2009,

Montes-Moreno et al. 2011). Jabaily and Sytsma (2010) also recovered different topologies when comparing chloroplast and nuclear DNA based trees of the bromeliad genus *Puya*. They explained the differences in Chilean Puya phylogenies with ancient chloroplast capture in conjunction with recent hybridization events.

### 4.2.4 Conclusion on the evolution

**Evolution of the genus**

The distribution areas of the extant genera of Pitcairnioideae s.str. overlap in N Argentina and S Bolivia, which makes it likely that this is the place of origin of the subfamily (Givnish et al. 2007, 2011). According to current chronograms that were based on cpDNA data (Givnish et al. 2011), the Pitcairnioideae s.str. arose about 13.4 mya in the rising chain of the Andes. The more mesophytic *Pitcairnia* and *Fosterella* lineages have their extant habitats mainly north of the so-called Andean knee – *Pitcairnia* continuously up to Central America. The members of the *Dyckia* clade (i.e. *Dyckia*, *Encholirium* and *Deuterocohnia*), however, apparently spread southwards along the eastern slopes of the Andes, as well as eastwards into the savannahs and forests of the Brazilian shield. Under the assumption that *Pitcairnia* reflects the ancestral conditions within the subfamily, its mesophytic habit has been maintained in *Fosterella*. *Pitcairnia* and *Fosterella* mainly differ by their flower morphologies: *Fosterella* has small and relatively inconspicuous, white flowers, which are very distinct from the much larger and more colourful ones of *Pitcairnia*. Given that the ancient character of having coloured, often bird-pollinated flowers was apparently maintained in the *Dyckia*-clade (which is sister to *Fosterella*), a shift of pollinators – from birds to insects – may have occurred in the common ancestor of the extant monophyletic *Fosterella* species. The members of the *Dyckia* clade became differentiated from their progenitor through the development of leaf succulence and CAM-photosynthesis in adaptation to xeric habitats. Varadarajan and Gilmartin (1988b) proposed that the aridity of Puna habitats could have triggered the split of the *Dyckia*-clade from the ancestor of *Fosterella*.

The most recent common ancestor of *Deuterocohnia* and *Dyckia/Encholirium* might have occurred in the already montane Andean regions of N Argentina and S Bolivia about 12.5 mya (Givnish et al. 2011), exhibiting a xerophytic rosette, a terminal, annual, simple or sparsely branched inflorescence and coloured flowers. Subsequently, the lineage of *Deuterocohnia* separated from the lineage leading to *Dyckia/Encholirium* by the development of perennial, conspicuously branched inflorescences and the formation of petal appendages. At the same time it extended its distribution area into the Inter-Andean dry valleys and eastern slopes of the Andes, climbing up to moderate or

even high altitudes. The progenitor of *Dyckia/Encholirium* [3] – or at least the ancestor of *Dyckia* – evolved a lateral inflorescence and connate stamina, and spread to the lowlands of Argentina and Brazil. After having diverged into the two lineages, the ancestors of *Deuterocohnia* and *Dyckia/Encholirium* were probably still able to hybridize with each other, but such events may have been rare, due to geographical, ecological, pre- and/or post fertilization barriers. Such an early hybridization between the two lineages may have taken place in SE Bolivia and might have caused chloroplast capture as described in chapter 4.2.1. Givnish et al. (2011) estimated that the age of the split of *Deuterocohnia* and *Dyckia/Encholirium* was approximately 8.5 mya. However, the restricted taxonomic sampling in their study did not reveal the paraphyly of *Deuterocohnia* in cpDNA data, which makes this age estimation not very reliable. Unfortunately, dated phylogenies of Bromeliaceae based on nuclear data are not available yet.

An interesting issue is the considerable difference in species number in *Dyckia* (about 130 spp., Luther 2008) on the one hand, and in *Deuterocohnia* (17 spp., present study), *Encholirium* (23 spp., Forzza 2005) and *Fosterella* (31 spp., Peters 2009) on the other. This is an especially intriguing question when comparing *Deuterocohnia*, *Encholirium* and *Dyckia*, which are all more or less similarly adapted to xeric conditions by their succulent leaves and CAM-photosynthesis (Crayn et al. 2000). As plant species richness decreases in exceptionally high or dry habitats (Givnish et al. 2001), this might be a reason for fewer species in *Deuterocohnia*, which is distributed mainly in high Andean mountain ranges. However, still the question remains of why *Deuterocohnia* could reach altitudes of almost 4000 m a.s.l., whereas it was not able to spread (like *Dyckia*) into the lowlands of Brazil. Various factors including climate (especially temperature regime), soils, differential sensitivity to fire, and/or availability of pollinators might have played a role in these differential adaptation processes, as well as habitat fragmentation (Krapp 2009). *Dyckia* could have spread into the Cerrado in dryer periods of the Late Tertiary. In more humid periods, the populations might have been restricted to rocky outcrops and genetic isolation subsequently triggered speciation processes. However, no recent revision is available for the genus *Dyckia*, and it is hence unclear yet whether all described taxa are actually good species.

[3] It is not clarified yet whether *Dyckia* and *Encholirium* are sister clades, or if *Dyckia* evolved from within *Encholirium* (Krapp 2009).

**Infrageneric evolution**

Essentially nothing is known about the historical biogeography of *Deuterocohnia* species so far. Correlating species distribution through time with the uplift of the Andes would be an intriguing task that nevertheless requires a well-established phylogeny of the genus, which has likewise been sparsely documented up till now. The present study provides a phylogenetic analysis of the genus based on cpDNA data from a relatively dense sampling of all of its species. However, the resulting topologies of tree and network reconstructions proved to reflect the geographical correlation between cpDNA haplotypes of *Deuterocohnia* rather than taxonomic relationships. Thus, specimens from the same geographical area usually share the same haplotype or closely related groups of haplotypes, regardless of the species they belong to. The situation is further complicated by the observation that the same species may have different haplotypes, if the corresponding populations grow in distant localities (e.g. *D. strobilifera* and *D. scapigera*, Fig. 3.31, 3.37). This suggests that extant populations of the different species are still connected by gene flow. On the other hand, morphological species boundaries seem to be maintained, because species that share the same or very similar haplotypes may be morphologically considerably distinct (e.g. *D. meziana* and *D. sanctae-crucis* [formerly *D. scapigera* ssp. *sanctae-crucis*], Fig. 3.32, 3.37).

The so-called porous genome concept aims to provide an interpretation for this kind of phenomena (Wu 2001). It brings together the morphological species concept (MSC) and a softened version of the biological species concept (BSC). The MSC is used mostly in plants, as it is the easiest to manage. The classical BSC presupposes reproductive isolation between species. As this is more complex to prove on the one hand, and hybridization between closely related plant species or even genera is a relatively frequent event, the BSC is not a very good descriptor for the situation in plant taxa. The porous genome concept allows some extent of gene flow between species at certain stages of differentiation, assuming that the species maintain their morphological integrity just with a few selective genes, called "speciation genes" (Rieseberg 1997). Other genes that are not subject to selection may then be interchanged between populations or even species without phenotypic consequences. Chloroplast capture can actually be regarded a special case of an exchange of such unselected genes. If the chloroplast genome does not comprise such "speciation genes" it might be interchanged between populations, without disturbing species boundaries. Under the porous gene concept, speciation genes are supposed to contribute to reproductive isolation and/or generate a favourable phenotype. Candidate genes may be involved in e.g. the regulation of anthocyanin production (changes in flower colour might cause pollinator shifts) or disease resistance genes (Rieseberg and Blackman 2010).

In accordance with the present study, Palma-Silva et al. (2011) also found a strong geographic rather than taxonomic pattern in their analyses of plastid microsatellites of four *Pitcairnia* species, which are distributed sympatrically over several inselbergs at the Brazilian coast around Rio de Janeiro. In contrast, species-related patterns were observed when microsatellites from the nuclear genome were used as genetic markers. A geographical distribution of chloroplast haplotypes independent of taxonomic boundaries was in fact reported by numerous other studies, indicating that this is a common phenomenon in recently diverged (or diverging) plant lineages (e.g. Palme et al. 2004, *Betula*; Bänfer et al. 2006, *Macaranga*; Scascitelli et al. 2010, *Helianthus*). More recently, similar observations were also made in animals: Maroja et al. (2009) analysed hybridizing cricket species and found introgression and more structured gene trees in housekeeping genes and genes from mitochondrial DNA, but near-zero introgression in two seminal protein coding genes, which might act as candidate barrier genes.

The low genetic variability within *Deuterocohnia* is reflected in the low resolution of the trees as well as in the haplotype network. By far most of the infrageneric cpDNA variation is responsible for the split between *Deuterocohnia* subclades A and B, and when we assume that this split is a consequence of an introgression event, the cpDNA of group B is actually derived from the *Dyckia/Encholirium* lineage and not from *Deuterocohnia*. Within each of the two subclades, only few mutational steps separate the different haplotypes from each other. A similarly low cpDNA variation was found in *Dyckia* (Krapp 2009) and might be explained by the young age of the two genera which has not allowed yet to accumulate a large number of mutations (Givnish et al. 2011). The lack of tree resolution is not only caused by low variation, but most probably also by ongoing interspecific gene flow (which of course is less hampered in young groups) that prevents stronger genetic differentiation. This is consistent with the finding that the Chilean *D. chrysantha* is one of the few well-supported monophyletic taxa in all analyses. The geographic isolation of this species apparently blocks gene flow to the other species of *Deuterocohnia* and thereby leads to genetic distinctness.

Although the cpDNA trees and networks do not reflect the species phylogeny they nevertheless contribute to our knowledge about the evolution of the species and thereby complement the morphological and biogeographical data. From the combined datasets, the following conclusions on the evolution of *Deuterocohnia* and its species can be drawn:

*Deuterocohnia longipetala* is supposed to represent the ancestral state within the genus. This assumption is supported by (1) the wide distribution of this species, covering a huge part of the genus' total distribution area; (2) the overlap in distribution area with species of *Dyckia* which may have evolved from the same common ancestor as *Deuterocohnia*; (3) the laxly flowered inflorescences, which are also typical for *Dyckia*; (4) the yellow petals with a greenish tip, which are typical for most other *Deuterocohnia* species.
The following six extant lineages of *Deuterocohnia* might have independently been derived from this ancestral state with a few changes each:

**(I) *D. meziana*, *D. brevispicata* and *D. seramisiana***

These three species have mostly reddish-greenish coloured flowers and occur in lowland up to montane areas of SE Bolivia. Similar to *D. longipetala, D. meziana* is characterized by laxly flowered partial inflorescences, which may be branched up to the 4$^{th}$ order. *Deuterocohnia meziana* has a relatively wide distribution area (ranging from lower and middle elevations of the Bolivian Andes to the lowlands of N Paraguay and W Brazil) and resides in very different ecoregions, ranging from the Tucuman-Bolivian dry forests to the Gran Chaco and the watershed of the Río Paraguay. Its different habitat preferences may account for the relatively strong infraspecific diversification. *Deuterocohnia meziana* ssp. *carmineo-viridiflora* climbs up the mountains of Cochabamba and Chuquisaca up to 2200 m a.s.l. *Deuterocohnia brevispicata* occurs at about the same elevation (1200–2200 m a.s.l.) of the same area, but develops much shorter and almost globose partial inflorescences. *Deuterocohnia seramisiana* is restricted to higher altitudes (2000–2400 m a.s.l.) and might have been derived from *D. brevispicata* in adaptation to different pollinators, which caused a change from reddish to yellow-greenish flower colour. These three species together formed a monophyletic group in AFLP studies (Horres 2003, Blank 2010). They are also closely related in the cpDNA based phylogeny of the present study.

**(II) *D. strobilifera***

This species is distributed at high elevations (2300–3900 m a.s.l.) in the Bolivian Puna and Prepuna regions of Potosí and Chuquisaca. In adaptation to their habitat, the size of the plants is reduced compared to *D. longipetala*. The leaves are conspicuously curved inwards, probably as a means to reduce the surface exposed to the sun and/or to reduce frost damage. The partial inflorescences are short and nearly globose as in *D. brevispicata* and *D. seramisiana*. One could therefore assume that *D. strobilifera* derived from this lineage, with a change to smaller plants and small,

completely yellow flowers. However, as the *meziana*-group is a distinct clade in all molecular analyses, *D. strobilifera* may rather have derived directly from *D. longipetala* or its progenitors.

**(III) *D. glandulosa***

The Bolivian species *D. glandulosa* resides in montane areas of the Andes, the flowers are similar to *D. longipetala* but covered with hairy indument and the partial inflorescences are more densely flowered. It might be a young, not well established species directly derived from *D. longipetala*.

**(IV) *D. haumanii*, *D. chrysantha*, *D. schreiteri* and *D. digitata***

These species all have in common the densely flowered partial inflorescences, which exhibit yellow flowers with or without greenish tips. *Deuterocohnia haumanii*, *D. schreiteri* and *D. digitata* occur in N Argentina, where *D. haumanii* and *D. schreiteri* dominate the vegetation in some areas. In contrast, *D. chrysantha* is endemic to Chile, and the only species of the genus found on the western side of the southern Andes. *Deuterocohnia chrysantha* exhibits large floral bracts, similar to the typical ones in *D. haumanii*, while the leaves, especially the leaf spines, are more reminiscent of *D. schreiteri*. As *D. chrysantha* is morphologically similar to the other species of this group, it might have evolved after an ancient long distance dispersal event from the eastern slopes of the Andes to the Atacama Desert on its Western side. Another explanation was highlighted by Zizka et al. (2009). The authors interpreted the isolated occurrence of *D. chrysantha* in Chile as a relict habitat that became separated from the remaining distribution area of *Deuterocohnia* by the uplift of the Andes. However, the geographic isolation of *D. chrysantha* is probably responsible for the genetic distinctness and monophyly in the cpDNA trees and networks. The AFLP study of Horres (2003) as well as the low copy nuclear marker trees in the present study (Fig. 3.38) revealed *D. chrysantha* to be sister to the remaining species of *Deuterocohnia*. This topology might also be a consequence of the geographic isolation of *D. chrysantha*. As there still might be gene flow between the *Deuterocohnia* species at the eastern slopes of the Andes that hampers strong genetic differentiation in large parts of the genome (see above), these samples cluster together in one clade, separated from the accessions of the genetically isolated *D. chrysantha*.

**(V) *D. recurvipetala***

The Argentinean species *D. recurvipetala* is endemic to the area of the Argentinean provenance Córdoba where it grows in the eastern Andean foothills. Its strongly recurved petals during anthesis combined with the laxly flowered branches are unique within the genus. It is likely that *D. recurvipetala* originated from *D. longipetala* populations – *D. longipetala* populations in the SE of

the genus distribution area are also more filigree and bear smaller flowers – and spread eastwards to lower elevations. Some morphological changes found in *D. recurvipetala* are also found in *Dyckia*, probably due to convergent evolution in adaptation to certain pollinators. For example, the flowers lost their greenish tip – neither present in *Dyckia* – and the petals are recurved, thereby conspicuously exposing the stamina as in many *Dyckia* species.

**(VI) *D. gableana*, *D. scapigera*, *D. sanctae-crucis*, *D. abstrusa*, *D. lotteae*, *D. brevifolia* (former *Abromeitiella* species, except *D. gableana*)**

These species all have considerably smaller rosettes than the other species of the genus. While *D. gableana*, *D. sanctae-crucis*, *D. scapigera* and *D. lotteae* are restricted to Bolivia, *D. abstrusa* and *D. brevifolia* occur mainly in Argentina. If we consider these group as a monophyletic evolutionary lineage derived from a *D. longipetala*-like ancestor, the plants may have become gradually smaller, the inflorescence shorter and less branched and the flowers slightly more greenish. This evolutionary stage is represented by *D. gableana*. Continuing selection in terms of size minimization and polster formation finally led to the evolution of the smallest species within the genus, *D. brevifolia*. As *D. gableana* and *D. sanctae-crucis* occur in altitudes of about 1000 to 2000 a.s.l. in central-south Bolivia, the remaining species of this group might have reached high elevations of more than 3000 m a.s.l. in two lineages. One lineage comprising only *D. scapigera* migrated westward into the mountains of the Bolivian Departments Potosi and Chuquisaca, whereas the other lineage including *D. brevifolia*, *D. lotteae* and *D. abstrusa* spread southward to Tarija and further to Argentina.

The evolution of the six lineages described above would have been accompanied by the evolution of a set of selected character states. The conclusions listed below can be drawn if we consider *D. longipetala* to carry the following ancient character states: (1) moderate plant size, (2) laxly flowered partial inflorescences with branches usually up to 2$^{nd}$ order and first branches in the second year, (3) yellow flowers with greenish tip and (4) erect petals.

(1) Leaf size has enlarged once in the *meziana*-group, but was reduced at least two times independently: in the *gableana*-group and in *D. strobilifera*. (2) Densely flowered partial inflorescences emerged several times independently, i.e. in the *meziana*-group, in the *haumanii*-group, in *D. glandulosa* and in *D. strobilifera*. Enlarged partial inflorescences with branches up to 4$^{th}$ order, which branch already in the first year, evolved once in *D. meziana*. (3) The flower colour yellow is present in most of the species. However, reddish to orange colour shades evolved two times independently, once in *D. lotteae* and a second time in the *meziana*-group. In *D. meziana* this character state diversified considerably, resulting in various colour shades and colour combinations of

sepals and petals. In *D. seramisiana* the ancestral state of yellowish petals re-evolved. The greenish petal tip typical for *D. longipetala* and most other *Deuterocohnia* species got lost three times independently, i.e. in *D. digitata* and *D. strobilifera* which are both distributed in high altitudinal ranges, and in *D. recurvipetala*, which occurs in the Andean foothills. (4) Recurved petals evolved two times independently, once in *D. strobilifera* and a second time in *D. recurvipetala*.

To summarize, the species of *Deuterocohnia* apparently originated in lower montane Andean regions and their ancestral character states are assumed to be represented by the extant *D. longipetala*. Six main lineages can be differentiated, which might represent three monophyletic groups. These are the *meziana*-group (I), the *gableana*/*brevifolia*-group (VI) and a lineage comprising the remaining four groups (II, III, IV, V). Each of these lineages conquered high Andean elevations independently. Morphologically, the species adapted to the environmental conditions at higher altitudes by developing smaller rosettes, densely flowered partial inflorescences and shorter flowers. In contrast, the species that spread into the lowlands developed larger plants, larger flowers and laxly flowered, amply branched inflorescences. Only two species spread to the eastern lowlands (*D. meziana* (I) and *D. recurvipetala* (V)). While in N Argentina some species of *Deuterocohnia* show high levels of occupancy in some of their habitats, the species found in Bolivia form more scattered populations in forest understorey or are restricted to rocky outcrops. Pollinator shifts, habitat fragmentation during the Andean uplift and Ice Ages as well as occasional long-distance dispersal are supposed to be key factors that triggered the diversification within the genus. Thus, vicariance or an ancient long distance dispersal event is assumed to be responsible for the evolution of the Chilean endemic *D. chrysantha*, and – given that the morphology of the plants from the Peruvian populations of *D. longipetala* is very similar to the morphology of those from Argentina – a more recent long distance dispersal event may explain the disjunct distribution area of *D. longipetala*.

# 5 TAXONOMIC TREATMENT

## 5.1 Generic description

***Deuterocohnia*** Mez, in Mart., Fl. bras. 3(3): 506-507. 1894. Type: *Dyckia longipetala* Baker. *Humboldt and Bonpland 3595* [holotype: B (not seen, probably destroyed), photo in F 11389!] ≡ *Deuterocohnia longipetala* (Baker) Mez.

= *Abromeitiella* Mez, Bot. Arch. 19: 460. 1927. Type: *Abromeitiella pulvinata* Mez. *Fiebrig 3573* [holotype: B (not seen, probably destroyed), isotypes: BM!, E, G!, K!, M!, photo ex E in WU!]

= *Meziothamnus* Harms, Notizbl. Bot. Gart. Berlin-Dahlem 10 (96): 575. 1929. Type: *Navia brevifolia* Griseb., Symb. fl. argent. in Abh. Königl. Ges. Wiss. Göttingen 24: 332. 1879. ≡ *Meziothamnus brevifolius* (Griseb.) Harms.

**Plants** small to large evergreen herbaceous chamaephytes, polycarpic, terrestrial or saxicolous, acaulescent or caulescent, often forming rings or cushions by sympodial branching, 2–60 × 2–75 cm, incl. inflorescence up to 200 cm. **Leaves** numerous (>20), rosulate, outer leaves inclined, inner leaves appressed, forming a dense, upright to arched rosette. **Sheaths** 0.5–5 × 1–10 cm, ample, broadly ovate to reniform, tightly surrounding the short stem, entire or slightly serrate, succulent with membranous margin, glabrous in the lower part, lepidote towards the blade, whitish to brownish. **Blades** 1.5–60 × 0.5–8 cm, simple, recurved or incurved, adaxially plane, concave or channelled, narrowly triangular, never constricted at base, narrowly acute towards the pungent apex, succulent, spinose with antrorsely or retrorsely curved, brownish spines of 1–5 mm length or margin rarely entire, lepidote on the adaxial surface, rarely densely lepidote, abaxially densely lepidote, green to greyish, rarely reddish. **Peduncle** usually present, incl. inflorescence 5–200 cm × 2–10 mm, erect, perennial, woody, glabrous, rarely absent. **Peduncle bracts** 2–11 × 0.2–2 cm, appressed, the lower ones exceeding the internodes, narrowly triangular, narrowly acute, spinose-serrate or entire, abaxially lepidote, sheaths inconspicuous, adnate to the peduncle. **Inflorescence** terminal, without peduncle and branches and 1–3-flowered or 4–70 [–100] cm long and branched or unbranched and many-flowered, spikes or racemes, compound or simple, branches of 1$^{st}$ to 4$^{th}$ order, perennial or annual. **Primary bracts** 3–50 × 2–15 mm, longer or shorter than the partial inflorescence or shorter than the sterile base of it, narrowly triangular

to ovate, narrowly acute to acute, entire, glabrous or lepidote, brownish. **Partial inflorescences** 4–40 cm long, ascending to inclined, densely to laxly flowered, axis visible or concealed, spikes or racemes, simple or branched, at times spheroidal or cylindrical, young axes glabrous or lanate, few to many-flowered. **Floral bracts** 2–15 × 2–8 mm, about equaling the sepals or much shorter, ovate or triangular, acuminate, acute or obtuse, mucronate or aristate, entire, herbaceous to scarious, laxly lepidote to glabrous, brownish, reddish or greenish. **Flowers** 11–50 × 3–5 mm, spirally arranged, ascending, perfect, actinomorphic, tubular, sessile, rarely with pedicels 0.5–15 mm long. **Sepals** 3, free, 5–20 × 3.5–6 mm, erect, asymmetric, ovate to lanceolate, obtuse to acute, often mucronulate, slightly carinate, entire, herbaceous, glabrous, papillose or slightly lepidote, greenish, yellowish or reddish colour shades, persistent. **Petals** 3, free, 11–45 × 4–11 mm, exceeding the sepals, erect, with slightly recurved apex or completely recurved during anthesis, erect afterwards, after anthesis more or less spirally twisted, symmetric, narrowly oblong to oblanceolate, slightly spathulate, rounded to obtuse, ecarinate, entire, membranous, glabrous, greenish, yellowish or reddish colour shades, persistent. **Petal appendages** present, each petal bearing a single basal, fringed appendage, 2–7 mm long, the base adnate to the petal. **Androecium** with 6 free stamina in two whorls, the antipetalous adnate to the base of the petals, erect. **Filaments** 8–35 mm long. **Anthers** 3–5 mm long, linear, erect, recurved or coiled at anthesis, sub-basifixed, longitudinally dehiscent, usually concealed, rarely exposed, greenish to yellowish. **Pollen** in monads, grains 40–48 × 23–30 μm, oblate, sulcate, reticulate to foveolate. **Gynoecium** 3-carpellate, syncarpous. **Ovary** 2.5–5 mm long, superior, ovoid, trilocular, axile placentation with numerous ovules, septal nectaries present. **Style** 10–40 mm long, terminal, filiform, whitish, greenish or reddish. **Stigma** trilobed, conduplicate-spiral, usually exposed, rarely concealed. **Fruits** 6–12 [–15] × 4–9 mm, capsular, ovoid to pyriform, septicidal, partially loculicidal, glabrous, brownish. **Seeds** 1.5–4 mm long, clavate to fusiform, dorsally and apically alate, brownish, the appendage fawn.

**Distribution.** Currently, 17 species are accepted, which all occur in Central South America between approx. 5°–34° S and 80°–56° W. The centre of diversity is located in S Bolivia and N Argentina. The genus appears also in N Peru, W Brazil and N Paraguay. One species (*D. chrysantha*) is endemic to N Chile.

**Habitat and ecology.** Ecoregions (numbers refer to Olsen et al. 2001, see 2.2.3): Peruvian Yungas (56), Andean Yungas (64), Tumbes/Piura dry forests (93), Marañon dry forests (94), Bolivian Montane Dry forest (95), Chaco savannas (96), Chiquitania dry forests (97), Arid Chaco (131), Humid Chaco (132), Córdoba montane savannas (134), Argentina Monte (136), Argentine Espi-

nal (137), Central Andean puna (156), Chilean mattoral (160). At elevations of 20–3900 m a.s.l. Terrestrial or saxicolous, on rocky slopes or bare rocks, in arid habitats. In open shrubland, in the understory of deciduous dry forests or in azonal habitats in evergreen forests. Ornithophilous and entomophilous.

**Etymology.** The name *Deuterocohnia* is dedicated to the German botanist and microbiologist Ferdinand Julius Cohen (1828–1898). As there had been already genera named *Cohnia* (syn. for *Cordyline* Comm. ex R. Br., Asparagaceae) and *Cohniella* (syn. for *Oncidium* Sw., Orchidaceae), this genus was named *Deuterocohnia* (Greek *deuteros* = second).

**Chromosome number**. 2n=50. (McWilliams 1974, Brown and Gilmartin, 1984, 1989, Horres 2003, Gitai et al. 2005). One sample of the former *D. lorentziana* exhibited 2n=100 (Horres 2003, Gitai et al. 2005).

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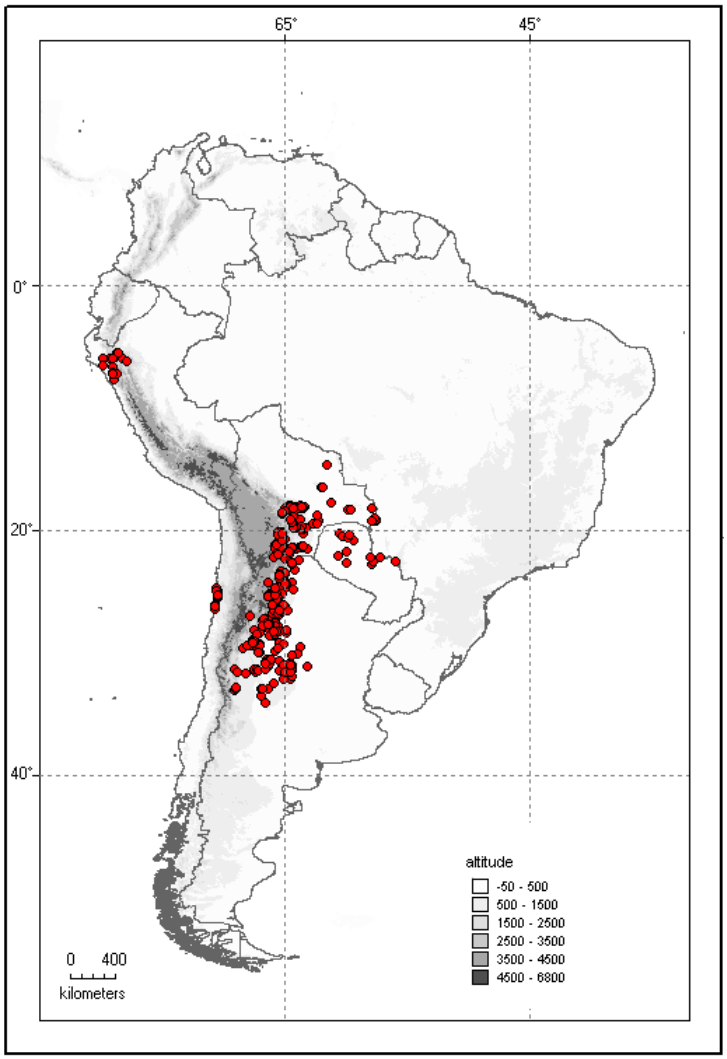


Fig. 5.1: Distribution of the genus *Deuterocohnia*.

## 5.2 Key to the species of the genus *Deuterocohnia* Mez #

1. Peduncle absent; inflorescence simple, annual, flowers few [1–4]; rosettes 2–12 [–15] cm in diam., forming extended cushions; leaf blades 1.5–8 cm long ..... 2

1. * Peduncle present, woody, conspicuously exceeding the rosette, rarely shorter, inflorescence compound, rarely simple, perennial, rarely annual; rosettes [7–] 10–100 cm in diam., forming rings or cushions; leaf blades 5–80 [–100] cm long ..... 4

2. Flowers reddish, S Bolivia ..... ***D. lotteae*** 181

2. * Flowers greenish, S Bolivia, N Argentina ..... 3

3. Rosettes 2–6 cm in diam.; leaf blades 1.5–4.5 cm long, adaxial side greenish lepidote, margin with many, few or without spines ..... ***D. brevifolia*** 142

3. * Rosettes 5–12 [–15] cm in diam., leaf blades 4–8 cm long, adaxial side greyish lepidote, margin with few spines ..... ***D. abstrusa*** 137

4. Peduncle concealed by the leaves or shortly exceeding the rosette; inflorescences simple, rarely compound, annual, rarely perennial; flowers 30–35 mm long, yellow-greenish; rosettes [7–] 10–20 cm in diam.; leaf blades 5–18 cm long, ..... 5

4. * Peduncle conspicuously exceeding the rosette (if shorter, then flowers 10–16 mm long); inflorescences compound (for some species simple in the first year of blooming #), perennial; flowers yellow, greenish, reddish or orange colour shades; rosettes 20–100 cm in diam.; leaf blades 8–80 [–100] cm long ..... 7

5. Peduncle shortly exceeding the rosette; pedicels distinct (1–3 mm); rosettes 15–20 cm in diam., leaf blades 12–18 cm long ..... ***D. gableana*** 161

5. * Peduncle concealed by the leaves; flowers sessile to subsessile; rosettes 7–15 cm in diam.; leaf blades 5–12 cm long ..... 6

6. Inflorescence simple, rarely branched; floral bracts 10–15 mm long, exceeding or equaling the sepals; rosettes 10–15 cm diam.; leaf blades 7–12 cm long; Bolivia, Dept. Chuquisaca and Potosí, 2400 to 3300 m a.s.l. ..... ***D. scapigera*** 206

6. * Inflorescence branched, rarely simple, floral bracts 5–10 mm long, shorter than the sepals; rosettes 6–12 cm diam.; leaf blades 5–10 cm long; Bolivia, Dept. Santa Cruz, 1200 to 2500 m a.s.l. ..... ***D. sanctae-crucis*** 202

7. Partial inflorescence laxely flowered, axes visible ..... 8
7. * Partial inflorescence globose or strobilate, the axes completely or almost completely concealed ..... 10

8. Inflorescence usually branched from the first year on; floral bracts 1–2 [–5] mm; flowers [20–] 30–50 cm long, sessile, subsessile or pedicellate, yellow, orange or reddish colour shades, always with a greenish tip; sepals 10–20 mm long, acuminate; leaf blades 25–80 [–100] cm long; Bolivia, Brazil, Paraguay ..... ***D. meziana*** 184
8. * Inflorescence usually starts branching in the second year; floral bracts 3–6 mm; flowers 10–27 mm long, sessile, yellow or yellow with greenish tip; sepals 6–12 cm long, obtuse; leaf blades 20–40 cm long; Argentina and border region to Bolivia, Peru ..... 9

9. Petals and anthers erect during anthesis; flowers 22–27 mm long; sepals greenish or yellow; petals 22–28 mm long, yellow with a greenish tip; leaf blades greenish or greyish lepidote ..... ***D. longipetala*** 172
9. * Petals and anthers recurved during anthesis; flowers 14–16 mm (recurved 10–11 mm) long; sepals yellow; petals 14–15 mm long, yellow; leaf blades greyish lepidote ..... ***D. recurvipetala*** 199

10. (Lower) primary bracts longer than the partial inflorescence; partial inflorescence short, globose ..... 11
10. * (Lower) primary bracts shorter than the partial inflorescence; partial inflorescence strobilate ..... 13

11. Flowers 12–16 mm long, yellow, single-coloured; petals and anthers recurved during anthesis; leaf blades 8–25 [–28] cm long, conspicuously incurved and greyish lepidote (might be recurved and greenish for cultivated plants) ..... ***D. strobilifera*** 217
11. * Flowers 17–24 mm long, reddish or yellow-greenish, with greenish tip; petals and anthers erect during anthesis; leaf blades 30–60 cm long ..... 12

12. Petals reddish with green apex; sepals reddish; floral bracts shorter than the sepals; leaf blades 35–60 [–70] cm long ..... ***D. brevispicata*** 148
12. * Petals yellow-greenish; sepals brownish-reddish; floral bracts longer than the sepals; leaf blades 30–45 cm long ..... ***D. seramisiana*** 214

13. Flowers 10–16 [–21] mm long, petals yellow or orange, rarely with greenish tip ..... 14

13. * Flowers larger (20–32 mm long), yellow with greenish tip, Argentina, Bolivia, Chile ..... 15

14. Peduncle long (20–30 cm); internodes between partial inflorescences 1.5–2 cm long; flowers 10–16 [–21] mm long; petals yellow, single-coloured; leaf blades adaxially greenish or greyisch lepidote ..... ***D. schreiteri*** 210

14. * Peduncle short (5–10 cm); internodes short, inflorescence subdigitate; flowers [10–] 14–15 mm long; petals orange-yellow, single-coloured; leaf blades slightly incurved and adaxially greyish lepidote ..... ***D. digitata*** 157

15. Floral bracts 10–15 mm long; flowers [25–] 30–32 mm long; sepals glabrous; anthers recurved; leaf blades bright reddish, often incurved (might be greenish and recurved for cultivated plants), leaf spines horizontal or retrorse, Chile, 20–800 m a.s.l. ..... ***D. chrysantha*** 153

15. * Floral bracts 4–12 mm long; flowers 20–29 mm long; sepals bearing glandular trichomes, rarely glabrous; anthers erect, leaf blades greenish or dark red, leaf spines antrorse; Bolivia, Argentina ..... 16

16. Floral bracts [4–] 8–10 [–12] mm long; flowers [20–] 22–29 mm long; sepals mucronulate; leaf blades 20–35 cm long; Argentina ..... ***D. haumanii*** 167

16. * Floral bracts 4–6 mm long; flowers 20–26[–28] mm long; sepals not mucronulate; leaf blades 30–45 cm long; Bolivia ..... ***D. glandulosa*** 163

# It has to be noticed, that several species generate secondary branches of the inflorescences not until the second year of maturity.

## 5.3 Species descriptions

***Deuterocohnia abstrusa*** (A. Cast.) N. Schütz, comb. nov. ≡ *Abromeitiella abstrusa* A. Cast., Anales Mus. Nac. Hist. Nat."Bernardino Rivadavia" 36: 369. Fig. 1, 5. 1931. Type: Argentina: Prov. Catamarca: Dept. Andalgalá: Cuesta de la Chilca, Cumbre del Pucará, 12 Jul. 1929. *Castellanos 29/60* [lectotype: BA! (2 sheets), photo ex BA in B!, K!, NY!, isolectotype: US, WU!].

− *Abromeitiella lorentziana* sensu Castellanos, Lilloa 10: 459. 1944. p. p.: *Castellanos 29/60*.

− *Abromeitiella lorentziana* sensu Smith and Downs (1974), Fl. Neotrop. Monogr. 14(3): 244, 245. 1974. p. p.: *Castellanos s.n.*, *Castillon 6458*, *Castellanos 30/404*, *Jörgensen 1773*, *Castellanos 28/2296*, *Castellanos 28/2297*, *Christobal and Türpe 111* [LIL!] (*Escalante and Agosti 87*, *Piccardo 30-A*, *Hunziker and Fulvio 19653* not seen).

**Plants** growing in dense cushions. **Rosettes** 7–14 [–20] × 5–12 [–15] cm. **Leaf sheaths** 0.5–1.3 × 1.5–2 cm. **Blades** 4–8 × 1–1.8 cm, recurved to straight, adaxially concave to plane, spinose-serrate, lepidote, greenish-greyish. **Peduncle** absent. **Inflorescence** simple, annual, 1–3-flowered. **Floral bracts** 9–13 × 3–4 mm, much shorter than the sepals, ovate, acute, mucronate, sparsely lepidote, greenish to brownish. **Flowers** 26–32 [–35] mm long, sessile. **Sepals** 10–14 × 3–4 mm, ovate to lanceolate, obtuse, mucronulate, sparsely lepidote, greenish. **Petals** 25–32 [–35] × 4–5 mm, erect during anthesis, after anthesis slightly spirally twisted, yellow-greenish, with green apex. **Petal appendages** 4–5 mm long, with short fringes. **Filaments** 20–25 mm long. **Anthers** 4–5 mm long, erect, concealed, greenish. **Ovary** 5–6 mm long. **Style** 20–30 mm long, stigma exposed. **Fruits** 10–12 [–15] mm diam. **Seeds** 3–4 mm long.

**Distribution.** BOLIVIA. Dept. Tarija. ARGENTINA. Prov. Jujuy, Salta, Tucumán, Catamarca, La Rioja. 21°40'–29°20' S, 64°30'–68°05' W.

**Habitat and ecology.** Ecoregions: Central Andean puna (156), Andean Yungas (64), Argentina Monte (136). At elevations of 1500–3200 m a.s.l. Terrestrial, forming cushions on open, rocky slopes, abundant at its localities. Dry scrub vegetation, in association with barrel cacti. Flowering time from September to February. Pollinated by insects or birds.

**Etymology.** The etymology was not explained by Castellanos. It may refer to the concealed inflorescence or the ramification hidden within the cushions. (Latin *abstrusus*: hidden, concealed).

**Affinities.** *D. abstrusa* is morphologically closely related to *D. brevifolia*, but is characterized by larger rosettes with a laxer leaf arrangement and usually a denser indument. For further information about the delimitation of *D. brevifolia* and *D. abstrusa* see 4.2.3.

**Notes and comments.** (a) *Abromeitiella abstrusa* has been formerly included in the synonymy of *A. lorentziana*. The *A. abstrusa* element is now re-established as an own species and transferred to *D. abstrusa*, whereas the *A. lorentziana* element is considered synonymous with *D. brevifolia*. (b) IUCN: *rare* (*D. lorentziana*; see 3.5.4).

**Further references.** Mez in Engler, Pflanzenr. IV. 32. (100): 279. 1934. Castellanos in Descole, Gen. Spec. Plant. Argent. 3: 188. 1945. Smith, Bromeliana 1(8): 3. 1964. Smith, Phytologia 15(3): 163, 198. 1967. Viers, Ann. Géogr. 76(416): 417. 1967. Janse, Succulenta (Netherlands) 47(10): 156. 1968. Smith and Downs, Fl. Neotrop. Monogr. 14(3): 244, 245. 1974. Rauh, Kakteen And. Sukk. 29(6): 146. 1978. Coester and Motschenbach, Bromelie 1: 74, 75. 1981. Varadarajan and Gilmartin, Syst. Bot. 12(4): 562–571. 1987 (micromorphological study). Schill et al., Beitr. Biol. Pflanzen 63: 221–252. 1988 (morphological study). Rauh, Bromelien: 410. 1990. Brown and Terry, Amer. J. Bot. 79(9): 1051–1071. 1992 (morphological study). Galetto and Bernardello, Bot. Acta 105(4): 292–299. 1992 (physiological study). Spencer and Smith, Bradea 6: 144. 1992. Horres and Zizka, Beitr. Biol. Pflanzen 69(1): 43–76. 1995 (anatomical study). Zuloaga and Morrone, Monogr. Syst. Bot. Missouri Bot. Gard. 60: 106, 109. 1996. Krömer et al., Selbyana 20(2): 207. 1999. López, Ecol. Bolivia 34: 45–70. 2000. López, Ecol. Bolivia 38(1): 42. 2003. Givnish et al., Int. J. Plant Sci. 165(4 Suppl.): S35–S54. 2004 (phylogenetic study). Givnish et al., Aliso 23: 3–26. 2007 (phylogenetic study). Paggi et al., Mol. Ecol. Resour. 8: 982. 2008 (molecular study). Zuloaga et al., Monogr. Syst. Bot. Missouri Bot. Gard. 107(1): 1–983. 2008. Jørgensen et al., Monogr. Syst. Bot. Missouri Bot. Gard. 45: 1–1286. 2010.

**Specimens seen.** BOLIVIA: **Dept. Tarija:** Prov. Avilés: 29 km on road from Tarija to Bermejo, at Rio Camachu, 21°42'15" S, 64°36'02" W, 1685 m, 11 Oct. 2006, *Schütz et al. 06-054* [LPB!]; ibid.: *Schütz et al. 06-056* [FR!]; ibid.: *Schütz et al. 06-057* [LPB!]; ibid.: *Schütz et al. 06-058* [FR!].
ARGENTINA: 1988, *Till, H. s.n.* [WU 2519!]; near Campana, 2000 m, 05 Sep. 1983, *Rauh 64065* [HEID! (2 sheets)]. **Prov. Jujuy:** Dept. Humahuaca: between Chuscalena and Senador Pérez (23°18' S, 65°21' W), 2800 m, 21 Jan. 1921, *Castellanos s.n.* [BA 1048!]; Dept. Tilcara: near Tilcara, Quebrada Huichaira, (23°34' S, 65°25' W), 3200 m, 25 Jan. 1999, *Beck and Paniagua 26545-A* [LPB!]; about 100 m from the road Tilcara a Garganta del Diablo, 23°34' S, 65°23' W, 2700–2800 m, 20 Feb. 1984, *Varadarajan et al. 1259* [GH!, MCNS!, US!]; Garganta del Diablo, (23°35' S, 65°22'30" W), 26. Jul. 1948, *Castellanos s.n.* [LIL 313257!]; Sierras de Tilcara, (23°35' S, 65°25' W), 3000 m, 10 Mar. 1957, *Cristobal and Türpe 111* [LIL!]; Garganta del Diablo, (23°35' S, 65°22'30" W), 2800 m, 13 Oct. 1985, *Palací 177* [MCNS! (2 sheets)]; ibid.: 18 Oct. 1986, *Palací 775* [MCNS!]; Quebrada de Huasamayo, (23°40' S, 65°25' W), 2600 m,

06 Feb. 1959, *Cabrera et al. 13167* [M!, US!]; 2,2 km north of Quebrada de Incahuasi, 100–200 m from the road, on east facing slopes, 23°40' S, 65°26' W, 2400–2450 m, 20 Feb. 1984, *Varadarajan et al. 1260* [US!]. Dept. Tumbaya: Volcán, (23°55' S, 65°08' W), 30 Nov. 1918, *Castillon 6458* [BA!, LIL!]. **Prov. Salta:** Valles Calchaquíes, *Schreiter s.n.* [LIL 34643!]. Dept. Rosario de Lerma: Quebrada del Toro, nearby the road from Chorrillos to Río Jucamayo, (24°45' S, 65°45' W), 2250 m, Oct. 1988, *Till, H. 88-149*, [WU!]. Dept. Chicoana: Huaira Huasi, km 30 auf RP 33 von RN 68, from Pulares to Payogasta and Cachi , 25°09'14" S, 65°43'11" W, 1796 m, 27 Nov. 2006, *Schütz et al. 06-085* [LIL!]; ibid.: *Schütz et al. 06-086*, [LIL!]; ibid.: *Schütz et al. 06-092*, [LIL!]. **Prov. Tucumán:** Dept. Lules: Quebrada de Lules, Nov. 1918, *Schreiter 27/2334* [WU!]. **Prov. Catamarca:** Dept. Belén: below the mine Farallón Negro–Hualfín, (27°15' S, 66°50' W), 1520 m, Dec. 1993, *Neuhuber and Amerhauser 697-2021*, [WU!]. Dept. Andalgalá: Apr. 1917, *Jörgensen 1773* [BA!, GH!, LIL!, SI, US!]; Capillitas, (27°21' S, 66°22' W), *O'Donell s.n.* [LIL 114012!]; Cuesta de la Chilca, 27°36' S, 66°20' W, 1850–1900 m, 23 Feb. 1984, *Varadarajan and Bilos 1271* [GH!, US!]; Cuesta de la Chilca, (27°38' S, 66°11' W), 1500 m, 03 Nov. 1930, *Schreiter 6417* [BA!, F 1403196!, LIL! (2 sheets)]; Cuesta de la Chilca, Cumbre del Pucará, (27°43' S, 66°02' W), 12 Jul. 1929. *Castellanos 29/60* [BA! (2 sheets), US, WU!, photo ex BA in B!, K!, NY!]. Dept. Tinogasta: Quebrada de San Buenaventura, (26°58' S, 67°50' W), 07 Feb. 1930, *Castellanos 30/404* [BA! (2 sheets), GH!, SI]; La Cripito to Vallecito, 3100 m, 06 Feb. 1930, *Schreiter 6258* [LIL! (2 sheets)]. **Prov. La Rioja:** Dept. Famatina: Cerro Famatina, Cuesta de los Duraznos Blancos, (28°51' S, 67°37' W), 18 Jan. 1928, *Castellanos 28/2296* [BA! (2 sheets)]; Río Famatina, (28°55' S, 67°31' W), 1700 m, 20 Apr. 1951, *Sparre 8705* [LIL!]. Dept. Chilecito: Cordón de Vilgo, near Cachiyuyal, (29°19' S, 67°44' W), 03 Feb. 1928, *Castellanos 28/2297* [BA! (2 sheets), K!].Sierra de Sañogasta (Famatina), Cuesta de Miranda, on RN 40 (+/- km 549) above Miranda, (29°20' S, 67°35' W), 1900 m, 05 Dec. 1969, *Hunziker 20218* [CORD!]; Cuesta de Miranda, (29°20' S, 67°46' W), 02 Feb. 1907, *Kurtz 14317* [CORD!]; 18 km W of Miranda, Cuesta Miranda, (29°20' S, 67°46' W), 1880 m, 08 Feb. 1990, *Till, W. 5108* [WU!]. Dept. Coronel Felipe Varela: near the road from Chilecito to Villa Union, km 502, after Puerto Allegre, before the bifurcation to Pagancillo, (29°20' S, 68°05' W), 1450 m, 20 Oct. 1987, *Till, H. 89* [WU!].

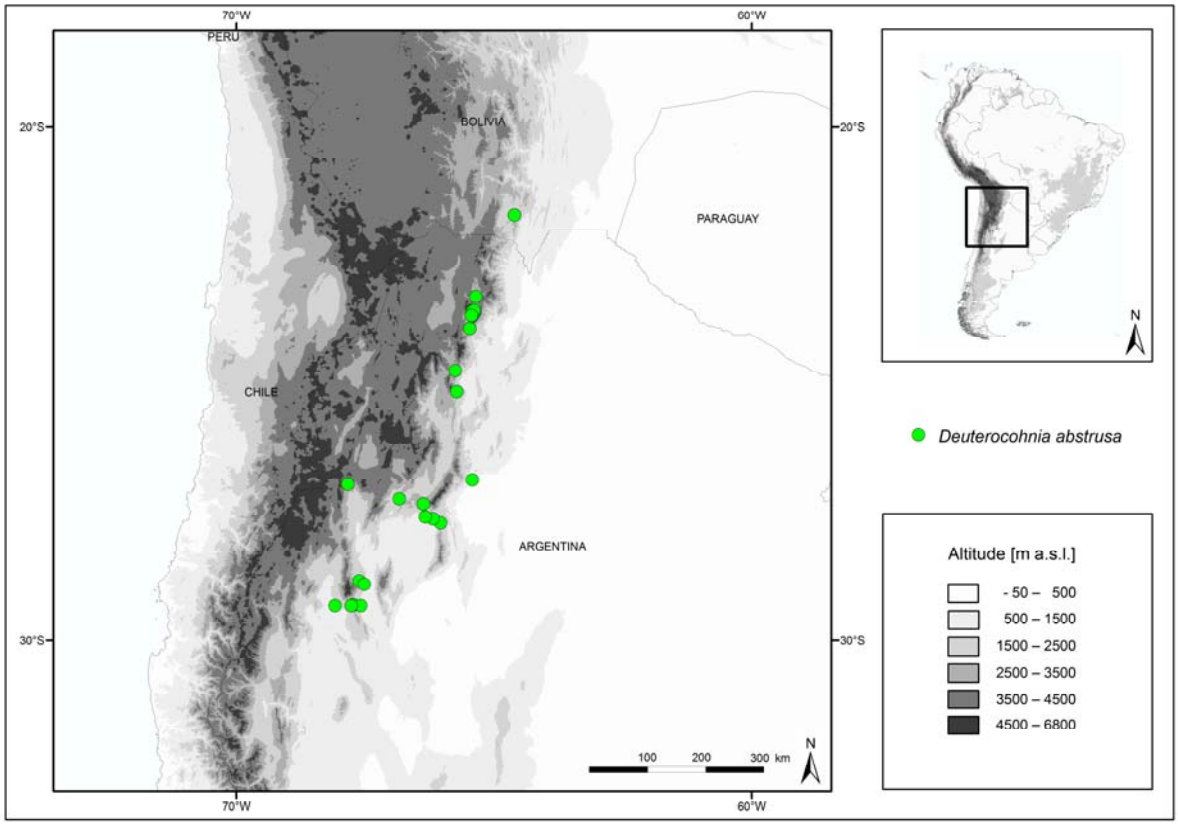


Fig. 5.2: Distribution of *D. abstrusa*.


Fig. 5.3: *D. abstrusa*. a: Natural habitat, Dept. Tarija, Bolivia, (*N. Schütz 06-054*). b: Flower. c: Plant (*W. Till 10098a*) in the greenhouse of the BG Vienna. d: Drawing of plant and floral elements by Castellanos (1945).

***Deuterocohnia brevifolia*** (Griseb.) M.A. Spencer & L.B. Sm., Bradea 6: 144: 1992. ≡ *Navia brevifolia* Griseb., Symb. fl. argent. in Abh. Königl. Ges. Wiss. Göttingen 24: 332. 1879. ≡ *Dyckia grisebachii* Baker, Handb. Bromel. 130. 1889. ≡ *Pitcairnia brevifolia* (Griseb.) R.E. Fr., Nova Acta Regiae Soc. Sci. Upsal. IV.1(1): 73. Fig. 1. 1905. ≡ *Lindmania brevifolia* (Griseb.) Hauman, Anales Mus. Nac. Hist. Nat. Buenos Aires 29: 413. Fig. 2, 3. 1917. ≡ *Meziothamnus brevifolius* (Griseb.) Harms, Notizbl. Bot. Gart. Berlin-Dahlem 10 (96): 576. 1929. ≡ *Abromeitiella brevifolia* (Griseb.) A. Cast., Anales Mus. Nac. Hist. Nat."Bernardino Rivadavia" 36: 371. 1931. Type: Bolivia, Dept. Tarija, Prov. O'Connor, Valle de Tambo, (21°25' S, 64°15' W), 11 Jun. 1873, *Lorentz and Hieronymus 947* [lectotype: GOET!, photo in NY!, isolectotype: CORD].

= *Pitcairnia lorentziana* Mez in C.DC., Monogr. phan. 9: 373. 1896. ≡ *Hepetis lorentziana*, Mez in C.DC., Monogr. phan. 9: 974. 1896. nom. nud. ≡ *Abromeitiella lorentziana* (Mez) A. Cast., Lilloa 10: 459. 1944. p.p. ≡ *Deuterocohnia lorentziana* (Mez) M.A. Spencer & L.B. Sm., Bradea 6: 144. 1992. p.p. Type: Argentina, Prov. Catamarca, Dept. Andalgalá, Cuesta de la Chilca, 13 Feb. 1872, *Lorentz s.n.* [holotype: B (not seen, probably destroyed), photo in F (negative 11386)!].

= *Tillandsia chlorantha* Speg., Comun. Mus. Nac. Buenos Aires 1: 87. 1899. ≡ *Lindmania chlorantha* (Speg.) Hauman, Anales Mus. Nac. Hist. Nat. Buenos Aires 29: 415, 416. 1917. ≡ *Pitcairnia chlorantha* (Speg.) A. Cast., Comun. Mus. Nac. Hist. Nat. „Bernardino Rivadavia" 2(14): 142. 1925. (synonymized by Castellanos, Anales Mus. Nac. Hist. Nat."Bernardino Rivadavia" 36: 371. 1931). ≡ *Abromeitiella chlorantha* (Speg.) Mez in Engler, Pflanzenr. IV. 32. (100): 279, 280. Fig. 67. 1934 (see "Notes and comments" below). ≡ *Abromeitiella brevifolia* (Griseb.) A.Cast. ssp. *chlorantha* (Speg.) Schultze-Motel, Bot. Jahrb. Syst. 96: 423. 1975. Type: Argentina, Prov. Salta, Dept. Guachipas, Pampa Grande, 3000 m a.s.l., Jan. 1897, *Spegazzini s.n.* [holotype: LP 200!].

= *Abromeitiella pulvinata* Mez, Bot. Arch. 19: 460. 1927. (synonymized by Smith, Phytologia 15(3): 163, 198. 1967). Type: Bolivia, Dept. Tarija, 1903–04, *Fiebrig 3573* [holotype: B (not seen, probably destroyed), isotypes: BM!, E, G!, K!, M!, photo ex E in WU!].

**Plants** growing in dense cushions. **Rosettes** 2–10 [–15] × 2–6 cm. **Leaf sheaths** 0.5–1 × 1–1.5 cm. **Blades** 1.5–4.5 × 0.5–1.5 cm, recurved to straight, adaxially concave to plane, spinose-serrate or entire, lepidote, greenish. **Peduncle** absent. **Inflorescence** simple, annual, 1–3-flowered. **Floral bracts** 9–13 × 4–5 mm, much shorter than the sepals, ovate, acute, mucronate, entire, sparsely lepidote, greenish to brownish. **Flowers** [20–] 25–30 mm long, sessile. **Sepals** 10–14 × 3–4 mm, ovate, obtuse, mucronulate, sparsely lepidote, greenish. **Petals**[20–] 25–30 × 5–6 mm, erect during anthesis, after anthesis slightly spirally twisted, yellow-greenish, with green apex. **Petal appendages** 4–5 mm long, with short fringes. **Filaments** 18–23 mm long. **Anthers** 3–4 mm long, erect, concealed, greenish. **Ovary** 4 mm long. **Style** 22–27 mm long, stigma exposed. **Fruits** 8–9 × 5–9 mm. **Seeds** 2-3 [–4] mm long.

**Distribution.** BOLIVIA. Dept. Tarija. ARGENTINA. Prov. Jujuy, Salta, Tucumán, Catamarca. 21°25'–27°40' S, 64°15'–66°25' W.

**Habitat and ecology.** Ecoregions: Andean Yungas (64), Bolivian Montane Dry forest (95). At elevations of 1000–3000 m a.s.l. Terrestrial or saxicolous, on stony slopes, moist rocks, open, thorny shrub vegetation. Growing together with *Larrea divaricata*, *Bulnesia schickendanzii* (all Zygophyllaceae), *Chuquiraga erinacea*, *Gochnatia glutinosa*, *Plazia spartioides* (all Asteraceae), *Buddleja tucumanensis* (Buddlejaceae), *Monnina angustifolia* (Polygalaceae), *Cassia crassiramea* (Caesalpiniaceae). Main flowering time from September to December, single collections with flowers also in July and August. Pollinated by insects or birds.

**Etymology.** The epithet refers to the short leaves (Latin *brevis* = short, little; *folium* = leaf).

**Affinities.** The species is closely related to *D. lotteae*, from which it differs in having greenish flowers (reddish in *D. lotteae*). *D. brevifolia* shows also similarity to *D. abstrusa*, but has smaller rosettes and less dense indumentum on the adaxial leaf surface. For further information about the delimitation of *D. brevifolia* and *D. abstrusa* see 4.2.3.

**Notes and comments.** (a) The taxonomic treatment of *Deuterocohnia brevifolia* and synonyms is quite complex and described in 3. (b) Mez (1934) established the new combination *Abromeitiella chlorantha* (Harms) Mez. Due to the epitheton "*chlorantha*", the combination should have been cited correctly as *Abromeitiella chlorantha* (Speg.) Mez. (c) On the voucher LIL 32, which is mentioned in the description of *Meziothamnus brevifolius*, the flower colour *green-red* is noted, the com-

mon flower of *D. lotteae*. (d) Harms (1930) mentioned also the name *Mezianthus* (p.67), probably an erroneous spelling of *Meziothamnus*. (e) Hauman (1917) indicated information about a *Navia brevifolia* Gris. forma *normalis* Kurtz, which exhibited larger and denser lepidote leaves than the taxa studied formerly. However, this taxon was not published anywhere. Probably it was a specimen of the current *D. abstrusa*, also noted by Castellanos (1931). (f) There are forms without any spines e.g. cultivated in the BGKS. (g) Mez in C.DC. (1896) cited the voucher from *Lorentz and Hieronymus 947* erroneously as collected in Argentina. (h) IUCN: *rare* (see 3.5.4).

**Further references.** Mez in C.DC., Monogr. phan. 9: 534. 1896. Gallardo, Anales Soc. Ci. Argent. 47: 297. 1899. Schumann, Just's Bot. Jahresber. 30 (2): 146. 1902. Hauman, Anales Mus. Nac. Hist. Nat. Buenos Aires 29: 240, 241. 1917. Fedde and Schuster, Just's Bot. Jahresber. 45 (1): 12. 1917. Wangerin, Just's Bot. Jahresber. 46 (1): 359. 1918. Castellanos, Comun. Mus. Nac. Hist. Nat. „Bernardino Rivadavia" 2(14): 142. 1925. Harms in Engler, Nat. Pflanzenfam. ed. 2, 15a: 67, 110. Fig.42. 1930. Mez in Engler, Pflanzenr. IV. 32. (100): 225. 1934. Castellanos in Descole, Gen. Spec. Plant. Argent. 3: 187. 1945. Foster, Contr. Gray Herb. 184: 39. 1958. Hunziker, Trab. Mus. Bot. Córdoba 2(10): 301. 1960. Smith, Bromeliana 1(8): 2–4 . 1964. Smith, Phytologia 14(8): 462, 490. 1967. Viers, Ann. Géogr. 76(416): 417. 1967. Janse, Succulenta (Netherlands) 47(10): 155, 156. 1968. Smith, Rhodora 71: 225. 1969. Ehler and Schill, Pollen & Spores 15(1): 34. 1973. Smith and Downs, Fl. Neotrop. Monogr. 14 (3): 241, 245. 1974. Schultze-Motel, Bot. Jahrb. Syst. 96: 425. 1975. Ehler, Trop. Subtrop. Pflanzenwelt: 20: 469–508. 1977 (micromorphological study). Rauh, Kakteen And. Sukk. 29(6): 145, 146. 1978. Coester and Motschenbach, Bromelie 1: 74, 75. 1981. Strehl and Winkler, Beitr. Biol. Pflanzen 56: 420, 430. 1981 (micromorphological study). Rauh, Trop. Suptrop. Pflanzenwelt 42: 37–44. 1983. Ravenna, Wrightia 7(3): 232. 1983. Winkler, Beitr. Biol. Pflanzen 61: 286, 306. 1986. Varadarajan and Gilmartin, Syst. Bot. 12(4): 562–571. 1987 (micromorphological study). Böhme, Trop. Subtrop. Pflanzenwelt 62: 125–232. 1988 (anatomical study). Rauh, Trop. Hochgebirgspfl.: 132, 133. 1988. Schill et al., Beitr. Biol. Pflanzen 63: 221–252. 1988 (morphological study). Varadarajan and Gilmartin, Amer. J. Bot. 75(6): 810. 1988 (morphological study). Rauh, Bromelien: 410. 1990. Galetto and Bernardello, Bot. Acta 105(4): 292–299. 1992 (physiological study). Halbritter, Grana 31: 197–212. 1992 (micromorphological study). Spencer and Smith, Bradea 6: 144. 1992. Martin, Bot. Rev. 60(1): 36. 1994 (physiological study). Horres and Zizka, Beitr. Biol. Pflanzen 69(1): 43–76. 1995 (anatomical study). Horres, Bromelie 3: 69, 70. 1996 (anatomical study). Zuloaga and Morrone, Monogr. Syst. Bot. Missouri Bot. Gard. 60: 106, 109. 1996. Krömer et al., Selbyana 20(2): 207. 1999. Antezana and Navarro, Rev. Bol. Ecol. 12: 22. 2002. López, Ecol. Bolivia 38(1): 42. 2003. Givnish et al., Int. J. Plant Sci. 165(4 Suppl.): S35–S54. 2004 (phylogenetic study). Gitaí et al., Pl. Syst. Evol. 253: 65–80. 2005 (cytogenetic study). Givnish et al., Aliso 23: 3–26. 2007 (phylogenetic study). Zuloaga et al., Monogr. Syst. Bot. Missouri Bot. Gard. 107(1): 1–983. 2008. Jørgensen et al., Monogr. Syst. Bot. Missouri Bot. Gard. 45: 1–1286. 2010. Wöhrmann and Weising, Theor. Appl. Genet. 123: 635–647. 2011 (methodological study).

**Specimens seen.** BOLIVIA: **Dept. Tarija:** 1903-04, *Fiebrig 3573* [B, BM!, E, G!, K!, M!, photo ex E in WU!]. Prov. O'Connor: Valle de Tambo, (21°25' S, 64°15' W), 11 Jun. 1873, *Lorentz and Hieronymus 947* [GOET!, CORD, photo ex GOET in NY!]. Cumbre del Cóndor, ca. 25 km W of Narvaez, ca. 65 km W of Entre Ríos, (21°25' S, 64°25' W), 2700 m, 15 Jul. 1982, *Till, W. 62* [WU!]; ibid.: 2650 m, 15 Jul. 1982, *Till, W. 62* [WU!]. Prov. Cercado:

20 km W of Junacas, near the road, (21°30' S, 64°30' W), 2100 m, 14 Jul. 1988, *Till, W. 59* [WU]. Prov. Avilés: Tarija via Padcaya, Colón Sud, (21°45' S, 64°40' W), 1950 m, 31 Oct. 1987, *Beck 14276* [U!]; between Padcaya and Honduras, (21°45' S, 64°35' W), 2800 m, 23 Sep. 1927, *Troll 390* [B!, GH, M!]. Prov. Arce: near Canas, (21°55' S, 64°55' W), Dec. 1995, *Gouda 95-18b* [WU!]; 69 km on road from Tarija to Bermejo, 21°57'37" S, 64°40'53" W, 2130 m, 11 Oct. 2006, *Schütz et al. 06-061* [FR!]; ibid.: *Schütz et al. 06-062* [LPB!]; ibid.: *Schütz et al. 06-063* [FR!].
ARGENTINA: *Muhr s.n.* [WU 260!]. **Prov. Jujuy:** Dept. Valle Grande: on the road to Valle Colorado from Valle Grande, about 5 km from Valle Grande, 23°27' S, 64°57' W, 1650–1700 m, 08 Feb. 1984, *Varadarajan 1231* [GH!]. Dept. Tilcara: 100–200 m from the road, on east facing slopes. 2.2 km N of Quebrada de Incahuasi, 23°40' S, 65°26' W, 2400–2450 m, 20 Feb. 1984, *Varadarajan et al. 1261* [US! (2 sheets)]. Dept. Tumbaya: Volcán, (23°55' S, 65°28' W), 27 Oct. 1964, *Cabrera 16333* [US!]; ibid.: Jul. 1922 *Castellanos 1049* [BA!]; ibid.: 2200 m, 30 Nov. 1918, *Castillon 6458* [A!, BA!]; ibid.: 07 Nov. 1974, *Schinini et al. 10177* [NY!]; Volcan, about 2 km N of Chilcaya, ca. 300 m W from the road Jujuy to La Quiaca, 23°55' S, 65°28' W, 2000–2100 m, 20 Feb. 1984, *Varadarajan et al. 1258* [MCNS!, US!]; Volcán, laguna 2 km W of the village, (23°56' S, 65°28' W), 2000 m, 22 Mar. 1989, *Novara 8713* [G!, M!, MCNS!, S!]; Laguna El Volcán, (23°56' S, 65°28' W), 01 Nov. 1974, *Subils 2032* [CORD!]. **Prov. Salta:** Cuesta de Cafayate, km 42 after crossing the river, road to Coronel Moldes,1400 m, Oct. 1988, *Till, H. 88-143* [WU!]. Dept. Santa Victoria: near Santa Victoria, Quebrada Negro Huaico, camino al oro, (22°15' S, 64°58' W), 2600 m, 10 Nov. 1991, *Charpin and Novara 23154* [G!]; Santa Victoria, surroundings of the village, (22°15' S, 64°58' W), 2500–2800 m, 13/16 Dec. 1988, *Novara 8339* [G!, M!, MCNS! S!]. Dept. La Caldera: Río Potrero, area "El zig-zag", 2 km N of the confluence with Río Wierna, (24°34' S, 65°33' W), 1900 m, 15 Oct. 1984, *Novara 4316* [G!, MCNS!]. Dept. Rosario de Lerma: Quebrada del Toro, near Inka ruins, (24°45' S, 65°45' W), Oct./Nov. 1988, *Till, H. s.n.* [WU 2514!]; station Chorrillos, km 48 on RN 51, near the station, (24°47' S, 65°44' W), 2220 m, 27 Feb. 2005, *Bruno et al. 12244* [MCNS!]; El Tunal, (24°48' S, 65°45' W), 1800 m, 12 Aug. 1923, *Parodi 5255* [BAA!]; Quebrada del Toro, El Tunal, (24°48' S, 65°45' W), Oct. 1988, *Till, H. 88-147* [WU!]: Quebrada del Toro, km 50, (24°50' S, 65°44' W), 2700 m, 05 Jan. 1990, *Palací 1131* [MCNS!]; Quebrada del Toro, km 38 on RN 51, (24°50' S, 65°43' W), 1850 m, 31 Jul. 1991, *Tolaba 208* [MCNS!]; El Alisal, RN 51, (24°51' S, 65°43' W), 1811 m, 16 Apr. 1978, *Novara 768* [CORD!, MCNS!]; El Alisal, Puerta Tastil to Río de Lerma, (24°51' S, 65°43 W), *Piccardo 30-B* [UC!, US!]; Quebrada del Toro, near Inka ruins, near Chorillos, (24°51' S, 65°43' W), Sep./Oct. 1988, *Till, H. s.n.* [WU 2513!]; Quebrada del Toro, km 33.2 on RN 51, near the viaduct of Río Toro, 8 km W of Campo Quijano, (24°53' S, 65°42' W), 1780 m, 16 Jan. 1988, *Novara 7469* [G!, MCNS!, S!]. Dept. Chicoana: at the beginning of Quebrada de Mal Paso, 24 km W from RN 68 Salta to Cafayate, 25°13' S, 65°45' W, 1825–1875 m, 21 Feb. 1984, *Varadarajan et al. 1265* [US!]. Dept. La Viña: mountains between La Viña and Amblayo, (25°30' S, 65°41' W), 16 Feb. 1943, *Castellanos 46643* [BA!]. Dept. Guachipas: Pampa Grande, (25°50' S, 65°28'30" W), 3000 m, Jan. 1897, *Spegazzini s.n.* [LP 200!]. Dept. La Candelaria: about 3 km from the road of El Tala to El Jardín, 26°03' S, 65°27' W, 1200 m, 07 Feb. 1984, *Varadarajan 1228* [US!]. **Prov. Tucumán:** Dept. Tafí Viejo: Quebrada La Hoyada, (26°30–45' S, 65°30–35' W), 1500 m, 24 Sep. 1920, *Schreiter 1366* [LIL!]; ibid.: 1600 m, 30 Sep. 1924, *Schreiter 4164* [F!, LIL!, UC!]; ibid.: 1000–1200 m, 01 Aug. 1922, *Schreiter 589* [BA!, GH!]; ibid.: 1500 m, 20 Nov. 1921, *Schreiter s.n.* [LIL 34645!]; ibid.: 1600 m, 30 Sep. 1924, *coll. ign.* [LIL 32!]; La Hoyada, (26°41' S, 65°32' W), 20 Nov. 1945, *Olea s.n.* [LIL 110374]; !]; ibid.: Oct. 1924, *Schreiter s.n.* [LIL 34642!]; ibid.: 1500 m, Jul. 1920, *Schreiter s.n.* [LIL 34640!]; ibid.: 1200 m, 26 Sep. 1920, *Schreiter s.n.* [LIL 34641!]; ibid.: 1500 m, Sep. 1922, *Venturi 1889* [GH!, LIL!, US!]; ibid.: 1600 m, 03 Oct. 1925, *Venturi 7255* [US!]. **Prov. Catamarca:** Dept. Andalgalá: near the road from Andalgalá to Capillitas, below the pass, (27°30' S, 66°25' W), 1800 m, Oct. 1988, *Till, H. 88-135* [WU!]; Potrero, (27°32' S, 66°20' W), 25 Oct. 1910, *Castillon s.n.* [LIL 34509!]; Camino to Andalgalá; Cuesta de

la Chilca, (27°38' S, 66°11' W), 1700–1900 m, *Borsini s.n.* [LIL 436768! (2 sheets)]; Cuesta de la Chilca (27°38' S, 66°11' W), *Lorentz s.n.* [B, GH!, photo ex B in F!].

s.loco: *Marnier-Lapostolle s.n.* [US 2479883–84!]; *Till, W. s.n.* [WU 2417!]; *coll. ign.* [M 124625!]; *coll. ign.* [M 124628!]; *coll. ign.* [US 2169604!]; *coll. ign.* [WU 2511!]; *coll. ign.* [WU 2515!]; *coll. ign.* [WU 2516!]; *coll. ign.* [WU 8628!].

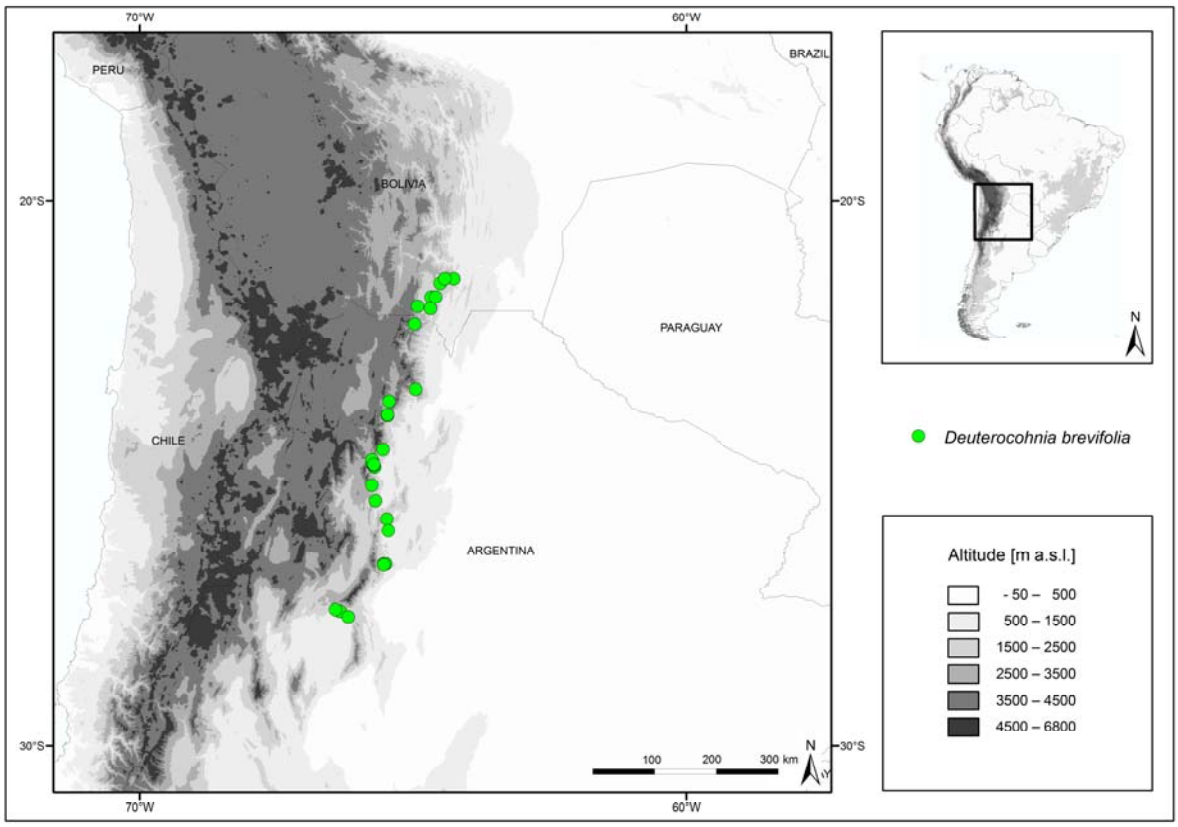


Fig. 5.4: Distribution of *D. brevifolia*.

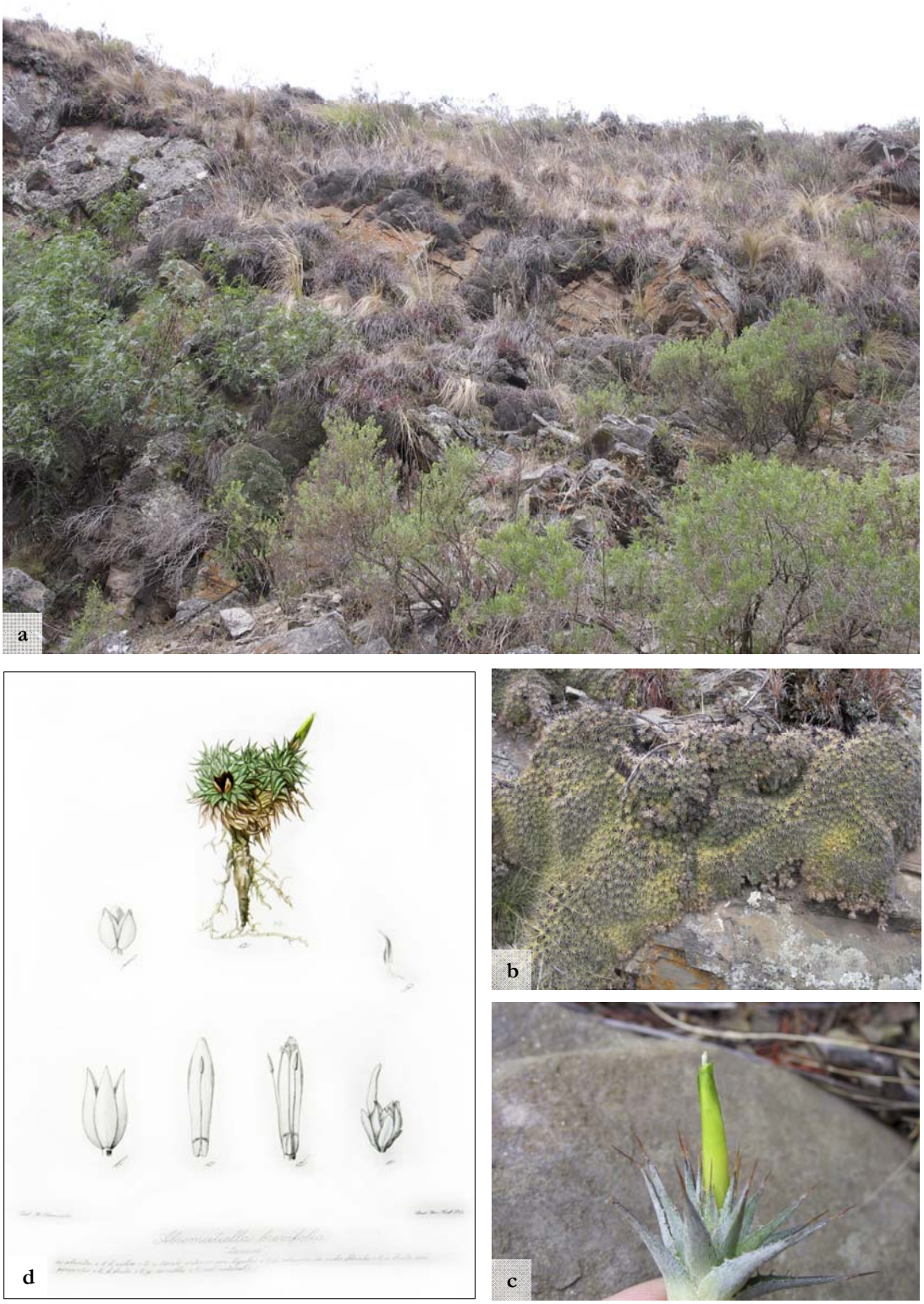


Fig. 5.5: *D. brevifolia*. a: Natural habitat, Dept. Tarija, Bolivia (*N. Schütz 06-061*). b: Cushion growing over rocks. c: Flower. d: Drawing of plant and floral elements by Castellanos (1945).

***Deuterocohnia brevispicata*** Rauh & L. Hrom. in Rauh, Trop. Subtrop. Pflanzenwelt 65: 5. 1988. Type: Bolivia, Dept. Chuquisaca, Prov. Tomina, near Serrania Inca Huasi, above Muyupampa, 1300 m a.s.l., without date of collection, *Hromadnik 5213* [holotype: HEID!].

**Plants** growing solitary or in groups. **Rosettes** 50–60 × 50–75 cm. **Leaf sheaths** 2.5–3.5 × [3–] 5–8 cm. **Blades** 35–60 [–70] × [3–] 5–8 cm, recurved, adaxially concave, spinose-serrate, lepidote, greyish–green. **Peduncle** present, incl. inflorescence 100–160 [–180] cm × 8–10 mm, erect, perennial, woody. **Peduncle bracts** 8–11 × 1.5–2 cm, spinose-serrate. **Inflorescence** 50–80 [–100] cm long, compound, branches of 1st or 2nd order, perennial. **Primary bracts** 3–5 [–8] × 1–1.5 cm, exceeding the partial inflorescence, narrowly triangular, narrowly acute, laxely spinose-serrate, lepidote. **Partial inflorescences** 4–6 [–8] cm long, densely flowered spikes, axis concealed, simple or branched, spheroidal, 10–20-flowered. **Floral bracts** 8–13 × 5–8 mm, about equaling the sepals, broadly ovate, acuminate, sparsely lepidote, brownish. **Flowers** 17–24 mm long, sessile. **Sepals** 8–14 × 4–5 mm, ovate, obtuse, mucronulate, sparsely lepidote, reddish. **Petals** 16–21 × 4–5 mm, erect during anthesis, after anthesis slightly spirally twisted, reddish, with green apex. **Petal appendages** 4–5 mm long, with short fringes. **Filaments** 14–15 mm long. **Anthers** 3–4 mm long, erect, concealed, greenish–yellow. **Ovary** [3–] 5 mm long. **Style** 11–17 mm long, stigma concealed or excerted. **Fruits** 8–9 × 5–6 mm. **Seeds** [1.5–] 2 [–3] mm long.

**Distribution.** BOLIVIA. Dept. Chuquisaca. 19°17'–19°52' S, 63°43'–64°22' W.
Besides the specimens seen during this revision, Kessler (2002) documented further localities in an ecological study: Dept. Cochabamba: Prov. Esteban Arce, Prov. Charcas. Dept. Chuquisaca: Prov. Jaime Zudáñez, Juana A. de Padilla, Belisario Boeto. Dept. Santa Cruz: Prov. Florida.

**Habitat and ecology.** Ecoregions: Bolivian montane dry forests (95) and Andean Yungas (64). At elevations of 1200–2200 m a.s.l. Terrestrial or saxicolous, at more open sites within semi-deciduous or deciduous montane forests, or on bare, steep slopes. Flowering plants documented in June, July and October. Pollination via hummingbirds (own observations), Kessler (2002) noted entomophily.

**Etymology.** The epithet refers to the short and dense partial inflorescence (Latin *brevis* = short, little; *spicatus* = grow spikes).

**Affinities.** Morphologically, *Deuterocohnia brevispicata* resembles *D. seramisiana*. Both exhibit a robust inflorescence and primary bracts longer than the spheroidal partial inflorescences. In contrast to *D. seramisiana*, *D. brevispicata* is characterized by reddish flowers and occurs in lower altitudinal ranges.

**Notes and comments.** (a) The type plant, which is cultivated in the botanical garden of Heidelberg, produced an inflorescence which, after 20 years, is still flowering. The inflorescence is about 2 m long.

**Further references.** Gross, Selbyana 19(2): 193. 1998. Spencer and Smith, Bradea 6: 145. 1992. Krömer et al., Selbyana 20(2): 207. 1999. Stolten, Bromelie 2: 42–49. 1999. Horres et al., Pl. Biol. (Stuttgart) 2(3): 309, 310. 2000 (phylogenetic study). Kessler, Bot. Rev. (Lancaster) 68(1): 123. 2002. Vásquez et al., Bromelie 1: 4–8. 2002. Bogner, Kakteen And. Sukk. 61 (2): 38–40. 2010.

**Specimens seen.** BOLIVIA: **Dept. Chuquisaca:** Prov. Tomina: 11 km from Padilla to Tomina on road between Padilla and Sucre, 19°17'23" S, 64°21'51" W, 2190 m, 20 Oct. 2001, *Vargas and Jordan 6282* [WU!]; 112 km on road from Monteagudo to Padilla, 19°23'06" S, 64°14'28" W, 2136 m, 04 Oct. 2006, *Schütz et al. 06-041* [FR!]; near Serrania Inca Huasi, above Muyupampa, (19°40' S, 64°15' W), 1300 m, without date of collection, *Hromadnik 5213* [HEID!]; along the road from Monteagudo to Lagunillas, about 5 km east of Muyupampa, (19°47' S, 64°17' W), 1230 m, 20 Jul. 1982, *Till, W. 110* [WU!]. Prov. Hernando Siles: 42 km de Monteagudo a Padilla, 19°38' S, 64°03' W, 1200 m, 28 Jun. 1995, *Kessler et al. 4948* [LPB!]; road from Monteagudo a Padilla, 19°47'13" S, 64°02'23" W, 1211 m, 03 Oct. 2006, *Schütz et al. 06-028* [FR!]; ibid.: *Schütz et al. 06-029* [FR!, LPB!]; 30 km on road from Monteagudo to Padilla, 1243 m, 04 Oct. 2006, *Schütz et al. 06-036* [FR!, LPB!]; ibid.: *Schütz et al. 06-037* [FR!]. Prov. Luis Calvo: Municipio de Villa Vaca Gúzman, Serrania de Incahuasi, bajando del abra del Incahuasi hacia Muyupampa, 19°51'13" S, 63°43'38" W, 1318 m, 19 Oct. 2005, *Llully et al. 445* [HSB!]; 45 km on road from Ipati to Lagunillas, 19°51'13" S, 63°43'44" W, 1410 m, 03 Oct. 2006, *Schütz et al. 06-022* [FR!].

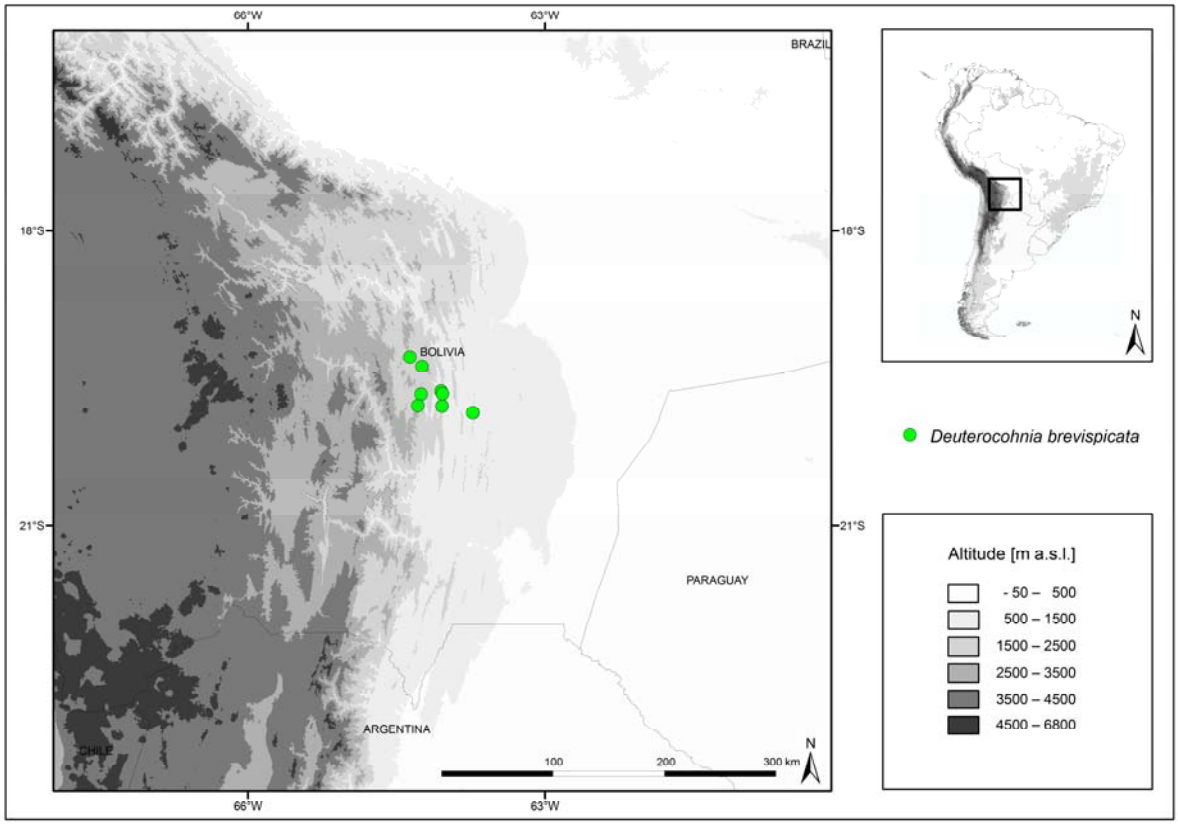


Fig. 5.6: Distribution of *D. brevispicata*.


Fig. 5.7: *D. brevispicata*. a: Natural habitat, Dept. Chuquisaca, Bolivia (*N. Schütz 06-037*). b: Plant growing on vertical, rocky slope. The most recent inflorescence arises form the centre of the rosette, an older one is hanging close to the rock. c: Partial inflorescence of the type collection (*L. Homadnik 5213*), growing in the BGHD.

***Deuterocohnia chrysantha*** (Phil.) Mez in Mart., Fl. bras. 3(3): 507. 1894. ≡ *Pitcairnia chrysantha* Phil., Fl. atacam.: 50. 1860. Type: Chile, Region III, Atacama, Prov. Chañaral: Pan de Azucar, 26°05' S, (70°39' W), Nov. 1853, *Philippi s.n.* [lectotype: SGO 46359!].

**Plants** growing in dense groups. **Rosettes** 15–25 × 20–30 cm. **Leaf sheaths** 2–2.5 × 3–6 cm. **Blades** [10–] 15–25 [–30] × [1.5–] 2.5–4 cm, recurved, lateraly curved, adaxially concave, spinose-serrate, lepidote, greyish–green, often reddish. **Peduncle** present, incl. inflorescence 70–100[140] cm × 5–7 mm, erect, perennial, woody. **Peduncle bracts** 3–8 cm × 3–5 mm, laxely spinose-serrate, upper ones shorter and entire. **Inflorescence** 15–40 cm long, compound, branches of 1st order, perennial. **Primary bracts** 10–15 × 3–4 mm, not exceeding the partial inflorescence, narrowly triangular, acuminate, entire or laxely spinose-serrate, glabrous or lepidote. **Partial inflorescences** [5–] 8–12 × 4 cm long, densely flowered spikes, axis concealed, simple, cylindrical to spheroidal, [20–] 30–40 [–60]-flowered. **Floral bracts** 9–15 × 5–7 mm, about equaling the sepals, broadly ovate, acuminate, mucronate to aristate, glabrous, brownish. **Flowers** [25–] 30–32 mm long, sessile. **Sepals** [10–] 12–13 [–15] × 4–5 mm, ovate, obtuse, mucronulate, glabrous, yellow. **Petals** 25–30 [–32] × 7–9 mm, erect during anthesis, after anthesis slightly spirally twisted, yellow, with greenish tip getting yellow at maturity. **Petal appendages** 5–7 mm long, with short fringes. **Filaments** [20–] 22–26 [–29] mm long, **Anthers** 4 mm long, recurved, concealed or exposed, greenish–yellow. **Ovary** 5–6 mm long. **Style** 24–28 mm long, stigma exposed. **Fruits** 10–12 × 6–7 mm. **Seeds** 2 mm long.

**Distribution.** CHILE. Region II/Antofagasta, Region III/Atacama. 24°40'–26°45' S, 70°25'–70°40' W. Documented also in the Prov. Copiapó (Atacama) by Squeo et al. (2008).

**Habitat and ecology.** Ecoregion: Chilean mattoral (160). At elevations of 20–800 m a.s.l. Terrestrial or saxicolous, in the Atacama desert, at wide, plane, stony areas near the Pacific coast, on cliffs, on steep slopes of ravines. Above 200 m a.s.l. coastal fog complements water supply. Accompanied by e.g. *Copiapoa* sp., *Eriosyce taltalensis*, *Eulychnia sp.* (all Cactaceae). Anthesis reported from November to February. Probably pollinated by hummingbirds and insects.

**Etymology.** The epithet refers to the yellow flower (Greek *chrysos* = gold).

**Affinities.** *Deuterocohnia chrysantha* is endemic to Chile, and is the only species of its genus occurring in this country. Morphologically, *D. chrysantha* is closely related to *D. haumanii*, but differs in having glabrous sepals, recurved anthers, fewer leaf spines and overall reddish leaf blades. CpDNA and ncDNA data revealed samples of *D. chrysantha* to be a well supported monophyletic group. According to nuclear sequence data of the present study and AFLP data from Horres (2000) *D. chrysantha* takes a basal positon within the genus. This is not the case in phylogenetic trees based on cpDNA data., where *D. chrysantha* takes a sister position to *D. longipetala* samples from Argentinean provinces Salta and La Rioja.

**Notes and comments.** (a) In the protologue from 1860 Philippi did not mention a voucher for typification. Mez noted in 1889 *Philippi 239* as a seen specimen, in 1896 he corrected the voucher number into *Philippi 939*. Muñoz (1966) noted *Philippi s.n.* [SGO 46359] as type of *D. chrysantha*. Smith and Downs (1974) designated *Philippi 939* [B] to be the holotype of *D. chrysantha*. The present revision selects the voucher *Philippi s.n.* (SGO 46359) to be the lectotype of *D. chrysantha*, because this is an extant specimen of the Philippi collection and had been collected before the publication of the protologue. The specimen of *Philippi 939* in Berlin [B] has been destroyed during the second world war. Photographs are deposited in F, GH and NY. (b) *Philippi 939* exhibits a notice "*Puya chrysantha*", which was probably a first idea of determination, but the name was never published. (c) Mez (1896) assigned also a collection from Bolivia (Kuntze s.n.) to *D. chrysantha*. This voucher was assigned to *D. longipetala* by Smith and Downs (1974). In the present revision this voucher is determined as *D. meziana*. (d) *D. chrysantha* is classified as *vulnerable* by IUCN red list of threatened plants (1997). Squeo et al. (2008) and Zizka et al. (2009) regarded this species as endangered, Hoffmann and Flores (1989) as vulnerable. (e) The vernacular name of *D. chrysantha* in Chile is "Chaguar de jote". (f) Plants cultivated in botanical gardens show more greenish coloured leaves (e.g. BOCH-0000-KA2-39).

**Further references.** Philippi, Reise Atacama: 17, 23, 34, 59, 60. 1860. Mez in Baker, Handb. Bromel.: 119. 1889. Mez in C.DC., Monogr. phan. 9: 466. 1896. Tietze, Z. Naturwiss. 78: 30. 1906. Reiche in Engler and Drude, Veg. Erde 8: 352. 1907. Reiche, Bot. Jahrb. Syst. 45(3): 346. 1911. Herzog, Meded. Rijks-Herb. 29: 82. 1916. Johnston, Contr. Gray Herb. 85: 22. 1929. Harms in Engler, Nat. Pflanzenfam. ed.2, 15a: 109. 1930. Mez in Engler, Pflanzenr. IV. 32. (100): 284. 1934. Muñoz, Espec. Pl. Descr. Philippi: 35. 1960. Smith, Bromeliana 1(4): 4. 1964. Smith, Phytologia 10(1): 48. 1964. Muñoz, Fl. silvestr. Chile: 39. Fig. 2. 1966. Smith and Downs, Fl. Neotrop. Monogr. 14 (3): 241. 1974. Rundel et al., Oecologia 46(2): 198, 200. 1980. Marticorena and Quezada, Gayana, Bot. 42: 81. 1985. Marticorena, Gayana, Bot. 47(3–4): 99. 1990. Rundel et al. Gayana, Bot. 53(2): 304, 310. 1996. Marticorena et al., Gayana, Bot 55(1): 73. 1998. Rundel and Dillon, Pl. Syst. Evol. 212: 261–278. 1998 (ecological study). Spencer and Smith, Bradea 6: 145. 1992. Zizka, J. Bromeliad Soc. 53(4): 147–150. 2003. Guerrero et al., Ediciones Univ. La Serena 19:

334. 2008. Squeo et al., Ediciones Univ. La Serena 4: 56. 2008. Squeo et al., Ediciones Univ. La Serena 6: 116. 2008. Squeo and Letelier, Ediciones Univ. La Serena Anexo 2: 419, 441. 2008. Zuloaga et al., Monogr. Syst. Bot. Missouri Bot. Gard. 107(1): 1–983. 2008. Zizka el al., Biodivers. & Conservation 18(9): 2449–2471. 2009.

**Specimens seen.** CHILE: **Region II, Antofagasta:** Prov. Antofagasta: Taltal, ca. 40km N of Paposo, near the coastal road to Antofagasta, 24°42,952' S, 70°33,934' W, 74 m, 28 Dec. 2006, *Zizka 8147* [FR!]; ibid. *Zizka 8148* [FR!]; !]; ibid. *Zizka 8149* [FR!]; !]; ibid. *Zizka 8150* [FR!]; !]; ibid. *Zizka 8151* [FR!]; !]; ibid. *Zizka 8152* [FR!]; Taltal, ca. 20km N of Paposo, near the coastal road to Antofagasta, 24°53,890' S, 70°31,563' W, 70 m, 28 Dec. 2006, *Zizka 8153* [FR!]; ibid. *Zizka 8154* [FR!]; ibid. *Zizka 8155* [FR!]; ibid. *Zizka 8156* [FR!]; Taltal, ca. 7 km N of Paposo along road to El Cobre, near ocean, 24°57' S, 70°29' W, 40 m, 14 Dec. 1987, *Dillon and Teillier 5270* [F!]; 20km S of Paposo near road to Taltal, 25°13,099' S, 70°26,298' W, 36 m, 28 Dec. 2006, *Zizka 8157* [FR!]; ibid. *Zizka 8158* [FR!]; ibid. *Zizka 8159* [FR!]; Taltal, 20 km N of Taltal on the road to Paposo, (25°15' S, 70°25'50" W), 20 m, 30 Jan. 1952, *Hutchison 400* [UC!]; 7 km NE of Taltal, towards the Panamericana, (25°23' S, 70°27' W), 280–400 m, 26 Nov. 1991, *Eggli and Leuenberger 1769* [B!. ZSS!]; Taltal, (25°24' S, 70°28'30" W), 01 Nov. 1940, *Grandjot 4223* [GH!]; Quebrada de Taltal, (25°24' S, 70°28'30" W), 120 m, 10 Sep. 1936, *Montero 2890* [GH!]; 6 km SE of Taltal, (25°24' S, 70°28'30" W), 15 Jan. 1939, *Morrison 17100* [GH! UC!]; hills SE of Taltal, 25°29' S, 70°27' W, 25 Nov. 1925, *Johnston 5097* [BA!, GH!, US!]; Quebrada de Taltal, 10 km W of Breas and 10 km E of Taltal, (25°30' S, 70°27' W), 350 m, 30 Jan. 1952, *Hutchison 396* [UC!]; Taltal, Oct. 1887, *Borchers s.n.* [SGO 046360!]; Paposo, 21 Feb. 1964, *Marticorena et al. 433* [SGO!]. **Region III, Atacama:** 24–26°S, s.d., *Philippi 939* [B (not seen, probably destroyed), photo in F!, GH!, NY!]; Prov. Chañaral: Pan de Azucar, 26°05' S, (70°39' W), Nov. 1853, *Philippi s.n.* [SGO 46359!]; vicinity of Caleta Pan de Azúcar, 26°07' S, 70°39' W, 18 Nov. 1925, *Johnston 5840* [GH!]; Parque Nacional Pan de Azúcar, Quebrada Coquimbo, ca. 100 km S of Taltal, 26°09' S, 70°39' W, 160–200 m, 05 Dec. 1987, *Dillon and Teillier 5092* [F!]; Parque Nacional Pan de Azúcar, Huanchillo, 26°09' S, 70°39' W, 300 m, 06 Feb. 1991, *Zizka 1565* [FR!]; Parque Nacional Pan de Azucar, Huanchillo, ca. 1000 m along gravel road, 26°09' m, 70°39' m, 200 m, 06 Mar. 1991, *Zizka 1566* [FR!]; Parque Nacional Pan de Azucar, Huanchillo, between Panamericana and Huanchillo, 26°09' S, 70°39' W, 06 Apr. 1991, *Zizka* 1567 [FR!]; Quebrada Los Infieles, ca. 6 km S of Chañaral, ca. 1,5–2 km inland from the mouth at El Caleuche, 26°23'10" S, 70°39'48" W, 100–250 m, 12 Dec. 1994, *Eggli and Leuenberger 2629 a* [B!]. s. loco: 20 Jun. 1964, *Rojas s.n.* [SGO 075562!]; *coll. ign.* [SGO 046358!].

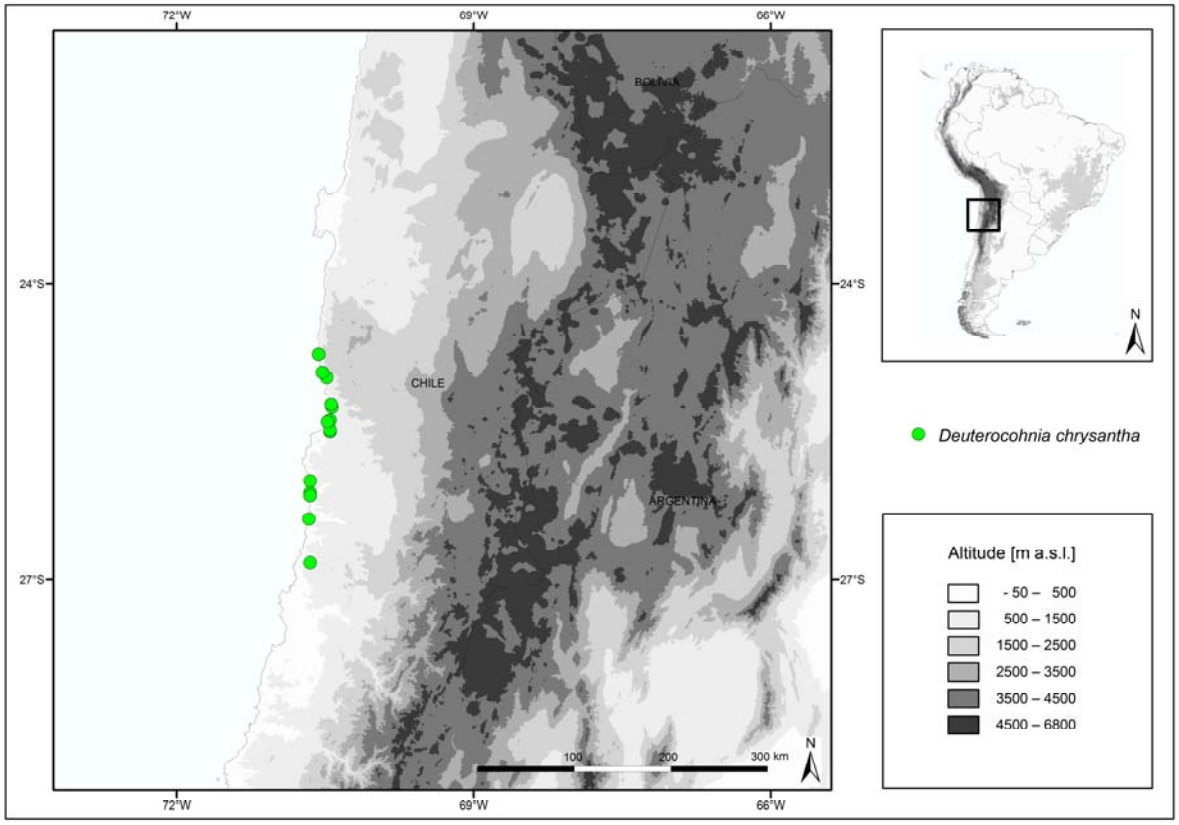


Fig. 5.8: Distribution of *D. chrysantha*.


Fig. 5.9: *D. chrysantha*. a: Natural habitat, Prov. Antofagasta, Chile. b: Upper part of the inflorescence. c: Reddish leaved rosettes. d: Partial inflorescense. Photos a-d: Georg Zizka. Additional photograph of the natural habitat close to the sea is shown in Fig. 3.18.

***Deuterocohnia digitata*** L.B. Sm., Phytologia 18(3): 137. 1969. Type: Argentina, Prov. Salta, Dept. Cachi, Cerros de Cachi, 07 Feb. 1943, *Castellanos s.n.* [holotype: BA 46636, photo in US!, isotype: US 88763!].

− "*Deuterocohnia strobilifera*" sensu Castellanos, Gen. Sp. Pl. Arg. 3: 194. Fig. 44, 126 b. 1945. p. p.: Argentinean plants.

**Plants** growing in groups or cushions. **Rosettes** 8–12 × [8–] 10–15 cm. **Leaf sheaths** 1.5–2.5 × 3–4 cm. **Blades** 8–15 × 1.5–3 cm, incurved, adaxially concave, spinose-serrate, densely lepidote on both sides, greyish. **Peduncle** present, incl. inflorescence 15–25 cm × 2–3 mm, erect, perennial, woody. **Peduncle bracts** 1.5–3.5 × 0.5 cm, laxely spinose-serrate or entire. **Inflorescence** 5–15 cm long, shortly exceeding the rosette, simple or compound, branches of 1st order, subdigitate, perennial. **Primary bracts** 2–10 × 1.5–2 mm, much shorter than the partial inflorescence, narrowly triangular, narrowly acute, entire, lepidote. **Partial inflorescences** 4–6 cm long, densely flowered spikes, axis concealed, simple, cylindrical, 20–30-flowered. **Floral bracts** 5–7 × 3.5–6 mm, about equaling the sepals or shorter, broadly ovate, acute, mucronate, glabrous, brownish. **Flowers** [10–] 14–15 mm long, sessile. **Sepals** 6–7 × 3–4 mm, ovate, obtuse, glabrous, yellow–orange. **Petals** 12–15 × 4–5 mm, yellow–orange, erect during anthesis, after anthesis not spirally twisted. **Petal appendages** 2 mm long, with short fringes. **Filaments** 8–10 mm long. **Anthers** 2.5–3.5 mm long, erect, concealed, greenish. **Ovary** 3 mm long. **Style** 10 mm long, stigma exposed. **Fruits** unknown. **Seeds** unknown.

**Distribution.** ARGENTINA. Prov. Salta. 24°10'–25°15' S, 65°45'–66°30' W.

**Habitat and ecology.** Ecoregion: Andean Yungas (64), Central Andean puna (156). At elevations of 2200–3200 [– 3800] m a.s.l. Terrestrial, in Inter-Andean dry valleys, on rocky hillsides with loose gravel and solid to weathered rock, open shrub cover. Associated with a.o. *Aristida adecencionis* (Poaceae), *Opuntia sulfurea* (Cactaceae), *Maihueniopsis* sp. (Cactaceae), *Cercidium andicola* (Fabaceae), *Bulnesia schickendanzii* (Zygophyllaceae). Flowering from September to March. No comments on potential pollinators available for this species, ornithophily as well as entomophily are conceivable.

**Etymology.** The epithet refers to the partial inflorescences, which may be arranged like fingers of a hand at older inflorescences (Latin *digitus* = finger).

**Affinities.** *Deuterocohnia digitata* is morphologically and ecologically similar to *D. strobilifera*. Both grow in dense, hemispherical groups at the upper limit of the genus' altitudinal range. While *D. strobilifera* occurs in southern Bolivia and the border district of Bolivia and Argentina, *D. digitata* is restricted to the northern Argentinean province Salta. *Deuterocohnia digitata* possesses shorter primary bracts, longer partial inflorescences, closed or only slightly opened flowers at anthesis, orange–yellow petals and erect anthers. The distribution areas of both species overlap.

**Notes and comments.** (a) Longer infloresecences of *D. digitata* may also develop partial inflorescences on lower parts of the axis, not only digitate or subdigitate ones at the apex. (b) *Crespo s.n.* [BA 37070] comprises locality and leaves as for *D. strobilifera*, the inflorescence is more like *D. digitata*. Even though the flower characters of *Crespo s.n.* cannot be evaluated due to immature flowers, this collection was assigned to *D. strobilifera*. (c) Zuloaga et al. (2008) listed *D. digitata* as synonym of *D. strobilifera*. (d) Classified as *vulnerable* by IUCN red list of threatened plants (1997).

**Further references.** Smith and Downs, Fl. Neotrop. Monogr. 14 (3): 239, 240. 1974. Brown and Gilmartin, Syst. Bot. 14(1): 125. 1989 (micromorphological study). Halbritter, Grana 31: 197–212. 1992 (micromorphological study). Spencer and Smith, Bradea 6: 145. 1992. Zuloaga and Morrone, Monogr. Syst. Bot. Missouri Bot. Gard. 60: 109. 1996. Krömer et al., Selbyana 20(2): 207. 1999. López, Ecol. Bolivia 34: 45–70. 2000. López, Ecol. Bolivia 38(1): 42. 2003. Zuloaga et al., Monogr. Syst. Bot. Missouri Bot. Gard. 107(1): 1–983. 2008.

**Specimens seen.** ARGENTINA: without precise locality: *Muhr s.n.* [WU 235!]; *Hromadnik s.n.* [WU 234!]. **Prov. Salta**: Dept. Los Andes: San Antonio de los Cobres, (24°13' S, 66°19' W), 3800 m, 18 Feb. 1986, Palaci 389 [MCNS!]. Dept. Rosario de Lerma: Gólgata, Quebrada del Toro, (24°41' S, 65°45' W), 2400 m, 11 Oct. 1901, *Fries 668* [S!]; near Gólgata station on railroad to Antonio de los Cobres, (24°41' S, 65°45' W), over 2500 m, 03 Mar. 1936, *West 6176* [GH!, UC!, photo ex UC in B!, MICH!]. Dept. Cachi: near Salta, Quebrada to Tin-Tin, (25°00' S, 66°00' W), 2700 m, Sep. 1983, *Rauh 64142* [HEID!]; road 33 from Chicoana to Cachi, 28 km W of the culmination ot the Cuesta del Obispo, 14 km E of Payogasta, 25°06'51" S, 66°00'06" W, 2900 m, 26 Nov. 2003, *Leuenberger and Eggli 4868* [B!, ZSS!]; km 4495 auf RN 40, between Cachi and Cafayate, Valle Calchaquíes, 25°08'44" S, 66°10'12" W, 2340 m, 27 Nov. 2006, *Schütz et al. 06-097* [LIL!]; ibid.: *Schütz et al. 06-099* [LIL!]; km 4492 auf RN 40, between Cachi and Cafayate, Valle Calchaquíes, 25°11'02" S, 66°11'26" W, 2290 m, 27 Nov. 2006 *Schütz et al. 06-101* [LIL!]; S of Cachipampa, 7 km W of the bifurcation to Amblayo, (25°12' S, 65°52' W), 3140 m, 10 Feb. 1993, *Till, W. 10187* [LIL!, WU]; 25°15' S, 66°15' W, Jan. 1897, *Spegazzini s.n.* [BA 29856!]; Cerros de Cachi, (25°15' S, 66°15' W), 07 Feb. 1943, *Castellanos s.n.* [BA 46636, US 88763!].

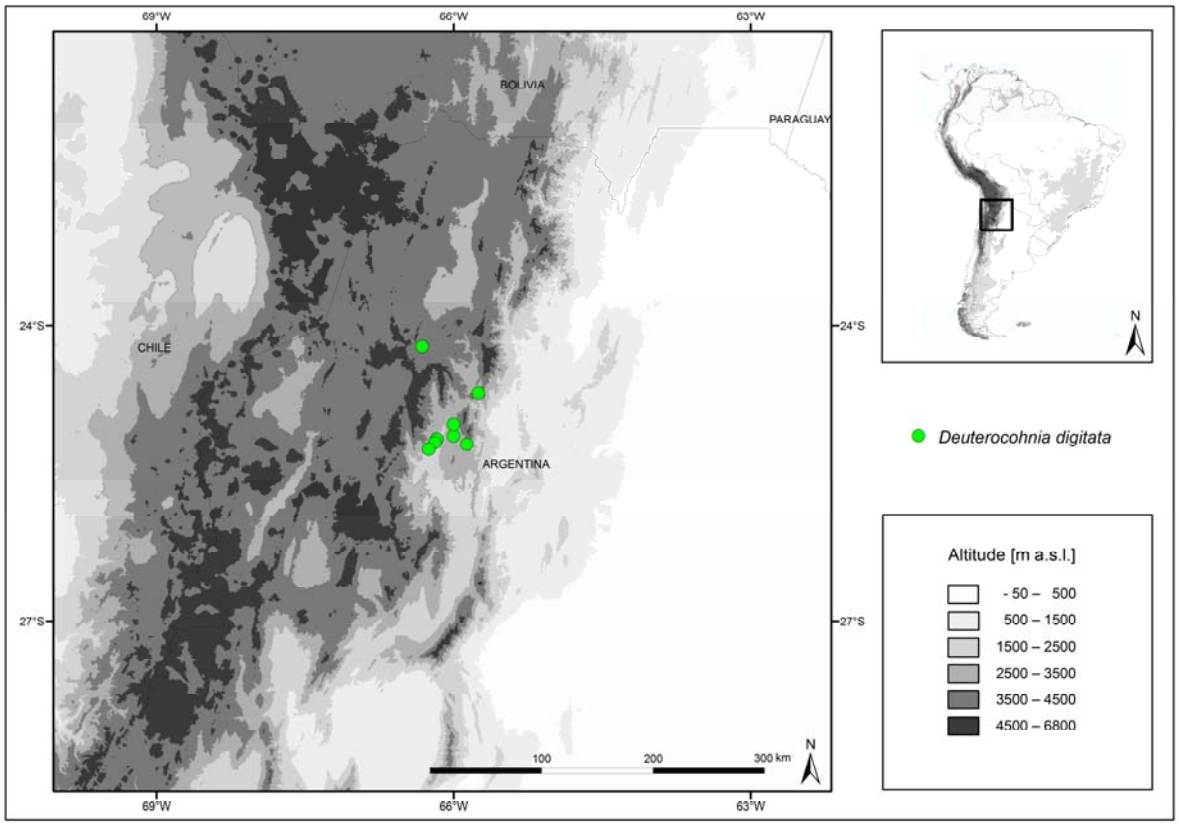


Fig. 5.10: Distribution of *D. digitata*.


Fig. 5.11: *D. digitata*. a: Natural habitat, Prov. Salta, Argentina (*N. Schütz 06-098*). b: Partial inflorescence with ants of the genus *Camponotus* (Formicinae) feeding on extrafloral nectaries. c: Flower in anthesis. d: Top view of cushion.

***Deuterocohnia gableana*** R. Vásquez & Ibisch, Vidalia 1(1): 40. 2003. Type: Bolivia, Dept. Santa Cruz, Prov. Florida, Refugio Los Volcánes, S of the Amboró National Park, 18°06' S, 63°35' W, 1150 m, 17 Sep. 2001, *Vásquez et al. 4253* [holotype: LPB!, isotypes: FR!, private herbarium of R. Vásquez!].

**Plants** growing in groups or cushions. **Rosettes** 10–15 × 15–20 cm. **Leaf sheaths** 2 × 3 cm. **Blades** 12–18 × 1.5–2 cm, recurved, adaxially concave, spinose-serrate, lepidote, greenish. **Peduncle** present, incl. inflorescence 15–20 cm × 2 mm, erect, annual, woody. **Peduncle bracts** 20–35 × 2–3 mm, spinose-serrate, upper ones almost entire, lepidote. **Inflorescence** 5–10 cm long, simple, rarely branched, spike or raceme, annual, 5–15 flowered. **Floral bracts** 5–15 × 2 – 3mm, about equaling the sepals, triangular to ovate, acute, aristate, rarely mucronate, abaxially with glandular trichomes. **Flowers** [28–] 30–36 mm long, subsessile to pedicellate, pedicels 0.5–3 mm long. **Sepals** 15–18 × 3–4 mm, lanceolate, acute, abaxially with glandular trichomes, greenish. **Petals** 30–35 × 4–6 mm, erect during anthesis, after anthesis slightly spirally twisted, yellow to greenish, with green apex. **Petal appendages** 2–3 mm long, with short fringes. **Filaments** 21–22 mm long. **Anthers** 5 mm long, erect, concealed, yellowish. **Ovary** 4–5 mm long. **Style** 26–30 mm long, stigma exposed. **Fruits** unknown. **Seeds** unknown.

**Distribution.** BOLIVIA. Dept. Santa Cruz. 18°06' S, 63°35' W.

**Habitat and ecology.** Ecoregion: Bolivian montane dry forests (95). At elevations of 1100–1200 m a.s.l. Saxicolous, on the Los Volcános sandstone mountains. Accompanied by e.g. *Cleistocactus samaipatanus* (Cactaceae), *Echeveria* sp. (Crassulaceae), *Fosterella floridensis*, *F. spectabilis*, *F. penduliflora*, *Pitcairnia cardenasii*, *P. longissimifolia*, *Puya sanctae-crucis*, *P. vasquezii*, *Tillandsia bermejoensis*, *T. edithae*, *T. samaipatensis* (all Bromeliaceae), *Furcraea* sp. (Agavaceae).

**Etymology.** The species is named after Caroline Gable, who provided an outstanding contribution to the conservation of the biodiversity of Bolivia.

**Affinities.** Morphologically, *D. gableana* is closely related to *D. sanctae-crucis* and *D. scapigera*. The flowers of the three species are highly similar, including colour, size and the glandular hairs on the sepals. The pedicellate flowers, the bigger rosette and the longer peduncle, which conspicuously exceeds the rosette, distinguishes *D. gableana* from the other two species.

**Notes and comments.** (a) Part of the type specimen in LPB does not correspond to *D. gableana*, the inflorescence probably belongs to the genus *Billbergia*. There must have been a mix-up while mounting the specimen. (b) Vásquez and Ibisch (2003) interpreted *D. gableana* to be a missing link between the species of the formerly separated genera *Deuterocohnia* and *Abromeitiella*. The flowers and the small rosettes are similar to the former *Abromeitiella* species, the short but distinct peduncle refers to the other species of *Deuterocohnia*. (c) The long aristate apex of the floral bracts are not shown in the drawing in the first description. (d) Although it has not been proven yet, the inflorescence of *D. gableana* may be able to flower more than one year, as it is sometimes the case for *D. scapigera*.

**Further references.** Luther and Rabinowitz, Selbyana 30(2): 147–189. 2010.

**Specimens seen.** BOLIVIA: **Dept. Santa Cruz:** Prov. Florida: Refugio Los Volcánes, S of the Amboró National Park, 18°06' S, 63°35' W, 1150 m, 17 Sep. 2001, *Vásquez et al. 4253* [FR!, LPB!, private herbarium of R. Vásquez!].
s.loco: *coll. ign.* [WU 7463!].

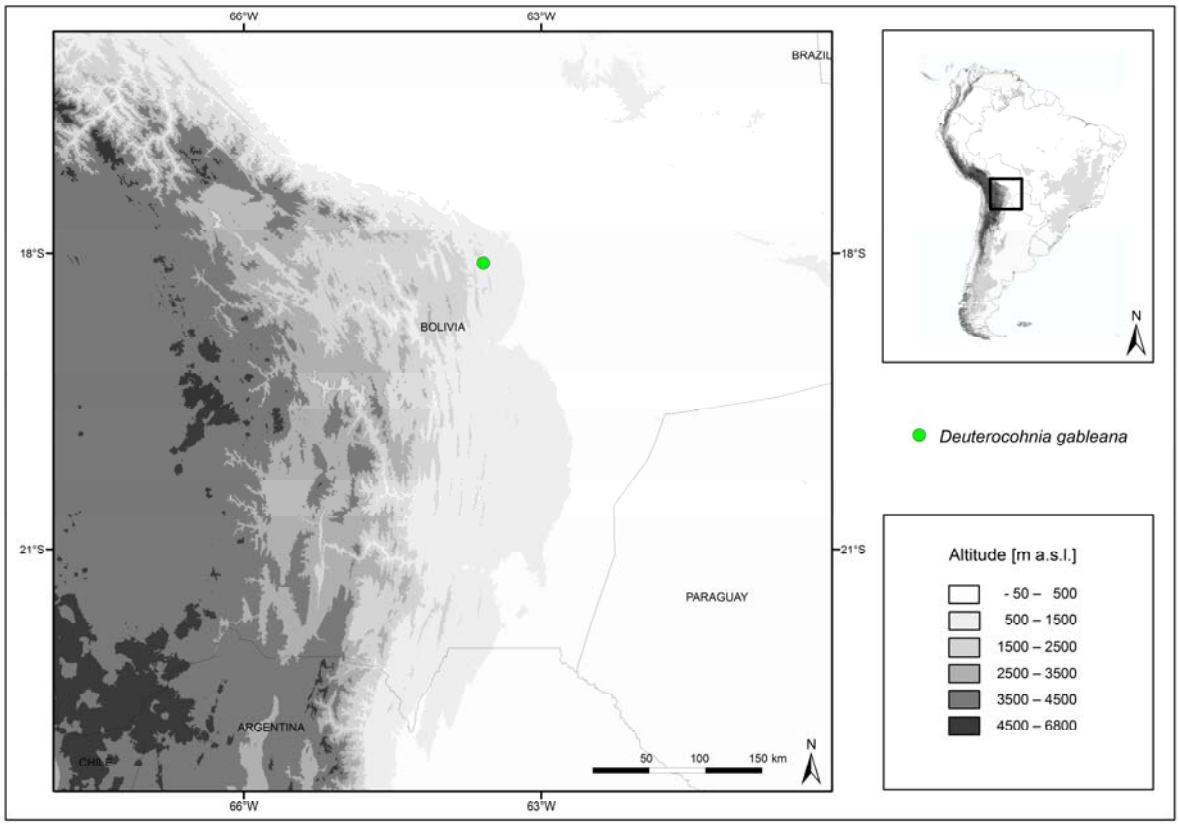


Fig. 5.12: Distribution map of *D. gableana*.

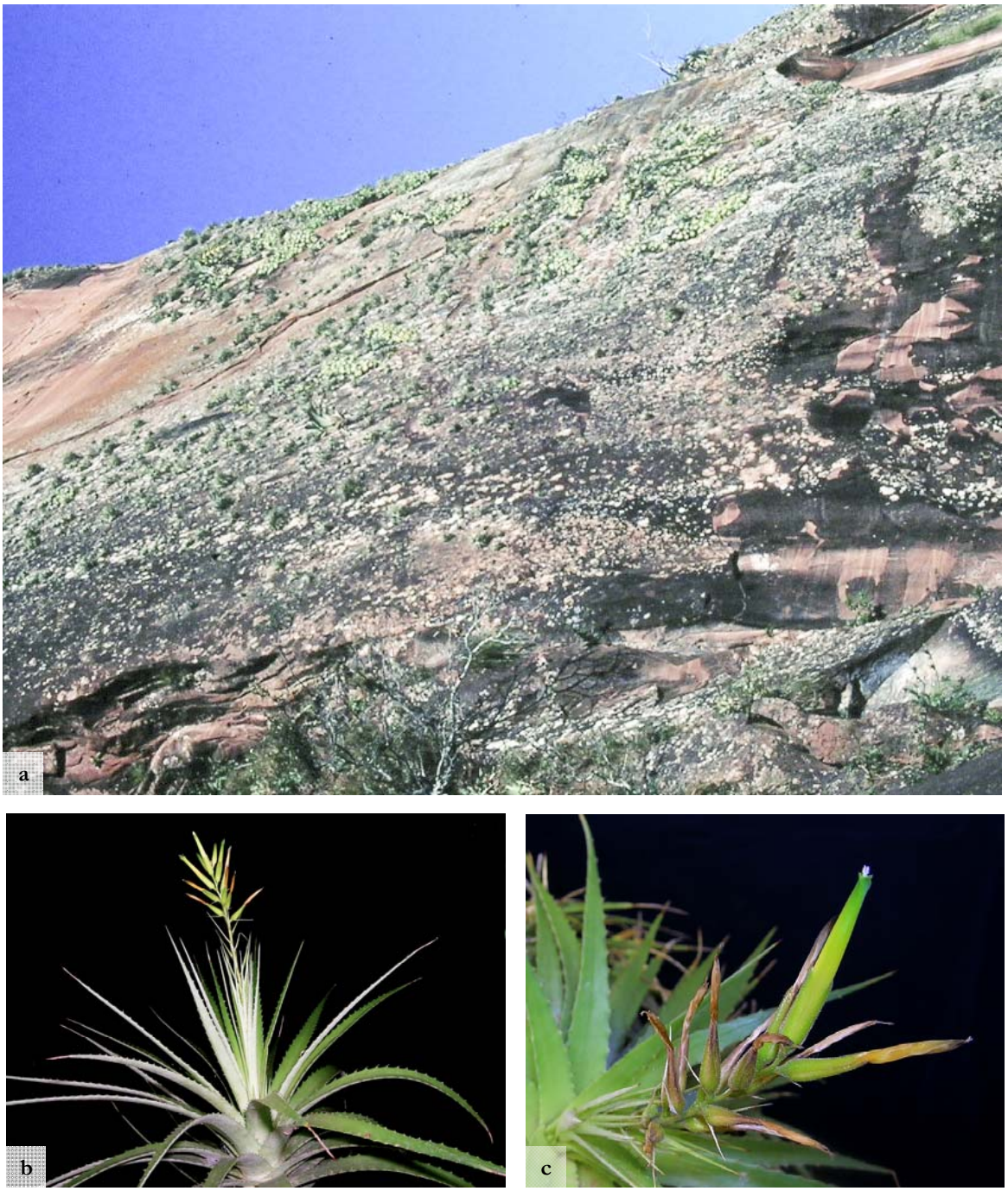


Fig. 5.13: *D. gableana*. a: Natural habitat, Dept. Santa Cruz, Bolivia (*R. Vásquez 4253*). b: Mature plant with inflorescence (*R. Vásquez et al. 4253*, private collection). c: Flowers. Photos a–c: Roberto Vásquez.

***Deuterocohnia glandulosa*** E. Gross in Rauh and Gross, Trop. Subtrop. Pflanzenwelt 75: 5. 1990. Type: Bolivia, Dept. Tarija, Prov. Gran Chaco, near Campo Serere, on the way to Villa Montes, 24 Jul. 1979. *Hromadnik 5167* [holotype: HEID!].

**Plants** growing solitary or in groups. **Rosettes** 30–40 × 40–50 cm. **Leaf sheaths** 5–6 × 4–5 cm. **Blades** 30–45 × 2–4 cm, recurved, adaxially concave, spinose-serrate, lepidote, greyish–green. **Peduncle** present, incl. inflorescence 80–120 cm × 4–6 mm, erect, perennial, woody. **Peduncle bracts** [2.5–] 4–5 cm × 3–4 mm, laxely spinose-serrate, upper ones shorter and entire. **Inflorescence** 30–50 cm long, simple or compound, branches of 1st or 2nd order, perennial. **Primary bracts** 10–20 × 3–4 mm, shorter than the partial inflorescence, narrowly triangular, narrowly acute, entire, lepidote. **Partial inflorescences** 5–12 × 3–4 cm long, densely to laxely flowered spikes, axis concealed, simple or branched, cylindrical, 10–25-flowered. **Floral bracts** 4–6 × 4 mm, much shorter than the sepals, ovate, acute, mucronate, abaxially with glandular trichomes, greenish-brownish. **Flowers** [20–] 25–28 mm long, sessile or subsessile. **Sepals** 10–14 × 3.5–4 mm, narrowly ovate, acute, abaxially with glandular trichomes, greenish. **Petals** [20–] 26–28 × 5–6 mm, erect during anthesis or with slightly recurved apex, after anthesis slightly spirally twisted, yellow, with greenish apex. **Petal appendages** 4–5 mm long, with short fringes. **Filaments** [12–] 15–19 mm long. **Anthers** 4–4.5 mm long, erect, concealed, yellowish. **Ovary** 4–5 mm long. **Style** 20–21 mm long, stigma exposed. **Fruits** 7 × 5 mm. **Seeds** 2–3 mm long.

**Distribution.** BOLIVIA, Dept. Santa Cruz, Tarija. 19°35'–21°30' S, 63°35'–64°20' W.

**Habitat and ecology.** Ecoregion: Andean Yungas (64). At elevations of 900–1200 m a.s.l. Terrestrial or saxicolous. Flowering time reported from August to September. Probably pollinated by hummingbirds and insects.

**Etymology.** The epithet refers to the glandular trichomes on the abaxial sepal surface.

**Affinities.** Morphologically, *D. glandulosa* shows affinities to *D. haumanii* and *D. longipetala*. From *D. haumanii* it can be distiguished by its less robust axes, smaller floral bracts and sepals without a mucronulate apex. Additionally, *D. glandulosa* has a distinct distribution area in Bolivia. Compared to *D. longipetala*, this species is characterized by its denser partial inflorescences and frequently glandular trichomes on the abaxial sepal surface.

**Notes and comments.** (a) Living plant of type locality is grown in the Botanical Garden of Heidelberg. (b) The glandular trichomes on the sepal surface are frequent, but not obligatory.

**Further references.** Spencer and Smith, Bradea 6: 145. 1992. Horres and Zizka, Beitr. Biol. Pflanzen 69(1): 43–76. 1995 (anatomical study). Gross, Selbyana 19(2): 193. 1998. Krömer et al., Selbyana 20(2): 207. 1999. Horres et al., Pl. Biol. (Stuttgart) 2(3): 309, 310. 2000 (phylogenetic study). Horres et al., Aliso 23: 27–43. 2007 (phylogenetic study). Givnish et al., Amer. J. Bot. 98(5): 872–895. 2011 (phylogenetic study).

**Specimens seen:** BOLIVIA: **Dept. Santa Cruz:** Prov. Cordillera: Valley of Tareira, Lagunillas, 1000 m, (19°39' S, 63°40' W), Aug. 1934, *Cárdenas 2850* [F!, GH!]; 14 km on road from Ipati to Lagunillas, 998 m, 19°42'23" S, 63°39'08" W, 03 Oct. 2006, *Schütz et al. 06-019* [FR!]; ibid.: *Schütz et al. 06-020* [FR!]; ibid.: *Schütz et al. 06-021* [LPB!]. **Dept. Tarija:** Prov. O'Connor: between Entre Rios and Tarija, (21°25' S, ca. 64°20' W), 04 Oct. 1986, *Fournet 715* [US!]; near Campo Serere, on the way to Villa Montes, (21°30' S, 63°30' W), 24 Jul. 1979, *Hromadnik 5167* [HEID!].
s.loco: *coll. ign.* [WU 4204! (2 sheets)]; *coll ign.* [WU 4111! (2 sheets)].

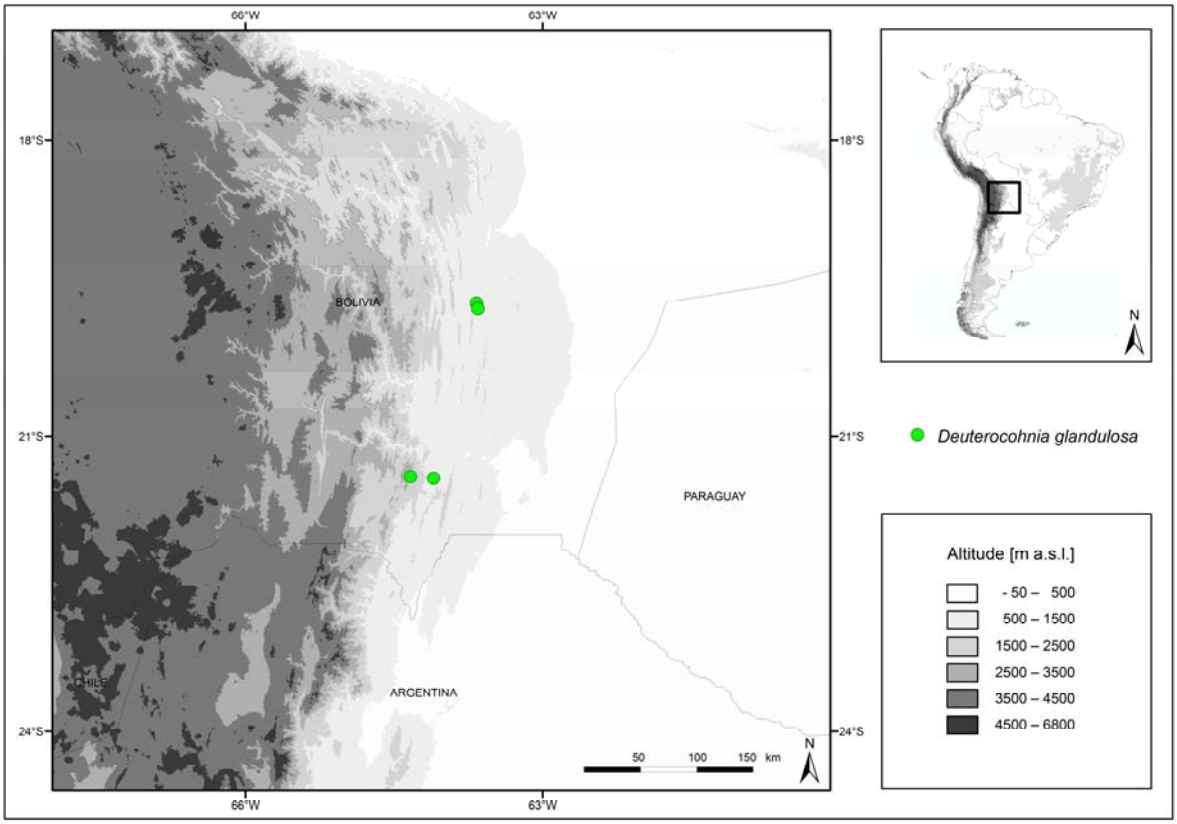


Fig. 5.14: Distribution of *D. glandulosa*.

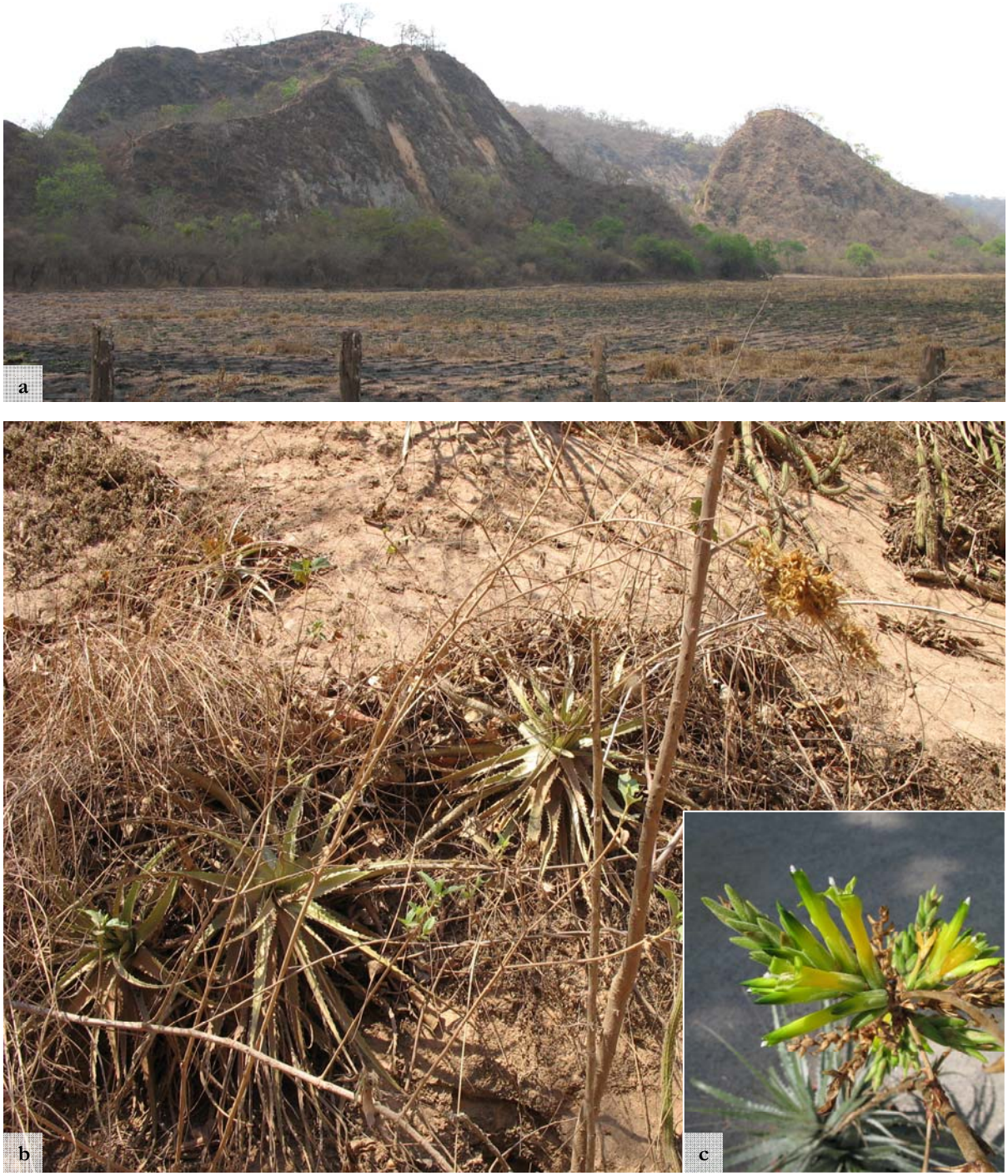


Fig. 5.15: *D. glandulosa*. a: Natural habitat. Dept. Santa Cruz, Bolivia (*N. Schütz 06-021*). b: Mature plant with compact partial inflorescences at the end of the fruiting period. c: Partial inflorescence of the type collection, (*L. Hromadnik 5167*), growing in the BGHD. Photo c: Timm Stolten.

***Deuterocohnia haumanii*** A. Cast., Anales Mus. Nac. Hist. Nat. „Bernardino Rivadavia" 36: 50. Fig. 13. 1929. Syntypes: Argentina, Prov. Salta, Dept. Cafayate, Valles Calchaquies, Nov. 1919, *Hauman s.n.* [BA 1110, photo in B!, K!, NY!, isosyntypes: K 321549!, GH]; Argentina, Prov. Catamarca, Dept. Santa María, Valle de Santa María, Quebrada de Balastro, Nov. 1915, *Schreiter s.n.* [LIL 34573!, isosyntype: A!].

**Plants** forming rings or cushions. **Rosettes** 15–25 × 25–40 cm. **Leaf sheaths** 3–4 × 4–6 cm. **Blades** 20–35 × [1.5–] 2–3.5 [–4.5] cm, recurved, adaxially concave, spinose-serrate, lepidote, greyish–green or reddish. **Peduncle** present, incl. inflorescence 70–120 cm × 4–7 mm, erect, perennial, woody. **Peduncle bracts** 40–60 × 3–5 mm, laxely spinose-serrate, upper ones entire. **Inflorescence** 30–40 cm long, simple or compound, branches of 1st order, perennial. **Primary bracts** 20–40 × 4-5 mm, shorter than the partial inflorescence, narrowly triangular, acute, entire, glabrous or lepidote. **Partial inflorescences** 5–15 [–25] × 2–3 [4.5] cm long, densely to laxely flowered spikes, axis concealed or visible, simple or rarely branched, cylindrical, [5–] 10–40 [–50]-flowered. **Floral bracts** [4–] 6–10 [–12] × 4–5 [–8] mm, about equaling the sepals or much shorter, broadly ovate, acute, abaxially with glandular trichomes, rarely glabrous, brownish. **Flowers** [20–] 22–29 mm long, sessile or subsessile. **Sepals** [8–] 10–13 [–15] × 4–5 mm, ovate to lanceolate, acute, mucronulate, abaxially with glandular trichomes, rarely glabrous, greenish. **Petals** 20–29 × 4–6 mm, erect during anthesis or with slightly recurved apex, after anthesis slightly spirally twisted, yellow, with greenish apex. **Petal appendages** 4–6 mm long, with short fringes. **Filaments** [12–] 17–19 mm long. **Anthers** 4 mm long, erect, concealed, greenish. **Ovary** 3–4 mm long. **Style** 16–20 mm long, stigma exposed. **Fruits** 11 × 7–8 mm. **Seeds** 2.5–3 mm long.

**Distribution.** ARGENTINA. Prov. Salta, Catamarca, Tucumán. 25°30'–26°30' S, 64°45'–66°10' W.

**Habitat and ecology.** Ecoregion: Andean Yungas (64) and Chaco savannas (96). At elevations of [500–] 1000–1900 m a.s.l. Terrestrial, on dry, rocky slopes, low, thorny shrub vegetation. Anthesis from September to February. Pollinators may be birds and insects.

**Etymology.** The species is named after the Belgian botanist Lucien Leon Hauman-Merck (1880–1965). He had a position at the University of Buenos Aires (1904–1925) and conducted a lot of investigations and publications of the Argentinean flora.

**Affinities.** *Deuterocohnia haumanii* comprises affinity to *D. longipetala* and *D. schreiteri*. It differs from the first in having more densely flowered branches and larger floral bracts and exhibits usually glandular trichomes on sepals, floral bracts and young branches. *D. haumanii* differs from *D. schreiteri* in noticeably larger floral bracts, larger flowers and the usually hairy floral parts. The distribution areas of the species overlap in Salta and Tucumán, where probably hybrids occur. In this regions various combinations of the distinguishing characters may be observed. Furthermore, *D. haumanii* shows similarities with two geographically distinct species, *D. glandulosa* and *D. chrysantha*. It can be distinguished from the Bolivian species *D. glandulosa* by its more robust axes, larger floral bracts and mucronulate sepals. From the Chilean species *D. chrysantha* it differs in having sepals with glandular trichomes, straight anthers, more leaf spines and greenish to dark reddish leaf blades.

**Notes and comments.** (a) The collection number *Venturi 1023* was probably assigned two times: *Deuterocohnia longipetala* [LIL, photo ex LIL in B!, K!] and *D. haumanii* [GH!]. (b) The syntype of *Schreiter s.n.* in LIL exhibits two herbarium numbers, 34573 on the label and 34593 on the sheet. The number on the label is treated here as the correct one, also seen on the label of the voucher in A. (c) In the protologue of *D. haumanii*, the peduncle bracts are described as deciduous. This might rather be due to external causes (animals, climate) than representing a species specific character. (d) Beside the specimens similar to the type voucher, there are some with less robust inflorescences and smaller floral bracts, especially in the area of Chicoana, Prov. Salta, Argentina. (e) The typical partial inflorescence of *D. haumanii* is densely flowered. However, laxer ones occur, potentially of hybrid origin. (f) The sepals often bear glandular trichomes, but also populations with glabrous sepals can be found. (g) Classified as *rare* by IUCN red list of threatened plants (1997).

**Further references.** Mez in Engler, Pflanzenr. IV. 32. (100): 283. 1934. Castellanos, Lilloa 10: 457. 1944. Castellanos in Descole, Gen. Spec. Plant. Argent. 3: 195. 1945. Smith, Bromeliana 1(4): 4. 1964. Smith and Downs, Fl. Neotrop. Monogr. 14 (3): 237. 1974. Varadarajan and Gilmartin, Syst. Bot. 12(4): 562–571. 1987 (micromorphological study). Varadarajan and Gilmartin, Amer. J. Bot. 75(6): 810. 1988 (morphological study). Varadarajan and Brown, Bot Gaz. 149(1): 86. 1988 (morphological study). Brown and Gilmartin, Amer. J. Bot. 76(5): 659. 1989 (cytogenetic study). Brown and Gilmartin, Syst. Bot. 14(1): 125. 1989 (micromorphological study). Rauh and Gross, Trop. Subtrop. Pflanzenwelt 75: 5, 8. 1990. Spencer and Smith, Bradea 6: 145. 1992. Zuloaga and Morrone, Monogr. Syst. Bot. Missouri Bot. Gard. 60: 109. 1996. Zuloaga et al., Monogr. Syst. Bot. Missouri Bot. Gard. 107(1): 1–983. 2008.

**Specimens seen.** ARGENTINA: **Prov. Salta:** Rio Grande, 650 m, 24 Sep. 1969, *Valenzuela s.n.* [LIL 556207!]. Dept. Cachi: RP 33 between Salta and Cachi, 25°10'25" S, 65°45'54" W, 2071 m, 27 Nov. 2006, *Schütz et al. 06-095*

[LIL!]. Dept. Chicoana: 2 km SW of Los Laureles, along the road to Cuesta del Obispo, (25°07'30" S, 65°36' W), 1480 m, 10 Feb. 1993, *Till, W. 10145* [WU!]; Quebrada de Malcante, RN 59, (25°08' S, ca. 65°45' W), 19 Oct. 1985, *Palaci and Gallardo 222* [MCNS!]; Quebrada de Escoipe, km 22 on RP 33, on road from El Carril nach Cachi, Peña Baya, 1564 m, 25°09'55" S, 65°39'08" W, 27 Nov. 2006, *Schütz et al. 06-80* [LIL!]; Quebrada de Escoipe, km 22 on RP 33, on road from El Carril nach Cachi, Peña Baya, 1601 m, 25°09'58" S, 65°38'58" W, 27 Nov. 2006, *Schütz et al. 06-82* [LIL!]. Pena Baya, 19 km west from RN 68 Salta to Cafayate, 50 m from the road to Cachi from Chicoana, 25°12' S (25°09"), 65°41' W, 1600–1650 m, 21 Feb. 1984, *Varadarajan 1262 et al.* [US!]; at the beginning of Quebrada del Mal Paso, 24 km west from the RN 68 Salta to Cafayate, 25°13' S, 65°45' W, 1875–2000 m, 21 Feb. 1984, *Varadarajan et al. 1266* [US!]; Cuesta del Obispo, (25°15' S, 65°45' W), 10 Nov. 2002, *Cocucci 2077* [CORD!]. Dept. La Viña: road of barrage Cabra Corral, 2 km after crossing the bridge, in direction to the weir General Belgrano, (25°17' S, 65°22–25' W), 1150 m, 28 Sep. 1999, *Novara 11356* [G!, MCNS!]; near Talapampa, (25°32' S, 65°34' W), 1300 m, Oct. 1948, *Cárdenas 4218* [GH!, LIL!]; Talapampa, (25°32' S, 65°34' W), 1100 m, 13 Dec. 1985, *Palaci 316* [MCNS!]; Quebrada de las Conchas, 5 km on road from Alemania to Cafayate, (25°38" S, 65°39' W), 1200 m, 27 Nov. 1933, *Peirano s.n.* [LIL 34592!, U!]; km 69 on RP 68 between Cafayate and Alemania, Las Abritas, 25°40'46" S, 65°41'27" W, 1385 m, 28 Nov. 2006, *Schütz et al. 06-117* [LIL!]; ibid.: *Schütz et al. 06-118* [LIL!]; *Schütz et al. 06-119* [LIL!]; *Schütz et al. 06-120* [LIL!]. Dept. Guachipas: Quebrada de Guachipas, (25°30' S, 65°30' W), 23 Jan. 1943, *Castellanos 46630* [BA!]; road from Salta to Cafayate, Quebrada del Río de las Conchas, (25°30'–26°00' S, 65°40–45' W), 1400–1500 20 Oct. 1983, *Charpin 18390* [G!]; Tres Cruces, between Cafayate and Alemania, (25°52' S, 65°42' W), 20 Jan. 1945, *Descole 3000* [LIL!]; ibid.: *Descole s.n.* [LIL 118245!, right side, together with a specimen of *D. schreiteri* on the left side]; Tres Cruces, km 41–42 from Cafayate to Salta, (25°52' S, 65°42' W), 1450 m, 12 Nov. 1984, *Subils 3556* [CORD!]; Tres Cruces, road from Alemania to Cafayate, (25°52'S, 65°42' W), 1500 m, 23 Sep. 1969, *Meyer 22921* [LIL!]; ibid.: 25 Sep. 1969, *Meyer 22922* [LIL!]; Quebrada de las Conchas, (25°30" S, 65°30' W), 17 Oct. 1985, *Palaci 223* [MCNS!]; Cuesta del Lajar, between La Viña and Guachipas, 32 km from Guachipas, (25°40'11" S, 65°29'27" W), 1820 m, 28 Nov. 2006, *Schütz et al. 06-123* [LIL!]; ibid.: *Schütz et al. 06-124* [LIL!]; *Schütz et al. 06-125* [LIL!]; RP 68 between Cafayate and Alemania, 1463 m, 25°54'30" S, 28 65°42'39" W, Nov. 2006, *Schütz et al. 06-114* [LIL!]; Valle de las Conchas, Alemania to Cafayate, (25°50' S, 65°40' W), 20 Oct. 1948, *Skottsberg s.n.* [GB s.n.!]; N of Guachipas, (25°30' S, 65°30' W), 20 Oct. 1948, *Smith 4655* [GH!, US!]; Quebrada de Guachipas (25°30' S, 65°30' W), Dec. 1896, *Spegazzini s.n.* [LP 209!]. Dept. Cafayate: Tolombón, (26°11' S, 65°56' W), 19 Oct. 1948, *Castellanos s.n.* [LIL 313266!]; Valles Calchaquíes, (26°00" S, 66°00' W), Nov. 1919, *Hauman s.n.* [BA 1110, GH!, K 321549!, photo ex BA in B!, K!, NY!]; amphitheater Orillas del Antiguo, road to Cafayate, (26°01'25" S, 65°50'13" W), 1600 m, 24 Oct. 1992, *Tolaba 415* [MCNS!]; 30 km from Cafayate, Alemania; (26°00' S, 65°45' W), 25 Sep. 1969, *Vaca 400* [LIL!]. Dept. La Candelaria: Santa Bárbara, 1200 m, 24 Nov. 1930, *Schreiter 6481* [LIL!]; Quebrada de Unquillo, Sierra del Castillejos, (26°12' S, 64°58' W), 1500 m, 07 Nov. 1931, *Schreiter 6618* [BA!; LIL!]; Unquillo, Quebrada del Chorro, (26°10' S 64°55' W), 1400 m, 07 Nov. 1931, *Schreiter 6726* [A!, LIL!, U!, BAB, US]. **Prov. Tucumán:** Dept. Burruyacú: ravine, Canal Florida, (26°30' S, 64°45' W), 550 m, 31 Oct. 1920, *Venturi 1023* [GH!]. **Prov. Catamarca:** Dept. Santa María: Valle de Santa María, Quebrada de Balastro, (26°58' S, 66°08' W), Nov. 1915, *Schreiter s.n.* [A!, BA, LIL 34573!]. s.loco: *Cubr 31096* [B!]; ibid.: *Schwertfeger 19602* [B!].

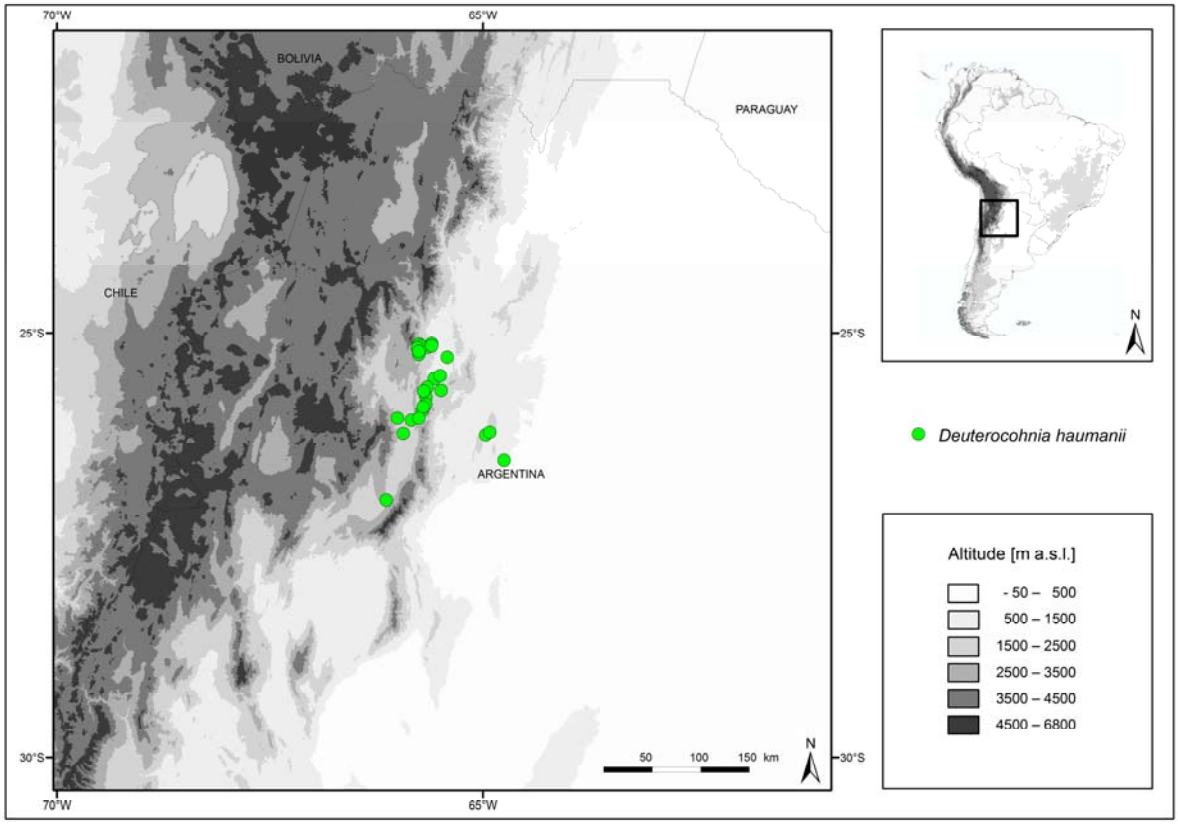


Fig. 5.16: Distribution of *D. haumanii*.

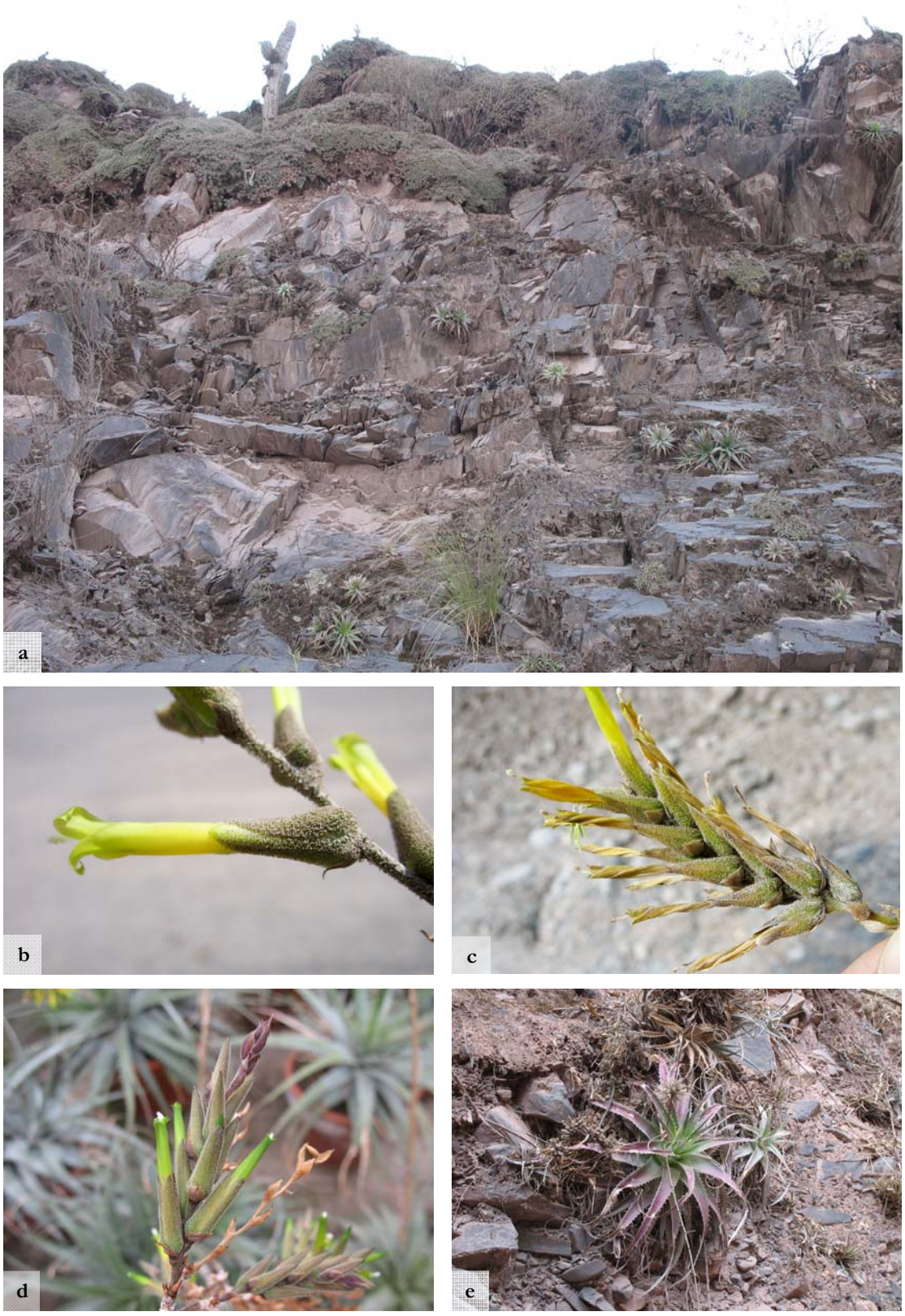


Fig. 5.17: *D. haumanii*. a: Natural habitat. Prov. Salta, Argentina (*N. Schütz 06-087*). b: Flower, the glandular trichomes on the sepals are covered with dust. c: Partial inflorescence. d: Partial inflorescence of the collection *W. Rauh 64157* in the BGHD. e: Rosette, with reddish coloured leaf parts.

***Deuterocohnia longipetala*** (Baker) Mez in Mart., Fl. bras. 3 (3): 507. Fig. 95. 1894. ≡ *Dyckia longipetala* Baker, Handb. Bromel.: 135. 1889. ≡ *Puya flava* Willd. ex Baker, Handb. Bromel.: 135. 1889. nom. nud. ≡ *Puya weberi* Schlumb. ex Lillo, Fl. Tucumán: 104. 1888. nom. nud. Type: Perú, Dept. Cajamarca, Río Marañon, Aug. 1802, *Humboldt and Bonpland 3595* [holotype: B (not seen, probably destroyed), photo in F, negative 11389!]. Epitype (designated in the present study): Perú, Dept. Cajamarca, Prov. Jaén, 2 miles E of Lac, Canyon of Río Chamaya, 850 m, 04 Oct. 1957, *Hutchison 1571* [UC!, isoepitypes US!, USM!. Cultivated in F!].

= *Dyckia decomposita* Baker, Handb. Bromel.: 136. 1889 (synonymized by Mez in C.DC., Monogr. phan. 9: 465. 1896). Syntypes: Argentina, Prov. Mendoza, Cerros de Chayados, *Miers 1098* [BM!]; Argentina, Prov. Mendoza, *Gillies s.n.* [K! Kew negative 7475].

= *Deuterocohnia longipetala* Mez f. *uberrima* A. Cast., Anales Mus. Argent. Ci. Nat. "Bernardino Rivadavia" 37: 495. 1933. (synonymized by Smith and Downs, Fl. Neotrop. Monogr. 14(1): 233. 1974). Type: Argentina, Prov. Tucumán, N of Dique, 650 m, 31 Oct. 1920, *Venturi 1023* [holotype: LIL! (2 sheets), photo in B!, K!, isotypes: A!, SI! (2 sheets)].

**Plants** growing solitary or in groups or forming rings. **Rosettes** 15–25 × 25–35 cm. **Leaf sheaths** 3–4 × 4–6 cm. **Blades** [12–] 20–30 [–40] × 2–4 cm, recurved, adaxially concave, spinose-serrate, lepidote, greenish, greyish or reddish. **Peduncle** present, incl. inflorescence 80–120 cm × 4–7 mm, erect, perennial, woody. **Peduncle bracts** 5–7 cm × 4–7 mm, laxely spinose-serrate, upper ones entire. **Inflorescence** 30–50 cm long, compound, branches of 1st, 2nd or 3rd order, perennial. **Primary bracts** 10–15 × 4–5 mm, shorter than the sterile base of the partial inflorescence, narrowly triangular to ovate, acute, entire, glabrous or lepidote. **Partial inflorescences** up to 25 cm long, laxely flowered spikes, axis visible, branched, 20–50-flowered. **Floral bracts** 4–6 [–10] × 4–5 mm, much shorter than the sepals, ovate, acute, mucronate, glabrous or rarely with glandular trichomes, brownish. **Flowers** [20–] 22–27 mm long, sessile. **Sepals** [5–] 8–12 [–15] × 4–5 mm, ovate, acute to obtuse, glabrous or rarely with glandular trichomes, yellow to greenish. **Petals** 22–28 × 4–6 mm, erect during anthesis or apex slightly recurved, after anthesis slightly spirally twisted, yellow, with greenish apex. **Petal appendages** 3–4 mm long, with short fringes. **Filaments** 15–18 mm long. **Anthers** 4–6 mm long, erect, concealed, greenish. **Ovary** 4–5 mm long. **Style** 17–20 mm long, stigma exposed. **Fruits** 8 × 6–7 mm. **Seeds** 2.5–3 [–4] mm long.

**Distribution.** PERU. Dept. Amazonas, Cajamarca, Lambayeque, La Libertad. BOLIVIA. Dept. Tarija. ARGENTINA. Prov. Jujuy, Salta, Tucumán, Catamarca, Santiago del Estero, La Rioja, San Juan, Córdoba, San Luis, Mendoza. [5°30'–] 21°14'–34°00' S, 63°09'–69°06' [–79°50'] W. *D. longipetala* comprises the widest distribution range among the species of *Deuterocohnia* and ist the only species with a conspicuously disjunct distribution area. The populations from N Peru are about 2000 km away from those occuring in Bolivia.

**Habitat and ecology.** Ecoregions: Peruvian Yungas (56), Tumbes/Piura dry forests (93), Marañon dry forests (94), Andean Yungas (64), Chaco savannas (96), Arid Chaco (131), Córdoba montane savannas (134), Argentine Monte (136) and Argentine Espinal (137). At elevations of 250–1500 m a.s.l. Terrestrial, on dry, rocky slopes, open shrub vegetation on sandstone as well as on granite, also on saline soil. Main anthesis from October to February. Hummingbirds are supposed to be the main pollinators.

**Etymology.** The epithet refers to the long petals.

**Affinities.** *Deuterocohnia longipetala* is similar to *D. haumanii*, but differs in having less densely flowered partial inflorescences, smaller floral bracts and usually glabrous floral parts. Furthermore, *D. longipetala* has affinities to *D. meziana*, which exhibits larger rosettes and branches up to 4$^{th}$ order, and which is usually pedicellate. Putative hybrids of both species occur along the border between Bolivia and Argentina. Putative hybrids between *D. longipetala* and *D. haumanii* seem to be common in Salta and Tucumán, Argentina.

**Notes and comments.** (a) The type specimen in Berlin was probably destroyed during second world war. (b) There is only a photograph of the type specimen of *D. longipetala* (F negative 11389) left. The photo provides only little information on the plant, just showing a small, flowerless part of the inflorescence. Therefore an epitype was choosen. This epitype (*Hutchison 1571*) was colleted – like the holotype – in Peru, and provides beside parts of the inflorescence, leaves and flowers. (c) The type locality of *D. longipetala* was erroneously cited as "Brazil" by Mez (Smith 1956). (d) Mez noted already in the first description of *Deuterocohnia longipetala* that *Dyckia decomposita* might be a synonym. He had only seen the diagnosis, but not the vouchers. (e) The collection number *Venturi 1023* was given to two different collections. One voucher, which is the type for *D. longipetala* f. *uberrima*, and another one, which belongs to *D. haumanii* [GH]. The latter erroneously has also been cited as type by Smith and Downs (1974). (f) The vouchers *Stuckert 11041*

and *Stuckert 12098* in G both carry a label with *D. gracilis* Mez. This name has never been published. (g) *Kurtz 119* [CORD!] noted "Paraguay" on the voucher, without precise locality, it would be the only documented specimen of *D. longipetala* from Paraguay. (h) *Bartlett 19977-A* (La Pampa, Hucal, Campo San Pedro, Laguna Veronica, 12 km NW of Bernasconi) [GH!, MICH, US] got probably a wrong label, as noted on the voucher by Cantino (in schedis). Therefore the locality of the specimen can not be verified. It would be the only collection in the Argentinean Dept. La Pampa. (i) *Wilson 65-690* [US!] notes Bahia (Brazil) as locality (see also Smith and Read 1975), but this seems to be unlikely, probably there was a mix-up of collection data. (j) Smith and Downs (1974) assigned *Kuntze s.n.* (*Deuterocohnia chrysantha* sensu Mez in C.DC. (1896) in part) to *D. longipetala*. This voucher is assigned to *D. meziana* in the present revision. (k) This term "*longipetala*" was probably chosen due to the distinctly shorter petals of the species belonging to the genus *Dyckia*. At first, the type specimen of *Deuterocohnia longipetala* had been assigned to *Dyckia*.

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**Specimens seen.** PERU: valley of Río Marañon, 370 m, 23 Dec. 1970, *Ellenberg 3605* [US!]. **Dept. Amazonas:** Prov. Bagua: Pongo de Rentema, Río Marañon, (05°30' S, 78°33' W), 380–400 m, 03 Mar. 1961, *Ferreyra 14218* [US!, USM!]; Valley of Río Marañon, 05°30' S, 78°30' W 400 m, 04 Feb. 1999, *Vásquez et al. 25930* [USM!]. Prov. Utcubamba: valley of Chamaya, Ingenio, (05°58' S, 78°10' W), 1200 m, 10 Aug. 1970, *Rauh 24611* [HEID! (2 sheets)]. Prov. Luya: valley of Río Marañon by Tupen, (06°12' S, 77°55' W), 800 m, Jan. 1905, *Weberbauer 4798* [B, F!, WRSL]. **Dept. Cajamarca:** 170 km towards Olmos, 740 m, 25 Dec. 1970, *Ellenberg 3648* [LPB!]; valley of Cajamarca, 800 m, 16 Aug. 1978, *Rauh s.n.* [US 2848091!]. Prov. Jaén: Rio Marañon, (05°30' S, 78°40' W), Aug. 1802, *Humboldt and Bonpland 3595* [B, photo in F 11389!]; Canyon of the Río Chamaya, 2 km E of Lac, (05°50' S, 78°50' W), 850 m, 04 Oct. 1957, *Hutchison 1571* [F!, UC!, US!, USM!]; Cajaruro, (06°00' S, 79°11' W), 10 Sep. 1952, *Diaz s.n.* [USM s.n.! (2 sheets)]; Pucará–Chamaya, (06°00' S, 79°00' W), 1000 m, 16 Sep. 1981, *López et al. 8953* [HUT!]. Prov. Santa Cruz: Santa Cruz, (06°40' S, 79°02' W), 500 m, Oct. 1973, *Rauh 35553* [HEID!]. Prov. San Miguel: between Quindén and Platanar, road to village of Unión Agua Blanca, (07°04' S, 78°58' W), 650–1100 m, 06 Oct. 2001, *Rodriguez et al. 2414* [F!, HUT!]. Prov. Contumazá: between Llallán and Tembladera, (07°11' S, 79°00' W), 600 m, 17 Aug. 1952, *Ferreyra 8605* [USM!, photo in NY!]; near Tambo, (07°20' S, 78°45' W), 700 m, 15 Jul. 1952, *Angulo et al. s.n.* [HUT 1729!]. Prov. Cajamarca: km 109 of road Pacasmayo to Cajamarca, (07°15' S, 78°42' W), 1100 m, 28 Nov. 1981, *Sánchez Vega 2720* [F!, USM!]. **Dept. Lambayeque:** Prov. Lambayeque: Olmos, (05°55' S, 79°45' W), 1000–2000 m, 08 Oct. 1954, *Rauh and Hirsch P2153* [HEID! (2 sheets), US!]; lower valley of Río Olmos, 16 km NE of the bifurcation from the Panamericana on road to Bagua, near Puente El Silencio, (06°30' S, 79°50' W), 400 m, 24 Jul. 1986, *Till, W. and Lindner 2038* [WU!]. **Dept. La Libertad:** Prov. Ascope: between Pampas de Jaguey and Quirripe, (07°41' S, 78°55' W), 850 m, 07 Dec. 1952, *Angulo s.n.* [HUT 2210!]. ibid.: 700 m, 07 Dec. 1952, *López 0917* [LIL!].
BOLIVIA: **Dept. Santa Cruz:** Prov. Cordillera: 0.3 km E of Comunidad Salinas from turnoff of the Camiri-Cuevo highway, 850 m, 20°13'38" S, 63°27'53" W, 06 Nov. 2000, *Nee 51213* [NY!]. **Dept. Chuquisaca:** Prov. Luis Calvo: road from Aratical to Vaca Guzmán, 1273 m, 19°53'31" S, 63°44'29" W, 03 Oct. 2006, *Schütz et al. 06-024* [FR!]; ibid.: *Schütz et al. 06-025* [FR!, LPB!]. **Dept. Tarija:** Prov. Gran Chaco: road between Entre Rios and Villamontes, 10 km

from Villamontes, near Río Pilcomayo, 21°14' S, 63°35' W, 800m, 30 Oct. 1993, *Ibisch 93.1298* [LPB!]; Villamontes, Río Pilcomayo, (21°15' S, 63°30' W), 500 m, 21 Oct. 1918, *Pflanz 943* [M!]; valley of Río Pilcomayo, Villamontes, (21°15' S, 63°30' W), 600 m, 14 Oct. 1927, *Troll 492* [B!, M!]. road between Entre Rios and Villamontes, (21°25' S, 63°40' W), 730 m, 10 Nov. 1993, *Billiet and Jadin 6154* [K!]; W of Villamontes, ravines of Rio Pilcomayo, 21°25' S, 63°30' W, 350 m, 01 Nov. 1993, *Billiet and Jadin 6013* [K!]. Prov. Aniceto Arce: 160 km on road from Tarija to Bermejo, near Rio Bermejo, 22°28'39" S, 64°28'59" W, 600 m, 11 Oct. 2006, *Schütz et al. 06-064* [FR! (3 sheets)]; ibid.: *Schütz et al. 06-065* [FR!, LPB!]; ibid.: *Schütz et al. 06-066* [LPB! (2 sheets)]; 167 km on road from Tarija to Bermejo, near Rio Bermejo, 22°29'29" S, 64°27'54" W, 593 m, 11 Oct. 2006, *Schütz et al. 06-067* [FR! (4 sheets), LPB! (2 sheets)].

ARGENTINA: 1500 m, 26 Sep. 1938, *Wall 22212* [S!]. **Prov. Jujuy:** Dept. Valle Grande: road to Valle Grande, Río Sunchal, 23°30' S, 64°58' W, 1290 m, 09 Oct. 1973, *Schiavone s.n.* [LIL!]. Dept. San Pedro: mountains SE of San Pedro, (24°15' S, 64°51' W), 16 Oct. 1964, *Cabrera and Fabris 16047* [LP!]; mountains of San Lucas, (24°17' S, 64°52' W), 08 Jan. 1971, *Fabris 7977* [C!]; mountains of San Lucas, about 3–5 km from San Lucas, 24°18' S, 64°50' W, 650–700 m, 08 Feb. 1984, *Varadarajan 1232* [US]; bluffs of Río San Pedro, between San Juancito and La Mendieta, station on F.C.C.N.A, (24°21' S, 65°00' W), 800 m, 16 Feb. 1937, *West 8386* [GH!, UC!]; between La Mendieta and Palpalá, RP 56, 24°21'16" S, 65°01'31" W, 901 m, 29 Nov. 2006, *Schütz et al. 06-126* [FR!]; Río Grande, 15 km SE of San Pedro, (24°22' S, 64°46'30" W), 1200 m, 30 Sep. 1938, *Eyerdam and Beetle 22312* [G!, GH!, K!, UC!]. Dept Palpalá: about 11 km before entering Carahunco from San Pedro by RN 56, 24°18' S, 65°10' W, 1200–1250 m, 08 Feb. 1984, *Varadarajan 1234* [GH!, US!], Dept. El Carmen: RN 9 from Salta to Jujuy, 24°24' S, 65°15' W, 1350–1400 m, 20 Feb. 1984, *Varadarajan et al. 1255* [US!]; 13 km S of Dique La Ciénaga, SW of Perico del Carmen, along the road to La Caldera, 8 km S of Las Lantas, 2 km NE of the provincial limits, (24°29' S, 65°17'30" W), 1420 m, 09 Feb. 1993, *Till, W. 10126* [WU!]; ravine of Santa Laura, (24°30' S, 65°17' W), 29 Oct. 1964, *Cabrera 16389* [LP!; US!]. **Prov. Salta:** Dept. Grl. San Martín: Piquirenda to Quebrada de Yacuy, (22°21' S, 63°48' W), 600 m, 03 Feb. 1925, *Schreiter 3610* [LIL! (2 sheets)]. Dept. Orán: from the international bridge of Río Bermejo, 8 km, road to Yacúlika, (22°43'30" S, 64°22' W), 21 Nov. 1974, *Ruiz et al. 10642* [LIL!]; border from Orán and San Martín, RN 34, ravine 500 m N of Río Bermejo, (23°14'30" S, 64°08' W), 23 Oct. 1991, *Charpin and Novara 22942* [G!, US!]. Dept. Grl. Güemes: station Aforo Mojotoro, (24°44' S, 65°00' W), 1069 m, 04 Oct. 1998, *Farquharson 1053* [MCNS!]. Dept. Metán: Cabra Corral, Peñas Azules, (25°10' S, 65°10' W), 900 m, 24 Oct. 1986, *Palací 795* [MCNS! (2 sheets)]; ibid.: *Palací 798 A* [MCNS!] . Dept. La Candelaria: about 2 km, NW of Potrerillo towards Pampa Grande, 2 km from Río Anta, 26°03' S, 65°27' W, 1000 m, 07 Feb. 1984, *Varadarajan 1227* [US! (3 sheets)]; Agua Caliente, (26°04' S, 65°05' W), 1000 m, 17 Oct. 1927, *Venturi 5483* [GH!, MO, MVM]. **Prov. Tucumán:** Nov. 1916, *Hauman 1112* [GH!]; N of Dique, 650 m, 31 Oct. 1920, *Venturi 1023* [A!, LIL! (2 sheets), SI! (2 sheets), photo ex LIL in B!, K!]. Dept. Trancas: San Pedro de Colalao, Las Tacanas, (26°14' S, 65°29' W), *coll. ign.* [LIL!]; 2 km N of the bifurcation to Gonzalo along the road to San Pedro de Colalao, (26°15' S, 65°30' W), 1130 m, 05 Feb. 1993, *Till, W. 10045* [WU!]; 3 km NE of Hualinchay along the road to San Pedro de Colalao, (26°18' S, 65°35' W), 1500 m, 05 Feb. 1993, *Till, W. 10050* [WU!]; Vipos, (26°29' S, 65°22' W), 23 Oct. 1888, *Lillo 517* [LIL!]; ibid.: 22 Dec. 1901, *Lillo 7272* [LIL!]; ibid.: 24 Sep. 1928, *Schreiter s.n.* [LIL 34657!]; ibid.: 750 m, *Schreiter s.n.* [LIL 95666!]; ibid.: 780 m, 28 Oct. 1923, *Schreiter 15* [LIL! (2 sheets)]; ibid.: 28 Oct. 1923, *Schreiter 17* [LIL!, UC!]; ibid.: 800 m, 28 Oct. 1923, *Venturi 2496* [LIL!, US! (2 sheets)]; ibid.: 800 m, 15 Nov. 1921, *Venturi 1572* [F!, LIL!, UC!]; Río Vipos, road about 10 km W of Vipos village and about 3 km before crossing the river, 26°29' S, 65°21' W, 400–450 m, 06 Feb. 1984, *Varadarajan 1224* [US!]; Jarami, near the confluence of Río Salí and el Vipos, (26°32' S, 65°13' W), 15 Apr. 1900, *Lillo 2490* [LIL!]. Dept. Tafí

Viejo: Cadillal, ravines of Río Sali (Río Loro), (26°37' S, 65°11' W), 24 Dec. 1916 *Castillon 7256* [LIL!]; ibid.: 500 m, 11 Nov. 1917, *Schreiter 269* [LIL!]; Dept. Lules: Quebrada de Lules (26°53' S, 65°25' W), Oct. 1905, *Castillon 41 a* [LIL!]; ibid.: 16 Oct. 1899, *Lillo 2328* [LIL!]; ibid.: Nov. 1919, *Schreiter s.n.* [LIL 34600!]; ibid.: 500 m, 28 Oct. 1919, *Schreiter 803* [A!, BA!, LIL!, MVM, NY!, U!]; ibid.; 500 m, 28 Oct. 1919, *Schreiter 8772* [LIL 34649! (2 sheets)]. Dept. Río Chico: Escaba, between Río Mora and Río Chorro, (27°30' S, 65°45' W), 600–800 m, 24 Nov. 1952, *Petersen and Hjerting 632* [C!]; Dept. J.B.Alberdi: Batiruana, (27°38' S, 65°45' W), 650 m, Dec. 1991, Neuhuber 91-480-1536 A [WU!]; Dept. Cocha: Los Pizarros, (27°45'30" S, 65°31' W), 11 Sep. 1969, *Figueroa s.n.* [LIL 576577!]; along the road 9 km from Juan B. Alberdi to Balcosna, 7 km below Dique Escaba, (27°45' S, 65°48' W), 670 m, 16 Feb. 1993, *Till, W. 10249* [LIL!, WU!]. **Prov. Catamarca:** 16 Jan. 1890, *Stuckert 6768* [G!]; San Rafael, 06 Oct. 1946, *Brizuela 339* [LIL!]. Dept. Belén: Cuesta de Belén, from Andalgalá to Belén, (27°45' S, 66°45' W), 900–1000 m, 02 Oct. 1988, *Till, H. 88-131* [WU! 2 sheets]; Cuesta de Belén, RN 62, km1558, (27°46' S, 66°45' W), 1140 m, 24 Feb. 1974, *Legname and Vervoorst 244* [C! (2 sheets)]. Dept. Andalgalá: with different collection dates, *Jörgensen 1580* [BA, GH! (2 sheets), LIL! (2 sheets), SI, UC!, US!]; Cuesta de la Chilca, 27°36' S, 66°20' W, 800–900 m, 23 Feb. 1984, Varadarajan 1269 [US!]; Cuesta de la Chilca, (27°38' S, 66°11' W), 1300–1600 m, 29 Nov. 1937, *Schreiter 10452* [LIL!]; Camino a Andalgalá; Cuesta de la Chilca, (27°38' S, 66°11' W), 1930, *Schreiter 6418* [BA!, BM!, F!, LIL! (3 sheets), UC!]; Quebrada del Río Cañada, 23 Oct. 1933, *Peirano 9902* [F!, LIL! (2 sheets)]; Dept. Tinogasta: Tinogasta to La Puntilla, (28°05' S, 67°30' W), 1200 m, 17 Feb. 1930, *Schreiter 6369* [LIL! (2 sheets)]. Dept. Pomán: Sierra de Ambato, falda oeste, between Pomán and Colana, (28°32' S, 66°13' W), 1160 m, 08 Dec. 1965, *Hunziker et al. 18396* [CORD!]; 4 km W of Joyango, "plants of the Bolson de Pipanaco and vicinity", (28°05' S, 66°10' W), 1100–1200 m, 19 Feb. 1973, *Cantino 657* [CORD!, GH!]. Dept. Ambato: 28 km N of Catamarca, (28°10' S, 65°46' W), 700 m, 29 Mar. 1995, *Saravia Toledo et al. 13068* [K!, LIL!]; between El Rodeo and Catamarca, (28°15' S, 65°53' W), 1300 m, 16 Mar. 1959, *Villa Carenzo and Legname 1198* [LIL!]. Dept. Capital: Alto de Choya, (28°25' S, 65°48' W), Dec. 1910, *Castillon 14114* [LIL!]; Catamarca, (28°25'S, 65°45' W), 15 Feb. 1945, *Krapovickas 1785* [LIL!]. Dept. F.M.Esquiú: Sierra de Gracián, (28°11' S, 65°45' W), 16 Jan. 1940, *Castellanos 33489* [BA, LIL!]. Dept. Paclín: between Catamarca and Cuesta del Totoral, (28°05'–28°20' S, 65°37' W), 16 Mar. 1959, *Villa Carenzo et al. 1121* [LIL!]. Dept. El Alto: road from Alijilán to Villa el Alto, (28°12' S, 65°28' W), 600 m, 26 Nov. 1979, *Legname et al. 6662* [LIL!]. Dept. Capayán: Sierra de Ambato, falda este, mountains between Miraflores and Los Angeles, (28°35' S, 65°56' W), 800 m, 27 Nov. 1965, *Hunziker et al. 18332* [CORD!]; 0,5 km NW of crossing of Río Casa de Piedra and locality with same name, low rocky hills on the left-hand side of the road and railway when coming on RN 33 from San Martín, 29°36'16" S, 65°31'59" W, 250 m, 26 Feb. 1994, *Leuenberger and Eggli 4370* [B!, CORD!]. Dept. La Paz: Recreo, (29°18' S, 65°03' W), 24 Feb. 1886, *Kurtz and Tatter 4319* [M!]. ibid.: 24 Febuar 1886 Kurtz 4339 [CORD!]; Ramblones, (29°10' S, 65°25' W), 23 Dec. 1946, *Brizuela 457* [LIL! (2 sheets)]. **Prov. Santiago del Estero:** Sierra de Mogotes, km 78 on road No. 64 from Santiago del Estero SW to Las Canas, behind Santa Catalina, 28°08'18.4" S, 64°48'58,8" W, 590 m, 29 Nov. 2008, *Dressler Arg16* [FR!]. Dept. Guasayán: Puerta Chiquita, (28°08' S, 64°52' W), 30 Sep. 1981, *Herrera 16* [LIL!]. **Prov. La Rioja:** Dept. San Blas de los Sauces: Alpasinche, (28°19' S, 67°03' W), 17 Feb. 1930, *Castellanos 30-403* [BA!]; along RN 40 from Pituil to Schaqui, 20 km NE of Pituil, (28°28'30" S, 67°16'30" W), 1370 m, 18 Feb. 1993, *Till, W. 10283* [LIL!]. Dept. Famatina: 13 km from Famatina towards Chilecito, 28°59'35" S, 67°30'52" W, 1420–1450 m, 16 Feb. 1994, *Leuenberger and Eggli 4223* [B!, CORD!, ZSS!]. Dept. Chilecito: 11 km N San Nicolas along the RN 40 to Famatina, (29°05' S, 67°28' W), 1100 m, 07 Feb. 1990, *Till, W. 5089* [WU! (3 sheets)]; alrededores de Chilecito, (29°10' S, 67°30' W), 28 Jan. 1927, *Parodi 7759 a* [BAA!]; hill behind the ACA-hotel, (29°10' S, 67°35' W), Feb. 1990, *Till, H. 90-s.n.* [WU 8533!]. Dept. Sanagasta: Sanagasta, (29°17' S, 67°02' W),

25 Nov. 1939, *Birabén et al. 1024* [LP!]. Dept. Cor.F.Varela: Cerro Bola, mountain side S, (29°33' S, 68°21' W), Feb. 1962, *Dawson 3433* [LP!]. Dept. Capital: mountains W of La Rioja, at km 17 (29°23' S, 66°59' W), 900 m, 12 Jun. 1948, *Alanis 137* [K! (2 sheets), LIL!, S!]; Dique Los Sauces, (29°24' S, 66°59' W), 1100 m, 16 Feb. 1944, *Parodi 14860 a* [BAA!]; Sierra Brava, (29°51' S, 65°48' W), 17 Feb. 1940, *Castellanos 33510* [BA, LIL!]. Dept. Independencia: Aguadita, Sierra de los Llanos, (29°19' S, 68°42' W), 1200 m, 03 Dec. 1906, *Kurtz 14118* [CORD!]. 31 km NW of Patquia along the RN 74 to Chilecito, Sierra de Los Colorados, near Los Colorados, (29°54' S, 67°09' W), 580 m, 06 Feb. 1990, *Till, W. 5068* [WU!]; Los Colorados, 29°58' S, 67°03' W, 11 Jan. 1964, *Giusti and Valla 3758* [BAA!]. Dept. Grl. A.Vicente Peñaloza: Sierra de Olta, Agua del Medio, (30°30' S, 66°25' W), 03 Feb. 1940, *Castellanos 33496* [BA, LIL!]. Dept. Chamical: Sierra de los Llanos, from Santa Bárbara uphill, Quebrada de La Bolsa, approximately 1 km from the hydrological station, (30°28' S, 66°19' W), 16 Nov. 1996, *Biurrun et al. 4438* [CORD!]. Dept. Grl. Belgrano: S of Sierra Brava, km 64, Recreo to Chamical, 30°28' S, 66°05' W, 300 m, 11 Oct. 1987, *Till, H. 8* [WU!]; vicinity of Dique de Olta, (30°38' S, 66°18' W), 25 Jun. 1959, *Hunziker and Di Fulvio 14437* [LP!]. Dept. Grl. J.Facundo Quiroga: 11 km E of Malanzan towards Olpas, 2 km E of Loma Larga, 2 km W of Casangate, 30°47'04" S, 66°30'29" W, 820 m, 13 Jan. 1995, *Leuenberger 4478 a* [B!]; northern foot of the Sierra de Porongo, 1 km W of Loma Larga, (30°48'15" S, 66°33' W), 1000 m, 13 Feb. 1990, *Till, W. 5185* [WU! (2 sheets)]; northern declivities of the Sierra de Porongo, 4 km E of Malanzan, (30°48'30" S, 66°34' W), 1100 m, 13 Feb. 1990, *Till, W.* 5182 [WU!]; Malanzan, (30°49' S, 66°37' W), Jan. 1940, *Vega s.n.* [MCNS s.n.!]; southern base of Sierra de Malanzan, near Malanzan, (30°50' S, 66°35' W), 950–1000 m, 12 Feb. 1990, *Till, W. 5165* [WU!]. Dept. Grl. Ocampo: 8.5 km from Los Mistoles towards Olpas, roadside slopes, (30°49' S, 66°16' W), 600 m, 13 Jan. 1995, *Leuenberger 4482 c* [B!]; Ambil, RN 79, between Tello and Santa Rosa de Catuna, (31°07' S, 66°21' W), 18 Feb. 1959, *Hunziker et al. 13875* [CORD!, LP!]. Dept. R.V. Peñaloza: Sierra de los Llanos, Río Totoral, ca. 5 km from Chelco(s), (31°13' S, 66°25' W), 05 Mar. 1959, *Hunziker et al. 14154* [LP!]; southern foot of the Sierra de Araganaraz, near Chepes Viejo, (31°15' S, 66°35' W), 800 m, 11 Feb. 1990, *Till, W. 5149* [WU!]. **Prov. San Juan:** Dept. Jáchal: Portezuelo, 1200 m, Nov. 1941, *Rodrigo 2928* [LP!]. Dept. Zonda: Pachaco, 89 km W of San Juan, (31°20' S, 69°05' W), 1200 m, 09 Jan. 1956, *Böcher et al. 2247* [C!]; Quebrada del Zonda, (31°30' S, 68°50' W), 28 Feb. 1926, *Castellanos 26-448* [BA, GH!, US!]. Dept. Caucete: mountains E of Marayes, RN 20, (31°19' S, 67°25' W), 600 m, 13 Dec. 1987, *Múlgura et al. 674* [NY! (2 sheets)]; Quebrada del Barro, road to Las Chacras, (31°20' S, 67°30' W), 04 Nov. 1992, *Lutz 190* [LIL!]; along the RN 141, 3 km E of the cross with RP 510, towards Marayes, (31°29' S, 67°20' W), 650 m, 11 Feb. 1990, *Till, W. 5146* [WU! (2 sheets)]; Marayes, 5 km SW, (31°30' S, 67°25' W), 650 m, 17 Feb. 1971, *Ellenberg 4529* [US!]; near Marayes, km 1074 on RN 20, (31°30' S, 67°20' W), 13 Jan. 1979, *Hunziker 23344* [CORD!]; Sierra de Pie de Palo, road up to Mogote Los Corralitos, in Quebrada del Molle, (31°39' S, 68°13' W), 28 Nov. 1980, *Hunziker et al. 23652* [CORD!]. **Prov. Córdoba:** Dique, Dec. 1891, *Kuntze s.n.* [NY s.n.! (2 sheets)]; Sierra de Córdoba, Nov. 1899, *Stuckert 7827* [G!]; Mar. 1925, *Lossen 255* [BH, F!, G!, GH!, M!]; Quebrada de los Angelitos, exceeding the ravine, 12 Oct. 1946, *Hunziker 6883* [LIL!]. Dept. Ischilín: along the street from Río Ceballos to the "Dique La Quebrada", near the dam, (30°09' S, 64°20'30" W), 750 m, 20 Feb. 1990, *Till, W. 5221* [WU! (4 sheets)]: Dept. Cruz del Eje: Serrezuela, Sierra de Guasapampa, (30°40' S, 65°23' W), 02 Feb. 1943, *Bartlett 19577* [UC!]: Dept. Punilla: Capilla del Monte, (30°51' S, 64°32' W), 02 Jan. 1951, *De la Sota 3586* [LIL!]; Los Cocos, near Capilla del Monte, (30°55' S, 64°30' W), *Hauman 1115* [GH!]; Sierra Chica, Loma de Calabalumba, (30°50' S, 64°30' W), 21 Dec. 1889, *Kurtz 6669* [LP!]; Cosquín, Sierra de Cuniputo, 10 km WNW of Capilla del Monte along the street to Sierra de San Marcos, (30°50' S, 64°35' W), 880 m, 05 Feb. 1990, *Till, W. 5038* [WU!]; Cerro Uritorco, (30°50'30" S, 64°28'30" W), Dec. 1904, *Claren s.n.* [CORD! herb. Kurtz 12863]; Sierra Chica, Cerro Uritorco, about 4 km E of Capilla del Monte, 30°53' S, 64°30' W, 1100–

1200 m, 17 Feb. 1984, *Varadarajan et al. 1244* [US!]; valley of Punilla, Huerta Grande, (31°04' S, 64°30' W), 20 Feb. 1947, *Rossi 810* [LIL!]; Cerro Pan de Azucar, 1400 m, 01 Jan. 1951, *Gutiérrez 220* [LIL!]; Río Yuspe, opposite to El Durazno, (31°20' S, 64°39'30" W), 15 Dec. 1949, *Meyer 15660* [LIL!]; Villa Carlos Paz, (31°25' S, 64°30' W), 24 Nov. 1949, *Palacios 4180* [LIL!]. Dept. Colón: along the road from La Cumbre to Candonga, 22 km SE of the bifurcation to Ascochinga, (31°00' S, 64°25' W), 1110 m, 04 Feb. 1990, *Till, W. 5025* [WU!]. Casa Bamba, (31°21' S, 64°24' W), 30 Dec. 1949, *De la Sota 1415* [LIL!]. Dept. Río Primero: Quinta, (31°04' S, 63°09' W), 10 Jan. 1902, *Stuckert 11041* [CORD, G!]. Dept. Pocho: 40 km W of Taninga, Los Tuneles, (31°23' S, 65°25' W), 1140 m, 06 Dec. 1958, *Boelcke 7740* [BAA! (2 sheets)]. Dept. Santa María: Ochoa, (31°24' S, 64°24' W), Nov. 1902, *Stuckert 12089* [CORD, G!]; El Diquesito on the way to San Roque from La Calera by road, 31°30' S, 64°28' W, 550–600 m, 16 Feb. 1984, *Varadarajan 1241* [US!]. Dept. Calamuchita: Valle de los Reartes, (31°55' S, 64°25' W), 02 Jan. 1918, *Castellanos 1116* [BA!]. **Prov. San Luis:** Jan. 1933, *Vignati 335* [LP! (2 sheets)]. Dept. Grl. San Martín: El Totoral, Bajo de Velis, Sierra de San Luís, (32°30' S, 65°55' W), 19 Feb. 1895, *Kurtz 8574* [CORD!]. Dept. La Capital: Sierra Varela, (34°00' S, 66°33' W), 22 Dec. 1925, *Castellanos 25-2784* [BA!]. **Prov. Mendoza:** *Gillies s.n.* [K! Kew negative 7475]; Cerros de Chayados, Paramillo de Mendoza, *Miers 1098* [BM!]. Dept. Las Heras: Punta de Las Lajas, (32°49' S, 68°58' W), 850 m, 08 Dec. 1944, *Semper 184* [NY!]; Challao, (32°51' S, 68°56' W), 17 Nov. 1885, *Loos 126* [CORD!]; ibid.: 23 Dec. 1949, *Melin and Araque 890* [LIL!]; Cacheuta (33°02' S, 69°06' W), Jan. 1908, *Hauman 1114* [BA!, GH!]; on dry hills near La Ripiera, 22 Sep. 1939, *Leal 6250* [LIL!]; arid mountains near Villa Hipistomo, 01 Dec. 1939, *Leal 6471* [LIL!]; Punta de Las Lajas, 850 m, 08 Dec. 1944, *Semper 181* [LIL!].
s.loco: 1889, *Andre s.n.* [K!]; *Cabrera 1000 II* [LP!]; 05 Dec. 2002, *Forzza et al. 2265* [RB!]; *Hromadnik s.n.* [WU!]; 28 Jul. 1889, *Schlumberger s.n.* [K!]; *coll. ign.* [HBG!]; *coll. ign.* [LIL!]; *coll. ign.* [LP!]; Sep. 1965, *Wilson et al. 65-690* [US!].

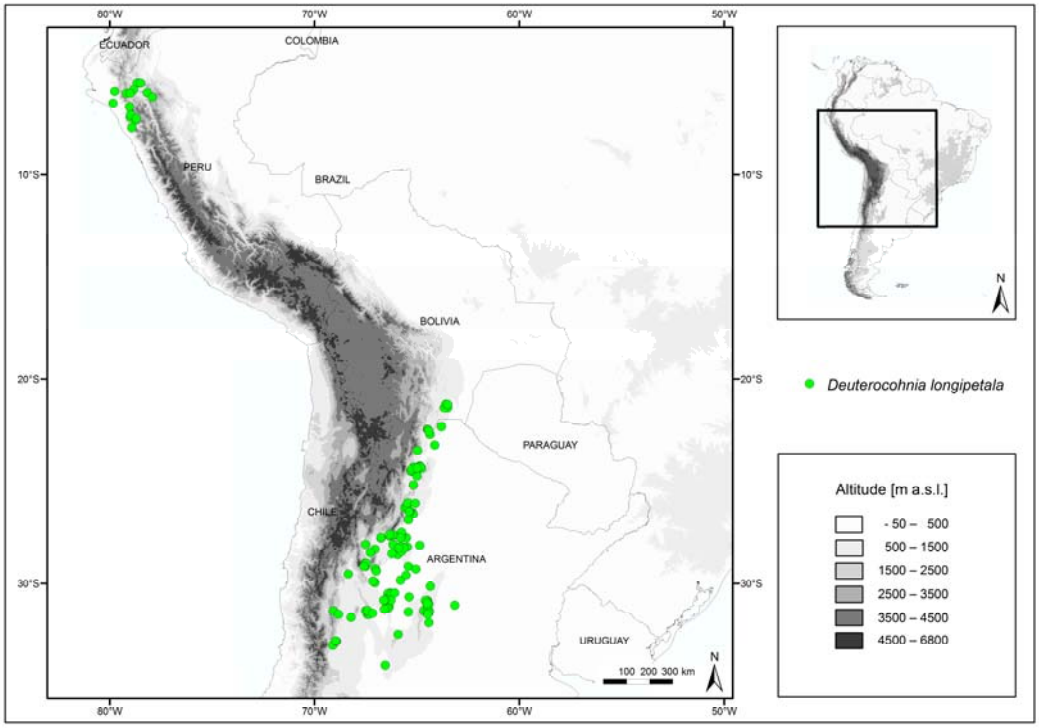


Fig. 5.18: Distribution of *D. longipetala*.


Fig. 5.19: *D. longipetala*. a: Natural habitat. Prov. Santiago del Estero, Argentina (*S. Dressler Arg16*). b: Partial inflorescence. c: Densely spinose rosette. d: Older inflorescence with many partial branches (*Laub 17*, BGHD). e: Flowers (*coll. ign.*, BGKS). Photos a–c: Stefan Dressler.

***Deuterocohnia lotteae*** (Rauh) M.A. Spencer & L.B. Sm., Bradea 6: 145. 1992. ≡ *Abromeitiella lotteae* Rauh, Trop. Suptrop. Pflanzenwelt 42: 37. 1983. Type: Bolivia, Dept. Tarija, Prov. Cercado, Cumbre del Condor, 2700 m a.s.l., 23 Aug.1979, *Hromadnik 5131* [holotype: HEID!].

**Plants** growing in dense cushions. **Rosettes** 2.5–7 × 3–6 [–8] cm. **Leaf sheaths** 0.5 × 0.5–1 cm. **Blades** 2–6 × 1–1.5 cm, recurved to straight, adaxially concave to plane, spinose-serrate, lepidote, greenish. **Peduncle** absent. **Inflorescence** simple, annual, 1–3-flowered. **Floral bracts** 11–14 × 3–4 mm, about equaling the sepals, broadly ovate, acuminate, mucronate to aristate, sparsely lepidote, brownish. **Flowers** 25–35 mm long, sessile. **Sepals** 10–14 × 3–4 mm, ovate, obtuse, mucronulate, sparsely lepidote, greenish-reddish. **Petals** 25–35 × 4–5 mm, erect during anthesis, after anthesis slightly spirally twisted, reddish-brownish, with green apex. **Petal appendages** 4–5 mm long, with short fringes. **Filaments** 18–25 mm long. **Anthers** 3–4 mm long, erect, concealed, greenish. **Ovary** 4–5 mm long. **Style** 20–30 mm long, stigma exposed. **Fruits** 8–9 × 5–7 mm. **Seeds** 2–3 mm long.

**Distribution.** BOLIVIA. Dept. Tarija. 21°20'–21°30' S, 63°45'–64°30' W.

**Habitat and ecology.** Ecoregions: Andean Yungas (64) and Chaco savannas (96). At elevations of 1400–2700 m a.s.l. Terrestrial or saxicolous. Pollinated by birds or insects.

**Etymology.** This species is dedicated to Lieselotte Hromadnik (Austria), who collected the type specimen together with her husband in 1979 in Bolivia.

**Affinities.** *Deuterocohnia lotteae* is morphologically closely related to *D. brevifolia*, but differs in having reddish–greenish petals. From *D. abstrusa* it is separated by smaller rosettes and more greenish leaf blades.

**Notes and comments.** (a) The collection number mentioned in the protologue (*Hromadnik 5131*) differs from the label on the herbarium voucher (*Hromadnik 5130*). No voucher *Hromadnik 5131* was seen in HEID or any other herbarium. Probably a mistake in numbers occurred while writing the herbarium label or the protologue. (b) The rosette sizes of *D. lotteae* may vary (Fig. 5.21d) as it is also the case for *D. brevifolia*.

**Further references.** Rauh, Bromelien: 410. 1990. Martin, Bot. Rev. 60(1): 36. 1994 (physiological study). Horres and Zizka, Beitr. Biol. Pflanzen 69(1): 43–76. 1995 (anatomical study). Horres, Bromelie 3: 67, 69, 70, 71. 1996 (anatomical study). Gross, Selbyana 19(2): 193. 1998. Krömer et al., Selbyana 20(2): 207. 1999. Crayn et al. in Wilson and Morrison, Monoc.: Syst. Evol.: 569–579. 2000 (phylogenetic study). Horres et al., Pl. Biol. (Stuttgart) 2(3): 308, 310. 2000 (phylogenetic study). Reinert et al, Biol. J. Linn. Soc. 80: 261–268. 2003 (phylogenetic study). Crayn et al., Proc. Natl. Acad. Sci. U.S.A. 101(10): 3705. 2004 (phylogenetic study). Horres et al., Aliso 23: 27–43. 2007 (phylogenetic study). Jørgensen et al., Monogr. Syst. Bot. Missouri Bot. Gard. 45: 1–1286. 2010. Givnish et al., Amer. J. Bot. 98(5): 872–895. 2011 (phylogenetic study).

**Specimens seen.** BOLIVIA. **Dept. Tarija:** Prov. O'Connor: Palos Blancos, (21°22' S, 63°55' W), 1430 m, *Hromadnik 9115* [HEID!]; Cumbre del Cóndor, ca. 25 km W of Narvaez, ca. 65 km W of Entre Ríos, (21°25' S, 64°25' W), 2700 m, 15 Jul. 1982; *Till, W. 62b* [WU!]. Prov. Cercado: Cumbre del Condor, (21°30' S, 64°30' W), 2700 m, 23 Aug.1979, *Hromadnik 5131* [HEID!].

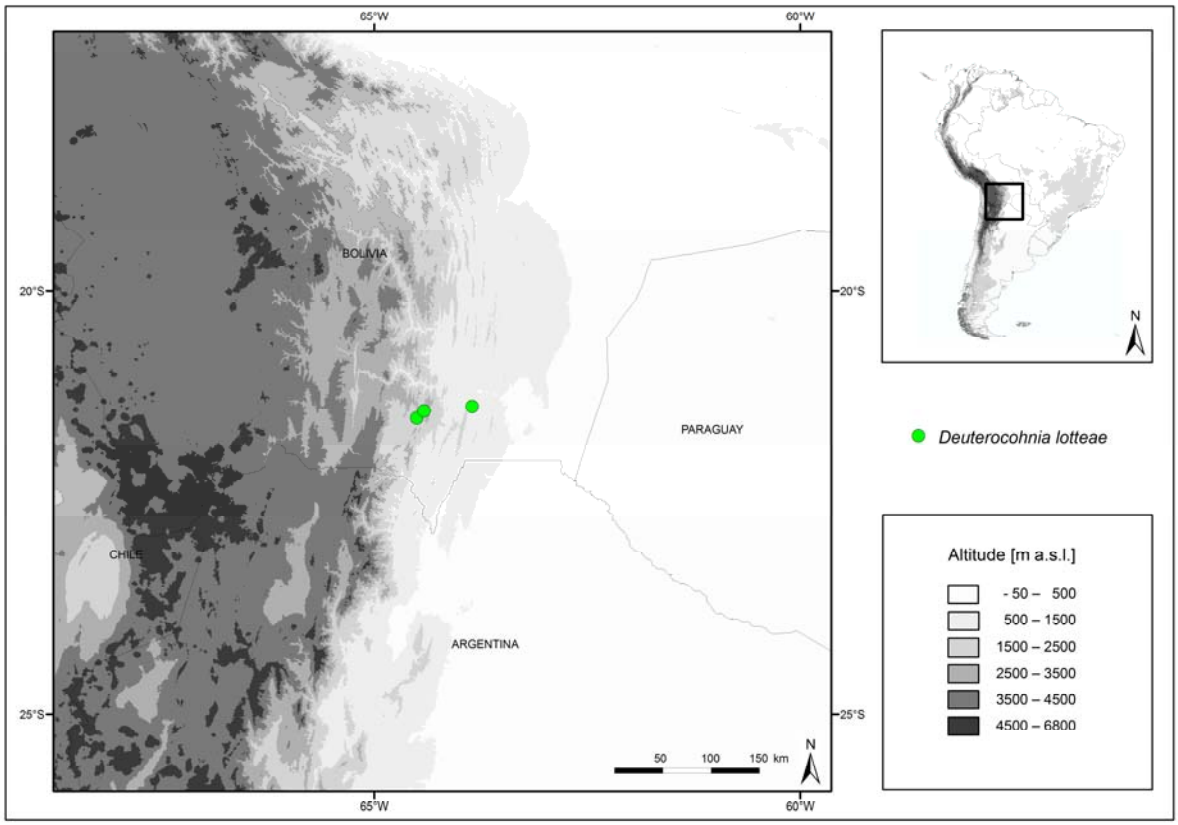


Fig. 5.20: Distribution of *D. lotteae*.


Fig. 5.21: *D. lotteae*. a and b: Natural habitat, Dept. Tarija, Bolivia (*W. Till 62b*). b: Detail of cushion with flowers. c: Flowers. d: Two different collections of *D. lotteae*, varying in the size of the rosette (left *L. Hromadnik 5131*, right *W. Till 62b*). Photos a, b: Walter Till, d: Timm Stolten.

***Deuterocohnia meziana*** Kuntze ex Mez in C.DC., Monogr. phan. 9: 465. 1896. Type: Brazil, Mato-Grosso, Corumbá, Aug. 1892, *Kuntze s.n.* [holotype: NY! (2 sheets), photo in GH!, R!, isotype B!].

**Plants** growing solitary or in groups. **Rosettes** 20–70 × 25–100 cm. **Leaf sheaths** 3–5 × 6–10 cm. **Blades** 25–80 [–100] × 4–9 cm, recurved, adaxially concave, spinose-serrate, lepidote, greenish or greyish. **Peduncle** present, incl. inflorescence 100–180 cm × 5–10 mm, erect, perennial, woody. **Peduncle bracts** 5–8 cm × 5–8 mm, laxely spinose-serrate, upper ones shorter than the internodes, entire. **Inflorescence** 40–70 cm long, compound, branches of 1st to 4th order, perennial. **Primary bracts** 3–4 × 2–3 mm, shorter than the sterile base of the partial inflorescence, triangular to ovate, narrowly acute to acute, entire, glabrous. **Partial inflorescences** up to 40 cm long, laxely flowered spikes, axis visible, branched, 10–40-flowered. **Floral bracts** 1–2 [–5] × 3–4 mm, much shorter than the sepals, broadly ovate, acute, mucronate, glabrous, reddish or brownish. **Flowers** [20–] 30–50 mm long, sessile to distinct pedicellate, pedicels 0.5–15 mm long. **Sepals** 10–20 cm × 5–6 mm, ovate to lanceolate, obtuse, mucronulate, glabrous, greenish, orange or reddish colour shades. **Petals** [20–] 30–45 × 7–10 mm, erect during anthesis, afterwards conspicuously spirally twisted, yellowish, orange or reddish colour shades, with greenish apex. **Petal appendages** 4–6 mm long, with short fringes. **Filaments** [15–] 25–35 mm long. **Anthers** 4–5 mm long, erect, concealed, greenish. **Ovary** 3–5 mm long. **Style** [15–] 25–40 mm long, stigma exposed or concealed. **Fruits** 10–12 × 6–8 mm. **Seeds** 3–4 mm long.

**Distribution.** BOLIVIA. Dept. Cochabamba, Chuquisaca, Santa Cruz, Tarija. BRAZIL. Est. Mato Grosso do Sul. PARAGUAY. Dept. Alto Paraguay, Amambay, Boquerón, Concepción. 14°30'–22°45' S; 56°00'–65°15' W.

Despite the broad morphological variation among populations of this species, distinct groups may be distinguished, which differ morphologically as well as geographically and ecologically (see also 4.2.3). Geographic distribution patterns are considered to be important for the recognition of infraspecific taxa (Stuessy 1989, Wendt et al. 2000) and the present study assigns four subspecies of *D. meziana*: (1) *D. meziana* ssp. *meziana*, (2) *D. meziana* ssp. *carmineo-viridiflora*, which formerly had been treated as a variety, (3) *D. meziana* ssp. *pedicellata*, which had been designated as a separate species (*D. pedicellata*), and (4) a new subspecies from Paraguay, *D. meziana* ssp. nov.

**Key to the subspecies.**

1. Leaf blades 60–90 [–100] cm long, inflorescence lax, many-flowered, floral bracts inconspicuous, flowers 25–35 mm long, sessile to shortly pedicellate (< 5 mm), sepals orange, petals orange to yellow with green tip. Lower eastern Andean slopes and lowlands of SE Bolivia (Chiquitania), Dept. Santa Cruz, adjacent areas in W Brazil and southwards along the Río Paraguay to N Paraguay, Dept. Amambay, Concepción. At elevations from 200 to 1400 m a.s.l. ..... ***D. meziana* ssp. *meziana*** **A**

1. * Flowers differently coloured ..... 2

2. Leaf blades 50–80 cm long, inflorescence lax, many-flowered, floral bracts inconspicuous, flowers 23–28 mm long (without pedicel), shortly to conspicuously pedicellate (< 15 mm), sepals green, petals yellow with green tip. Inter-Andean dry valleys of Chuquisaca, Bolivia. At elevations from 900 to 1400 m a.s.l. ..... ***D. meziana* ssp. *pedicellata*** **D**

2. * Flowers reddish ..... 3

3. Leaf blades 30–60 cm long, inflorescence very lax, few-flowered, floral bracts inconspicuous, flowers 35–45 mm long, sessile to shortly pedicellate (< 5 mm), sepals rose, petals rose to magenta with green tip. N of Paraguay (Grand Chaco), Dept. Boqueron, Alto Paraguay and Presidente Hayes. At elevations from 100 to 300 m a.s.l. ..... ***D. meziana* ssp. nov.** **C**

3. * Leaf blades 40–70 cm long, inflorescence lax or more dense, many-flowered, floral bracts short up to 5 mm, flowers 25–35 (–55) mm long, sessile to shortly pedicellate (< 5 mm), sepals magenta to carmine, petals magenta to carmine with green tip. Bolivian Andes, close to the Andean knee, Dept. Cochabamba and Santa Cruz. At elevations from 1200 to 2200 m a.s.l. ..... ***D. meziana* ssp. *carmineo-viridiflora*** **B**

**Specimens not assignable to one of the subspecies** (due to insufficient herbarium material): BOLIVIA. without precise locality: 16 Jul. 1978, *Rauh s.n.* [US 00386035!]. **Dept. Santa Cruz:** Prov. Nuflo de Chavez: Lomerios at 359 km, 59°03' W, 300–400 m, 30 Oct. 1999, *Agreda and Wood 30* [USZ!]. Prov. Caballero: Comarapa to Vallegrande, 17°55' S, 64°30' W, 2100 m, Nov. 1947, *Cárdenas 4007* [US!]; 3 km (air line) WSW of Comarapa, 2.9 km by road from highway at Comarapa, on gravel road to Chilón, 17°55' S, 64°33' W, 1960 m, 26 Nov. 1999, *Nee 50662* [NY!, USZ!]; Saipina; 3 km E of Los Thacras, 18°03'18" S, 64°33'40" W, 1660 m, 20 Jan. 1995, *Balcazar 100* [USZ!]; 7 km from Saipina, E side of Río Mizque, near archaeological pictograph site, 18°05' S, 64°35' W, 1450 m, 07 Aug. 1987, *Nee and Coimbra 35574* [NY!]; 5.4 km E of Saipina on road to Pulquina, 18°05'38" S, 64°32'34" W, 1465 m, 10 Dec. 2005, *Nee et al. 53741* [NY!]. Prov. Cordillera: Estancia Isla Verde, vicinity of Bañados del Izozog, Río Parapeti, 20 km air line NE of the Estancia, 19°25' S, 62°40' W, 300 m, 17 Aug. 1997, *Fuentes and Navarro 1992* [USZ!]; Hacienda Yatihuiwa, 19°53' S, 63°31' W, 870 m, 25 Jul. 1998, *Portugal et al. 198* [LPB!]; Estancia Cerro Colorado, near

Cerro Colorado, 12 Dec. 1993, *Navarro 2153* [USZ!]. **Dept. Tarija:** Prov. Gran Chaco: Palos Blancos 3 km towards Puerto Margarita via Rio Pilcomayo, 21°25' S, 63°45' W, 625 m, 24 Dec. 1983, *Beck and Liberman 9727* [LPB! (2 sheets), USZ!].
PARAGUAY: Near Mayor Santa Cruz, 22 Oct. 1980, *Fernández Casas 4405* [NY!]; s.d., *Collins 9-19* [GH!].
s. loco: *Arenas s.n.* [US 2825570!]; *coll. ign.* [HEID 600156!].

Putative hybrids: Prov. Vallegrande: Road from Vallegrande to Villa Serrano, between Pucara and the bridge Santa Rosa over Río Grande, 18°42'20" S, 64°16'40" W, 1470 m, 29 Sep. 2009, *Schütz et al. 09-004* [FR!, LPB!]; ibid.: *Schütz et al. 09-005* [LPB!]; *Schütz et al. 09-006* [LPB!]; *Schütz et al. 09-007* [LPB!].

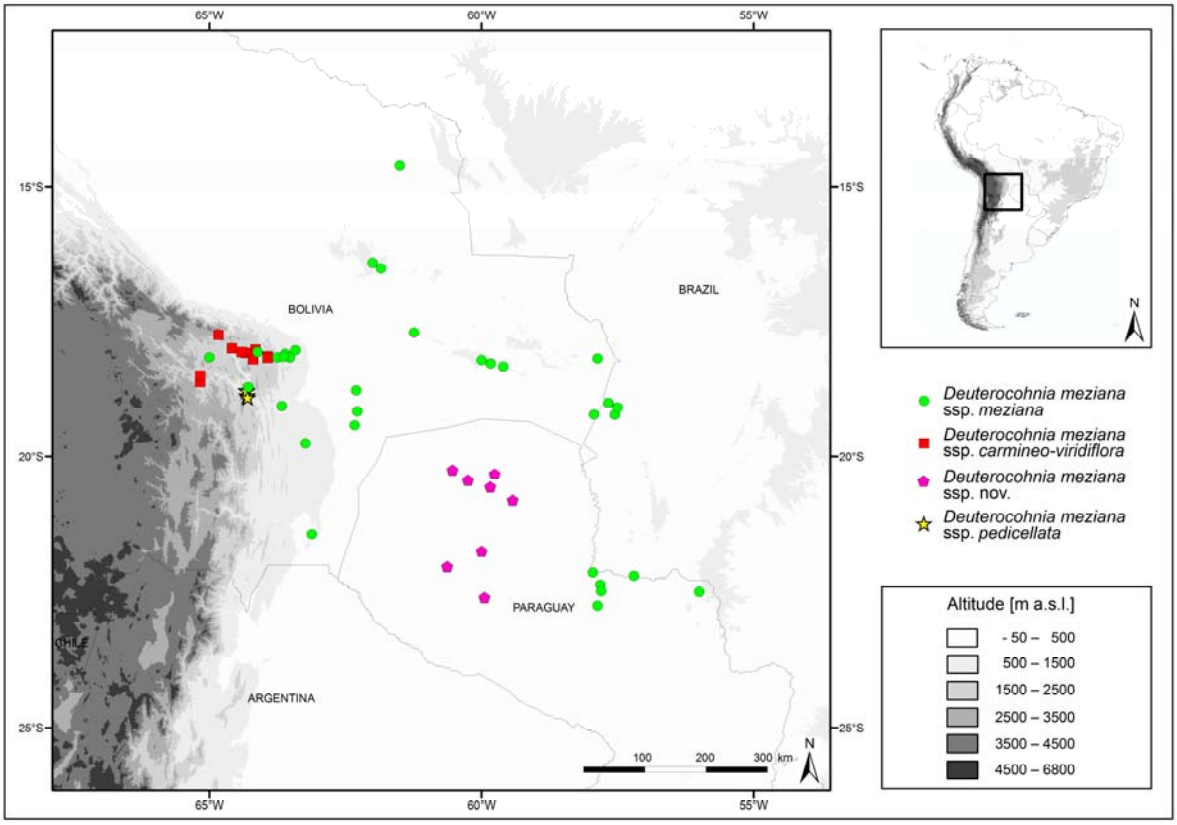


Fig. 5.22: Distribution of *D. meziana* and its subspecies.

**A. *Deuterocohnia meziana* ssp. *meziana*** Kuntze ex Mez in C.DC., Monogr. phan. 9: 465. 1896. Type: Brazil, Mato-Grosso, Corumbá, Aug. 1892, *Kuntze s.n.* [holotype: NY! (2 sheets), photo in GH!, R!, isotype B!].

= *Deuterocohnia paraguariensis* Hassl., Annuaire Conserv. Jard. Bot. Genève 20: 298. 1919. (synonymized by Mez in Engler, Pflanzenr. IV. 32. (100): 283. 1934). ≡ *Deuterocohnia divaricata* Mez, Repert. Spec. Nov. Regni Veg. 16(1): 9. 1919. (synonymized by Harms in Engler, Nat. Pflanzenfam. ed. 2, 15a: 109. 1930). Type: Paraguay, Cerro Margarita, Sierra de

Amambay, *Rojas* in herb. *Hassler 11098* [holotype *D. paraguariensis*: G!, photo in F!, GH!, isotype: BAF. holotype *D. divaricata*: B, not seen, probably destroyed].

−"*Deuterocohnia chrysantha*" sensu Mez in C.DC., Monogr. phan. 9: 466. 1896. p. p.: *Kuntze s.n.*

**Distribution.** BOLIVIA. Dept. Santa Cruz, Tarija. BRAZIL. Est. Mato Grosso do Sul. PARAGUAY. Dept. Amambay, Concepción. 14°30'–22°45' S; 56°00'–64°20' W.

**Habitat and ecology.** Ecoregions: Chaco savannas (96), and its border to Andean Yungas (64), Chiquitania dry forests (97), Humid Chaco (132). At elevations of 150–1400 m a.s.l. Terrestrial or saxicolous, on limestone, on laterite and granitic outcrops, on sandstone. In open dry forest or shrubland, also close to the river, in seasonally flooded riverside forests. Growing together with *Commiphora leptophloeos* (Burseraceae), *Echinopsis hammerschmidii*, *Frailea chiquitana*, *Gymnocalyccium chiquitanum*, *Monvillea kroenleinii* (all Cactaceae), *Sapium argutum* (Euphorbiaceae), *Vellozia tubiflora* (Velloziaceae) on granitic outcrops in the Chiquitania dry forests. Main flowering period from July to December, flowers also reported from the rest of the year. Pollinated by hummingbirds and occasionally by insects.

**Etymology.** The species is dedicated to the German botanist Carl Christian Mez (1866–1944) whose research focused on plant taxonomy and physiology. He established the genus *Deuterocohnia* in 1894.

**Affinities.** *Deuterocohnia meziana* ssp. *meziana* is morphologically closely related to the other subspecies of *D. meziana*, but differs in having orange sepals and yellow to orange petal colour shades (with a greenish apex as in other subspecies). The rosettes are large, with broad, robust leaves. Together with *D. brevispicata*, *D. meziana* ssp. *meziana* provides the largest plants among species of *Deuterocohnia*. The subspecies is mainly distributed in SO Bolivia, the border to Brazil and NO Paraguay. Some plants that occur in the border region of Santa Cruz and Chuquisaca or Cochabamba may actually represent intermediate forms between *D. meziana* ssp. *pedicellata* and *D. meziana* ssp. *carmineo-viridiflora*.

**Notes and comments.** (a) In 1919 Mez described *D. divaricata* from Paraguay, based on the collection of *Rojas* in herb. *Hassler 11098*, which probably was located in the herbarium of Berlin. A voucher of the same collection located in the herbarium of Geneve was used to describe the spe-

cies *D. paraguariensis* by Hassler (1919) six months earlier (and therefore preceded the name *D. divaricata*, which was synonymized to *D. paraguariensis* by Harms in 1930). Thus the two species belong to the same collection, with type vouchers in different herbaria. Concerning the type of *D. divaricata*, there is neither a voucher of *Hassler 11098* found in B, nor a photograph of it among the Berlin negatives in F. (b) The first description of *D. meziana* notes only yellow as flower colour, the same for *D. divaricata*. Probably the authors referred only to the petals. (c) Classified as *rare* by IUCN red list of threatened plants (1997), (*endangered* in Bolivia, Brazil, *vulnerable* in Paraguay).

**Further references.** Tietze, Z. Naturwiss. 78: 30. 1906. Fedde and Schuster, Just's Bot. Jahresber. 47 (2): 6. 1919. Mez, Repert. Spec. Nov. Regni Veg. 16: 454. 1919. Krause, Bot. Jahrb. Syst. 56(1): 5. 1920. Greenman and Payson, Bot. Abstr. 7(1): 81. 1921. Broadway and Smith, Proc. Amer. Acad. Arts 68(5): 188, 189. 1933. Foster, Natl. Hort. Mag. 24: 19, 21. 1945. Smith, Smithsonian Misc. Collect. 126: 45, 46. 1956. Smith, Bromeliana 1(4): 4. 1964. Smith and Downs, Fl. Neotrop. Monogr. 14 (3): 236. 1974. Zanoni and Schofield, Brittonia 33(2): 251. 1981. Böhme, Trop. Subtrop. Pflanzenwelt 62: 125–232. 1988 (anatomical study). Schill et al., Beitr. Biol. Pflanzen 63: 221–252. 1988 (morphological study). Brown and Terry, Amer. J. Bot. 79(9): 1051–1071. 1992 (morphological study). Spencer and Smith, Bradea 6: 145. 1992. Horres and Zizka, Beitr. Biol. Pflanzen 69(1): 43–76. 1995 (anatomical study). Horres, Bromelie 3: 69, 70. 1996 (anatomical study). Navarro, Rev. Bol. Ecol. 2: 15. 1997. Krömer et al., Selbyana 20(2): 207. 1999. Crayn et al. in Wilson and Morrison, Monoc: Syst. Evol.: 569–579. 2000 (phylogenetic study). Mostacedo et al., Acta Amazon. 31(1): 11–25. 2001. Antezana and Navarro, Rev. Bol. Ecol. 12: 22. 2002. Reinert et al., Biol. J. Linn. Soc. 80: 261–268. 2003 (phylogenetic study). Lira et al., Revista Biol. Ci. Terra 4(1). 2004. Crayn et al., Proc. Natl. Acad. Sci. U.S.A. 101(10): 3705. 2004 (phylogenetic study). Zuloaga et al., Monogr. Syst. Bot. Missouri Bot. Gard. 107(1): 1–983. 2008. Forzza et al., Catálogo Pl. Fung. Brasil 1: 792. 2010. Jabaily and Sytsma, Amer. J. Bot. 97(2): 337–356. 2010 (phylogenetic study). Pott et al., Brazil. J. Biol. 71(1) suppl.: 272. 2011.

**Specimens seen.** BOLIVIA. **Dept. Santa Cruz:** Sierra de Santa Cruz, 2000 m, May 1892, *Kuntze s.n.* [NY!]. Prov. Velasco: Santa Rosa de la Roca, diversion to Moira/Piso Firme, km 65, 14°37' S, 61°30' W, 300 m, 25 Aug. 1983, *Ibisch et al. 93.0636* [LPB!]. Prov. Nuflo de Chavez: Est. Sebastian, 40 km S of Concepcion on road to Lomerio, 16°25' S, 62°00' W, 450 m, 17 Sep. 1985, *Killeen 1220* [F!, GH! (2 sheets), LPB!, NY!, US!]; Lomerio, 12 km N of the community Las Trancas, permanent tracts of the project "BOLFOR", Las Trancas-95, 16°31'13" S, 61°50'47" W, 450 m, 20 Feb. 1995, *Mamina 463* [USZ!]; Estancia San Miguelito, 200 km NE of Santa Cruz, 4 km NO of San Pablo, 17°0'9" S, 400 m, 14 Dec. 1995, *Fuentes 1449* [USZ!]. Prov. Chiquitos: 57 km W of San José, road to Santa Cruz, 17°42'36" S, 61°14'24" W, 270 m, 29 Jan. 2004, *Solís Neffa et al. 1313* [LPB!]; Cerro Mutún, 7 km NE of the landing runway of the miners' camp, 25 km S of Puerto Suárez, 18°11'18" S, 57°52'42" W, 400–500 m, 17–20 Oct. 1994, *Vargas 3377* [NY!, USZ!]; Robore, 18°16'31" S, 59°49'58" W, 320 m, 03 Dec. 2002, *Forzza et al. 2253* [LPB!, RB! (4 sheets)]; 4 km SW of Santiago de Chiquitos, 18°20' S, 59°36' W, 400 m, 22 Nov. 1989, *Saldias et al. 959* [NY!, USZ! (3 sheets)]; Serrania Santiago, 15 km NW of Limoncito, 18°13' S, 60°00' W, 350 m, 28 Jul. 1982, *Till, W. 137* [WU! (2 sheets)]; stream going down to the mining camp of Cerro Mutum, Germán Busch, 19°12'52" S, 57°55'54" W, 180 mm 19 Aug. 2004, *Zárate et al. 1766* [USZ!]. Prov. Florida: On road from Comarapa to Mariana,

1 km S of Los Negros, 18°04' S, 64°07' W, 1350 m, 08 Aug. 1987, *Nee et al. 35601* [LPB!, NY!, US! (2 sheets), USZ!]; Refugio Los Volcánes; 3 km NE of Bermejo, 18°06' S, 63°36' W, 1150 m, 04 Oct. 1997, *Kessler et al. 12307* [LPB!]; between Santa Cruz and Bermejo, road to Samaipata, 18°08'40" S, 63°37'31" W, 1000 m, 26 Sep. 2009, *Schütz et al. 09-002* [FR!, LPB!]; road from Santa Cruz to Samaipata, 36 km before Samaipata, 18°10' S, 63°45' W, 28 Mar. 2006, *Cubr 43830* [U! (2 sheets)]. Prov. Andrés Ibáñez: Samaipata to Santa Cruz, 40 km W of Santa Cruz, 18°02' S, 63°25' W, 800 m, 25 Aug. 1976, *Rauh 40673* [HEID! (6 sheets)]; between Santa Cruz and Bermejo on the road to Samaipata, 18°10'02" S, 63°31'08" W, ca. 1000 m, 26 Sep. 2009, *Schütz et al. 09-001* [FR!, LPB!]. Prov. Vallegrande: Road from Vallegrande to Villa Serrano, between Pucara and the bridge Santa Rosa over Río Grande, 18°42'20" S, 64°16'40" W, 1470 m, 29 Sep. 2009, *Schütz et al. 09-004* [FR!, LPB!]; ibid.: *Schütz et al. 09-005* [LPB!]; *Schütz et al. 09-006* [LPB!]; *Schütz et al. 09-007* [LPB!]; road from Vallegrande to Villa Serrano, between Pucara and the bridge Santa Rosa over Río Grande, 18°42'22" S, 64°17'09" W, 1371 m, 29 Sep. 2009, *Schütz et al. 09-008* [FR!, LPB!]; near Río Grande, 19°03'29" S, 63°40'09" W, 557 m, 02 Oct. 2006, *Schütz et al. 06-017* [LPB!]; ibid.: *Schütz et al. 06-018* [FR! (2 sheets)]. Prov. Cordillera: Curuyuqui, 18°46' S, 62°18' W, 350 m, 26 Oct. 1991, *Gentry and Pena 75390* [USZ!]; Aguarati Izozog, near road to Cerro Colorado, 27 km from the airfield of Rancho Nuevo, 19°09'19" S, 62°16'58" W, 24 Sep. 1998, *Bourdy 2141* [LPB!]; Cerro Colorado, 19°25' S, 62°20' W, 400–540 m, 27 Oct. 1991, *Gentry and Foster 75351* [USZ! (2 sheets)]; Río Charagua, 7 km air line NO of Charagua, 19°45'30" S, 63°14' W, 1000 m, 14 Apr. 1990, *Quevedo 111* [USZ!]. **Dept. Tarija:** Prov. Gran Chaco: Palo Marcado, Pilcomayo, 21°26' S, 63°07' W, 450 m, 02 Nov. 1927, *Troll 190* [B!, M!].

BRAZIL: **Dept. Mato Grosso do Sul:** 12 Mar. 1979, *Burle Marx 69275* [HB!]; 20 Sep. 1940, *Foster 1064* [GH!]; FAN, 24 May 1978, *Martinelli 4551* [RB!]. Prov. Caracol: Caracol, 30–40 km W, 22°12' S, 57°12' W, 17 Mar. 1985, *Hatschbach and Silva 49207* [C!, HBG!]; Prov. Corumbá: Bandalta, 25 Oct. 1953, *Pereira et al. 497* [RB! (3 sheets)]; Leque, 10 Nov. 1977, *Rodrigues et al. 376* [RB!]; Prov. Corumbá/Sapezal: Corumbá, area of pantanal, 19°00' S, 57°40' W, 02 Jun. 1984, *Elias de Paula 1769* [HB!, NY!]; ibid.: 12 Sep. 1985, *Elias de Paula 1853* [NY!]; ibid.: Jul. 1911, *Hoehne 3542* [R!]; ibid.: Jul. 1911, *Hoehne 3543* [R!, photo in G!]; ibid.: Jul. 1911, *Hoehne 3544* [R!]; ibid.: Jul. 1911, *Hoehne 4614* [R!]; ibid.: Aug. 1892, *Kuntze s.n.* [B!, GH!, NY! (2 sheets), R!]; near Corumbá, Morro do Urucum, 19°13' S, 57°33' W, 550 m, 18 Sep. 1940, *Foster 1045*, [GH!, US!]; Corumbá, Rod. Br 262, Serra do Urucum, 19°13' S, 57°33' W, 14 Apr. 1972, *Hatschbach 29493* [C!, NY!, UC!]; 35 km SE of Corumbá, Fazenda Vale do Paraiso, 19°5' S, 57°30' W, 10 Dec. 1976, *Krapovickas 29820* [C!].

PARAGUAY: Jardín Botánico, 05 Oct. 1944, *Rojas s.n.*(Herb.Hassler) [LIL!]; **Dept. Amambay:** Distr. Pedro Juan Caballero: Sierra de Amambay, Cerro Margarita, 22°30' S, 56°00' W, Apr. 1907–08, *Rojas 11098* [F!, G!, GH!, NY!]; **Dept. Concepción:** Distr. Concepción: Puerto Fonciere, alto Paraguay, 22°29' S, 57°48' W, Dec. 1916, *Rojas 2270* [BA!, GH! (2 sheets)]; Itapucú-mi, 22°45' S, 57°52' W, 19 Sep. 1893, *Lindman A-2097* [GH!, S! (5 sheets)]; Distr. San Lázaro: Vallemi, Cerro Pucú; 22°08'29" S 57°57'12" W, 300 m, 04 Nov. 2001, *Zardini and Vera 57359* [WU! (5 sheets)]; Colonia Risso, 22°22' S, 57°49' W, 28 Nov. 1896, *Anisits 2419* [GH!, S! (3 sheets)].


Fig. 5.23: *D. meziana* ssp. *meziana*. a: Natural habitat, Dept. Santa Cruz, Bolivia (*N. Schütz 09-001*). b: Mature plant growing on a rocky slope. c: Partial inflorescence with orange-greenish coloured flowers.

**B. *Deuterocohnia meziana* ssp. *carmineo-viridiflora*** (Rauh) N. Schütz stat. nov. ≡ *Deuterocohnia meziana* var. *carmineo-viridiflora* Rauh, Trop. Subtrop. Pflanzenwelt 52: 20. 1985. Type: Bolivia, Dept. Cochabamba, near Pojo, Jul. 1973 (24 Aug. 1976 ?, see notes), *Rauh 40642* [holotype: HEID! (6 sheets, see notes)].

**Distribution.** BOLIVIA. Dept. Cochabamba, Santa Cruz. 17°45'–18°40' S; 63°55'–65°10' W.

**Habitat and ecology.** Ecoregion: Bolivian montane dry forests (95). At elevations of 1300–2200 m a.s.l. Terrestrial or saxicolous, on argillaceous soils with few organic material. Growing together with columnar cacti, sometimes dominating the understory vegetation. Flowers reported from September to November. Pollinated by hummingbirds and occasionally by insects.

**Etymology.** The name of the subspecies refers to the colour of the flower (*carmineo* = carmine red shade; Latin *viridis* = green; *florus* = to flower).

**Affinities.** *Deuterocohnia meziana* ssp. *carmineo-viridiflora* is similar to *D. meziana* ssp. nov., both subspecies share the long, sessile to pedicellate flowers in reddish colour shades, spread on a long and branched inflorescence. This separates both taxa conspicuously from the other taxa of *Deuterocohnia*. *Deuterocohnia meziana* ssp. *carmineo-viridiflora* differs from the new subspecies in having more densely flowered secondary branches, larger floral bracts, carmine-greenish petals and longer leaf blades. Furthermore, the latter occurs in the Chaco savannas of Paraguay, while *Deuterocohnia meziana* ssp. *carmineo-viridiflora* belongs to the mountain range of the Bolivian departments Cochabamba and Santa Cruz. Some plants that occur in the border region of Cochabamba and Santa Cruz or Chuquisaca may actually represent intermediate forms between *D. meziana* ssp. *meziana* and *D. meziana* ssp. *pedicellata*.

**Notes and comments.** (a) There are some discrepancies between the description in the protologue and the notes on the herbarium voucher: Collection date: Jul. 1973 vs. 24 Aug. 1976, altitude 200 vs. 1700 m a.s.l. (Pojo at ca. 2800 m a.s.l.), sepal colour rose vs. sepal colour dirty-carmine. Probably Rauh collected in 1976 (during his trip to Bolivia and other countries) the plant with the collection number 40642 near Pojo, Cochabamba, in an altitude of about 1700 m a.s.l. The sheets 4, 5 and 6 of the type voucher in HEID might be from the type locality, they represent older inflorescences with broken parts, typical for plants in natural habitats. A handwritten note on sheet 5 mentions beside the date, dirty-carmine floral bracts and sepals. This

fits well to the taxon *carmineo-viridiflora*. However, sheet 3 of the type voucher 40642 represents a young inflorescence, with longer secondary branches, smaller floral bracts and flowers more distant to each other. Like the corresponding plant 103653 in the BGHD this sheet does not fit well to the taxon *carmineo-viridiflora*. The colour of the sepals is rose, the petals are magenta (this plant is more similar to the *D. meziana* ssp. nov.-populations in Paraguay). The protolog seems to be a mixture of both, Rauh referred to the plant (103653) in the garden as well as to his notes from the field. It still remains to be clarified whether the plant 103653 is really from the type locality and why the protologe cites the collection date 1973, (in this time Rauh went to Brazil and other countries) and the altitude of 200 m a.s.l. (b) In the protologue of *D. meziana* var. *carmineo-viridiflora*, SO Brazil is erroneously cited as part of the distribution area of *D. meziana var. meziana*. This should be SO Bolivia. (c) Vouchers in US (Rauh s.n., US 2848092-93) and WU (Rauh 40642/46774, WU 11819) are labeled as isotypes, but not isotype is declared in the protologe. (d) The collection of *HR 5264* is related to Rauh 50852 and the locality description Sucre–Santa Cruz on the voucher in HEID. This differs from the database entry of HEID and the voucher in WU, which note Rauh 50824 and the locality Villa Granado–Omereque.

**Further references.** Spencer and Smith, Bradea 6: 145. 1992. Gross, Selbyana 19(2): 194. 1998. Till, Vidalia 2(2): 42. 2004. Jørgensen et al., Monogr. Syst. Bot. Missouri Bot. Gard. 45: 1–1286. 2010.

**Specimens seen.** BOLIVIA: without precise locality: *Rauh s.n.* [US 2848092, -93! (2 sheets)]. **Dept. Cochabamba:** Prov. Campero: Sucre to Santa Cruz, Villa Granado to Omereque, 18°10' S, 65°00' W, 2000 m, 31 Jul. 1979, *Hromadnik 5264* [HEID!, WU! (7 sheets)]; 45 km S Aiquile on road to Sucre, 18°30' S, 65°10' W, 1740 m, 08 Jul. 1982, *Till, W. 8* [WU!]; Río Grande, Puente Arce, 18°35' S, 65°10' W, 1700 m, 16 Jul. 1979, *Hromadnik 5030* [HEID! (2 sheets), WU! (2 sheets)]. Prov. Carrasco: NW of Comarapa, near Pojo, 17°45' S, 64°50' W, 1700 m, Jul. 1973/24 Aug. 1976, *Rauh 40642* [HEID! (6 sheets)]; ibid.: *Rauh 46774* [HEID! (3 sheets), WU!]. **Dept. Santa Cruz:** Sierra de Santa Cruz, 2000 m, May 1892, *Kuntze s.n.* [NY! s.n.]; vertical walls above Río Blanco, Cerro Hosana, 1300 m, 02 Sep. 1917, *Steinbach 3444* [LIL! (2 sheets)]. Prov. Caballero: Mountain S of Comarapa, 18°00' S, 64°35' W, 2200 m, 19 Mar. 1999, *Hromadnik 24090* [WU! (2 sheets)]; Pulquina, vicinity of the village and the botanical garden of Pulquina, 18°04' 06"S, 64°24'18" W, 1557 m, 04 Oct. 2003, *Mendoza and Gusman 551* [USZ! (2 sheets)]; Comarapa, 30 km towards Santa Cruz, 18°05' S, 64°20' W, 2000 m, 28 Sep. 1981, *Beck 7073* [LPB!, US!]. Prov. Florida: Los Negros to Vallemoso, 18°01'19" S, 64°08'58" W, 1300 m, 01 Oct. 2006, *Schütz et al. 06-012* [FR!, LPB!]; between Mataral and Comarapa, 18°08'27" S, 64°15'17" W, 1485 m, 30 Sep. 2009, *Schütz et al. 09-013* [FR!, LPB!]; road from Samaipata to Vallegrande, 18°08'55" S, 63°55'48" W, 1530 m, 01 Oct. 2006, *Schütz et al. 06-002* [FR!]; ibid.: *Schütz et al. 06-003* [LPB!]; ibid.: *Schütz et al. 06-006* [LPB!]; road from Samaipata to Vallegrande, 18°09'13" S, 64°06'00" W, 1240 m, 01 Oct. 2006, *Schütz et al. 06-010* [FR!, LPB!]; between Samaipata and Mairana, 18°09'48" S, 63°55'29" W, 1690 m, 28 Sep. 2009, *Schütz et al. 09-003* [FR! (2 sheets), LPB!]; road from Samaipata to Vallegrande, 18°09'43" S, 63°55'28" W, 1696 m,


Fig. 5.24: *D. meziana* ssp. *carmineo-viridiflora*. a: Natural habitat, Dept. Santa Cruz, Bolivia (*N. Schütz 06-002*). b and c: Mature plant and flowers with carmine-greenish petals. d and e: Plant (*L. Hromadnik 5030*) growing in the BGHD, collected in the Dept. Cochabamba, Bolivia. Photos d, e: Timm Stolten.

01 Oct. 2006, *Schütz et al. 06-001* [FR!, LPB!]. Prov. Vallegrande: Road from Vallegrande to Mataral, 18°11'41" S, 64°11'27" W, 1500 m, 30 Sep. 2009, *Schütz et al. 09-011* [FR!, LPB!]; ibid.: *Schütz et al. 09-012* [FR!].

**C. *Deuterocohnia meziana* ssp. nov.** Type: Paraguay, Dept. Presidente Hayes, Distr. Puerto Pinasco: Laguna Ganso, 22°34'05" S, 59°35'08" W, (120 m), 10 Dez. 2010, *Vogt 970* [holotype: FCQ!, isotype: FACEN].

**Distribution.** PARAGUAY, Dept. Alto Paraguay, Boqueron, Presidente Hayes. 20°15'–22°40'S; 59°25'–60°45' W.

**Habitat and ecology.** Ecoregion: Chaco savannas (96). At elevations of 100–300 m a.s.l. Terrestrial, on clay soils, on arenaceous underground, between rocks, in the understorey of open dry forests and shrublands, solitary or in groups. Growing together with *Aspidosperma* (Apocynaceae), *Bulnesia sarmientoi* (Zygophyllaceae), *Capparis* (Capparaceae), *Deinacanthon urbanianum*, *Dyckia ferox* (Bromeliaceae), *Ruprechtia trifolia* (Polygonaceae), *Prosopis sericantha* (Fabaceae), *Maytenus vitis-idea* (Celastraceae) and *Trithrinax schizophylla* (Arecaceae). Flowers reported from September to February. Pollinated probably by hummingbirds as is the case for the other subspecies of *D. meziana*.

**Affinities.** *Deuterocohnia meziana* ssp. nov. is similar to *D. meziana* ssp. *carmineo-viridiflora*, both subspecies share the long, sessile to pedicellate flowers in reddish colour shades, spread on a long and branched inflorescence. This separates both taxa conspicuously from the other taxa of *Deuterocohnia*. *Deuterocohnia meziana* ssp. nov. differs from *D. meziana* ssp. *carmineo-viridiflora* in having more laxely flowered secondary branches, minute floral bracts, magenta-greenish petals and shorter leaf blades. Furthermore, the latter occurs in the mountain range of the Bolivian departments Cochabamba and Santa Cruz, while *Deuterocohnia meziana* ssp. nov. belongs to the Chaco savannas of Paraguay.

**Specimens seen.** PARAGUAY: **Dept. Alto Paraguay:** Tyto. Lageranza–4 de Mayo, 20°07'34" S, 60°31'55" W, 17 Mar 1996, *Mereles and Degen 6330* [FCQ!]; Parque Nacional Defensors del Chaco, 20°15'23" S, 59°45'32" W, 14 Aug. 1998, *Mereles et al. 7381* [FCQ!]. Distr. Mayor Pablo Lagerenza: SW of Cerro Leon, 20 km before Capitan Pablo Lagerenza, 20°15' S, 60°32' W, 295 m, 1996, *Amerhauser 96-11* [WU! (2 sheets)]; proposed Biosphere Reserve "Gran Chaco Americano", Madrejon–Agua Dulce, 20°19'22" S, 59°45'32" W, 170 m, 07 Feb. 2002, *Zardini and Gomez-Cabrera 58178* [WU! (2 sheets)]; Cerro León, 20°26' S, 60°15' W, 02 Oct. 1979, *Schinini and Bordas 1782*0 [UC!];


Fig. 5.25: *D. meziana* ssp. nov. a: Plants in the natural habitat, Dept. Presidente Hayes, Paraguay (*C. Vogt 997*). b: Partial inflorescence with typical long, rose to magenta-coloured flowers. c: Rosettes, growing in the understory of semideciduous dry forest. Photos a–c: Christian Vogt.

ibid.: 25 Aug. 1981 *Schinini et al. 21173* [C!]; Parque National Defensores del Chaco, 20°33'24" S, 59°50'28" W, 12 Feb. 1999, *Zardini and Godoy 50020* [WU!]; Reserva Riacho Florida, 20°47'55" S, 59°25'37" W, 110 m, 19 Sep. 2007, *Vogt 688* [FCQ!]. **Dept. Boquerón:** Ayoreo-settlement "Jesudi", 19 Jan. 2004, *Vogt 115* [FCQ!, PY]; ibid. *Vogt 117* [FCQ!]; Colony Fernheim, 7 km from the village Hohenau, 22°36'26.2" S, 59°56'24.6" W, 18 Feb. 2005, *Vogt 197* [FCQ!]; road between Tte. Montania and Mcal. Estigarribía, 21°50'34.6" S, 60°08'43.5" W, 07 Feb. 2005, *Vogt and Mereles 227* [FCQ!]. Distr. Grl. Eugenio Garay: Fortin Teniente Montania–Fortin Madrejon, km 38, 21°45' S, 60°00' W, 12 Oct. 1977, *Evrard 8117* [US!]; Distr. Mariscal José Felíx Estigarribia: 22°02' S, 60°38' W, Dec. 1936, *Rojas 7515* [GH!]; Chaco Paraguay, López de Filippi, 22°02' S, 60°38' W, 06 Nov. 1945, *Rojas s.n.* [LIL!]. **Dept. Presidente Hayes:** Distr. Puerto Pinasco: Laguna Ganso, 22°34'05" S, 59°35'08" W, (120 m), 10 Dez. 2010, *Vogt 970* [FACEN, FCQ!].

**D. *Deuterocohnia meziana* ssp. *pedicellata*** (W. Till) N. Schütz stat. nov. ≡ *D. pedicellata* W. Till, Vidalia 2 (2): 42. 2004. Type: Bolivia, Dept. Chuquisaca, Prov. Belisario Boeto, 30 km after crossing the Río Grande on the road from Vallegrande to Villa Serrano, 18 km before Siberia al Nuevo Mundo, 18°54'03" S, 64°17'49" W, 1200 m a.s.l., 21 Oct. 2001, *Vargas 6285* [holotype: WU! (5 sheets), isotype: LPB, MO!].

**Distribution.** BOLIVIA. Dept. Chuquisaca. 18°30'–19°00'S; 64°15'–64°30' W.

**Habitat and ecology.** Ecoregion: Bolivian montane dry forests (95). At elevations of 900–1400 m a.s.l. Terrestrial, on slopes in dry forests of Intern-Andean valleys. Flowers reported in October and November. Pollinated probably by hummingbirds and insects as it is the case for the other subspecies of *D. meziana*.

**Etymology.** The name of the subspecies refers to the conspicuous flower stalk. (Latin *pediculatus* = stalked).

**Affinities.** Morphologically, *D. meziana* ssp. *pedicellata* is closely related to *D. longipetala*, but differs in having shorter floral bracts, distinct pedicels (> 5 mm), more laxely flowered inflorescences and larger rosettes. Usually, the inflorescence branches in the first year, while the lateral branches of the inflorescence of *D. longipetala* grow in the second year. *Deuterocohnia meziana* ssp. *pedicellata* is distinct form the other subspecies, due to the long pedicel and the greenish sepals. Usually the flowers are slightly shorter. Some plants that occur in the border region of Chuquisaca and Santa Cruz or Cochabamba may actually represent intermediate forms between *D. meziana* ssp. *meziana*

and *D. meziana* ssp. *carmineo-viridiflora*. Southwards, in Tarija, hybrids with *D. longipetala* may be located.

**Notes and comments.** (a) The type voucher *Vargas 6285* notes "Villa Seroño", probably "Villa Serrano" was meant. (b) The first description mentions the petal colour as distinct from a typical yellow or yellow–greenish colour of many *Deuterocohnia* species, probably in relation to the description on the type voucher ("flores de color café amarillo en la base"). Nevertheless, on-site findings showed a yellowish flower with green petal tips.

**Further references.** Jørgensen et al., Monogr. Syst. Bot. Missouri Bot. Gard. 45: 1–1286. 2010.

**Specimens seen.** BOLIVIA: **Dept. Chuquisaca:** Prov. Belisario Boeto: 5 km after crossing the bridge Santa Rosa over the Río Grande, on the road from Pucara to Villa Serrano, 18°46'22" S, 64°18'48" W, 956 m, 29 Nov. 2009, *Schütz et al. 09-010* [LPB!]; 10 km after crossing the bridge Santa Rosa over the Río Grande, on the road from Pucara to Villa Serrano, 18°47' S, 64°19' W, 1000 m, 29 Nov. 2009, *Schütz et al. 09-015* [LPB!]; 25 km after crossing the bridge Santa Rosa over the Río Grande, on the road from Pucara to Villa Serrano, 18°51.67' S, 64°18.22' W, 1400 m, 29 Nov. 2009, *Schütz et al. 09-009* [FR! (2 sheets), LPB! (2 sheets)]. 30 km after crossing the Río Grande on the road from Vallegrande to Villa Serrano, 18 km before Siberia al Nuevo Mundo, 18°54'03" S, 64°17'49" W, 1200 m, 21 Oct. 2001, *Vargas et al. 6285* [LPB, MO!, WU! (5 sheets)].


Fig. 5.26: *D. meziana* ssp. *pedicellata*. a: Natural habitat, Dept. Chuquisaca, Bolivia (*N. Schütz 09-009*). b: Mature plant bearing a laxely flowered inflorescence. c: Conspicuously pedicellate flowers. d: Habitat, valley of Río Grande. e: Rosette.

***Deuterocohnia recurvipetala*** E. Gross, Trop. Subtrop. Pflanzenwelt 79: 5. 1991. Type: Argentina, Cerro Colorado, 500 m a.s.l., Sep. 1983, *Rauh 64236* [holotype: HEID!].

**Plants** growing form unknown. **Rosettes** 30–40 × 40–50 cm. **Leaf sheaths** 3–5 × 6–10 cm. **Blades** 25–35 × 3–4 cm, recurved, adaxially concave, spinose-serrate, densely lepidote on both sides, greyish–green. **Peduncle** present, incl. inflorescence 100–120 cm × 6–10 mm, erect, perennial, woody. **Peduncle bracts** 45–55 × 7–9 mm, spinose-serrate, upper ones shorter than the internodes, entire. **Inflorescence** 30–50 cm long, simple or compound, branches of 1st, 2nd or 3rd order, perennial. **Primary bracts**, 5 × 3.5 mm, shorter than the sterile base of the partial inflorescence, triangular, acuminate, glabrous or lepidote. **Partial inflorescences** up to 30 cm long, laxely flowered spikes, axis visible, simple or branched, 10–50-flowered. **Floral bracts** 3–4 × 3 mm, much shorter than the sepals, broadly ovate, obtuse, mucronulate, glabrous, brownish. **Flowers** 14–16 mm (recurved 10–11 mm) long, sessile. **Sepals** 6–8 × 4 mm, ovate, obtuse, glabrous, yellow–greenish. **Petals** [12–] 14–15 × 4 mm, recurved during anthesis, afterwards erect, after anthesis not spirally twisted, yellow. **Petal appendages** 4–5 mm long, with short fringes. **Filaments** 9–10 mm long. **Anthers** 4 mm long, recurved, exposed, yellowish. **Ovary** 2.5 mm long. **Style** 10 mm long, stigma exposed. **Fruits** 7–8 × 5–6 mm. **Seeds** 1.5–2 mm long.

**Distribution.** ARGENTINA. Prov. Córdoba.
The protologue only provides the information "Argentina, Cerro Colorado". As there are many "Cerro Colorado" in Argentina, it is not possible to determine the type locality unequivocally. The voucher of *Hunziker 12171* [CORD] is located in Tulumba, a department of Córdoba. Nearby is a famous mountain and populated place called "Cerro Colorado". Probably this is the type locality.

**Habitat and ecology.** Ecoregion: Chaco savannas (96). At elevations of 500–600 m a.s.l. On rocky slopes at Cerro Colorado. According to *Hunziker 12171* [CORD] flowering time is around May. In the greenhouse plants of *D. recurvipetala* flower continuously for about 2 months, usually two flowers are in anthesis per day and per partial inflorescence. There is no information about pollinators in natural habitats. In the greenhouse the flowers produce seeds, pollinated via selfing or insects.

**Etymology.** The epithet refers to the petals, which are recurved during anthesis.

**Affinities.** Morphologically, *D. recurvipetala* is closely related to *D. longipetala*. It differs from the latter by shorter flowers, recurved petals during anthesis and recurved anthers. According to molecular analyses based on cpDNA data, *D. recurvipetala* is closely related to *D. longipetala* samples from La Rioja, Córdoba and San Juan.

**Notes and comments.** (a) It is difficult to recognize *D. recurvipetala* on a herbarium voucher, because the recurved petals are erect after anthesis. Especially in the south of the distribution area of *D. longipetala*, the flowers get smaller and the branches of the inflorescence become more delicate and thus more similar to *D. recurvipetala*. Probably some vouchers from this area determined as *D. longipetala* belong to *D. recurvipetala*. (b) In the protologue the sepals are described as symmetric, but they are also slightly asymmetric.

**Further references.** Gross, Selbyana 19(2): 194. 1998. Zuloaga and Morrone, Monogr. Syst. Bot. Missouri Bot. Gard. 60: 109. 1996. Zuloaga et al., Monogr. Syst. Bot. Missouri Bot. Gard. 107(1): 1–983. 2008.

**Specimens seen.** ARGENTINA: Cerro Colorado, 500 m, Sep. 1983, *Rauh 64236* [HEID!]. **Prov. Santiago del Estero:** Dept. Ojo de Agua: Cerro de la Cruz, (29°30' S, 63°40' W), 29 Nov. 1944, *Balegan 157* [LIL!]. **Prov. Córdoba**: Dept. Tulumba: (30°06' S, 63°56' W, 600 m), 05 May 1959, *Hunziker 12171* [CORD!].

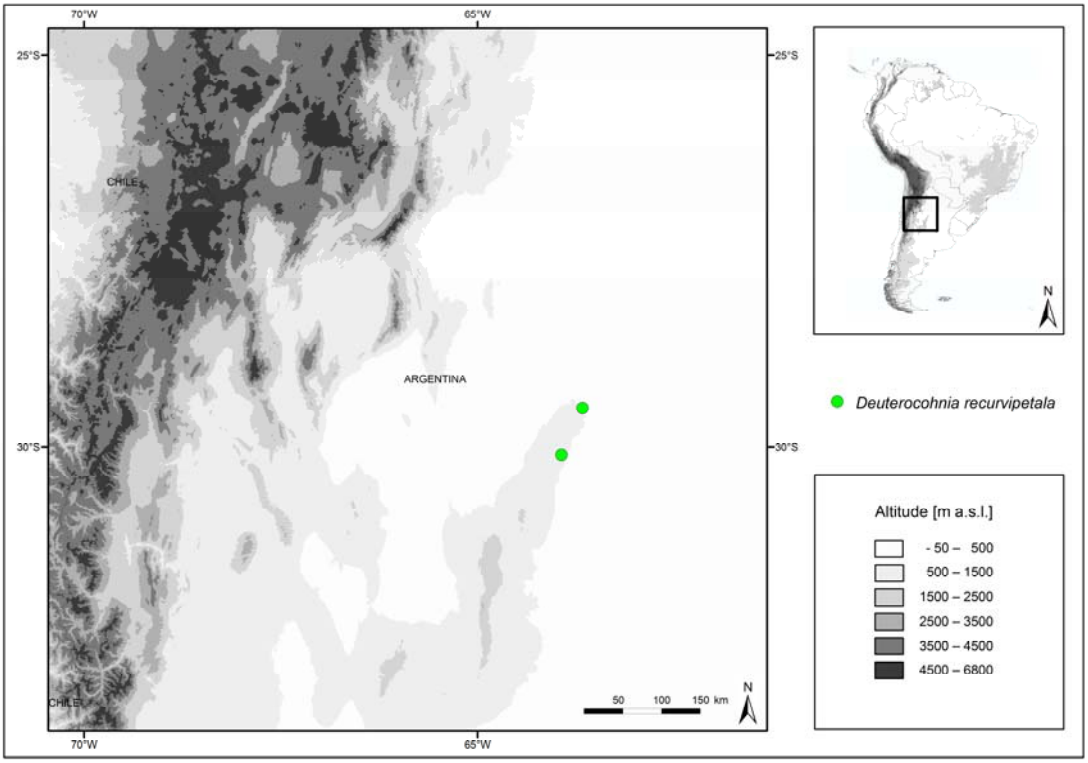


Fig. 5.27: Distribution of *D. recurvipetala*.


Fig. 5.28: *D. recurvipetala*. a: Mature plant (*W. Rauh 64236*, BGHD) with ramet, both bearing inflorescences. b: Partial inflorescence. c: Flower in anthesis, with recurved petals and anthers (*W. Rauh 64236*, BGKS). Photos a, b: T. Stolten.

***Deuterocohnia sanctae-crucis*** (R. Vásquez & Ibisch) N. Schütz stat. nov. ≡ *Deuterocohnia scapigera* ssp. *sanctae-crucis* R. Vásquez & Ibisch, Vidalia 1(1): 43. 2003. Type: Bolivia, Dept. Santa Cruz, Prov. Florida, 1500 m a.s.l., 24 Jun. 2000, *Müller 259* [holotype: LPB, isotype: USZ]. Paratypes: Bolivia, Dept. Santa Cruz, Prov. Florida, 6 km W of Mataral on the road between Mataral and Comarapa, Quebrada del Río El Salto, (18°07' S, 64°15' W), 1450 m, 29 Dec. 1999, *Vásquez 3523* [FR!, private herbarium of R. Vásquez]; ibid.: *Vásquez and Rivero 3017* [private herbarium of R. Vásquez]; ibid., 500–700 m a.s.l. SE of the sculptured rock of El Fuerte, 18°10'54"S, 63°49'28"W, 1900 m a.s.l., 25 Nov. 2001, *Vargas 6649* [USZ]; Bolivia, Dept. Santa Cruz, Prov. Vallegrande, Palma Amarillas, 8–10 km NE of Vallegrande, 18°25'°S, 64°75' W, 1900 m a.s.l., 19 Jul. 1994, *Vargas 3185* [USZ, NY!].

**Plants** growing in groups or cushions. **Rosettes** 10–12 × 6–12 cm, the inflorescence slightly exceeding the rosette. **Leaf sheaths** 1.5 × 2 cm. **Blades** 5–10 × 1–2 cm, recurved to straight, adaxially concave to plane, spinose-serrate, lepidote, greenish. **Peduncle** present, incl. inflorescence 6–7 cm × 1–2 mm, erect, perennial, woody. **Peduncle bracts** 20–35 × 2–5 mm, spinose-serrate, lepidote. **Inflorescence** 4–5 cm long, simple or branched, spike or raceme, annual or perennial. **Primary bracts**, 5 × 3–4 mm, shorter than the partial inflorescence, triangular, acute, aristate, glabrous or lepidote. **Partial inflorescences** up to 4 cm long, densely flowered spikes, axis concealed, simple, 5–10-flowered. **Floral bracts** 5–10 × 2–3 mm, about equaling the sepals or much shorter, triangular to ovate, acute, aristate, abaxially with glandular trichomes, brownish. **Flowers** 30–35 mm, sessile or subsessile. **Sepals** 10–15 × 3–4 mm, ovate to lanceolate, obtuse, abaxially with glandular trichomes, yellow–greenish. **Petals** 30–35 × 4–6 mm, erect during anthesis, after anthesis slightly spirally twisted, yellow, with green apex. **Petal appendages** 2–3 mm long, with short fringes. **Filaments** 20–25 mm long. **Anthers** 4–5 mm long, erect, concealed, yellow-greenish. **Ovary** 4–5 mm long. **Style** 25–30 mm long, stigma slightly exposed. **Fruits** unknown. **Seeds** unknown.

**Distribution.** BOLIVIA. Dept. Cochabamba, Santa Cruz, Chuquisaca. 18°05'–19°35' S, 63°45'–65°00' W.

**Habitat and ecology.** Ecoregions: Bolivian montane dry forests (95) and Andean Yungas (64). At elevations of 1200–2500 m a.s.l. Saxicolous on rocky slopes. Flowering time is around No-

vember to December. There is no information about pollinators in natural habitats, probably the plants are entomophilous and/or ornithophilous.

**Etymology.** The species name is related to the Bolivian province Santa Cruz, where the type specimen was collected.

**Affinities.** Morphologically, *D. sanctae-crucis* shows affinities to *D. scapigera* and *D. gableana*. The flowers are highly similar, including colour, size and the glandular hairs on the sepals. *D. sanctae-crucis* is characterized by smaller ramets, less robust inflorescences and shorter floral bracts than the other two species. The inflorescence may be branched conspicuously and exhibit more flowers. In contrast to the pedicellate flowers of *D. gableana*, *D. sanctae-crucis* and *D. scapigera* have sessile to subsessile flowers.

**Notes and comments.** (a) Holotype (*Müller 259*) not seen in LPB, isotype not seen in USZ. As *D. scapigera* ssp. *sanctae-crucis* has been described quite recently, types may be stuck somewhere in the mounting or related processes. It is assumed, that they are not lost in the herbaria, thus no neotype is chosen. (b) The floral bracts of voucher *coll. ign.* [WU 7365!] exhibit shorter apices. (c) The change of the taxonomic status of *D. sanctae-crucis* is discussed in 4.2.3.

**Further references.** Krömer et al., Selbyana 20(2): 207. 1999. López, Ecol. Bolivia 34: 45–70. 2000. Vásquez et al., Bromelie (1): 9. 2002. Jørgensen et al., Monogr. Syst. Bot. Missouri Bot. Gard. 45: 1–1286. 2010.

**Specimens seen.** BOLIVIA: **Dept. Santa Cruz:** Prov. Florida: 5 km W of Mataral, (18°07' S, 64°15' W), 1700 m, 1994, *Balfanz 126* [HEID!]; 6 km W of Mataral on the road between Mataral and Comarapa, Quebrada del Río El Salto, (18°07' S, 64°15' W), 1450 m, 29 Dec. 1999, *Vásquez 3523* [FR!]; between Mataral y Comarapa, 18°08'37" S, 64°15'54"W, 1550 m, 30 Oct. 2009, *Schütz et al- 09-014* [FR!, LPB!]. Prov. Vallegrande: Palma Amarillas, 8–10 km NE of Vallegrande, 18°25'°S, 64°75' W, 1900 m, 19 Jul. 1994, *Vargas 3185* [NY!, USZ]. **Dept. Chuquisaca:** Prov. Tomina: 72 km from Monteagudo to Padilla; at the road, 19°33' S, 64°09' W, 1200 m, 04 Jul. 1995, *Kessler et al. 5085* [LPB!].
s.loco. Svoboda s.n. [WU 5099!]; Svoboda s.n. [ZSS 1882!]; *coll. ign.* [WU 7365!].

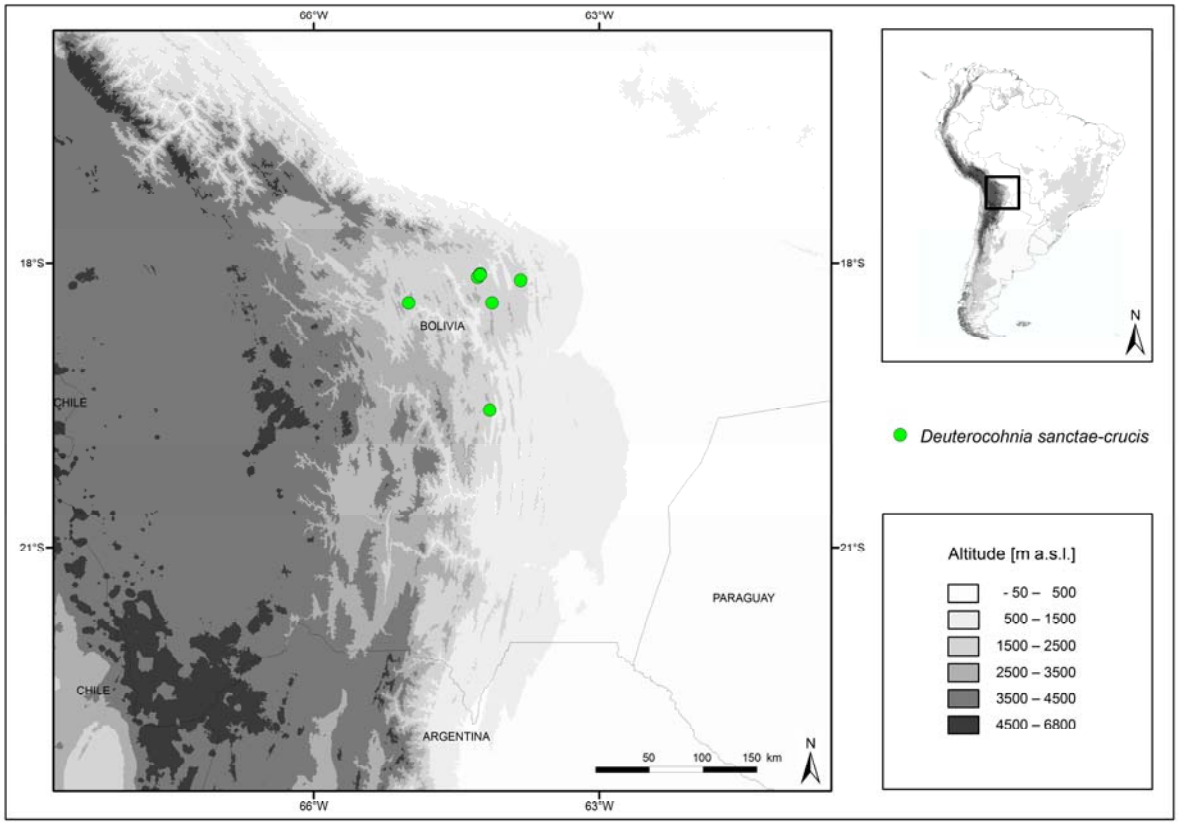


Fig. 5.29: Distribution of *D. sanctae-crucis*.


Fig. 5.30: *D. sanctae-crucis*. a: Natural habitat, Dept. Santa Cruz, Bolivia (*N. Schütz 09-014*). b: Plant growing on vertical, rocky slope. c: Branched inflorescence with several mature and immature flowers (*R. Vásquez 3523*, private collection) . d: Flowering rosette. Photos c, d: Roberto Vásquez.

***Deuterocohnia scapigera*** (Rauh & L. Hrom.) M.A. Spencer & L.B. Sm., Bradea 6: 145. 1992. ≡ *Abromeitiella scapigera* Rauh & L. Hrom. in Rauh, Trop. Subtrop. Pflanzenwelt 60: 5. 1987. Type: Bolivia, Potosí, 2400 m a.s.l., Aug. 1979, *Hromadnik 5275* [holotype: HEID! (alcohol material), isotype: HEID! (herbarium voucher)].

**Plants** growing in groups or cushions. **Rosettes** 12–18 × 10–15 cm, the inflorescence slightly exceeding the rosette. **Leaf sheaths** 2 × 2–3 cm. **Blades** 7–12 × 1–2 cm, recurved to straight, adaxially concave to plane, spinose-serrate, lepidote, greenish. **Peduncle** present, incl. inflorescence 6–8 cm × 1–2 mm, erect, perennial, woody. **Peduncle bracts** 20–40 × 5 mm, spinose-serrate, lepidote. **Inflorescence** 4–5 cm long, simple, rarely branched, spike or raceme, annual or perennial, 3–10-flowered. **Floral bracts** 10–16 × 2–4 mm, about equaling the sepals or much shorter, triangular to ovate, acute, aristate, abaxially with glandular trichomes, brownish. **Flowers** [28–] 30–38 cm long, sessile or subsessile. **Sepals** 10–15 × 3–4 mm, ovate to lanceolate, obtuse, rounded or mucronulate, abaxially glabrous or with glandular trichomes, yellow–greenish. **Petals** 30–35 × 4–6 mm, erect during anthesis, after anthesis slightly spirally twisted, yellow, with green apex. **Petal appendages** 2–4 mm long, with short fringes. **Filaments** 21–26 mm long. **Anthers** 4–5 mm long, erect, concealed, yellowish. **Ovary** 5 mm long. **Style** 25–30 mm long, stigma slightly exposed. **Fruits** unknown. **Seeds** unknown.

**Distribution.** BOLIVIA. Dept. Potosí, Chuquisaca. 20°40'–21°45' S, 65°00'–65°30' W.

**Habitat and ecology.** Ecoregion: Bolivian montane dry forests (95) and Central Andean puna (156). At elevations of 2400–3300 m a.s.l. Saxicolous on rocky slopes. Growing together with *Blossfeldia* cf. *liliputana*, *Cleistocactus tupizensis*, *Parodia maxima* (all Cactaceae), *Tillandsia lotteae*, *Tillandsia* sp. (Bromeliaceae). Flowering time is around November to February. There is no information about pollinators in natural habitats, probably the plants are entomophilous and/or ornithophilous.

**Etymology.** The epithet refers to the short peduncle of this species. (Latin *scapus* = stem, stalk; *ger* = to bear). This was a delimiting character of the formerly separated genus *Abromeitiella*, whose species did not exhibit a peduncle. The expression "scape" is sometimes used in descriptions of bromeliads synonymously to peduncle.

**Affinities.** Morphologically, *D. scapigera* is closely related to *D. sanctae-crucis* and *D. gableana*. The flowers are highly similar, including colour, size and the glandular hairs on the sepals. They mainly differ in the size of the rosettes and the peduncles, where *D. scapigera* takes an intermediate position between the larger *D. gableana* and the smaller *D. sanctae-crucis*. In contrast to the pedicellate flowers of *D. gableana*, *D. scapigera* and *D. sanctae-crucis* have sessile to subsessile flowers. *D. scapigera* occurs in the Bolivian departments of Chuquisaca and Potosí (S of Río Pilcomayo), whereas *D. sanctae-crucis* and *D. gableana* are distributed in Santa Cruz, Cochabamba and Chuquisaca (N of Río Pilcomayo). From *D. abstrusa* this species differs in having a peduncle, a higher number of flowers and less dense indument on the adaxial leaf surface.

**Notes and comments.** (a) The holotype refers to alcohol material. The herbarium voucher is an isotype. (b) In cpDNA analyses *Hromadnik 5275* occurs in the subclade B. All other samples of *D. scapigera* belong to subclade A. (c) Peduncles may slightly exceed the rosette, as observed in the greenhouse in BGHD (*Hromadnik 5275)*. (d) Inflorescences of a rosette may flower for more than one year (*Hromadnik 5275*).

**Further references.** Rauh, Bromelien: 410. 1990. Halbritter, Grana 31: 197–212. 1992 (micromorphological study). Horres and Zizka, Beitr. Biol. Pflanzen 69(1): 43–76. 1995 (anatomical study). Horres, Bromelie 3: 69, 70. 1996 (anatomical study). Krömer et al., Selbyana 20(2): 207. 1999. Gross, Selbyana 19(2): 193. 1998. Horres et al., Pl. Biol. (Stuttgart) 2(3): 308, 310. 2000 (phylogenetic study). López, Ecol. Bolivia 34: 45–70. 2000. Kessler, Bot. Rev. (Lancaster) 68(1): 123. 2002. Vásquez et al., Bromelie 1: 9. 2002. López, Ecol. Bolivia 38(1): 42. 2003. Horres et al., Aliso 23: 27–43. 2007 (phylogenetic study). Jørgensen et al., Monogr. Syst. Bot. Missouri Bot. Gard. 45: 1–1286. 2010.

**Key to the varieties.**

| | | | |
|---|---|---|---|
| 1. | Petals greenish-yellowish, sepals abaxially covered with glandular trichomes ..... | *D. scapigera* var. *scapigera* | A |
| 1. * | Petals orange-yellowish, sepals glabrous ..... | *D. scapigera* var. nov. | B |

**A. *Deuterocohnia scapigera*** (Rauh & L. Hrom.) M.A. Spencer & L.B. Sm. **var. *scapigera***

**Distribution.** BOLIVIA. Dept. Potosí, Chuquisaca. 20°40'–21°45'S, 65°00'–65°30'W.

**Specimens seen.** BOLIVIA: **Dept. Chuquisaca:** Prov. Nor Cinti: 24 km SW of Camargo, valley of Río Tumusla, (20°45' S, 65°15' W), 2450 m, 11 Jul. 1982, *Till, W. 38* [WU!]. **Dept. Potosí:** Prov. Nor Chichas Valley of Río Grande de Cotagaita, W of Palca Grande, (20°42' S, 65°23' W), 2400 m, Aug. 1979, *Hromadnik 5275* [HEID!]. Prov. Modesto Omiste: between Mojo and Toro, (21°45' S, 65°30' W), 3300 m, 21 Jul. 1997, *Hromadnik 5103* [HEID!]. s.loco: Braun 701 [HEID!]; *coll. ign.* [WU BRO 03805!].

**B. *Deuterocohnia scapigera*** (Rauh & L. Hrom.) M.A. Spencer & L.B. Sm. **var. nov.** Type: Bolivia, Dept. Chuquisaca, Prov. Nor Cinti, Valley of Río Tumusla, 2400 m, 19 Jun. 1979, *Hromadnik 5076* [holotype: HEID!, isotypes: FR!, WU!].

**Distribution.** BOLIVIA. Dept. Chuquisaca. 20°45' S, 65°15' W.

**Specimens seen.** BOLIVIA: **Dept. Chuquisaca:** Prov. Nor Cinti: Valley of Río Tumusla, (20°45' S, 65°15' W), 2400 m, 19 Jun. 1979, *Hromadnik 5076* [HEID!, FR!, WU!].

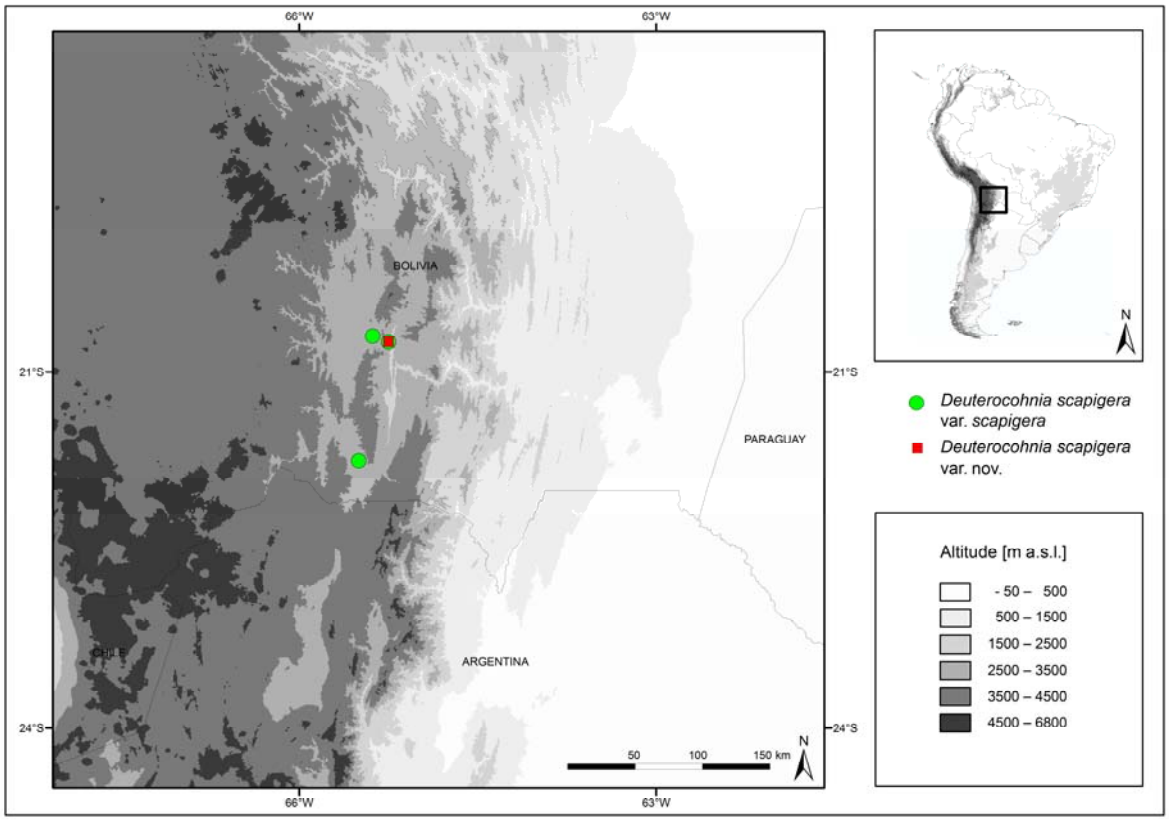


Fig. 5.31: Distribution of *D. scapigera*.


Fig. 5.32: *D. scapigera*. a and b: Plant of *D. scapigera* ssp. *scapigera* from the type locality growing in BGHD (*L. Hromadnik 5275*). Older inflorescences occur below the younger ramets and may flower for more than one season (b). c: Inflorescence of *D. scapigera* ssp. nov. with orange coloured petals (*L. Hromadnik 5076*). Photo a, c: Timm Stolten.

***Deuterocohnia schreiteri*** A. Cast., Anales Mus. Nac. Hist. Nat. „Bernardino Rivadavia" 36: 51. Fig. 1. 1929. Type: Argentina, Prov. Tucumán, Dept. Trancas, Valles Calchaquíes, Las Arquitas, 2500 m a.s.l., 16 Feb. 1920. *Schreiter 1098* [holotype: LIL! (3 sheets), photo in B!, F!, K!, NY!, isotype: BA, US! (fragment)].

**Plants** forming rings or cushions. **Rosettes** 15–25 × 20–30 cm. **Leaf sheaths** [2–] 3–4 × [3–] 5–6 cm. **Blades** 15–25 [–35] × 2.5–3.5 cm, recurved, adaxially concave, spinose-serrate, lepidote, greyish–green. **Peduncle** present, incl. inflorescence 50–80 cm × 5–7 mm, erect, perennial, woody. **Peduncle bracts** 4–7 × 0.5 cm, laxely spinose-serrate, upper ones entire. **Inflorescence** 20–50 cm long, compound, simple or compound, branches of 1st order, perennial. **Primary bracts** [5–] 10–20 × 0.5 cm, shorter than the partial inflorescence, narrowly triangular, acute, laxely spinose-serrate or entire, glabrous or lepidote. **Partial inflorescences** [3–] 5–12 [–18] × 1.5–3 cm long, densely to laxely flowered spikes, axis concealed, simple or rarely branched, cylindrical, [10–] 25–50 [–80]-flowered. **Floral bracts** 3–6 × 3–4 mm, about equaling the sepals, ovate, acute, mucronate, glabrous, brownish. **Flowers** 11–16 [–21] mm long, sessile. **Sepals** 5–6 × 4–5 mm, broadly ovate, obtuse, glabrous, greenish-brownish. **Petals** 11–16 × 4–5 mm, erect during anthesis, after anthesis not spirally twisted, yellow. **Petal appendages** 2.5 cm long, with short fringes. **Filaments** 9–12 [–14] mm long. **Anthers** 3 mm long, erect, concealed, yellow. **Ovary** 2.5–3.5 mm long. **Style** 10–13 [–15] mm long, stigma slightly exposed. **Fruits** 6–7 × 5 mm. **Seeds** 1.5–2 mm long.

**Distribution.** ARGENTINA. Prov. Salta, Tucumán, Catamarca. 25°00'–27°45' S, 65°15'–66°30' W.

**Habitat and ecology.** Ecoregions: Mainly in the northern part of Argentine Monte (136), spreading into Central Andean puna (156), Andean Yungas (64). At elevations of [850–] 1000–2500 [–2900] m a.s.l. Terrestrial or saxicolous, on sandstone slopes or on weathered granite, dry, thorny shrub vegetation with e.g. *Larrea*, *Zuccagnia*, *Cassia* (Fabaceae). Co-occurs with *Deuterocohnia lorentziana*. Flowering time from November to February. Varadarajan and Brown (1988) assumed insect pollination, Bernardello et al. (1991) also mentioned pollination by birds.

**Etymology.** The species is dedicated to the German naturalist Carlos Rodolfo Schreiter (1877–1955), who was employed at the Museum of Natural Historia in San Miguel de Tucumán, Argentina. He collected the type specimen.

**Affinities.** *Deuterocohnia schreiteri* is morphologically close to *D. haumanii*, but differs in noticeably smaller floral bracts, smaller flowers and laxely spinose leaves. The distribution areas of both species overlap in parts of Salta and Tucumán, where probably hybrids occur. From *D. digitata* it can be distinguished by its longer peduncle and inflorescence and the yellow flowers.

**Notes and comments.** (a) The holotype *Schreiter 1098* [LIL 34585] consists of three sheets. One of them is deposited as photograph in B, F, K, NY. (b) The type locality, Valles Calchaquíes, is assigned to the Argentinean department Trancas in the province of Tucumán. Actually, the Valles Calchaquíes are mainly located in the province Salta.

**Further references.** Mez in Engler, Pflanzenr. IV. 32. (100): 283. 1934. Castellanos, Lilloa 10: 457. 1944. Castellanos in Descole, Gen. Spec. Plant. Argent. 3: 197. 1945. Smith, Bromeliana 1(4): 4. 1964. Ehler and Schill, Pollen & Spores 15(1): 34. 1973. Smith and Downs, Fl. Neotrop. Monogr. 14 (3): 237. 1974. Simpson, Oecologia 27(3): 209. 1977. Schill et al., Beitr. Biol. Pflanzen 63: 221–252. 1988 (morphological study). Varadarajan and Gilmartin, Amer. J. Bot. 75(6): 810. 1988 (morphological study). Varadarajan and Brown, Bot. Gaz. 149(1): 83, 86, 88, 89. 1988 (morphological study). Rauh, Bromelien: 414. 1990. Bernardello et al., Ann. Bot. (Oxford) 67(5): 401–411. 1991. Spencer and Smith, Bradea 6: 145. 1992. Zuloaga and Morrone, Monogr. Syst. Bot. Missouri Bot. Gard. 60: 109. 1996. Pierce et al., Amer. J. Bot. 88(8): 1380. 2001. Zuloaga et al., Monogr. Syst. Bot. Missouri Bot. Gard. 107(1): 1–983. 2008.

**Specimens seen.** ARGENTINA: without precise locality: *Hromadnik s.n.* [WU 2975!]. **Prov. Salta:** Dept. Cachi: La Paya, 4 km W of RN 40, and 8 km S of Cachi, (25°10'30" S, 66°14' W), 2400–2700 m, 30 Mar. 2001, *Novara 11537* [MCNS!]; Dept. Molinos: Seclantás a Brealito, (25°17' S, 66°19' W, 2900 m), 20 Jul. 1945, *Meyer 9149* [LIL!]; side road of RN 40 near Seclantas, in direction to Brealito, 25°18'18" S, 66°20'02" W, 2355 m, 27 Nov. 2006, *Schütz et al. 06-102* [FR!]; ibid. *Schütz et al. 06-103* [FR!]; Valles Calchaquíes 25°22'04" S, 66°16'48" W, 2300 m, 27 Nov. 2006, *Schütz et al. 06-105* [FR!]; Valles Calchaquies, Churcal, (25°22' S, 66°14' , 2100 m), 06 Feb. 1943, *Castellanos 46635* [BA!]; Valles Calchaquíes, 5 km S of Puerta de Paya, immediately N of San José de Escalchi along the road to Molinos, (25°25' S, 66°20' W), 2300 m, 11 Feb. 1993, *Till, W. 10191* [LIL!, WU!]. Dept. La Viña: slopes near the highway 68, 3 km S before the road from Alemania joins with the highway 68, (25°36' S, 65°36' W), 1400–1500 m, 18 Feb. 1984, *Varadarajan 1250* [US!]. Dept. Guachipas: Tres Cruces, between Cafayate and Alemania, (25°52' S, 65°42' W), 20 Jan. 1945, *Descole s.n.* [LIL 118245!, left side, together with a specimen of *D. haumanii* on the right side]. Dept. Cafayate: km 16 on RP 68, between Cafayate and Alemania, 1550 m, 26°01'14" S, 63°50'02"°W, 28 Nov. 2006, *Schütz et al. 06-109* [LIL!]; ibid.: *Schütz et al. 06-112* [LIL!]; 16 km from Cafayate, on the road to La Vina, 1 km south of La Punilla, 26°02' S, 65°53' W, 1650 m, 18 Feb. 1928, *Varadarajan 1249* [US!]; Cafayate, (26°05' S, 66°00' W, 2000 m), 06 Feb. 1935 *Castellanos 14650* [BA, GH!, MCNS!, WU!]; El Divisadero, (26°05' S, 66°00' W, 2000 m), 02 Jan. 1943, *Castellanos 46618* [BA!]; Cafayate, (26°05' S, 66°00' W), 1050 m, *Hayward 2138* [LIL!]; Santa Teresita (26°05' S, 66°00' W), 1710 m, 25 May 1945, *Lourteig 1038* [LIL!]; 3 km S of Cafayate along the road to Tolombón, (26°05' S, 66°00' W), 1730 m, 13 Feb. 1993, *Till, W. 10229* [LIL!, WU!]; Divisadero, (26°05' S, 66°00' W), 1900 m, 24 Aug. 1949, *Vesvoorst 489* [LIL!]; RN 40; 7 km S of Cafayate (26°08' S, 65°58' W), 1600 m, 02 Jan. 1972, *Krapovickas 20589* [GH!]; Cafayate por Tolombón, Ruta 40, 6 km al sur de Cafayate, (26°08' S, 65°58' W, 2000 m), 11 Feb. 1978,

*Novara 625* [CORD!, MCNS!]; 7,5 km from Cafayate to Tolombón auf RN 40, 26°08'15" S, 65°57'56" W, 1650 m, 28 Nov. 2006, *Schütz et al. 06-106* [FR!]; ibid. *Schütz et al. 06-107* [FR!]; Valles Calchaquies, about 10 km S of Cafayate, on the east facing slopes, 26°10' S, 65°57' W, 1700 m, 18 Feb. 1984, *Varadarajan 1247* [US!]. Cerca de Tolombón, (26°11' S, 65°56' W, 1600 m), 21 Jan. 1945, *Descole 3029* [K!, LIL!]; Cerca de Tolombón (26°11' S, 65°56' W, 1600 m), Feb. 1945, *Descole s.n.* [A (ex LIL 113777)!]; taking turnoff 5 km S of Tolombón (plaza) on the road under construction that eventually will unite with the road connecting Lara with Hualinchay, 13 km from the RN 40, 26°13,13' S, 65°48,69' W, 1980 m, 23 Nov. 2003, *Leuenberger 4842* [B!, ZSS!]. **Prov. Tucumán:** Dept. Tafí del Valle: Quebrada de las Arcas (26°30' S, 65°50' W), 1800 m, 03 Feb. 1927, *Schreiter 5528* [LIL!, U!]; Amaicha to Tiopunco, (26°30' S, 65°55' W), 1800 m, Dec. 1931, *Schreiter 7179* [LIL!]; Las Arcas, (26°30' S, 65°50' W), 2000 m, 26 Dec. 1926, *Venturi 4835* [LIL!, US!]. **Prov. Catamarca:** Dpto: Andalgalá: Agua de las Palomas, Cuesta de la Chilca, (27°36' S, 66°10' W), 1200–1500m, *Till, H. 88-s.n.* [WU 6945!]; Cuesta de la Chilca, 27°36' S, 66°20' W, 800–900 m, 23 Feb. 1984, *Varadarajan 1270* [US!]; Camino a Andalgalá; Cuesta de la Chilca, (27°38' S, 66°11' W), 1930, *Schreiter 6418* [BA!, BM!, F!, LIL! (3 sheets), UC!]; 9 km SE of Andalgalá, via road to Cuesta de la Chilca, (27°40' S, 66°20' W), 1010 m, 20 Nov. 1972, *Cantino 452* [GH!]; near the base of the Cuesta de la Chilca, (27°40' S, 66°20' W), 1200–1400 m, 30 Nov. 1972, *Cantino 472* [CORD!, GH!]. Dept. Trancas: Valles Calchaquíes, Las Arquitas, 2500 m, 16 Feb. 1920. *Schreiter 1098* [BA!, LIL! (3 sheets), US! (fragment), photo ex LIL in B!, F!, K!, NY!].

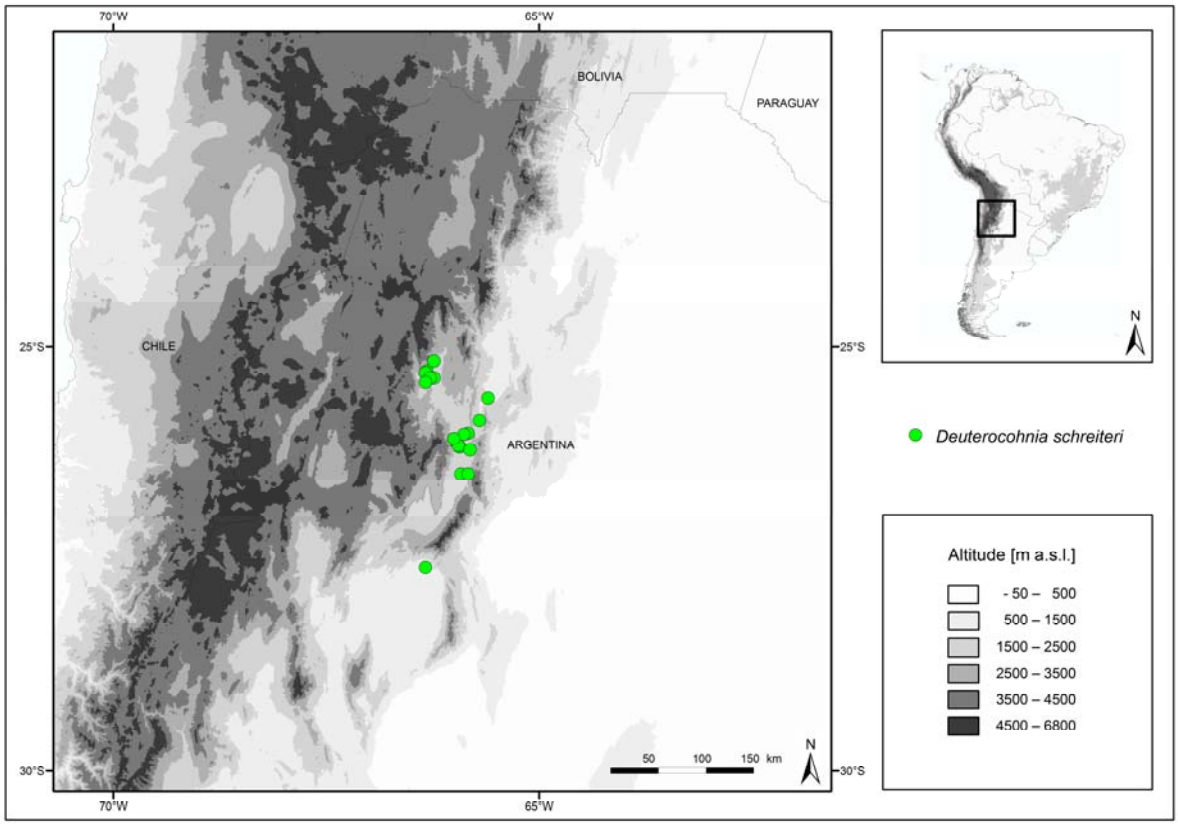


Fig. 5.33: Distribution of *D. schreiteri*.


Fig. 5.34: *D. schreiteri*. a: Natural habitat, Prov. Salta, Argentina (*N. Schütz 06-106*). b: Cluster of ramets from clonal propagation. The oldest ramets within the centre are already decomposed. c: Mature plant (*coll. ign.*, BGHD 130148) with inflorescences. d: Partial inflorescence. Photos c, d: Timm Stolten.

***Deuterocohnia seramisiana*** R. Vásquez, Ibisch & E. Gross, Bromelie 1: 4. 2002. Type: Bolivia, Dept. Chuquisaca, Prov. Zudañez/Tomina, between Thuru Mayu and Tomina, 19°08' S, 64°29' W, 2300 m a.s.l., 21 May 2001, *Vásquez and Ric 4093* [holotype: LPB!].

**Plants** growing solitary or in groups. **Rosettes** 20–30 × 40–50 cm. **Leaf sheaths** 1–3 × [3–] 5–7 cm. **Blades** 30–45 × 5–6 cm, recurved, adaxially concave, spinose-serrate, lepidote, greyish–green. **Peduncle** present, incl. inflorescence 70–120 cm × 6–10 mm, erect, perennial, woody. **Peduncle bracts** [5–] 7–10 × 1.5–2 cm, spinose-serrate. **Inflorescence** 30–50 cm long, compound, branches of 1st or 2nd order, perennial. **Primary bracts** 3–5 × 1 cm, exceeding the partial inflorescence, narrowly triangular, narrowly acute, laxely spinose-serrate, lepidote. **Partial inflorescences** 3–4 cm long, densely flowered spikes, axis concealed, simple or branched, spheroidal, 3–4-flowered. **Floral bracts** 13–15 × 6–8 mm, about equaling the sepals, broadly ovate, acuminate, sparsely lepidote, brownish. **Flowers** 18–20 mm long, sessile. **Sepals** 10–11 × 4–5 mm, ovate, obtuse, mucronulate, sparsely lepidote, yellow–brownish. **Petals** 17–18 × 4–5 mm, erect during anthesis, after anthesis not or slightly spirally twisted, yellow, with greenish apex. **Petal appendages** 3–4 mm long, with short fringes. **Filaments** 14–15 mm long. **Anthers** 2.5 mm long, erect, concealed or exposed, greenish. **Ovary** 3–5 mm long. **Style** 14–16 mm long, stigma exposed. **Fruits** 8–9 × 5–6 mm. **Seeds** 2 mm long.

**Distribution.** BOLIVIA. Dept. Chuquisaca. 19°05'–19°10'S, 64°25'–64°35'W.

**Habitat and ecology.** Ecoregions: Bolivian montane dry forests (95). At elevations of 2000–2400 m a.s.l. Terrestrial or saxicolous, on rocky slopes in forests in Inter-Andean dry valleys. According to first description the main blooming period is from February to June, some flowers also found in October. Probably pollinated by hummingbirds. Accompanied by *Tillandsia recurvata*, *T. loliacea*, *T. funebris*.

**Etymology.** The epithet refers to the trademark SERAMIS®. Within the context of the BIOPAT initiative (http://www.biopat.de), people, companies or institutions can adopt a sponsorship for newly discovered species. With their financial support, they contribute to the research on biodiversity and its conservation.

**Affinities.** *Deuterocohnia seramisiana* exhibits conspicuous morphological similarity to *D. brevispicata*. Both exhibit a robust inflorescence and primary bracts longer than the spheroidal partial inflores-

cences. In contrast to *D. brevispicata*, *D. seramisiana* exhibits yellow-greenish flowers and occurs in higher altitudinal ranges.

**Notes and comments.** (a) The first description characterizes the adaxial surface of the leaf blade as glabrous. However, the examined specimens exhibit peltate trichomes adaxially and abaxially, although the trichomes are larger on the abaxial leaf side. (b) The type locality is documented in the province Zudañez. Nevertheless, the related coordinates refer to the province Tomina.

**Further references.** Luther and Rabinowitz, Selbyana 30(2): 147–189. 2010.

**Specimens seen.** BOLIVIA: **Dept. Chuquisaca**: Prov. Tomina: between Thuru Mayu and Tomina, 19°08' S, 64°29' W, 2300 m, 21 May 2001, *Vásquez and Ric 4093* [LPB!]; road from Padilla to Sucre, 10 km from Tomina, 19°08'40" S, 64°31'09" W, 2078 m, 05 Oct. 2006, *Schütz et al. 06-042* [FR!]; ibid.: *Schütz et al. 06-043* [FR!, LPB!].

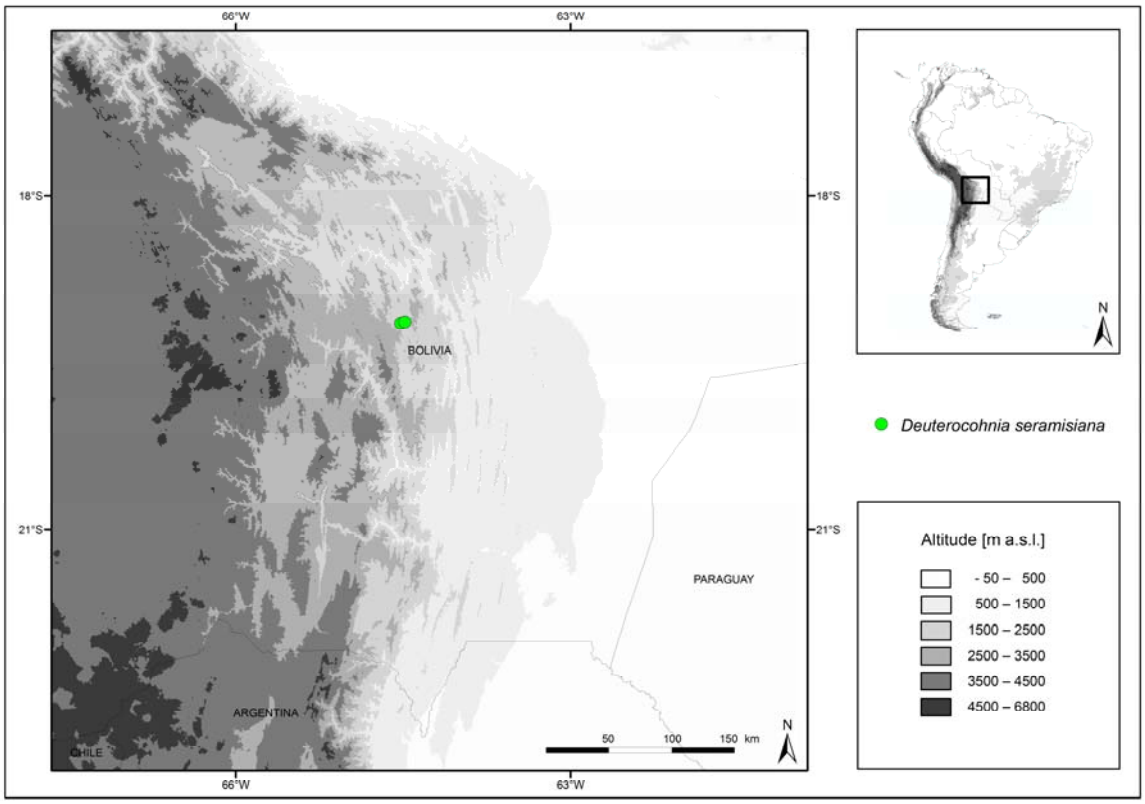


Fig. 5.35: Distribution of *D. seramisiana*.


Fig. 5.36: *D. seramisiana*. a: Natural habitat, Dept. Chuquisaca, Bolivia (*N. Schütz 06-042*). b: Partial inflorescence with large primary bract. c: Mature plant with inflorescence.

***Deuterocohnia strobilifera*** Mez, Repert. Spec. Nov. Regni Veg. 3: 15. 1906. Type: Bolivia, Dept. Chuquisaca, Prov. Sud Cinti, Camataqui, 2500 m a.s.l., 10 Feb. 1904, *Fiebrig 2933* [holotype: B!, photo ex B in GH!, F!].

= *D. bracteosa* W. Till & L. Hrom., Bromélia 4 (1): 19. 1997. Type: Bolivia, Dept. Chuquisaca, Prov. Sud Cinti, valley about 10 km W of Villa Abecia, 3000 m a.s.l., Feb. 1995. *Hromadnik 19029* [holotype: WU!].

**Plants** forming rings or cushions. **Rosettes** 10–20 [–25] × 10–20 cm. **Leaf sheaths** 1.7–3 [–4] × 3.5–5.5 cm. **Blades** 7.5–25 [–28] × 1.5–4 cm, incurved, channelled, spinose-serrate or entire, densely lepidote on both sides, abaxial greyish, adaxial greenish to reddish. **Peduncle** present, incl. inflorescence 20–40 cm × 3–4 [–7] mm, erect, perennial, woody. **Peduncle bracts** [4–] 8–16 × 0.5–1.5 cm, laxely spinose-serrate. **Inflorescence** 10–20 cm long, compound, branches of 1st order, perennial. **Primary bracts** 6–9 × 0.6–1.5 cm, shorter than the partial inflorescence, narrowly triangular, narrowly acute, laxely spinose-serrate or entire, lepidote. **Partial inflorescences** 2–4 cm long, densely flowered spikes, simple, axis concealed, spheroidal, 10–25-flowered. **Floral bracts** 6–8 × 0.5–0.8 mm, about equaling the sepals, broadly ovate, acuminate, sparsely lepidote, brownish. **Flowers** 12–16 mm long, sessile. **Sepals** [4.5–] 6–9 × 3–5 [–6] mm, ovate, obtuse, mucronulate, glabrous, yellow-brownish. **Petals** [8–] 11–15 × [2–] 3–5 mm, glabrous or adaxially with some glandular trichomes, recurved during anthesis, after anthesis not spirally twisted, yellow. **Petal appendages** 3–5 mm long, with long fringes. **Filaments** [5.5–] 10–12 mm long. **Anthers** [1.5–] 2–3.5 mm long, recurved, exposed, yellow. **Ovary** [2–] 3 mm long. **Style** [4–] 7–9 mm long, stigma exposed. **Fruits** 8–9 × 4–5 mm. **Seeds** 3 mm long.

**Distribution**. BOLIVIA. Dept. La Paz (see "Notes and comments"), Chuquisaca, Potosí, Tarija. ARGENTINA. Prov. Jujuy: Dept. Santa Catalina. [16°45' –] 18°15'–22°15' S, 65°00'–65°50' [–68°30'] W. In additon to the specimens seen during this revision, Kessler (2002) documented further localities in an ecological study: Dept. Cochabamba: Prov. Narciso Campero.

**Habitat and ecology.** Ecoregion: Bolivian montane dry forests (95) and Central Andean puna (156). At elevations of 2300–3900 m a.s.l. Terrestrial, on rocky slopes in Prepuna and Semihumid Puna regions, open areas with sparse vegetation. Associated with cacti and xerophytic shrubs, a.o. *Acacia feddeana*, *Caesalpinia trichocarpa*, *Cercidium andicola*, *Prosopis ferox* (all Fabaceae), *Corryocactus tarijensis*, *Oreocereus celsianus* (Cactaceae), *Gochnatia cardenasii* (Asteraceae). Main anthesis from No-

vember to March. Bernardello et al. (1991) proposed ornithophily. Nevertheless, the small, opened flowers and the single-coloured petals may indicate entomophily (Benzing 2000), which is also assumed by Kessler (2002).

**Etymology.** The epithet refers to the dense partial inflorescences (Greek *strobilus* = pine-cone).

**Affinities.** *Deuterocohnia strobilifera* is morphologically and ecologically similar to *D. digitata*. Both grow in dense groups or cushions at the upper limit of the genus' altitudinal range. While *D. strobilifera* occurs in southern Bolivia and the border district of Bolivia and Argentina, *D. digitata* is restricted to the northern Argentinean province Salta. *Deuterocohnia strobilifera* possesses longer primary bracts, shorter partial inflorescences, conspicuously opened flowers at anthesis, yellow petals and recurved anthers.

**Notes and comments.** (a) The voucher of *Krach 7488* [US] notes the Bolivian province Ingavi (Dept. La Paz) as collection locality. Due to the fact that no other specimen of *Deuterocohnia* has been collected in La Paz nor in Oruro, and that the next populations of *D. strobilifera* are more than 500 km farther south, this locality is kind of uncertain, but possible. (b) Mez mentioned in the initial description of *D. strobilifera* only Bolivia as distribution area. Castellanos (1945) and others included also the departments Cachi and Molinas in Argentina. Later on, those Argentinean collections were recognized as a new species (*D. digitata*) by Smith (1969). In the monograph of Bromeliaceae from Smith and Downs (1974) still a collection from Salta is noted as *D. strobilifera*: *West 6176* [UC]. This voucher is assigned to *D. digitata* in the present revision, due to its erect, orange–yellow petals, erect anthers and short primary bracts. (c) The inflorescences often seem to be quite short on herbarium vouchers. This is in most cases due to a broken peduncle. Subsequently, partial inflorescences appear in between the leaf apices. This complicates the measurement of the inflorescences. (d) The varieties are well distinguishable, but there are also intermediates, comprising just one or two spines on one leaf (e.g. *Schütz et al. 06-074*). (e) The voucher of *López 771* [LPB] comprises both varieties, demonstrating that plants with and without leaves may occur within the same population. (f) Till noted already in 1997 on the type voucher of *D. bracteosa* (*Hromadnik 19029* [WU]), that it belongs to *D strobilifera*. (g) *Deuterocohnia strobilifera* was classified as *vulnerable/endangered* by IUCN red list of threatened plants (1997). (h) Zuloaga et al. (2008) listed *D. digitata* as synonym of *D. strobilifera*.

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## Key to the varieties.

| | | | |
|---|---|---|---|
| 1. | Leaves laxly spinose-serrate, spines about 5 mm long | *D. strobilifera* var. *strobilifera* | A |
| 1. * | Leaves entire | *D. strobilifera* var. *inermis* | B |

## A. *Deuterocohnia strobilifera* Mez var. *strobilifera*

**Distribution.** BOLIVIA. Dept. Chuquisaca, Potosí, Tarija. ARGENTINA. Prov. Jujuy. 20°00'–22°15' S, 65°00'–65°50' W.

**Specimens seen.** BOLIVIA: without precise locality: 1979, *Hromadnik 5083* [HEID!]. **Dept. Chuquisaca:** Prov. Nor Cinti: N of Camargo, (20°30' S, 65°10' W), 2500 m, 19 Jul. 1979, *Hromadnik 5064* [HEID!]; 15 km on road from Camargo to Tarija, 20°45'51" S, 65°14'01" W, 2360 m, 10 Oct. 2006, *Schütz et al. 06-048* [FR!, LPB!]; ibid.: *Schütz et al. 06-049* [FR!, LPB!]. Prov. Sud Cinti: Camataqui, (21°00' S, 65°23' W), 2500 m, 10 Feb. 1904, *Fiebrig 2933* [B!, F!, photo ex B in GH!].3,5 km on road from El Puente to Impora, 21°14'02"S, 65°13'11"W, 2425 m, 13 Oct. 2006, *Schütz et al. 06-069* [FR!, LPB!]; ibid.: *Schütz et al. 06-070* [FR!, LPB!]; 69 km on road from El Puente, between Impora and Hornillos, 21°23'05" S, 65°20'05" W, 3595 m, 13 Oct. 2006, *Schütz et al. 06-072* [FR]. **Dept. Potosí:** Prov. Nor Chichas: 84 km from Potosí via Cotagaita to Tupiza, antes de Vitichi, (20°7,5' S, 65°30' W), 3500 m, 28 Dec. 1986, *Beck 14122* [LPB!]. Prov. Sud Chichas: 39 km from Tupiza to Potosí, between Hornillos and Santiago de Cotagaita, 21°10'08" S, 65°36'34" W, 3340 m, 14 Oct. 2006, *Schütz et al. 06-074* [LPB!]; Tupiza, (21°30' S, 65°45' W), 2950 m, 08 Feb. 1941, *Crespo s.n.* [BA 37070!]; in ravines of Río San Juan de Oro, near Tupiza, near the bridge passing Quebrada Seca, (21°30' S, 65°20' W), 3150 m, 08 Aug. 1990, *Palaci 1199* [WU!]. Prov. Modesto Omiste: going up from Hi-

guieras to Villazón, 21°54' S, 65°26'09" W, 3000 m, 09 Mar. 1998, *Beck et al. 23800* [LPB!]. **Dept. Tarija:** Prov. Méndez: Cantón Paycho, 3200 m, 27 Feb. 1991, *Garcia 2394* [LPB!]; 7 km on road from El Puente to Tarija, 21°15'29" S, 65°12'40" W, 2370 m, 10 Oct. 2006, *Schütz et al. 06-051* [FR!, LPB!]; ibid.: *Schütz et al. 06-052* [FR!]; between Tomayapo and Iscayachi, 21°18'15" S, 65°02'30" W, 2800 m, 08 May 2003, *López et al. 771* [LPB!]; Iscayachi 18 km to Cieneguillas, via Potosí, (21°30' S, 65°05' W), 3450 m, 09 Nov. 1993, *Beck et al. 22042* [LPB!]. ARGENTINA. **Prov. Jujuy:** Dept. Santa Catalina: Cuesta de Toquero, road to Santa Catalina, (22°10' S, 65°50' W), 3900 m, 31 Jan. 1943, Cabrera 7789 [LP!].

**B. *Deuterocohnia strobilifera*** Mez **var*. inermis*** L.B. Sm., Contr. U.S. Natl. Herb. 29(11): 535. 1954. Type: Bolivia, Dept. Chuquisaca, Prov. Nor Cinti, near Sivingamayu, 3400 m, Dec. 1949, *Cárdenas 4094* [holotype: US!, isotype: LIL!].

**Distribution.** BOLIVIA. Dept. Chuquisaca, Potosí, [La Paz]. [16°45' –] 20°00'–22°00' S, 65°14'–65°45' [– 68°30'] W.

**Etymology.** The name of the variety refers to the spineless leaves (Latin *inermis* = defenseless).

**Specimens seen.** BOLIVIA: **Dept. La Paz**: Prov. Ingavi: on road La Paz–Oruro, 12 km N of the bridge over Quebrada Honda, almost plane area, 3600 m, 29 Dec. 1979, *Krach 7488* [US!]. **Dept. Chuquisaca**: Prov. Nor Cinti: Otavi 22 km to Camargo, (20°10' S, 65°15' W), 3530 m, 23 Mar. 1979, *Beck 683* [LPB!]; from Otavi to Padcayo, 20°11'02" S, 65°14'50" W, 3500 m; 09 Oct. 2006, *Schütz et al. 06-047* [FR]; just N of Padcaya on road from Camargo to Potosí, (20°15' S, 65°10' W), 3500 m, 04 Mar. 2000; *Wood 15904* [HSB!, K!, LPB!]; near Sivingamayu, (20°20' S, 65°10' W), 3400 m, Dec. 1949, *Cárdenas 4094* [LIL!, US!].Tajsara chain, (20°40' S, 65°00' W), 3320 m, 22 Jan. 1982, *Gerold 25* [LPB!]. **Dept. Potosí**: near Potosi, *Knize s.n.* [ZSS 9225!]. Prov. José María Linares: 92 km on road from Otavi to Padcayo, 20°07'55" S, 65°19'51" W, 3280 m, 09 Oct. 2006, *Schütz et al. 06-046* [FR!, LPB!]. Prov. Nor Chichas: 151 km on road from Tupiza to Potosí, between Tumusla and Vitichy, 20°22'09" S, 65°31'53" W, 2940 m, 14 Oct. 2006, *Schütz et al. 06/075* [FR]. Prov. Sud Chichas: between Oploca and Atocha, (21°10' S, 65°45' W), 3000 m, Dec. 1946, *Cárdenas 3741* [GH!, LIL!, US!]. Prov. Modesto Omiste: Quebrada Tenalpa, 20 km east of Villazón on road to Tarija, (21°55' S, 65°30' W), 12 Feb. 1937, *West 8379* [GH!, UC!]. **Dept. Tarija:** Prov. Méndez: between Tomayapo and Iscayachi, 21°18'15" S, 65°02'30" W, 2800 m, 08 May 2003, *López 771* [LPB!].

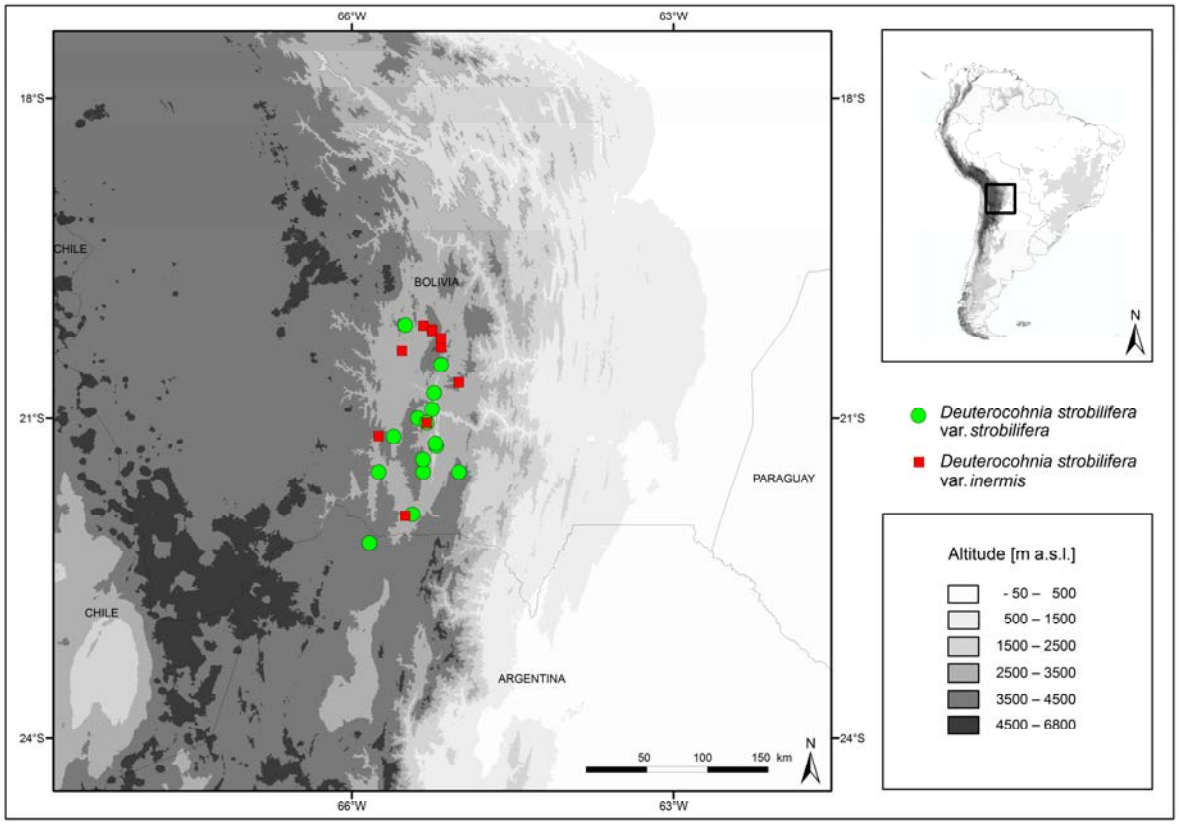


Fig. 5.37: Distribution of *D. strobilifera*.


Fig. 5.38: *D. strobilifera*: a and b: Natural habitat, Dept. Chuquisaca, Bolivia (*N. Schütz 06-046, 06-070*). c: partial inflorescence. d: Mature plant from the greenhouse (*L. Hromadnik 5064*) with notably different habit than in nature (e). e: Cluster of ramets, centre already decomposed.

# 6 SUMMARY

The present study investigates the systematics and evolution of the Neotropical genus *Deuterocohnia* Mez (Bromeliaceae). It provides a comprehensive taxonomic revision as well as phylogenetic analyses based on chloroplast and nuclear DNA sequences and presents a hypothesis on the evolution of the genus.

A broad morphological, anatomical, biogeographical and ecological overview of the genus is given in the first part of the study. For morphological character assessment more than 700 herbarium specimens from 39 herbaria as well as living plant material in the field and in the living collections of botanical gardens were carefully examined. The arid habitats, in which the species of *Deuterocohnia* grow, are reflected by the morphological and anatomical characters of the species.

Important characters for species delimitation were identified, like the length of the inflorescence, the branching order, the density of flowers on partial inflorescences, the relation of the length of the primary bracts to that of the partial inflorescence, the sizes of floral bracts, sepals and petals, flower colour, the presence or absence of a pedicel, the curvature of the stamina and the petals during anthesis.

After scrutinizing the nomenclatural history of the taxa belonging to *Deuterocohnia* – including the 1992 syonymized genus *Abromeitiella* – 17 species, 4 subspecies and 4 varieties are accepted in the present revision. Taxonomic changes were made in the following cases: (I) New combinations: *A. abstrusa* (A. Cast.) N. Schütz is re-established – as defined by Castellanos (1931) – and transfered to *D. abstrusa*; *D. brevifolia* (Griseb.) M.A. Spencer & L.B. Sm. includes accessions of the former *D. lorentziana* (Mez) M.A. Spencer & L.B. Sm., which are not assigned to *D. abstrusa*; *D. bracteosa* W. Till is synonymized to *D. strobilifera* Mez; *D. meziana* Kuntze ex Mez var. *carmineo-viridiflora* Rauh is classified as a subspecies of *D. meziana* (ssp. *carmineo-viridiflora* (Rauh) N. Schütz); *D. pedicellata* W. Till is classified as a subspecies of *D. meziana* (ssp. *pedicellata* (W. Till) N. Schütz); *D. scapigera* (Rauh & L. Hrom.) M.A. Spencer & L.B. Sm ssp. *sanctae-crucis* R. Vásquez & Ibisch is classified as a species (*D. sanctae-crucis* (R. Vásquez & Ibisch) N. Schütz); (II) New taxa: a new subspecies of *D. meziana* Kuntze ex Mez is established; a new variety of *D. scapigera* is established; (the new taxa will be validly published elsewhere); (III) New type: an epitype for *D. longipetala* was chosen.

All other species were kept according to Spencer and Smith (1992) or – in the case of more recently described species – according to the protologue. Beside the nomenclatural notes and the detailed descriptions, information on distribution, habitat and ecology, etymology and taxonomic delimitation is provided for the genus and for each of its species. An key was constructed for the identification of currently accepted species, subspecies and varieties. The key is based on easily detectable morphological characters.

The former synonymization of the genus *Abromeitiella* into *Deuterocohnia* (Spencer and Smith 1992) is re-evalutated in the present study. Morphological as well as molecular investigations revealed *Deuterocohnia* incl. *Abromeitiella* as being monophyletic, with some indications that a monophyletic *Abromeitiella* lineage arose from within *Deuterocohnia*. Thus the union of both genera is confirmed.

The second part of the present thesis describes and discusses the molecular phylogenies and networks. Molecular analyses of three chloroplast intergenic spacers (*rpl*32-*trn*L, *rps*16-*trn*K, *trn*S-*ycf*3) were conducted with a sample set of 119 taxa. This set included 103 *Deuterocohnia* accessions from all 17 described species of the genus and 16 outgroup taxa from the remainder of Pitcairnioideae s.str. (*Dyckia* (8 sp.), *Encholirium* (2 sp.), *Fosterella* (4 sp.) and *Pitcairnia* (2 sp.)). With its high sampling density, the present investigation by far represents the most comprehensive molecular study of *Deuterocohnia* up till now. All data sets were analyzed separately as well as in combination, and various optimality criteria for phylogenetic tree construction were applied (Maximum Parsimony, Maximum Likelihood, Bayesian inferences and the distance method Neighbour Joining). Congruent topologies were generally obtained with different algorithms and optimality criteria, but individual clades received different degrees of statistical support in some analyses. The *rps*16-*trn*K locus was the most informative among the three spacer regions examined. The results of the chloroplast DNA analyses revealed a highly supported paraphyly of *Deuterocohnia*. Thus, the cpDNA trees divide the genus into two subclades (A and B), of which *Deuterocohnia* subclade B is sister to the included *Dyckia* and *Encholirium* accessions, and both together are sister to *Deuterocohnia* subclade A.

To further examine the relationship between *Deuterocohnia* and *Dyckia*/*Encholirium* at the generic level, two nuclear low copy markers (PRK exon2-5 and PHYC exon1) were analysed with a reduced taxon set. This set included 22 *Deuterocohnia* accessions (including members of both cpDNA subclades), 2 *Dyckia*, 2 *Encholirium* and 2 *Fosterella* species. Phylogenetic trees were constructed as described above, and for comparison the same reduced taxon set was also analysed at

the three cpDNA data loci. In contrast to the cpDNA results, the nuclear DNA data strongly supported the monophyly of *Deuterocohnia*, which takes a sister position to a clade of *Dyckia* and *Encholirium* samples.

As morphology as well as nuclear DNA data generated in the present study and in a former AFLP analysis (Horres 2003) all corroborate the monophyly of *Deuterocohnia*, the apparent paraphyly displayed in cpDNA analyses is interpreted to be the consequence of a chloroplast capture event. This involves the introgression of the chloroplast genome from the common ancestor of the *Dyckia*/ *Encholirium* lineage into the ancestor of *Deuterocohnia* subclade B species.

The chloroplast haplotypes are not species-specific in *Deuterocohnia*. Thus, one haplotype was sometimes shared by several species, where the same species may harbour different haplotypes. The arrangement of haplotypes followed geographical patterns rather than taxonomic boundaries, which may indicate some residual gene flow among populations from different *Deuteroccohnia* species. Phenotypic species coherence on the background of ongoing gene flow may then be maintained by sets of co-adapted alleles, as was suggested by the porous genome concept (Wu 2001, Palma-Silva et al. 2011).

The results of the present study suggest the following scenario for the evolution of *Deuterocohnia* and its species. *Deuterocohnia longipetala* may be envisaged as a representative of the ancestral state within the genus. This is supported by (1) the wide distribution of this species; (2) the overlap in distribution area with species of *Dyckia*; (3) the laxly flowered inflorescences, which are also typical for *Dyckia*; (4) the yellow petals with a greenish tip, present in most other *Deuterocohnia* species. The following six extant lineages within *Deuterocohnia* might have independently been derived from this ancestral state with a few changes each: (I) *D. meziana*, *D. brevispicata* and *D. seramisiana* (Bolivia, lowland to montane areas, mostly reddish-greenish coloured, very laxly to very densely flowered); (II) *D. strobilifera* (Bolivia, high Andean mountains, yellow flowers, densely flowered); (III) *D. glandulosa* (Bolivia, montane areas, yellow-greenish flowers, densely flowered); (IV) *D. haumanii*, *D. schreiteri*, *D. digitata*, and *D. chrysantha* (Argentina, Chile, E Andean mountains and Atacama desert, yellow-greenish flowers, densely flowered); (V) *D. recurvipetala* (Argentina, foothills of the Andes, recurved yellow flowers, laxly flowered); (VI) *D. gableana*, *D. scapigera*, *D. sanctae-crucis*, *D. abstrusa*, *D. brevifolia*, *D. lotteae* (former *Abromeitiella* species, Bolivia, Argentina, higher Andean mountains, greenish-yellow flowers, inflorescence usually simple).

Originating from the lower montane Andean regions, at least four lineages of the genus (I, II, IV, VI) adapted in part to higher altitudes by developing densely flowered partial inflorescences, shorter flowers and – in at least three lineages (II, IV, VI) – smaller rosettes, whereas species spreading into the lowlands (I, V) developed larger plants, laxly flowered, amply branched inflorescences and in part larger flowers (I).

# 7 ZUSAMMENFASSUNG

Die vorliegende Arbeit befasst sich mit der Systematik und Evolution der xerophytischen, neotropisch verbreiteten Gattung *Deuterocohnia* Mez (Bromeliaceae). Sie beinhaltet sowohl eine umfassende taxonomische Revision als auch phylogenetische Analysen mittels Chloroplasten- und Kern-DNA Daten.

Im ersten Teil der Ergebnisse der vorliegenden Untersuchung wird ein Überblick über die Morphologie, Anatomie, Biogeographie und Ökologie der Gattung *Deuterocohnia* und ihrer Arten gegeben. Die Basis für diese Untersuchungen bildeten über 700 Herbarbelege aus 39 Herbarien sowie Lebendmaterial, das während zweier Feldaufenthalte in Bolivien und Argentinien und in den Sammlungen zahlreicher Botanischer Gärten untersucht wurde. Die ariden Habitate, in denen alle *Deuterocohnia*-Pflanzen wachsen, spiegeln sich in den morphologischen und anatomischen Merkmalen der Arten wieder.

Mit Hilfe der morphologischen Analysen konnten einige Merkmale ermittelt werden, die zur Artabgrenzung gut geeignet sind. Dies sind insbesondere die Länge der Infloreszenz und deren Verzweigungsgrad, die Dichte der Blüten an den Teilinfloreszenzen, das Verhältnis der Länge der primären Hochblätter zu den Teilinfloreszenzen, die Größe der Floralbrakteen, der Sepalen und der Petalen, die Blütenfarbe, das Vorhandensein oder Fehlen eines Blütenstiels sowie die Krümmung der Stamina und der Petalen während der Anthese.

Nach intensiver Untersuchung der Morphologie sowie der Nomenklatur der *Deuterocohnia*-Arten – einschließlich der 1992 (Spencer und Smith) syonymisierten Gattung *Abromeitiella* – werden 17 Arten, 4 Unterarten und 4 Varietäten in der vorliegenden Arbeit anerkannt. Taxonomische Änderungen wurden in den folgenden Fällen durchgeführt: (I) Umkombinationen: *A. abstrusa* (A. Cast.) N. Schütz wird – entsprechend Castellanos (1931) – wieder aufgestellt und zu *D. abstrusa* transferiert; *D. brevifolia* (Griseb.) M.A. Spencer & L.B. Sm. umfasst jetzt zusätzlich die Akzessionen der ehemaligen *D. lorentziana* (Mez) M.A. Spencer & L.B. Sm., die nicht *D. abstrusa* zugeordnet werden; *D. bracteosa* W. Till wird als Synonym von *D. strobilifera* Mez geführt; *D. meziana* Kuntze ex Mez var. *carmineo-viridiflora* Rauh wird als Unterart klassifiziert (*D. meziana* ssp. *carmineo-viridiflora* (Rauh) N. Schütz); *D. pedicellata* W. Till wird als Unterart von *D. meziana* geführt (*D. meziana* ssp. *pedicellata* (W. Till) N. Schütz); *D. scapigera* (Rauh & L. Hrom.) M.A. Spencer & L.B. Sm. ssp. *sanctae-crucis* R. Vásquez & Ibisch wird als Art klassifiziert (*D. sanctae-crucis* (R.

Vásquez & Ibisch) N. Schütz); (II) Neue Taxa: eine neue Unterart von *D. meziana* Kuntze ex Mez wird etabliert; eine neue Varietät von *D. scapigera* wird aufgestellt; (die neuen Taxa werden an anderer Stelle gültig publiziert); (III) Neuer Typus: ein Epitypus wurde für *D. longipetala* ausgewählt. Alle weiteren Taxa entsprechen der Klassifizierung von Spencer und Smith (1992), im Falle von später beschriebenen Arten der zugehörigen Erstbeschreibung. Kritische Taxa und taxonomische Veränderungen werden im Diskussions-Teil aufgezeigt und erläutert. Der spezielle taxonomische Teil bildet den Abschluss der vorliegenden Arbeit und beinhaltet Gattungs- und Artbeschreibungen sowie Bestimmungsschlüssel für alle derzeit anerkannten Arten, Unterarten und Varietäten. Jede Artbeschreibung umfasst neben der Nomenklatur auch Informationen zu Verbreitung, Lebensraum und Ökologie sowie zur Etymologie und zur Differenzierung von nahe stehenden Arten.

Auch die Synonymisierung der Gattungen *Abromeitiella* und *Deuterocohnia* durch Spencer und Smith (1992) wurde in der vorliegenden Arbeit kritisch untersucht. Sowohl morphologische als auch molekulare Daten unterstützen *Deuterocohnia* inkl. *Abromeitiella* als monophyletische Gruppe und bestätigen die Vereinigung beider Gattungen. Dennoch deuten einige Anzeichen darauf hin, dass eine monophyletische *Abromeitiella*-Linie innerhalb von *Deuterocohnia* entstanden sein könnte.

Im zweiten Ergebnis-Teil werden die molekularen Phylogenien und Netzwerke dargestellt und erläutert. Molekulare Analysen von drei intergenischen Bereichen des Chloroplasten-Genoms (*rpl*32-*trn*L, *rps*16-*trn*K, *trn*S-*ycf*3) wurden mit einem Probenset von 119 Taxa durchgeführt. Dieses Set beinhaltet 103 *Deuterocohnia*-Akzessionen, die zusammen alle 17 beschriebenen Arten der Gattung abdecken, sowie 16 weitere Taxa der Pitcairnioideae s.str. (*Dyckia* (8), *Encholirium* (2), *Fosterella* (4) und *Pitcairnia* (2)). Mit dieser hohen Sampling-Dichte ist die vorliegende Untersuchung die bisher umfassendste molekulare Analyse der Gattung *Deuterocohnia*. Alle Datensätze wurden einzeln sowie in Kombination analysiert und es wurden verschiedene Optimalitätskriterien und Algorithmen für die phylogenetischen Baumrekonstruktionen angewendet (Maximum Parsimony, Maximum Likelihood, Bayesian Inference und die Distanz-Methode Neighbour Joining). Die unterschiedlichen Rechenmethoden resultierten in weitestgehend kongruenten Baumtopologien für die jeweiligen Taxon-Sets, zum Teil erhielten allerdings einige Gruppen unterschiedlich gute statistische Unterstützung. Die Region *rps*16-*trn*K erwies sich als die informativste der drei cpDNA-Spacer-Regionen. Die Ergebnisse der Chloroplasten-DNA-Analysen zeigten eine statistisch sehr gut gestützte Paraphylie von *Deuterocohnia*. Die Arten der Gattung teilen sich demnach in zwei Untergruppen (A und B) auf, von denen *Deuterocohnia* Untergruppe B eine Schwester-

gruppen-Position zu den *Dyckia*- und *Encholirium*-Proben einnimmt und beide Gruppen zusammen wiederum eine Schwestergruppen-Position zu *Deuterocohnia* Untergruppe A einnehmen. Die beiden Untergruppen sind nicht nur molekular, sondern auch morphologisch und geographisch deutlich voneinander differenziert.

Zur weiteren Untersuchung der Frage der Monophylie vs. Paraphylie von *Deuterocohnia* wurden zwei nukleäre low-copy-Marker (PRK exon2-5 und PHYC exon1) sequenziert. Dies erfolgte mit einem reduzierten Taxon-Set, da ausschließlich die Beziehung der Gattungen *Deuterocohnia* und *Dyckia/Encholirium* zueinander untersucht werden sollte. Dieses Set umfasste 22 *Deuterocohnia*-Akzessionen (wobei beide Untergruppen aus der cpDNA-Analyse berücksichtigt wurden), sowie jeweils zwei Proben der Gattungen *Dyckia*, *Encholirium* und *Fosterella*. Phylogenetische Bäume wurden wie oben beschrieben rekonstruiert, zum Vergleich wurde das gleiche Taxon-Set mit cpDNA-Daten untersucht. Im Gegensatz zu den Ergebnissen der cpDNA-Analyse unterstützen die Kerndaten deutlich die Monophylie von *Deuterocohnia*. Dabei steht *Deuterocohnia* in einem Schwestergruppen-Verhältnis zu den Proben von *Dyckia* und *Encholirium*.

Da sowohl die Morphologie als auch die Kern-DNA-Daten der vorliegenden Studie und einer früheren AFLP-Analyse (Horres 2003) die Monophylie von *Deuterocohnia* bestätigen, ist die Paraphylie in den cpDNA-Analysen vermutlich auf ein frühes „Chloroplast-capture"-Ereignis zurückzuführen, bei dem das Chloroplasten-Genom von dem gemeinsamen Vorfahren von *Dyckia/Encholirium* in die Linie der *Deuterocohnia*-Untergruppe B aufgenommen wurde.

Innerhalb der beiden Untergruppen von *Deuterocohnia* zeigen die Chloroplasten-Haplotypen keine artspezifische Verteilung. So kommt z.B. der gleiche Haplotyp oftmals in mehreren Arten vor. In anderen Fällen treten in derselben Art unterschiedliche Haplotypen auf. Insgesamt zeigt jedoch die Verteilung der Haplotypen ein deutliches geographisches Muster. Dies deutet darauf hin, dass zwischen Populationen aus verschiedenen, sympatrisch verbreiteten *Deuterocohnia*-Arten ein gewisser Genfluss besteht. Die phänotypische Kohärenz der Arten bei beständigem Genfluss kann durch das Auftreten von einigen wenigen „Speziations-Genen" erklärt werden, wie es das „Porous-Genome"-Konzept (Wu 2001, Palma-Silva et al. 2011) beschreibt.

Neben der Erörterung der Taxonomie und der Interpretation der molekularen Daten werden in der Diskussion der vorliegenden Untersuchung auch Hypothesen zur Evolution der *Deuterocohnia*-Arten vorgestellt. Die gewonnenen Erkenntnisse legen das folgende Szenario für die Evolution

von *Deuterocohnia* und den zugehörigen Arten nahe: *Deuterocohnia longipetala* kann als Vertreter des ursprünglichen Zustands innerhalb der Gattung betrachtet werden. Dies wird unterstützt durch (1) die weite Verbreitung dieser Art; (2) die überlappende Verbreitung mit Arten von *Dyckia*, die sich wahrscheinlich aus einem gemeinsamen Vorfahren mit *Deuterocohnia* entwickelt haben; (3) die entfernt stehenden Blüten an den Teilinfloreszenzen, die auch typisch für *Dyckia* sind; (4) die gelben Petalen mit grünlicher Spitze, die auch typisch für die meisten anderen *Deuterocohnia* Arten sind. Innerhalb von *Deuterocohnia* könnten die folgenden sechs Linien unabhängig voneinander aus dieser ursprünglichen Form entstanden sein: (I) *D. meziana*, *D. brevispicata* und *D. seramisiana* (Bolivien, Tiefland bis montane Regionen, meist rötlich-grünlich gefärbte Blüten, sehr locker bis sehr dicht stehende Blüten), (II) *D. strobilifera* (Bolivien, Hochanden, gelbe Blüten, sehr dicht stehende Blüten), (III) *D. glandulosa* (Bolivien, montane Bereiche, gelb-grünlichen Blüten, dicht stehende Blüten); (IV) *D. haumanii*, *D. schreiteri*, *D. digitata* und *D. chrysantha* (Argentinien, Chile, höhere Lagen der östlichen Anden und Atacama-Wüste, gelb-grünliche Blüten, dicht stehende Blüten), (V) *D. recurvipetala* (Argentinien, am Fuße der Anden, zurückgebogene, gelbe Blüten, locker stehende Blüten), (VI) *D. gableana*, *D. scapigera*, *D. sanctae-crucis*, *D. abstrusa*, *D. brevifolia*, *D. lotteae* (ehemalige *Abromeitiella*-Arten, Bolivien, Argentinien, höhere Lagen der Anden, grünlich-gelbe Blüten, dicht stehende Blüten, Blütenstand meist einfach).

Die aus niedrigeren Höhenstufen der Anden hervorgegangenen Linien haben sich demnach mindestens viermal (in I, II, IV, VI) unabhängig an das Leben in höheren Lagen angepasst und dabei verkürzte Teilinfloreszenzen mit dicht stehenden Blüten, kürzere Blüten und – in drei Linien (II, IV, VI) – kleinere Rosetten entwickelt. Arten im Tiefland (I, V) hingegen entwickelten tendenziell größere Pflanzen, große, lockere Infloreszenzen mit voneinander entfernt stehenden Blüten und zum Teil größere Blüten (I).

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# 9 APPENDIX

## Appendix 1: Haplotypes and the related accessions

z: *D.lotteae*_HEID_Till62b_N137_BO_Tarija
*D.schreiteri*_HEID_unknown_N145_unknown
*D.digitata*_FR_Schütz06098_N192_AR_Salta
*D.digitata*_FR_Schütz06099_N193_AR_Salta
*D.digitata*_FR_Schütz06101_N195_AR_Salta
*D.schreiteri*_FR_Schütz06106_N199_AR_Salta
*D.schreiteri*_FR_Schütz06108_N201_AR_Salta
*D.brevifolia*_FR_unknown_N222_unknown
*D.lotteae*_HEID_Hromadnik5131_N247_unknown
*D.longipetala*_WU_Till10050_N259_AR_Tucuman
*D.digitata*_WU_TillH88_151_N261_AR_Salta

s: *D.schreiteri*_FR_Schütz06102_N196_AR_Salta

a1: *D.chrysantha*_FR_Zizka8148_C148_CH_Antofagasta
*D.chrysantha*_FR_Zizka8152_C152_CH_Antofagasta
*D.chrysantha*_FR_Zizka8154_C154_CH_Antofagasta
*D.chrysantha*_FR_Zizka8156_C156_CH_Antofagasta
*D.chrysantha*_FR_Zizka8159_C159_CH_Antofagasta
*D.chrysantha*_FR_Katzsn_H196_CH_Antofagasta
a2: *D.longipetala*_FR_Schütz06118_N208_AR_Salta
*D.longipetala*_WU_Till5089_N271_AR_LaRioja
*D.longipetala*_WU_TillHsn_N280_AR_LaRioja
a3: *D.longipetala*_FR_Schütz06124_N210_AR_Salta

b1: *D.strobilifera*_var_*in*_FR_Schütz06075_N180_BO_Potosí
b2: *D.scapigera*_FR_Hromadnik5076_N113_BO_Potosi
*D.strobilifera*_var_*in*_FR_Schütz06046_N167_BO_Chuquisaca
*D.strobilifera*_FR_Schütz06072_N177_BO_Chuquisaca
*D.strobilifera*_FR_Schütz06074_N179_BO_Potosi
*D.scapigera*_HEID_Braun701_N253_unknown
*D.scapigera*_WU_Till38_N268_BO_Potosi
*D.strobilifera*_FR_unknown_N279_unknown
b3: *D.scapigera*_var_*nov*_HEID_Hromadnik5076_N252_BO_Potosi
b4: *D.strobilifera*_HEID_Hromadnik5083_N248_BO_unknown

c1: *D.haumanii*_HEID_Rauh64157_N143_AR_Salta

c2: *D.haumanii*_FR_Schütz06094_N189_AR_Salta

*D.haumanii*_FR_Schütz06096_N190_AR_Salta

c3: *D.longipetala*_WU_Till10126_N264_AR_Jujuy

c4: *D.longipetala*_WU_Till10082_N260_AR_Jujuy

d1: *D.lorentziana*_FR_Schütz06085_N183_AR_Salta

*D.lorentziana*_FR_Schütz06092_N187_AR_Salta

*D.lorentziana*_WU_Till10156_N265_AR_Salta

e1: *D.longipetala*_HEID_Tillsn_N245_AR_unknown

*D.longipetala*_WU_Till10045_N257_AR_Tucuman

e2: *D.longipetala*_B_Tillsn_N127_AR_unknown

f1: *D.digitata*_HEID_Rauh64142_N141_AR_Salta

*D.digitata*_FR_Schütz06097_N191_AR_Salta

*D.schreiteri*_FR_Schütz06104_N197_AR_Salta

*D.schreiteri*_FR_Schütz06105_N198_AR_Salta

g1: *D.longipetala*_HEID_Leuenberger4478a_N131_AR_LaRioja

*D.longipetala*_WU_Till5038_N270_AR_Cordoba

*D.longipetala*_WU_Till5165_N273_AR_LaRioja

g2: *D.longipetala*_WU_Till5131_N272_AR_SanJuan

g3: *D.recurvipetala*_FR_Rauh64236_N111_AR_unknown

*D.recurvipetala*_HEID_Rauh64236_N144_AR_unknown

g4: *D.longipetala*_B_unknown_N116_unknown

g5: *D.longipetala*_WU_Till10249_N267_AR_Tucuman

g6: *D.longipetala*_WU_Till5068_N284_AR_LaRioja

h1: *D.brevifolia*_FR_unknown_N106_unknown

*D.lorentziana*_B_unknown_N120_unknown

*D.brevivolia*_HEID_Balfanz075_N138_BO_Tarija

*D.brevifolia*_HEID_Hromadnik5124_N139_BO_Tarija

*D.lorentziana*_FR_Schütz06054_N171_BO_Tarija

*D.lorentziana*_FR_Schütz06056_N172_BO_Tarija

*D.lorentziana*_K_Taylorsn_N255_unknown

*D.lorentziana*_WU_Till62a_N275_BO_Tarija

*D.brevifolia*_WU_Till59_N277_BO_Tarija

*D.lorentziana*_FR_unknown_N281_unknown

h2: *D.brevifolia*_FR_Schütz06061_N173_BO_Tarija

i1: *D.strobilifera*_FR_Schütz06048_N168_BO_Chuquisaca

i2: *D.strobilifera*_FR_Schütz06051_N170_BO_Tarija

*D.strobilifera*_HEID_Hromadnik5064_N251_BO_Chuquisaca

i3: *D.strobilifera*_FR_Schütz06049_N169_BO_Chuquisaca

i4: *D.scapigera*_HEID_Hromadnik5103_N135_BO_Potosi

i5: *D.longipetala*_FR_Schütz06067_N176_BO_Tarija

i6: *D.glandulosa*_FR_Schütz06025_N161_BO_Chuquisaca

*D.longipetala*_FR_Schütz06066_N175_BO_Tarija

i7: *D.lorentziana*_HEID_Gouda95_18b_N136_BO_Tarija

i8: *D.glandulosa*_FR_Schütz06021_N159_BO_SantaCruz

i9: *D.glandulosa*_HEID_Hromadnik5167_N134_BO_Tarija

*D.longipetala*_WU_Till79_N276_BO_Tarija

i10: *D.lotteae*_B_Hromadnik5175_N121_BO_unknown

i11: *D.lotteae*_HEID_Hromadnik5131_N133_BO_Tarija

*D.lotteae*_HEID_Hromadnik9115_N140_BO_Tarija

j1: *D.seramisiana*_FR_Schütz06042_N165_BO_Chuquisaca

j2: *D.gableana*_LPB_Vasquez4253_N214_BO_SantaCruz

j3: *D.meziana*_FR_Schütz06011a_N213_BO_SantaCruz

*D.meziana*_FR_Schütz06011e_N224_BO_SantaCruz

j4: *D.scapigera*_HEID_Balfanz126_N249_BO_SantaCruz

*D.scapigera*_var_*san*_FR_Schütz09014_N295_BO_SantaCruz

j5: *D.brevispicata*_FR_Schütz06037_N163_BO_Chuquisaca

j6: *D.scapigera*_var_*san*_FR_Vasquez3017_N215_BO_SantaCruz

j7: *D.meziana*_HEID_Gouda9521_N244_BO_SantaCruz

j8: *D.meziana*_FR_Schütz06007d_N225_BO_SantaCruz

j9: *D.pedicellata*_FR_Schütz09009_N293_BO_Chuquisaca

j10: *D.meziana*_var_*car*_HEID_Rauh40642_N130_BO_Cochabamba

*D.meziana*_var_*car*_HEID_Rauh46774_N132_BO_Cochabamba

*D.meziana*_FR_unknown_N296_unknown

j11: *D.scapigera*_HEID_Hromadnik5275_N142_BO_Potosi

j12: *D.meziana*_HEID_Hromadnik5264_N254_BO_Cochabamba

j13: *D.brevispicata*_FR_Schütz06041_N164_BO_Chuquisaca

j14: *D.brevispicata*_B_Hromadnik5213_N112_BO_Chuquisaca

*D.brevispicata*_HEID_Hromadnik5213_N129_BO_Chuquisaca

*D.brevispicata*_FR_Schütz06022_N160_BO_SantaCruz

j15: *D.meziana*_HEID_Hromadnik5030_N246_BO_Cochabamba

y1: *E.horridum*_HEID_Schindhelmsn_N223_BR_MinasGerais

y2: *Dy.spec*_FR_Laubsn_N126_AR_unknown

y3: *Dy.spec*_HEID_Laub17_N250_AR_Catamarca

y4: *Dy.ferox*_HEID_Horst375_N242_BR_Bahia

y5: *Dy.maritima*_WU_unknown_N286_BR_unknown

y6: *E.inerme*_HEID_Horst386_N243_BR_MinasGerais

y7: *Dy.goehringii*_HEID_Rauh67622_N148_BR_MinasGerais

*Dy.marnier_lapostollei*_FR_MarnierLapostollesn_N219_BR_unknown

y8: *Dy.estevesii*_HEID_EddieEstevesPereirasn_N226_BR_Goias

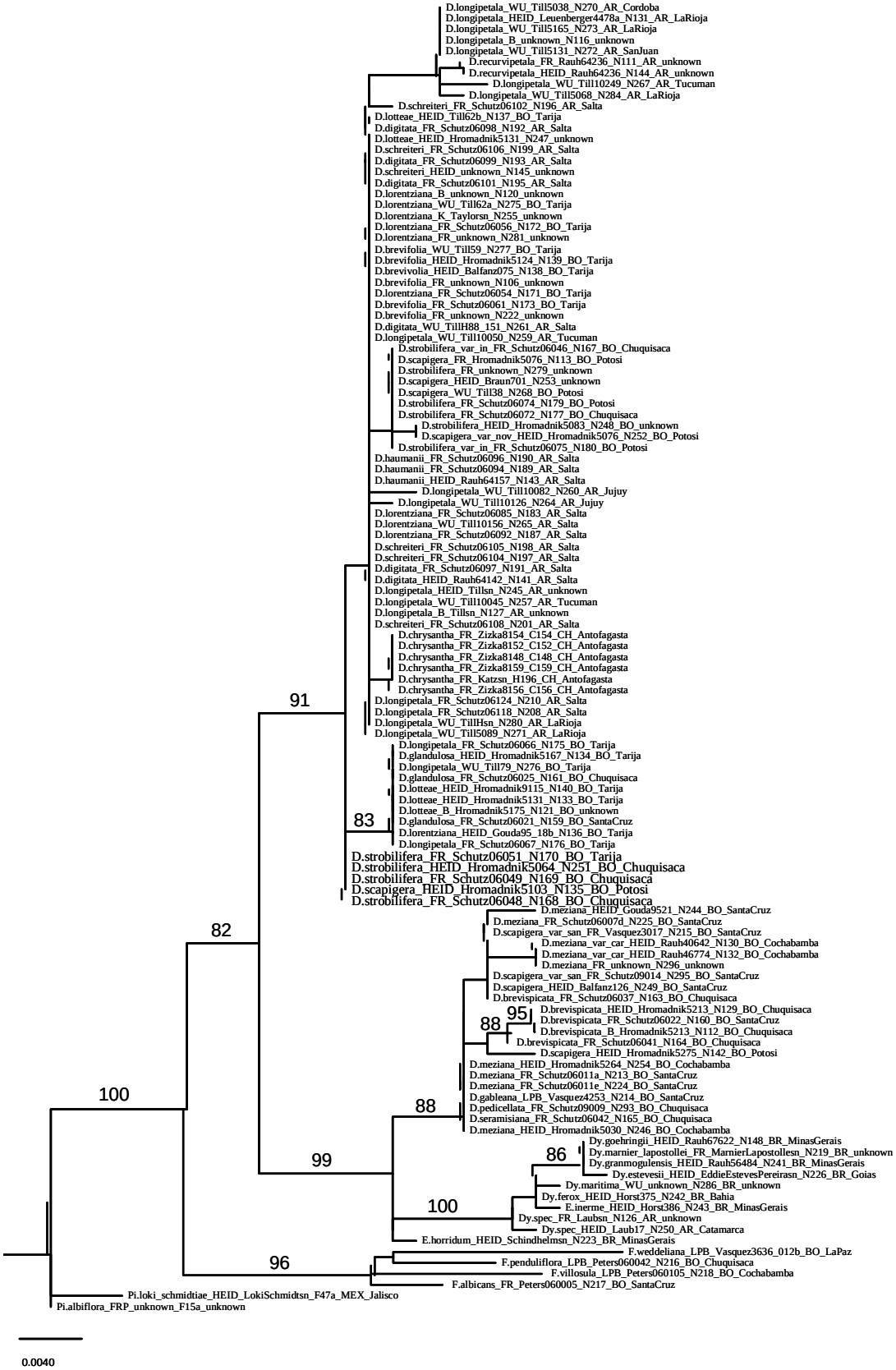
y9: *Dy.granmogulensis*_HEID_Rauh56484_N241_BR_MinasGerais

**Appendix 2: electronic Appendix: Alignment of the combined chloroplast sequence data in NEXUS format including simple indel coding**

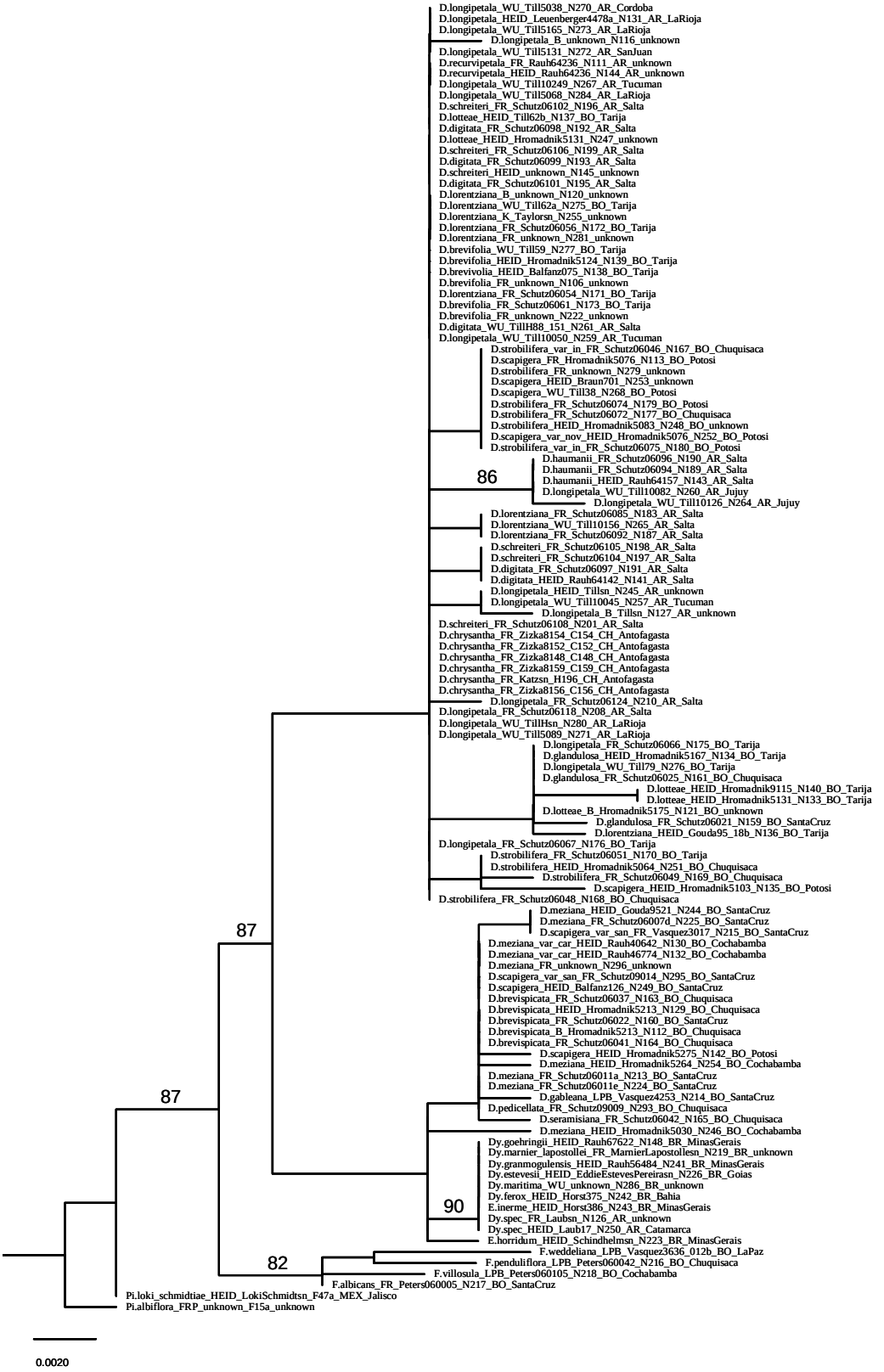
**Appendix 3: electronic Appendix: Alignment of the combined nuclear sequence data in NEXUS format including simple indel coding**

**Appendix 4: Phylogenetic tree resulting from Maximum Likelihood (RAxML) analyses of the chloroplast intergenic spacer *rpl*32-*trn*L**

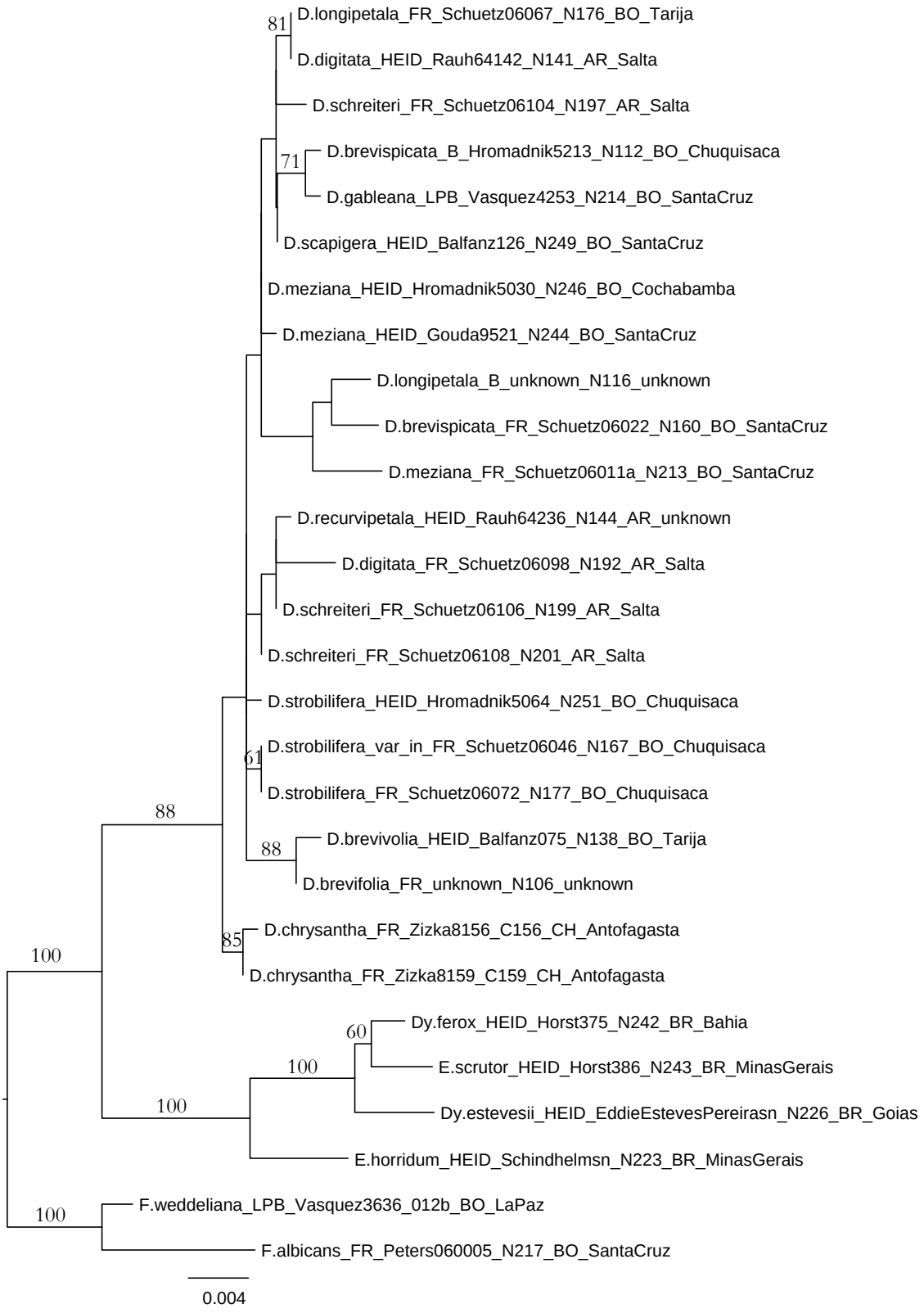
## Appendix 5: Phylogenetic tree resulting from Maximum Likelihood (RAxML) analyses of the chloroplast intergenic spacer *rps*16-*trn*K



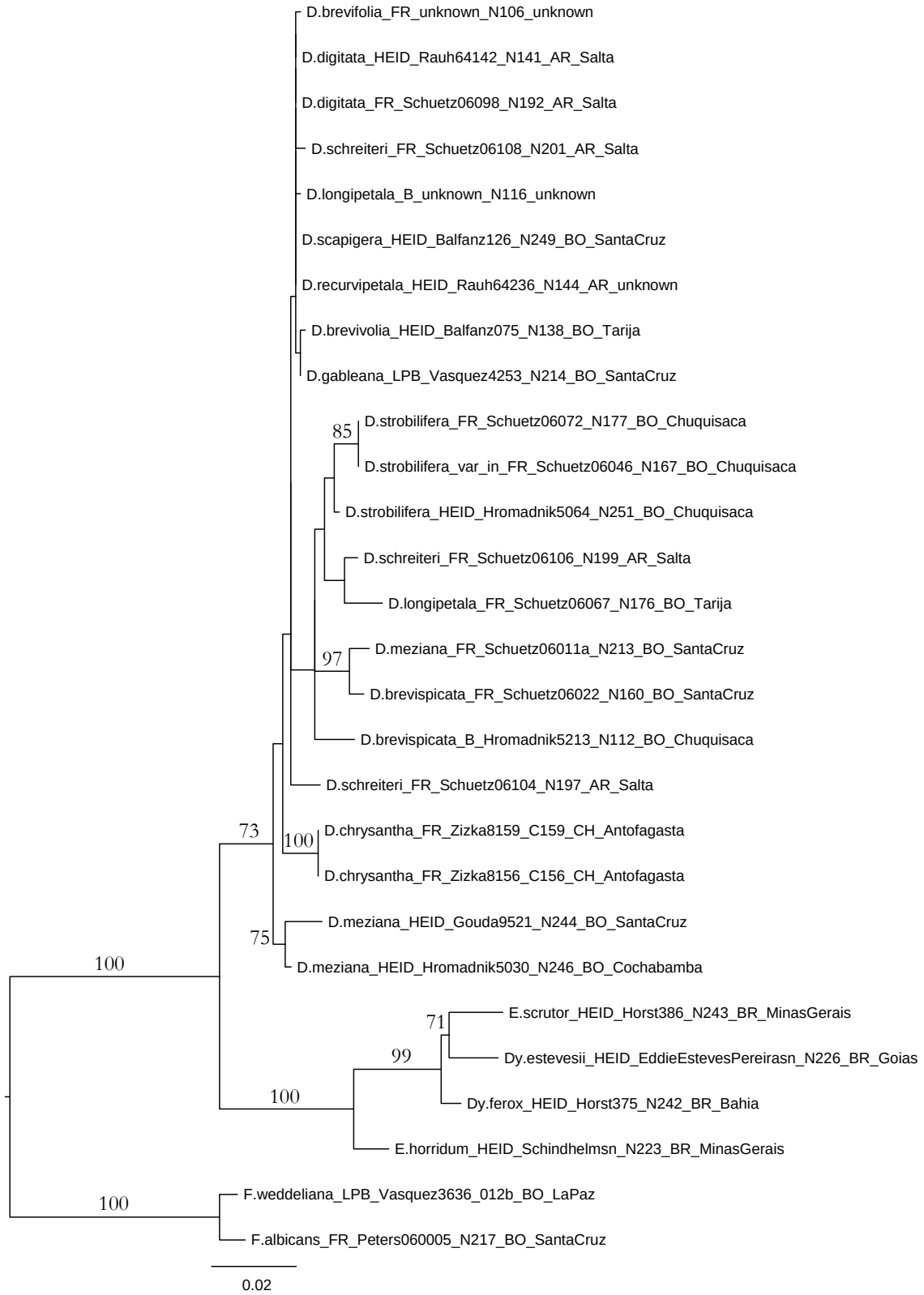
## Appendix 6: Phylogenetic tree resulting from Maximum Likelihood (RAxML) analyses of the chloroplast intergenic spacer *trn*S-*ycf*3



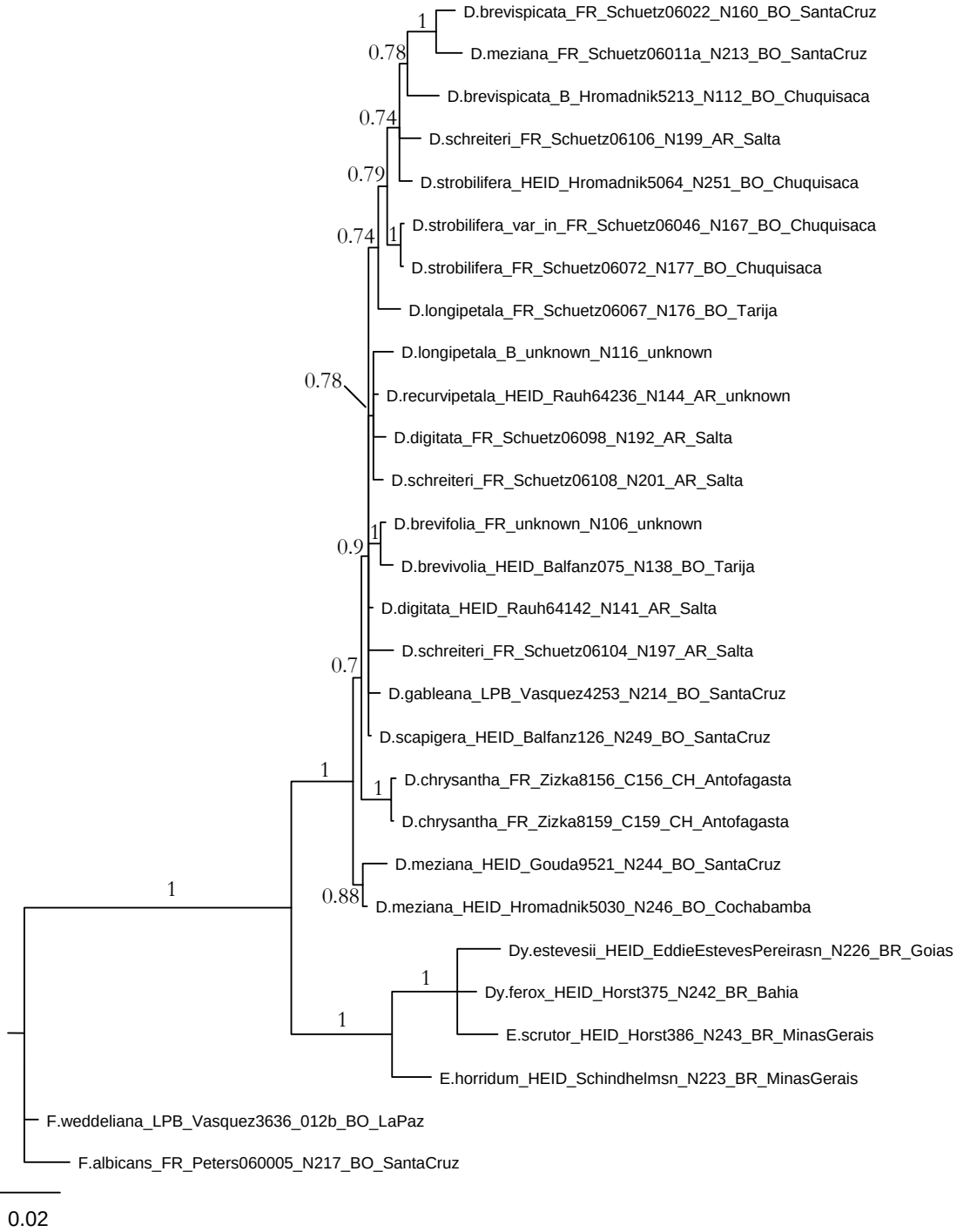
**Appendix 7: Phylogenetic tree resulting from Maximum Likelihood (RAxML) analyses of the nuclear low copy marker PHYC exon1**



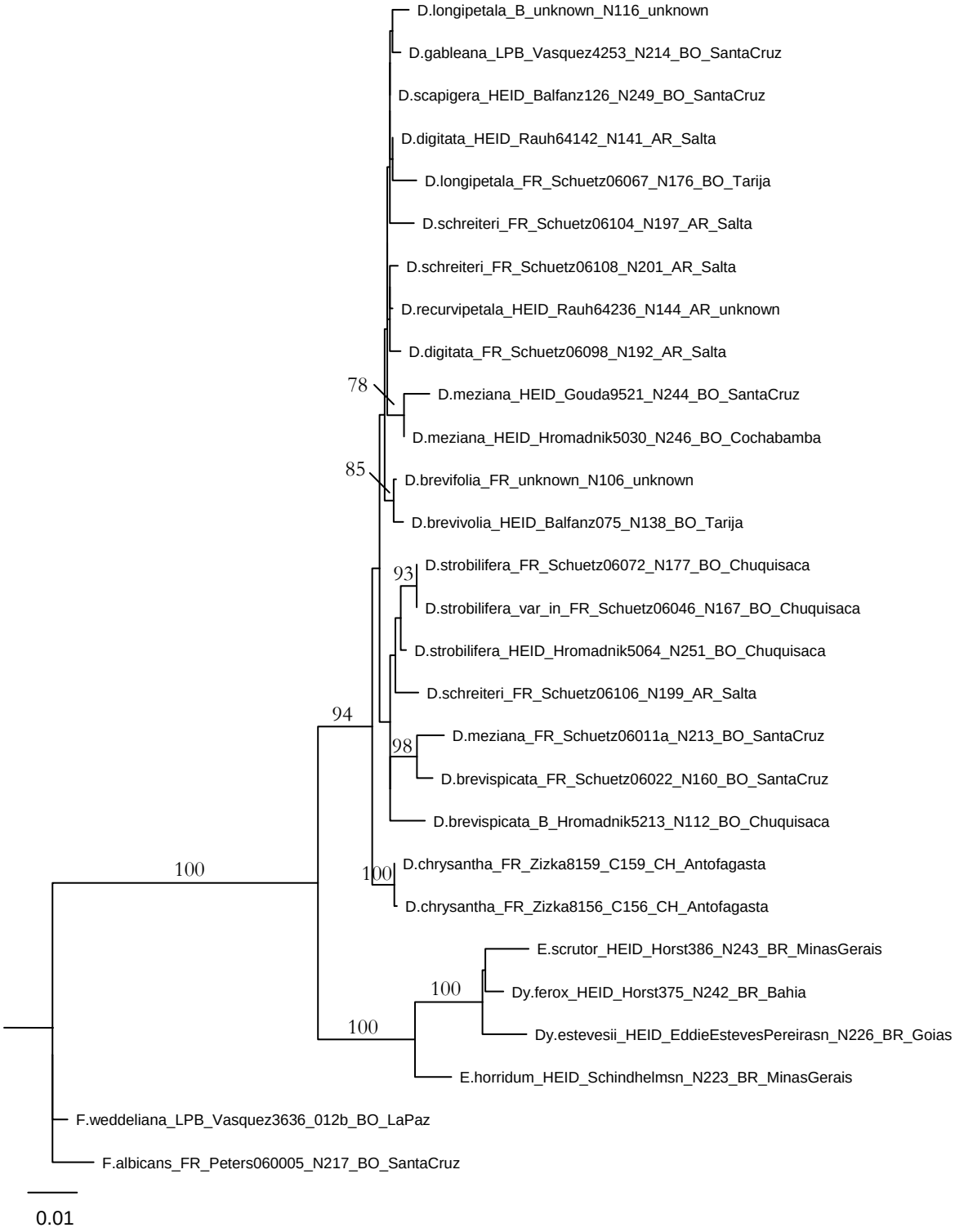
## Appendix 8: Phylogenetic tree resulting from Maximum Likelihood (RAxML) analyses of the nuclear low copy marker PRK exon2–5



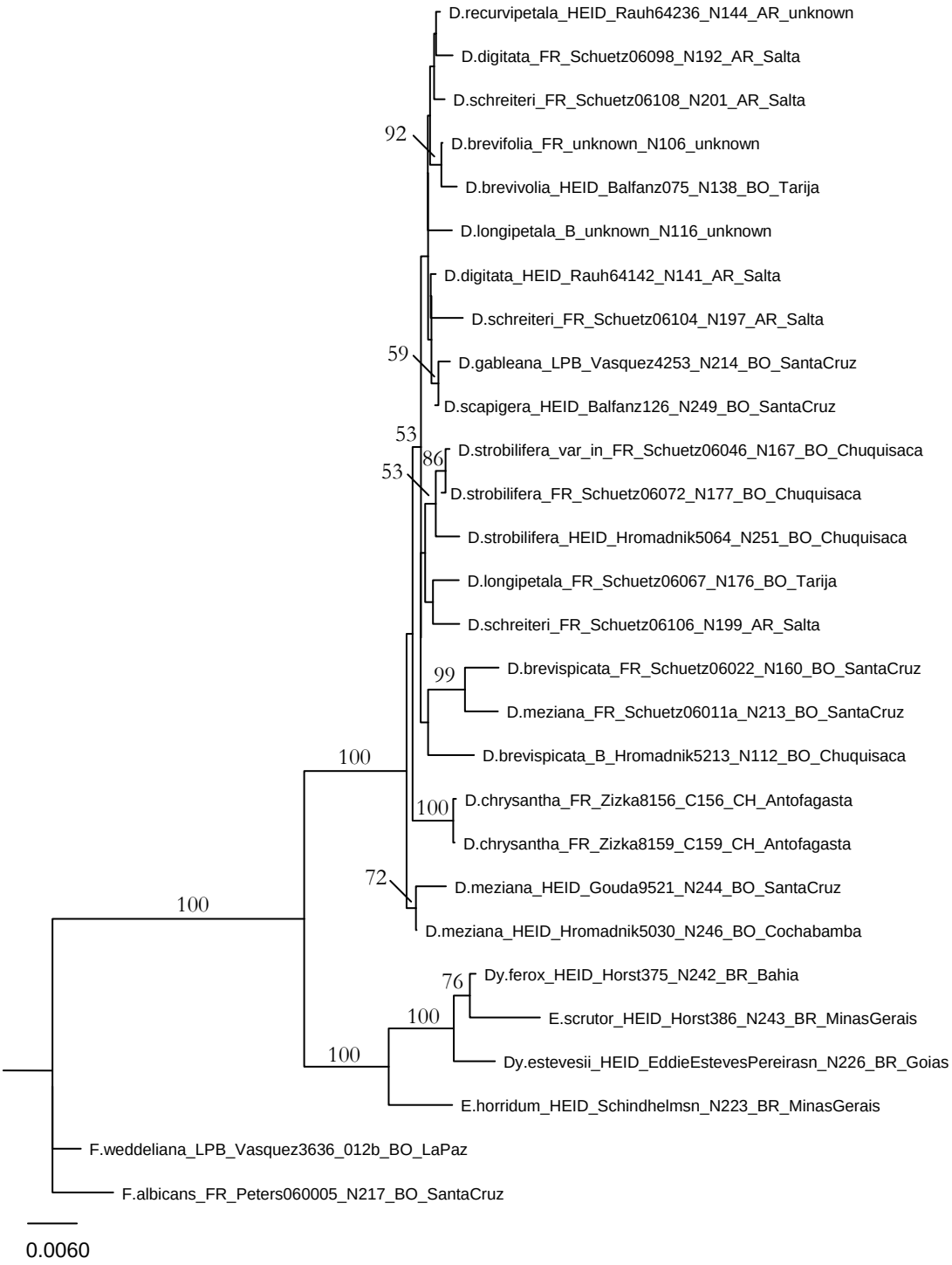
## Appendix 9: Phylogenetic tree resulting from Bayesian analyses of the combined nuclear data set



**Appendix 10: Phylogenetic tree resulting from Maximum Likelihood (RAxML) analyses of the combined nuclear data**

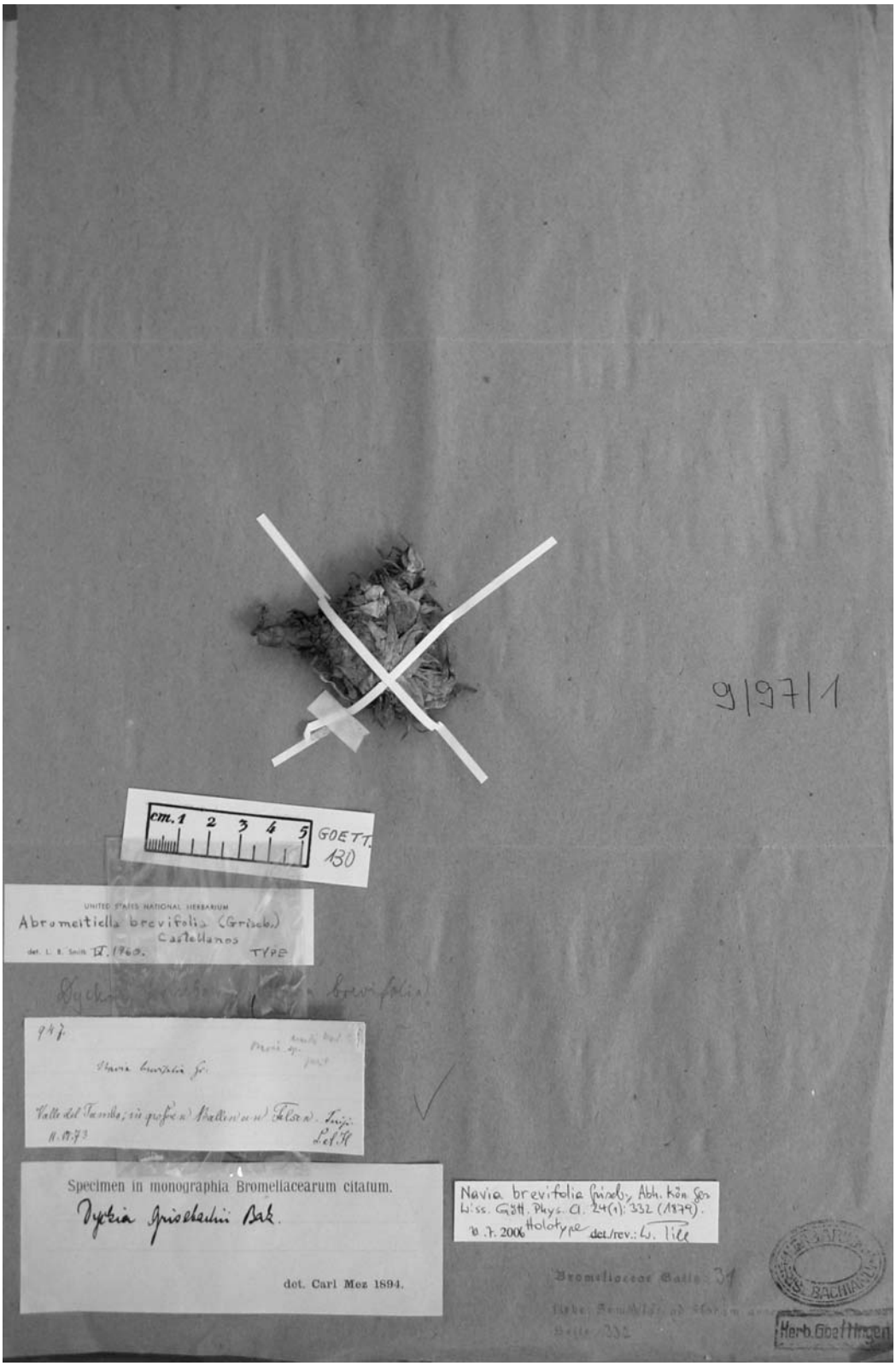


## Appendix 11: Phylogenetic tree resulting from Neighbour Joining analyses of the combined nuclear data

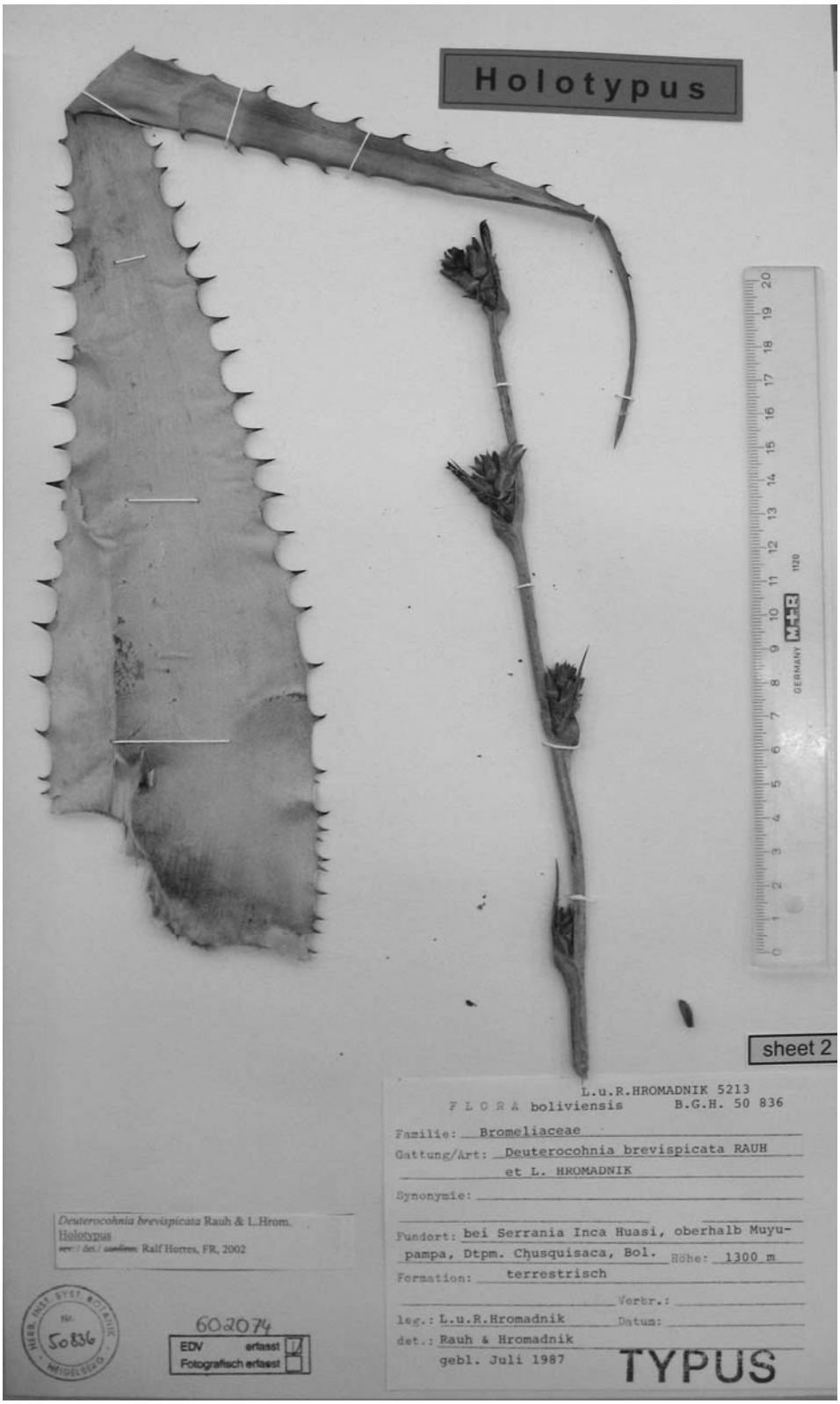


## Appendix 12: Photographs of type specimens

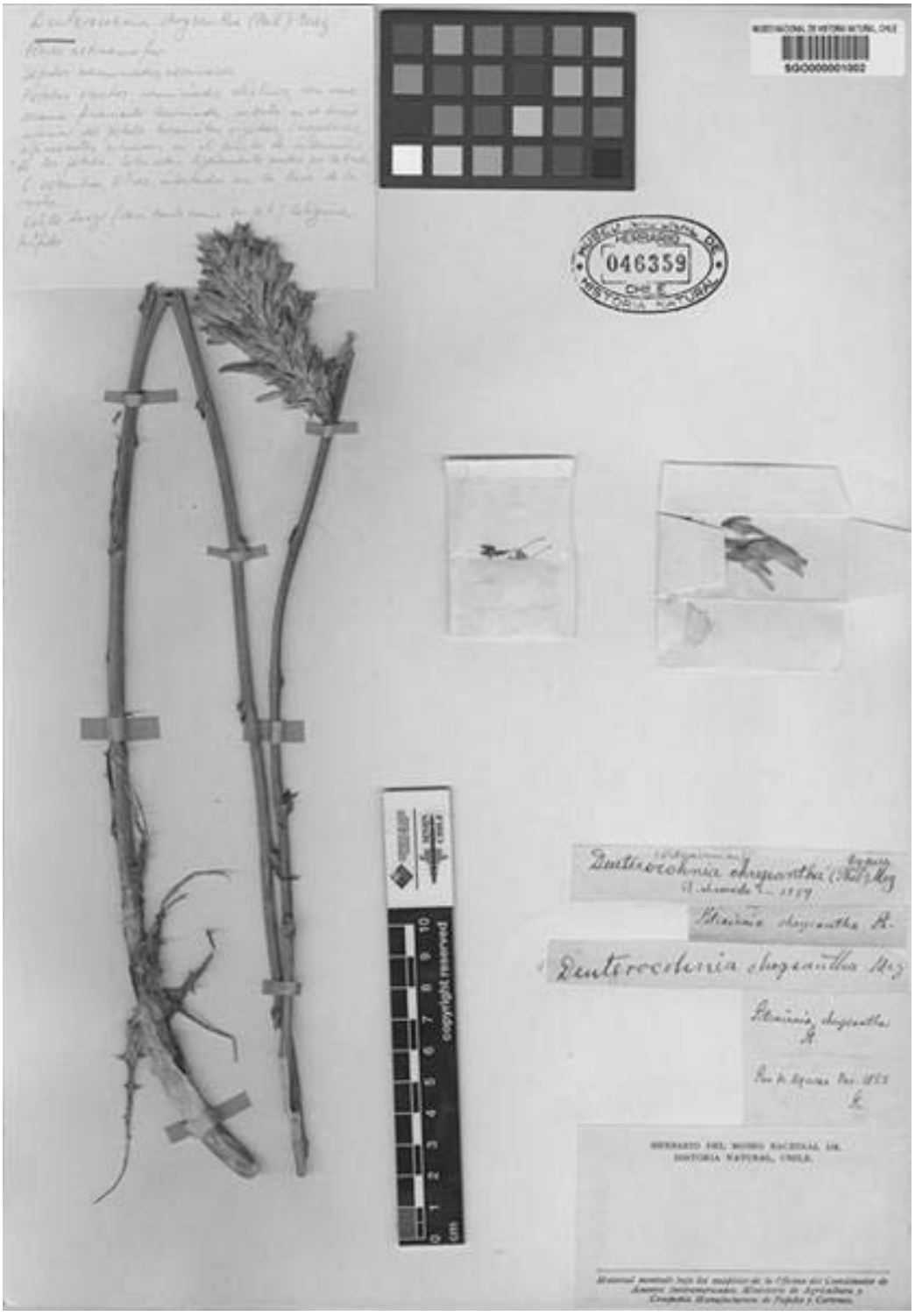

Castellanos 29/60: lectotype of *D. abstrusa* (A.Cast.) N. Schütz, sheet 1 of 2 [BA].




Lorentz and Hieronymus 947: lectotype of *D. brevifolia* (Griseb.) M.A. Spencer & L.B. Sm. [GOET].

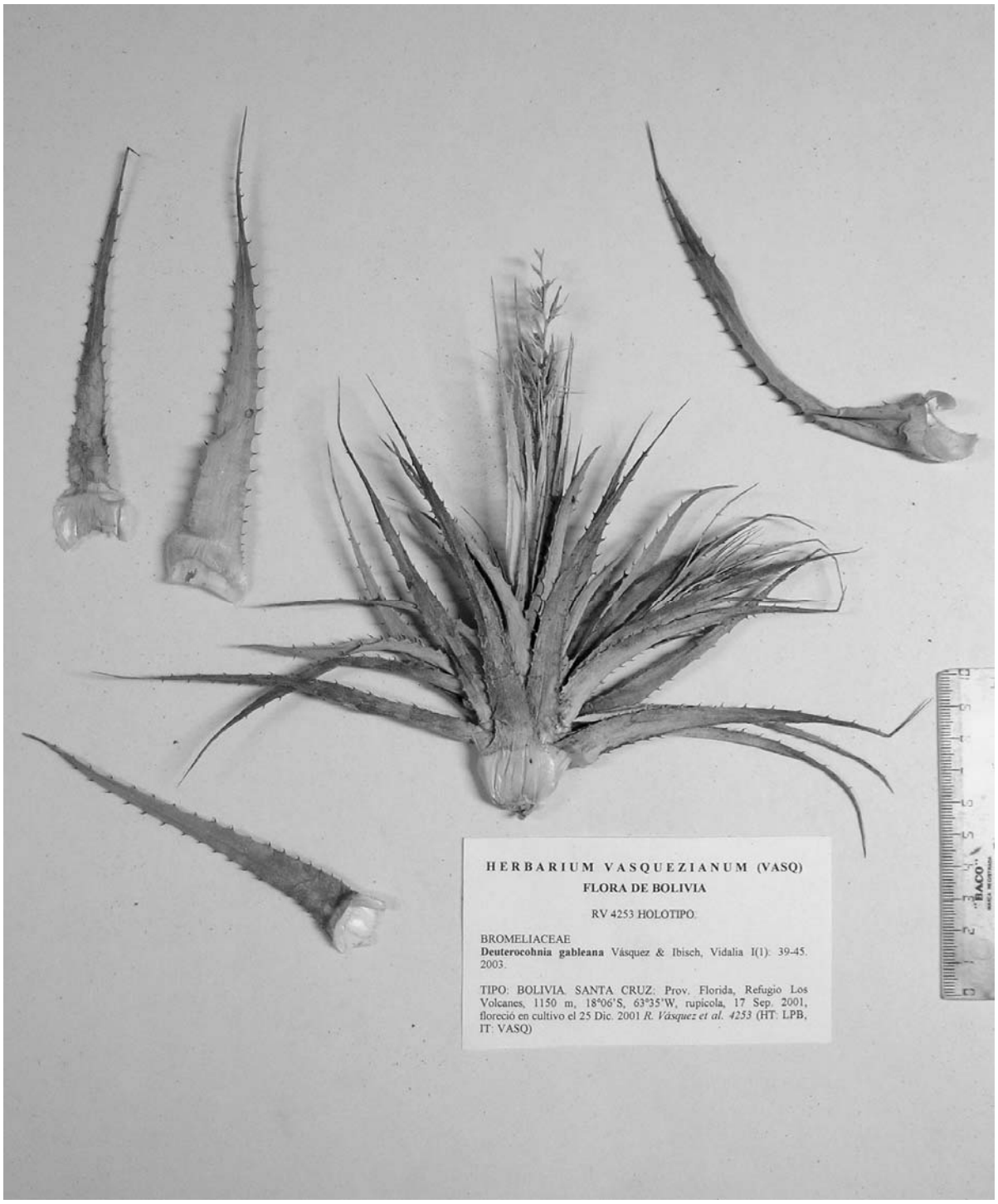



Hromadnik 5213: holotype of *D. brevispicata* Rauh & L. Hrom., sheet 2 of 2, [HEID].

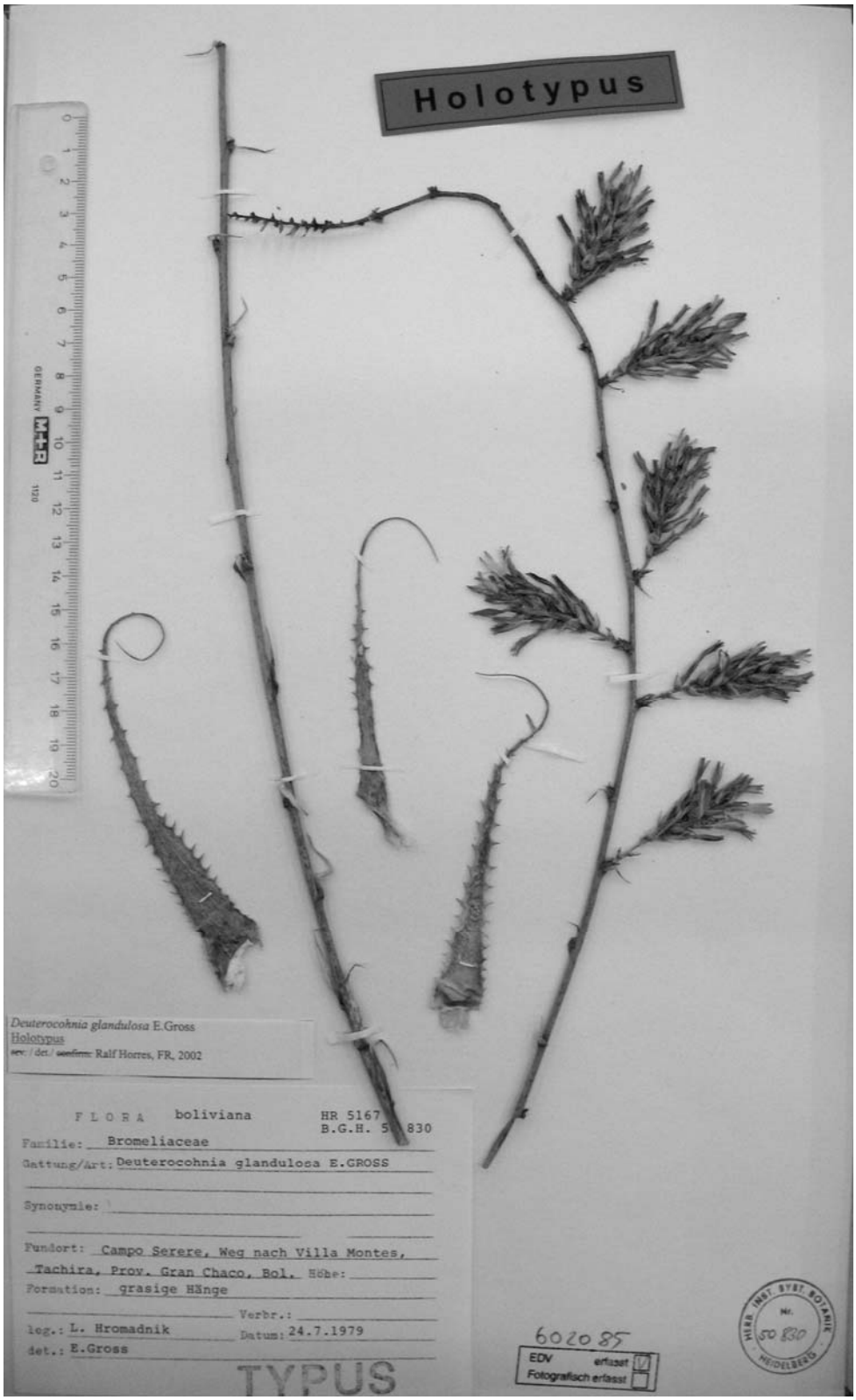



Philippi s.n.: photo of the lectotype of *D. chrysantha* (Phil.) Mez [SGO 46359].


Castellanos s.n.: isotype of *D. digitata* L.B. Sm. [US]. Photo ex US.



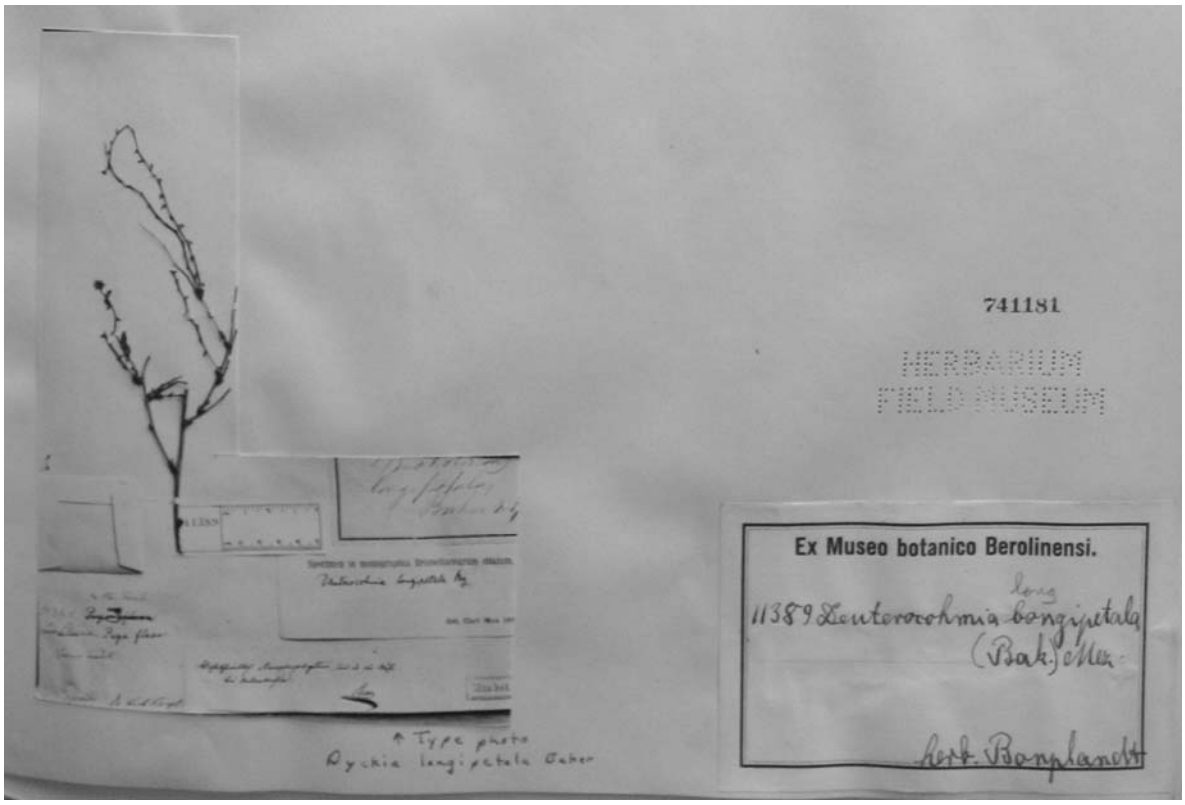

Vásquez 4253: isotype of *D. gableana* R. Vásquez & Ibisch [private collection of Roberto Vásquez, VASQ]. Photo from Roberto Vásquez.



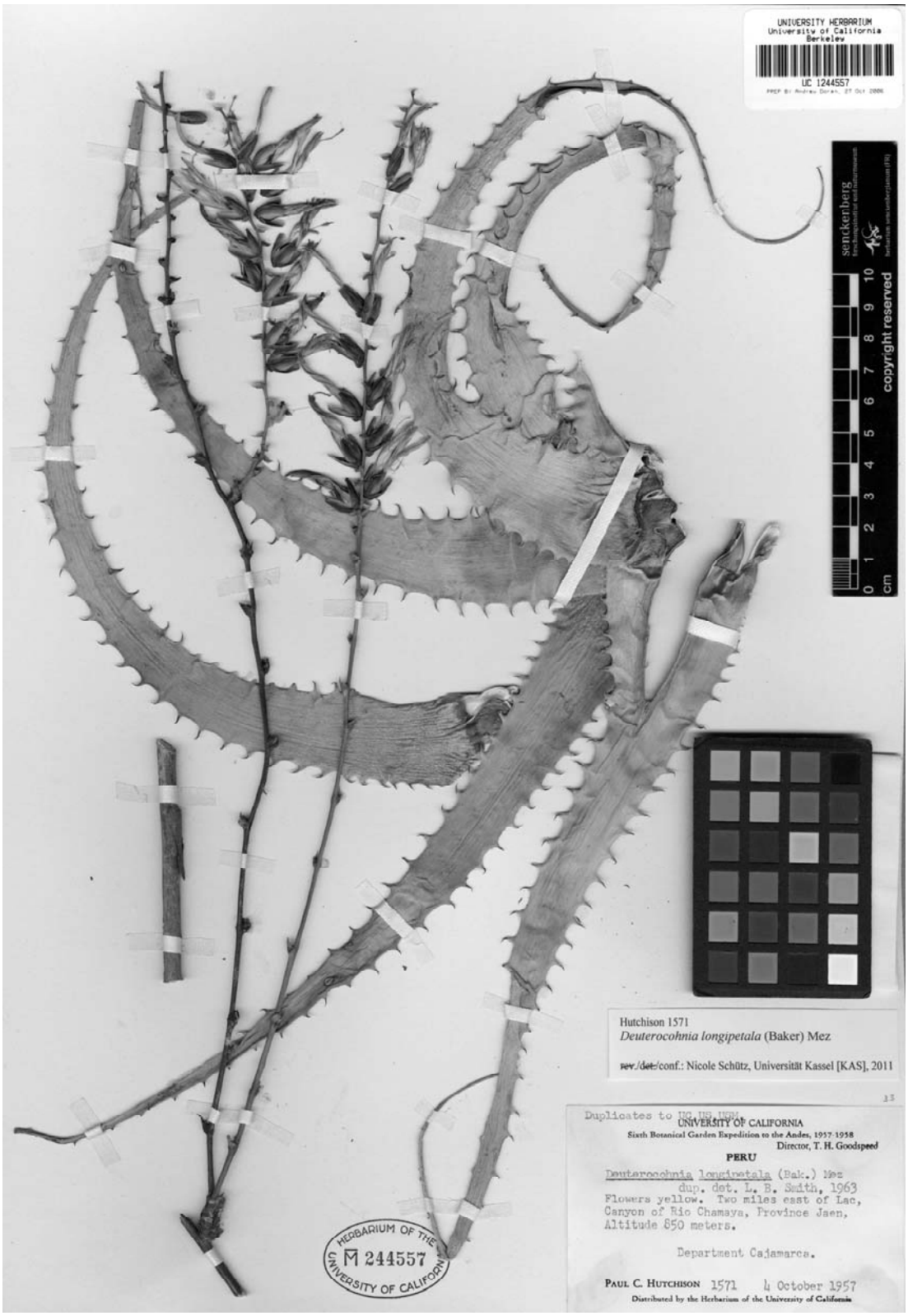

Hromadnik 5167: holotype of *D. glandulosa* E. Gross [HEID].


Schreiter s.n.: syntype of *D. haumanii* A. Cast. [LIL]. Photo ex JSTOR, www.jstor.org.

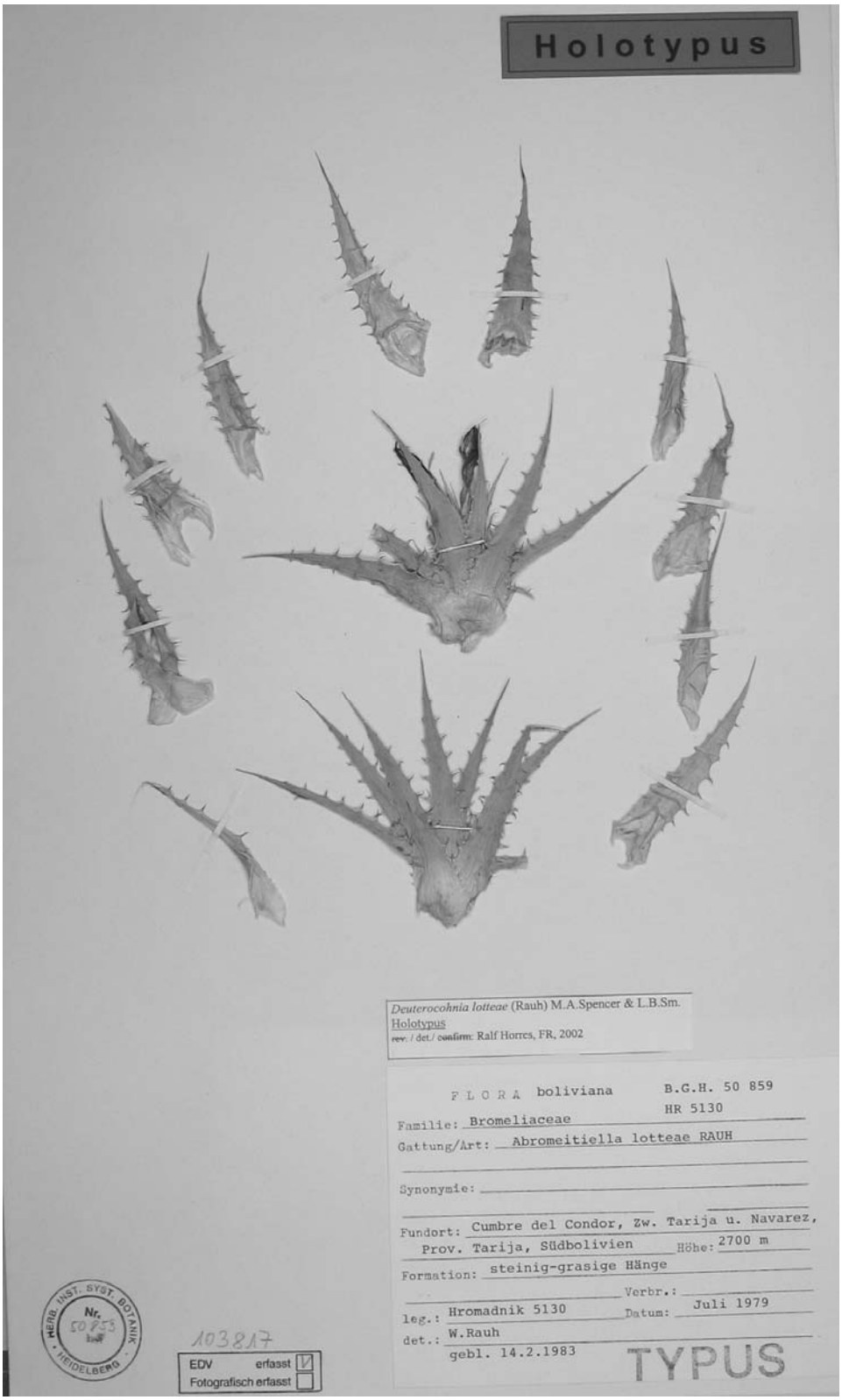

Hauman s.n.: syntype of *D. haumanii* A. Cast. [BA].



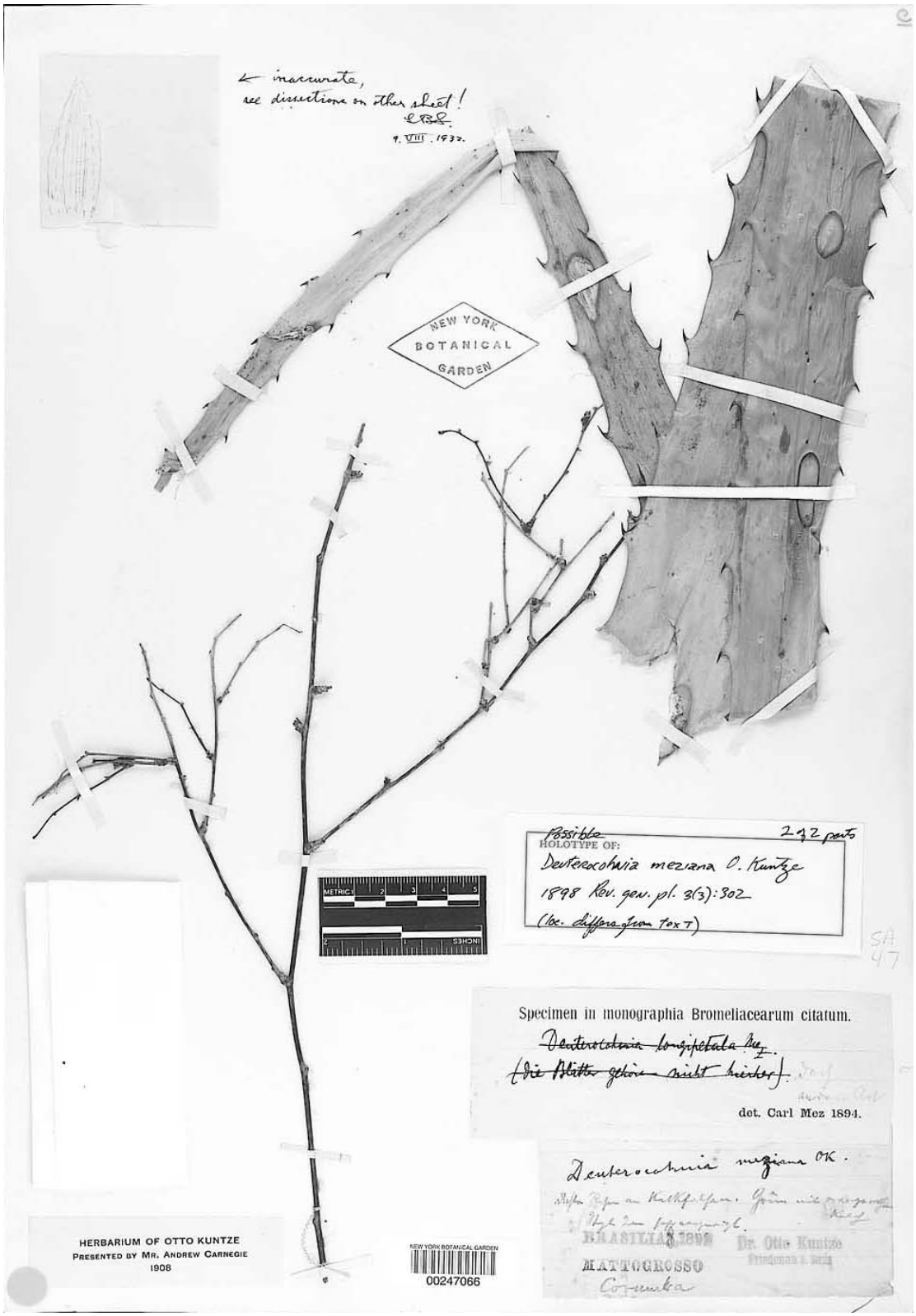

Humboldt and Bonpland 3595: photograph of holotype of *D. longipetala* (Baker) Mez [F].




Hutchison 1571: epitype of *D. longipetala* (Baker) Mez [UC].

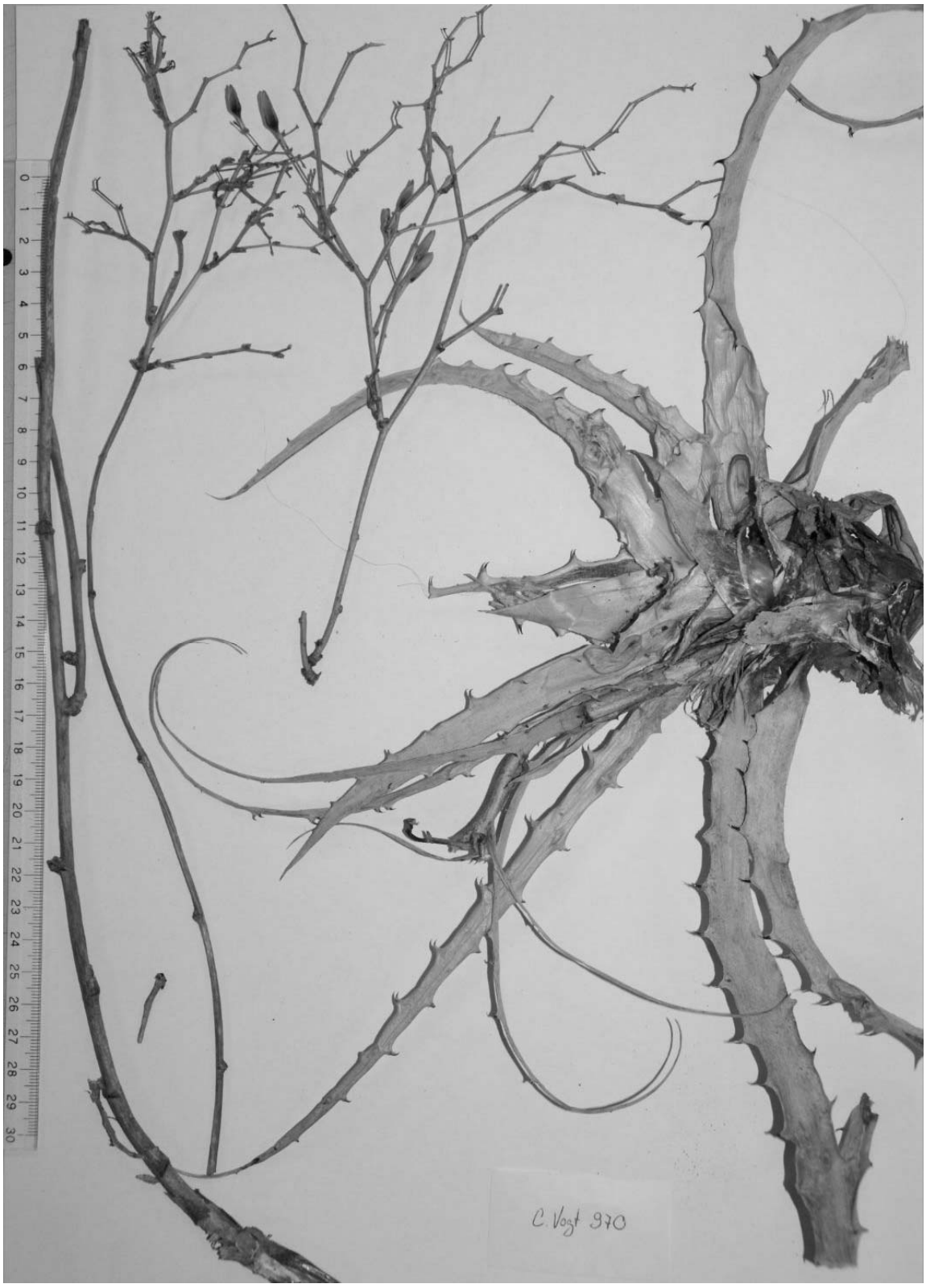



Hromadnik 5130 (5131): holotype of *D. lotteae* (Rauh) M.A. Spencer & L.B. Sm. [HEID].



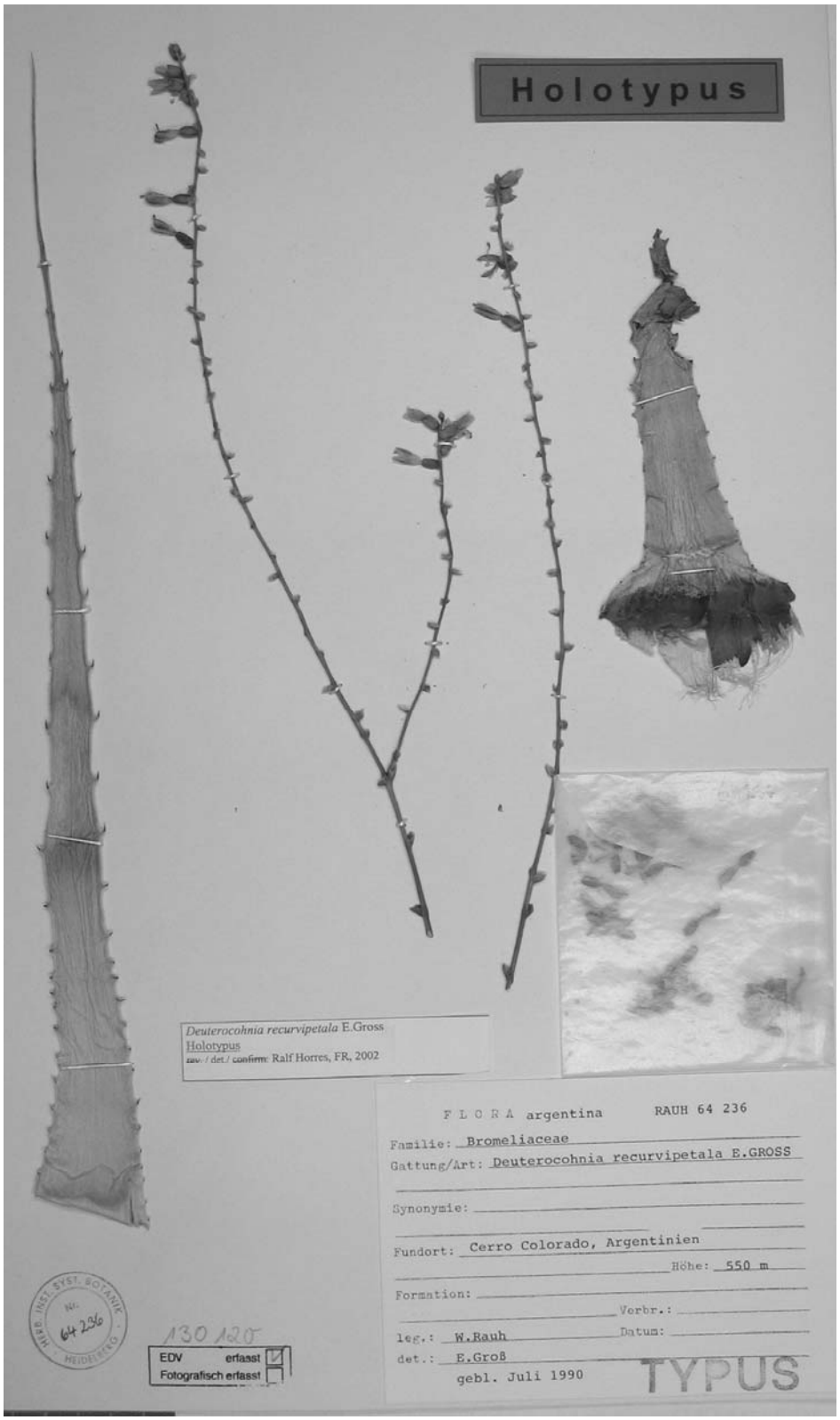

Kuntze s.n.: holotype of *D. meziana* Kuntze ex Mez, sheet 2 of 2, [NY]. Photo ex NY.


Rauh 40642: holotype of *D. meziana* ssp. *carmineo-viridiflora* (Rauh) N. Schütz, sheet 5 of 6, [HEID].



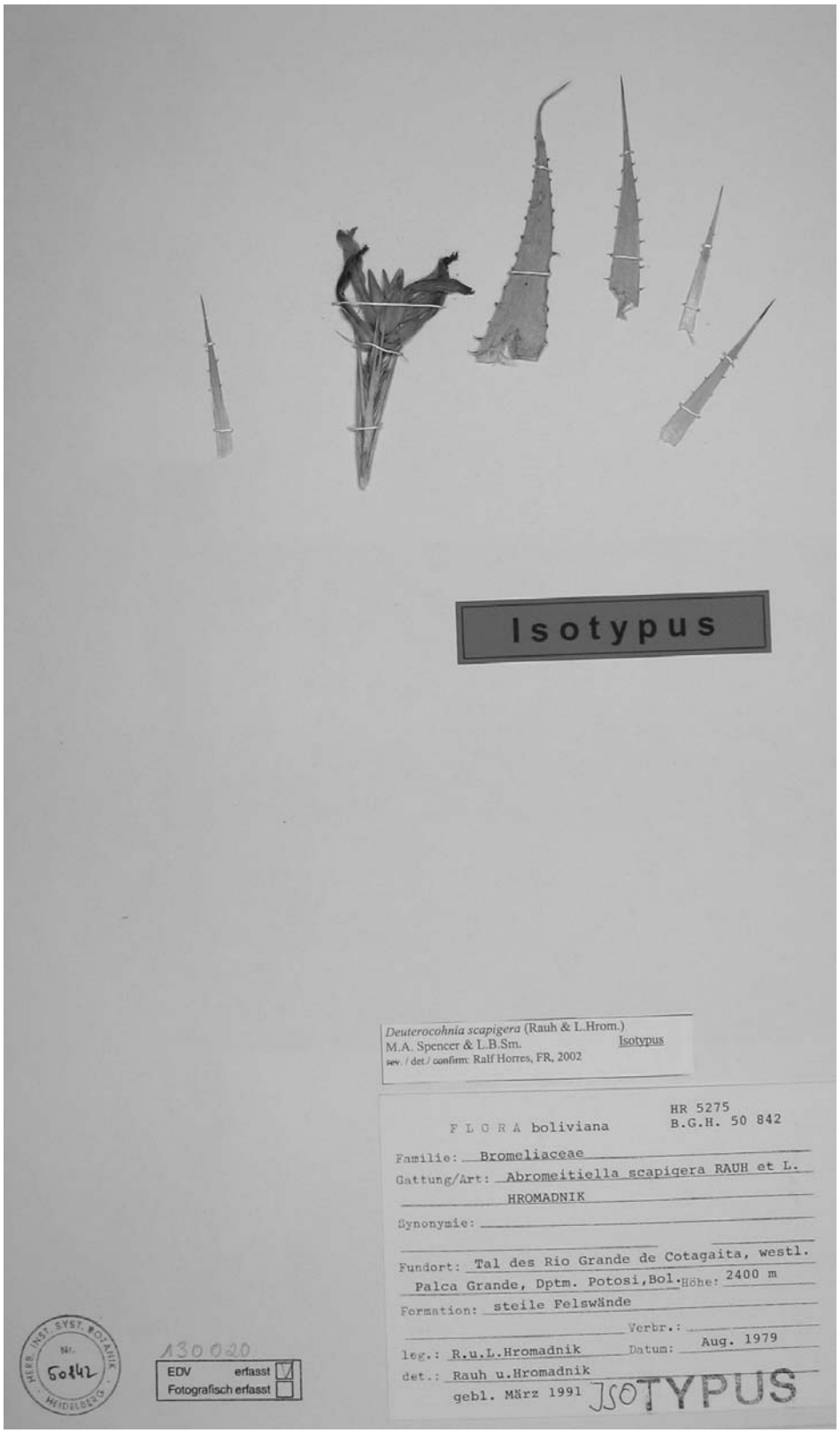

Vogt 970: holotype of *D. meziana* ssp. nov. [FCQ]. Photo from Christian Vogt.


Vargas 6285: holotype of *D. meziana* ssp. *pedicellata* (Till) N. Schütz, sheet 1 of 5, [WU]. Photo ex WU



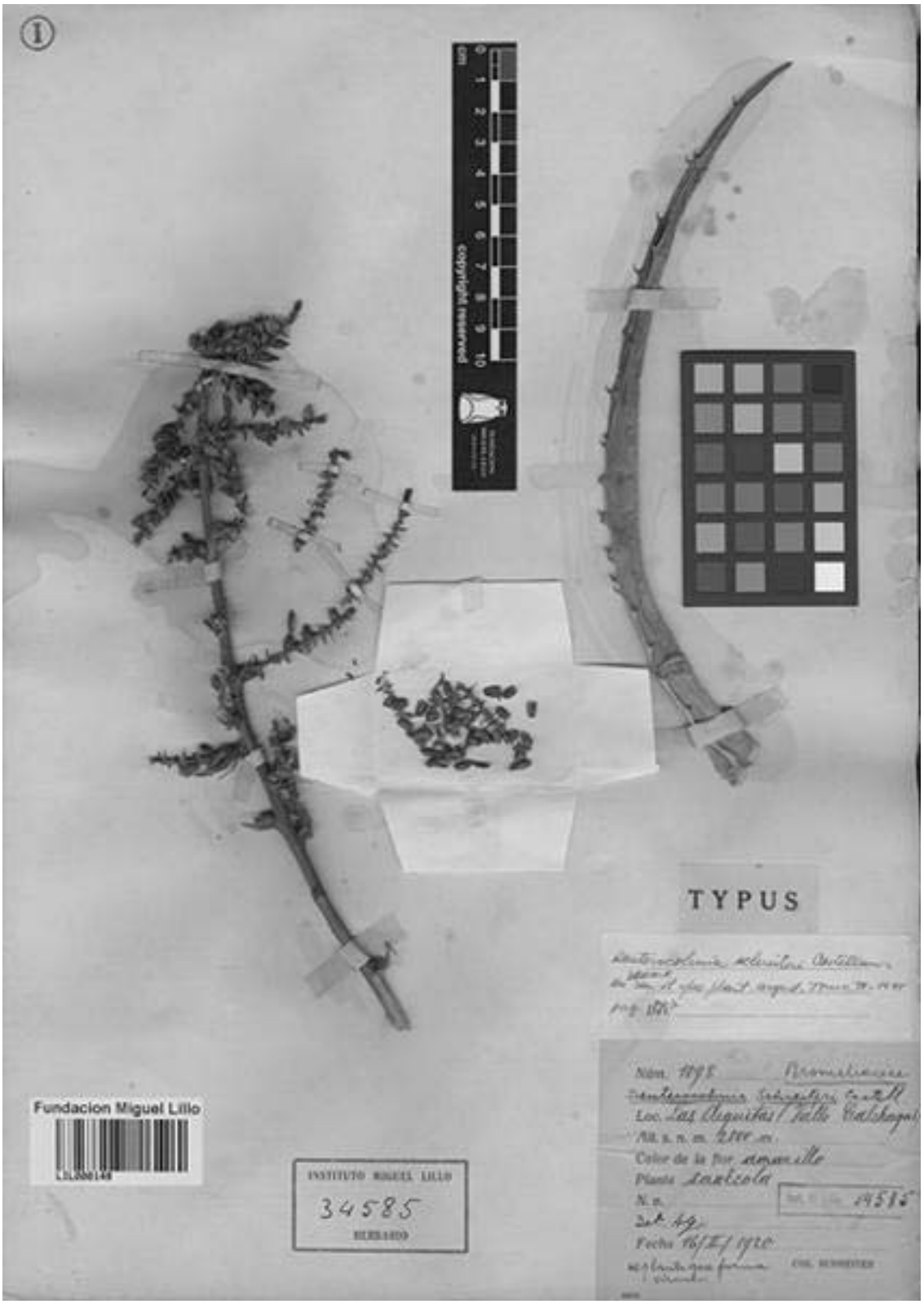

Rauh 64236: holotype of *D. recurvipetala* E. Gross [HEID].


Vargas 3185: paratype of *D. sanctae-crucis* (R. Vásquez & Ibisch) N. Schütz, [NY].

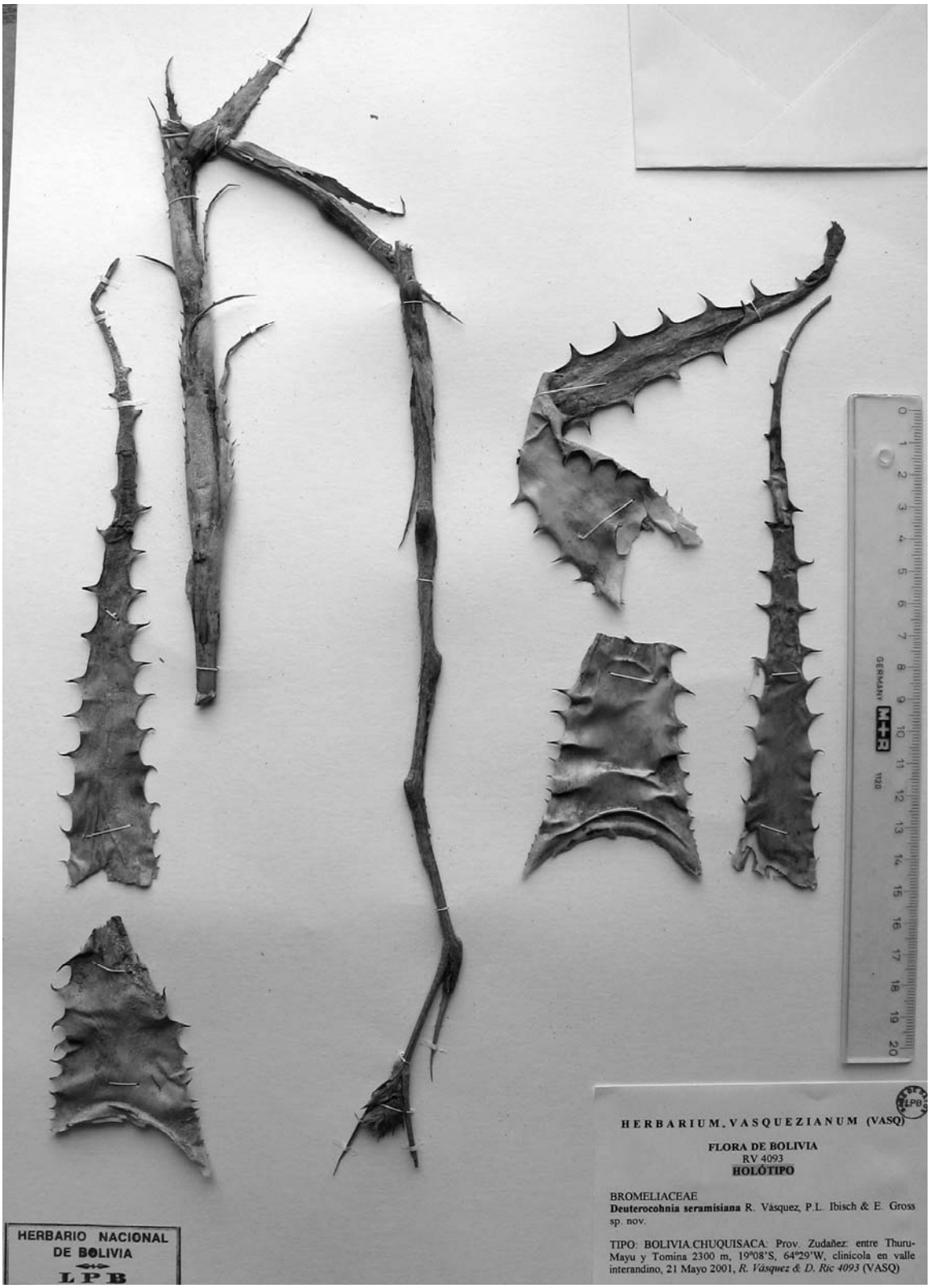



Hromadnik 5275: isotype of *D. scapigera* (Rauh & L. Hrom.) M.A. Spencer & L.B. Sm. [HEID].


Hromadnik 5076: isotype of *D. scapigera* var. nov. [WU].




Schreiter 1098: holotype of *D. schreiteri* A.Cast., sheet 1 of 3, [LIL]. Photo ex JSTOR, www.jstor.org.




Vásquez and Ric 4093: holotype of *D. seramisiana* R. Vásquez, Ibisch & E. Gross [LPB].


Fiebrig 2933: holotype of *D. strobilifera* Mez [B].


Cárdenas 4094: holotype of *D. strobilifera.* var. *inermis* L.B. Sm. [US]. Photo ex US.

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