Ann. Bot. Fennici 49: 239–247 ISSN 0003-3847 (print) ISSN 1797-2442 (online)
Helsinki 31 August 2012

Taxonomy of the *Lessingianthus saltensis* (Vernonieae, Asteraceae) species complex

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Received 27 Dec. 2011, final version received 14 Feb. 2012, accepted 16 Feb. 2012

Angulo, M. B. & Dematteis, M. 2012: Taxonomy of the *Lessingianthus saltensis* (Vernonieae, Asteraceae) species complex. — *Ann. Bot. Fennici* 49: 239–247.

In this study, three species of *Lessingianthus saltensis* complex are described and illustrated, including two new species. The new taxa *L. membranifolius* and *L. coriarius* are diploid (2n = 2x = 32), while *L. saltensis* is tetraploid (2n = 4x = 64). *Lessingianthus membranifolius* is distinguished from the other taxa in the complex by the membranaceus leaves, phyllaries with a rounded apex and leaf blades basally obtuse with serrate margins. *Lessingianthus coriarius* can be easily separated from the other taxa of the group by the combination of coriaceus leaves, phyllaries apically acute and leaf blades acute at the apex, with entire margins. A lectotype is designated for *L. saltensis*.

Introduction

The genus *Lessingianthus* (Vernonieae, Asteraceae) was initially established to accommodate the species originally placed in *Vernonia* sect. *Lepidaploa* subsection *Macrocephalae* (Bentham & Hooker 1873). It is widely distributed in South America, including Venezuela, Colombia, Peru, Brazil, Bolivia, Paraguay, Argentina and Uruguay (Robinson 2007). The species are perennial herbs or shrubs with xylopodia, having medium- or large-sized heads and seriate-cymose inflorescences (Robinson 1988). The genus currently comprises more than 120 species that mostly occur in *campo cerrado* and *campo rupestre* habitats (Bremer 1994).

This group can be distinguished from the other American members of the tribe by its pollen type, anther appendages and chromosome number, among other features. The pollen grains of *Lessingianthus* have been named type "B" and they are tricolporate, echinolophate, with a discontinuous tectum, very long germinal furrows that converge at the poles, lacunae disposed in a regular pattern, and lacking a polar lacuna (Keeley & Jones 1979, Angulo & Dematteis 2010). The anther appendages in *Lessingianthus* commonly lack glands, whereas some related genera have glandular appendages (Robinson 1988, Dematteis 2007). The basic chromosome number is x = 16, differing from the majority of the New World Vernonieae which have a base number of x = 17 (Dematteis 2002, Angulo & Dematteis 2012).

There are several closely related and morphologically similar species complexes within *Lessingianthus* that may hybridize naturally. Among these complexes are those formed around *L. glabratus*, *L. mollissimus*, *L. rubricaulis* and *L. saltensis* (Angulo & Dematteis 2009a). At present, only the *L. rubricaulis* complex has been studied (Dematteis 2004). This complex includes four

species, *L. rubricaulis*, *L. laniferus*, *L. pusillus* and *L. pseudoincanus*, that can be distinguished by their habit, underground parts, indumentum type, and leaf size and shape.

In the present study, we analyzed the *L. saltensis* complex, which is distributed in the northwestern Argentina and Bolivia and shows wide morphological and karyological variation. The analysis of external morphological features, pollen morphology, microcharacters and chromosomes revealed three species, two of them new. These species are described, including full synonymy and a key to distinguish the taxa.

Material and methods

This study was based on morphological analysis of specimens deposited at BAB, CORD, CTES, G, K, LP and SI (Holmgren *et al*. 1990). The line drawings were made from herbarium specimens using a camera lucida with a Leica MZ6 stereo microscope. The journal abbreviations are from *Botanico Periodicum Huntianum* (Lawrence *et al*. 1968).

Pollen samples were obtained by removing one or two florets from herbarium specimens of the species. The pollen grains were acetolysed according to the procedure suggested by Erdtman (1966). For light microscopy (LM) the pollen samples were mounted in glycerin jelly on glass slides and then examined with a Zeiss Axioplan microscope. Permanent slides were deposited at the Palynological Laboratory of the Universidad Nacional del Nordeste (PAL-CTES). The terminology applied for pollen grain description in general follows Erdtman (1966) and Punt *et al*. (2007).

Mitotic chromosome preparations were made from root meristems obtained from germinating seeds. The roots were pretreated for about five hours in 0.002 M 8-hydroxyquinoline solution at room temperature, fixed in 3:1 absolute alcohol/acetic acid and then stained using Feulgen's technique. Permanent microscope slides were prepared by mounting in Euparal. In all samples at least 20 counts of 7–10 individuals were made to verify the observations. Nomenclature used for the karyotype description is that suggested by Levan *et al*. (1964). The chromosome morphology was determined using the centromeric index (ci = [short arm] × 100/[total chromosomal length]). Accordingly, the chromosomes were classified into metacentrics (m): 50–37.5, submetacentrics (sm): 37.5–25 and subtelocentrics (st): 25–12.5. The karyological parameters, total length of karyotype (TLK), the mean chromosome length (ML), the average centromeric index (CI) and the ratio between the longest and the shortest chromosome pair (*R*) were evaluated. The karyotype asymmetry has been determined using the intrachromosomal (A_1) and interchromosomal index (A_2) suggested by Romero Zarco (1986).

To examine micro-characters, the florets were obtained from herbarium specimens and softened in boiling water to which a drop of detergent was added, dissected under a stereomicroscope, mounted in Hoyer's solution (Anderson 1954) and studied with a light microscope.

Results and discussion

Chromosome number and karyotype

Lessingianthus saltensis was found to be tetraploid with 2n = 4x = 64 (Fig. 1A), which agrees with prior counts from a population of Jujuy (Argentina) by Dematteis (1998). The chromosome numbers of *L. membranifolius* (Fig. 1E) and *L. coriarius* (Fig. 1G) were determined here for the first time. Both taxa were diploids having 2n = 2x = 32. The somatic chromosome number, karyotype formula, mean chromosome length, total length of karyotype, centromeric index and asymmetric index of the species in the *L. saltensis* complex are indicated in Table 1 (*see* also Fig. 2).

Pollen morphology

The species of the *L. saltensis* complex all have type "B" pollen grains (Fig. 1B and C). This type of pollen grain is tricolporate, echinolophate, with a discontinuous tectum, very long germinal furrows that converge at the poles, and lacunae distributed in a regular pattern but lacking a polar lacuna (Keeley & Jones 1979, Dematteis

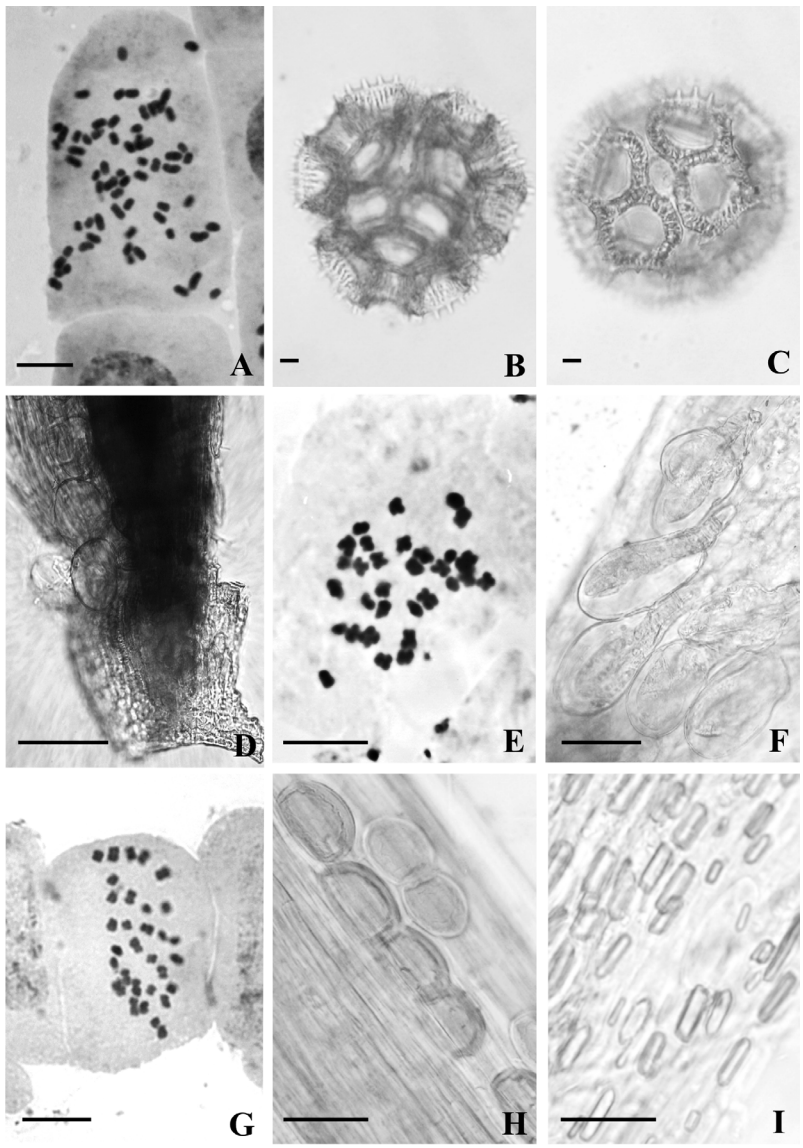

Fig. 1. Somatic chromosomes, microcharacters and pollen grains in the *Lessingianthus saltensis* complex. **A**–**D**: *L. saltensis* (*Dematteis et al. 2952*, CTES). — **A**: Metaphase plate, 2n = 64. — **B**: Pollen grain, polar view. — **C**: Pollen grain, equatorial view. — **D**: Glandular trichomes of cypsela. **E** and **F**: *L. membranifolius* (from the holotype). — **E**: 2n = 32. — **F**: Corolla lobe apex with glandular trichomes. **G**–**I**: *L. coriarius* (from the holotype). — **G**: Metaphase plate, 2n = 32. — **H**: Idioblasts. — **I**: Crystals of achene wall. Scale bars = 10 μm.

& Pire 2008, Angulo & Dematteis 2010). The type "B" pollen is characteristic of the genus (Robinson 1988, Dematteis & Pire 2008, Angulo & Dematteis 2010). For pollen characteristics *see* Table 2.

Morphological characters

Previously described *Lessingianthus* species are distinguished from the other American members of the tribe by their eglandular anther appendages, lack of a basal style node, and cubic crystals in the achene wall (Robinson 1999). The species of the *L. saltensis* complex lack of basal stylar node. The anther appendages are eglandular and the species have anthers basally calcarate and sagittate similar to those found in the congeneric taxa. Additionally, they have glandular trichomes on the corolla lobes (Fig. 1F). The surface of the cypselas have eglandular trichomes in *L. coriarius*, while *L. saltensis* has eglandular and glandular trichomes (Fig. 1D) and the cypselas of *L. membranifolius* are glabrous. The crystals are cubic and prismatic of varying size on the fruits walls (Fig. 1I). Numer-

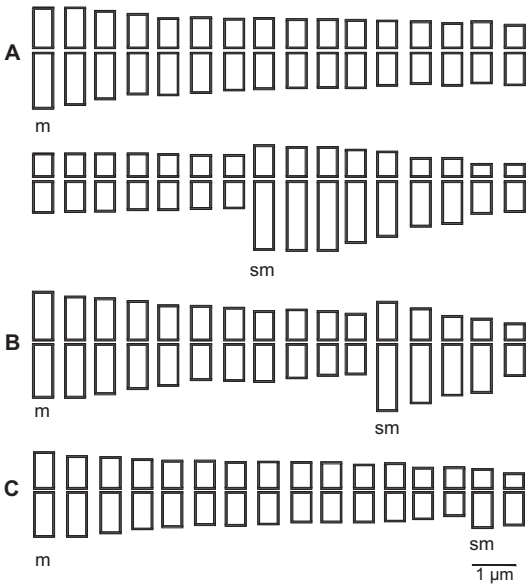

Fig. 2. Idiograms of species in the *Lessingianthus saltensis* complex. — **A**: *L. saltensis*, 2n = 64 = 46 m +18 sm. — **B**: *L. membranifolius*, 2n = 32 = 22 m + 10 sm. — **C**: *L. coriarius*, 2n = 32 = 28 m + 4 sm.

ous idioblasts were observed in the three species of the complex (Fig. 1H and Table 3).

Taxonomic treatment

The taxa are described and illustrated below and they can be distinguished by the following key.

Key to species of the *Lessingianthus saltensis* complex

1. Fruits with glandular trichomes; chromosome number 2n = 64 ..... *L. saltensis*
1. Fruits without glandular trichomes; chromosome number 2n = 32 2
2. Leaves membranaceus, base obtuse, margins serrate; phyllaries with rounded apex ..... *L. membranifolius*
2. Leaves coriaceus, base attenuate, margin entire; phyllaries with acute apex. ..... *L. coriarius*

Lessingianthus saltensis (Hieron.) H. Rob.

Proc. Biol. Soc. Wash. 101: 948. 1988.

Vernonia saltensis Hieron., Bot. Jahrb. Syst. 22: 691. 1897. — Type: Argentina. Salta im Gebüsch an den Flussufern bei San José, 10 Feb. 1873, *Lorentz & Hieronymus 227* (holotype B†). Lectotype (designated here): Argentina. Salta. San Jose, 10 Feb. 1873, *Lorentz & Hieronymus 227* (CORD 00005615!; isolectotypes CORD 00005614!, K 000485959!, photo F 14609).

Table 1. Chromosome number, karyotype formula, chromosome size, total chromosome length, centromeric index ± SE (CI); and intra- (A_1) and interchromosomal (A_2) indexes in the species of the *Lessingianthus saltensis* complex.

Species	2n	Karyotype formula	Chromosome size [mean (range)] (µm)	Total chromosome length (µm)	CI	A_1	A_2
L. saltensis	64	46 m + 18 sm	1.51 (1.32–2.15)	96.64 ± 0.20	42.40 ± 0.15	0.247	0.231
L. membranifolius	32	22 m + 10 sm	1.73 (1.08–2.15)	55.96 ± 0.04	39.82 ± 0.50	0.313	0.256
L. coriarius	32	28 m + 4 sm	1.74 (1.04–3.72)	54.58 ± 0.04	42.42 ± 0.30	0.260	0.345

Table 2. Polar axis (*P*), equatorial diameter (*E*), and their ratio (*P*/*E*), exine thickness, spine length, and lacunae diameter of pollen grains from species of the *L. saltensis* complex. Shown are minimum(mean)maximum values.

Species	*P* (µm)	*E* (µm)	*P*/*E*	Shape	Exine thickness (µm)	Spine length (µm)	Lacuna diameter (µm)
L. saltensis	42.1(43.5)44.8	40.8(43.2)44.8	1.01	prolate-spheroidal	5.4(6.1)6.8	2.0(2.7)3.4	8.1(9.6)10.8
L. membranifolius	46.2(48.2)51.6	44.8(47.6)50.3	1.01	prolate-spheroidal	5.4(6.1)6.8	2.0(2.7)3.5	9.5(10.3)10.8
L. coriarius	51.6(52.9)55.7	50.3(52.5)53.0	1.01	prolate-spheroidal	5.0(5.7)6.5	2.0(2.7)3.5	9.5(11.5)13.6

Erect branched shrubs, 0.5–1.5 m tall. Stems glabrous or pubescent, leafy to apex. Leaves membranaceus, shortly petiolate, gradually decreasing in size towards stem apex. Leaf blades lanceolate to ovate-lanceolate, 6–9 cm long, 2.5–4 cm wide, entire or serrulate, acute and mucronulate at apex, basally attenuate, shortly pubescent on both leaves surface, pinnately nerved. Inflorescence seriate-cymose with numerous capitula. Capitula sessile, solitary. Bracts of inflorescence leafy, regularly reduced upwards, always longer than heads. Involucre campanulate, 7–9 mm high, 5–7 mm wide. Phyllaries in 5–6 series, appressed, apically rounded and mucronulate, pilose and ciliate on margin, inner phyllaries oblong-lanceolate, 7–9 mm high, 1.6–1.9 mm wide, middle phyllaries lanceolate, 5–6 mm high, 2.5–3 mm wide and outer ones oblong-lanceolate to ovate, 3.5–4 mm high, 2–2.5 mm wide. Florets purple, 12–25 per head. Corolla with glandular trichomes in lobes apex, 7–8 mm long. Anthers basally calcarate, sagittate, thecae 4–4.5 mm long, apical appendages lanceolate to ovate-lanceolate, 0.8 mm long. Style 7.5–8 mm long, without basal style node. Cypselas turbinate, ribbed, 2.5–3 mm long, shortly pubescent with glandular trichomes on fruit base, idioblasts among ribs, achene wall with cubic and prismatic crystals, carpopodium cylindrical. Pappus white, biseriate, inner bristles 6–7 mm long, outer scales lanceolate, fimbriate, variable length. Pollen grains type "B". 2n = 64. Flowering and fruiting between December and August.

Distribution and ecology: Distributed from southern Bolivia, Paraguay and western Brazil to northwestern and central Argentina in deciduous forests, between 340–1300 m a.s.l.

The original material studied by Hieronymus (1897) was deposited at B, which was destroyed in World War II. Therefore, the specimen of CORD is designated here as the lectotype because it is in accordance with the protologue.

Additional specimens examined: **Argentina**. Catamarca: Dept. Ambato, *C. Saravia Toledo et al. 13180* (CTES); *C. Saravia Toledo et al. 12813* (CTES). — Córdoba: Dept. Sobremonte, *F. Kurtz 6725* (CORD, CTES). Dept. Tulumba, *A. T. Hunziker 12180* (CORD, CTES). — Jujuy: Dept. El Carmen, *O. Ahumada et al. 6572* (CTES). Dept. Ledesma, *M. Dematteis et al. 2952* (CTES); *M. Dematteis et al. 521* (CTES); *A. L. Cabrera 34702* (CTES); *M. Dematteis et al. 520* (CTES). Dept. San Pedro, *A. Krapovickas & A. Schinini 39295* (CTES). — La Rioja: Dept. Capital, *F. Biurrun & E. Pagliari 4630* (CTES). — Salta: Dept. Anta, *C. S. Toledo 1007* (CTES). Dept. Capital, *A. L. Cabrera 3021* (CTES, BAB); *J. H. Hunziker & J. C. Gamerro 12607* (CTES). Dept. Campo Santo, *A. Krapovickas & C. L. Cristobal 46617* (CTES). Dept. Gral, *S. Bruno 9881* (CTES); Dept. Guachipas, *R. Pozner & M. J. Belgrano 454* (CTES, SI); Dept. Orán, *S. A. Pierotii 7362* (CTES); Dept. San Martín, *A. Krapovickas & A. Schinini 30824* (CTES). — Santiago del Estero: Dept. Guasayán, *A. M. Molina et al. 1365* (CTES). — Tucumán: Dept. Trancas, *R. Renolfi 227* (CTES). **Bolivia**. Chuquisaca: Prov. Azero, *V. Solis Neffa et al. 1954*

Table 3. Morphological features of the species in the *Lessingianthus saltensis* complex.

	L. saltensis	*L. membranifolius*	*L. coriarius*
Leaf size (cm)	6–9 × 2.5–4	10–11 × 4.5–5	4–4.5 × 2.5–3
Leaf apex	acute and mucronulate	acute	acute
Leaf base	attenuate	obtuse	attenuate
Leaf margin	entire or slowly serrate	serrate	entire
Leaf texture	membranaceus	membranaceus	coriaceus
Phyllary apex	acute	rounded	acute
Glandular trichomes on corolla lobes	present	present	present
Basal stylar node	absent	absent	absent
Apical appendages of anthers	lanceolate to ovate-lanceolate	ovate-lanceolate	ovate-lanceolate
Anther bases	calcarate and sagittate	calcarate and sagittate	calcarate and sagittate
Achene indumentum	pilose	glabrous	pilose
Glandular trichomes of fruit	present	absent	absent
Carpopodium	cylindrical to turbinate	cylindrical to turbinate	cylindrical to turbinate
Crystals in the achene wall	cubic and prismatic	cubic and prismatic	cubic and prismatic
Idioblasts	present	present	present

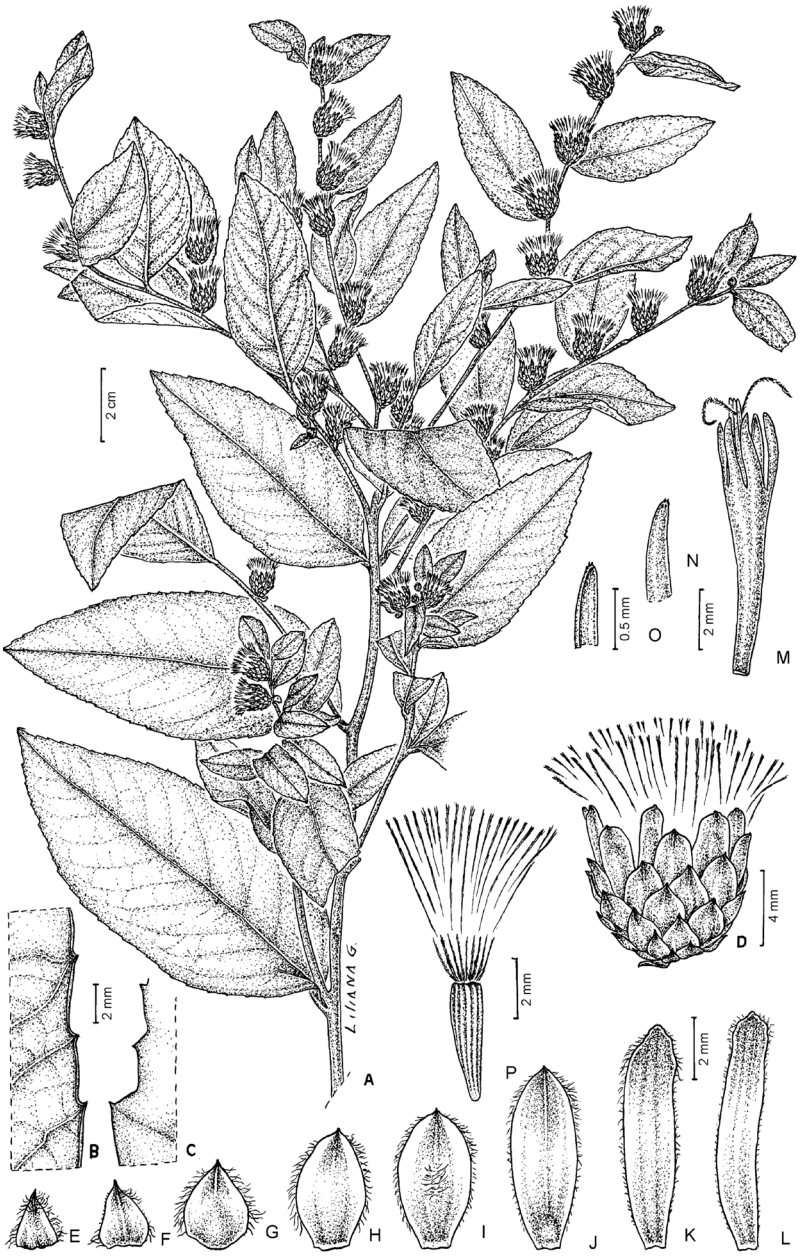

Fig. 3. *Lessingianthus membranifolius* (from the holotype). — **A**: Habit. — **B**: Abaxial surface of leaf margin. — **C**: Adaxial surface of leaf margin. — **D**: Involucre. — **E**–**G**: Outer phyllaries. — **H**–**J**: Middle phyllaries. — **K**–**L**: Inner phyllaries. — **M**: Corolla. — **N**: Apex of corolla lobe, dorsal view. — **O**: Apex of corolla lobe, ventral view. — **P**: Cypsela with pappus.

(CTES); *J. G. Seijo et al. 3150* (CTES). Prov. Calvo, *C. Saravia Toledo et al. 11452* (CTES). — Cochabamba: Prov. Campero, *M. Dematteis et al. 2413* (CTES). — Santa Cruz: Prov. Florida, *S. G. Beck 23603* (CTES); Prov. Chiquitos, *V. Solis Neffa et al. 1892* (CTES); *M. Dematteis et al. 2334* (CTES); *M. Dematteis et al. 2297* (CTES). Prov. Cordillera, *R. Chávez de Michel RM 2772* (CTES). — Tarija. Prov. Gran Chaco, *C. Saravia Toledo et al. 11360* (CTES). **Brazil**. Mato Grosso, *G. Hatschbach et al. 66770* (CTES); *G. Hatschbach et. al. 73005* (CTES). — Corumbá, *Forzza et al. 829* (CTES). **Paraguay**. Boquerón, *A. Krapovickas et al. 45327* (CTES). — Nueva Asunción, *A. Schinini & R. Palacios 25721* (CTES).

Lessingianthus membranifolius M.B. Angulo, *sp. nova* (Fig. 3)

Type: Bolivia. Dept. Santa Cruz. Prov. Caballero. 5 km E of Saipina, on the Road to Aiquile, 12 Apr. 2006 *M. Dematteis, G. E. Pieszco, M. S. Ferrucci & J. D. Urdampilleta 2383*

(holotype CTES 510529!, isotypes G!, SI!). — PARATYPE. Bolivia. Santa Cruz: Prov. Caballero, 47 km W de Venadillos, camino a Comarapa, 11 Apr. 2006 *M. Dematteis*, *M. S. Ferrucci*, *G. Pieszco & J. D. Urdampilleta 2362* (CTES).

ETYMOLOGY: The specific epithet refers to the membranaceus leaves.

Erect shrubs 70–100 cm high. Stems striate, leafy to apex. Leaves sessile to subsessile, membranaceus, 10–11 cm long × 4.5–5 cm wide. Leaf blades ovate-lanceolate, serrate, acute at apex, basally obtuse, upper and lower surface shortly pubescent, pinnately nerved. Inflorescence terminal, seriate-cymose. Bracts of inflorescence leafy, longer than involucres. Capitula numerous, sessile, solitary, disposed on axil of leafy bracts. Involucre campanulate, 9–10 mm high. × 7–9 mm wide. Phyllaries in 7–8 series, appressed, rounded and mucronulate at apex, pilose and ciliate on margin, inner phyllaries oblong-lanceolate, 7.5–8 mm long, 1.6–1.8 mm wide, middle phyllaries ovate-lanceolate, 4–5.5 mm long, 2.6–2.7 mm wide, outer phyllaries ovate-lanceolate, 3–4 mm long, 2.3–2.4 mm wide. Florets violet, 25–30 per head. Corolla 8–9 mm long, with glandular trichomes on lobes apex. Anthers basally calcarate, sagittate, 4.5–5 mm long, apical appendage non glandular, ovate-lanceolate, 0.6–0.7 mm long. Style 10–11 mm long, basal stylar node absent. Cypselas obconical, ribbed, glabrous, 4–4.5 mm long, with numerous idioblasts and cubic and prismatic crystals of varying size on fruit wall, carpopodium cylindrical. Pappus biseriate, white, outer scales fimbriate, linear, variable length, inner bristles 6-8 mm long. Pollen grains type "B". 2n = 32.

Almost all the available flowering specimens were collected between February and April.

DISTRIBUTION AND HABITAT: This species is known only from the department Santa Cruz in Bolivia (province Caballero). It grows on the hill slopes and stony soil.

Lessingianthus coriarius M.B. Angulo, *sp. nova* (Fig. 4)

TYPE: Bolivia. Santa Cruz: Prov. Cordillera, 3 km N de Abra de Quiñe, 9 Apr. 2009 *M. Dematteis, J. P. Coulleri, E. Meza Torres & A. Vega 3660* (holotype CTES 0017988!, isotypes K!, LPB!). — PARATYPES: Bolivia. Chuquisaca: Zudañez. Tarabuco ca. 30 km hacia Zudañez, 7 Mar. 1981 *S. G. Beck 6252* (CTES, LPB). Santa Cruz: Cordillera. Estancia Rancho Chico (Puesto Nuevo) y alrededores, 22 May 1998, *A. Fuentes 2372* (CTES, LPB).

ETYMOLOGY: The specific epithet refers to the leathery leaves.

Erect shrubs 0.5–1 m high, branched toward inflorescence, with deciduous leaves on stem. Leaves coriaceus, subsessile, 4–4.5 cm long, 2.5–3 cm wide. Leaf blades ovate-lanceolate, entire, revolute at margin, apically acute, attenuate at base, shortly pubescent on both surfaces. Inflorescence cymose. Capitula numerous, sessile, solitary, disposed on axil of leafy bracts. Bracts of inflorescence leafy, gradually reduced upwards, longer than heads. Involucre campanulate, 9–11 mm high, 7–8 mm wide. Phyllaries in 6–8 series, appressed, acute and mucronulate at apex, pilose and ciliate on margin, inner phyllaries oblong-lanceolate, 7.5–8 mm long, 1.9–2 mm wide, middle phyllaries ovate-lanceolate, 6–6.5 mm long., 2.6–2.7 mm wide, outer ones ovate-lanceolate, 3.5–4 mm long, 2–2.3 mm wide. Florets violet, 15–30 per head. Corollas 7–8 mm long, with glandular trichomes on lobes tips. Anthers basally calcarate, sagittate, thecae 2–2.5 long, apical appendages ovate-lanceolate, 0.4 mm long. Style 8–8.5 mm long, basal nodule of style absent. Cypselas cylindrical to turbinate, ribbed, pubescent, 3–3.5 mm long, with idioblasts between ribs and cubic and prismatic crystals on their wall, carpopodium cylindrical to turbinate. Pappus white, biseriate, outer scales lanceolate, fimbriate, 0.9 mm long, inner bristles, 6–7 mm long. Pollen grains type "B". 2n = 32. Flowering and fruiting between February and May.

DISTRIBUTION AND HABITAT: This taxon grows in Bolivia, on stony soils in the Departments of Santa Cruz and Chuquisaca.

Acknowledgements

We would like specially to thank the keepers and staff of the visited herbaria for their collaboration. Mirta Liliana Gómez of the Instituto de Botánica del Nordeste prepared the drawings. This work was supported by grants from the Consejo Nacional de Investigaciones Científicas y Tecnológicas (CONICET), the Secretaría General de Ciencia y Técnica de

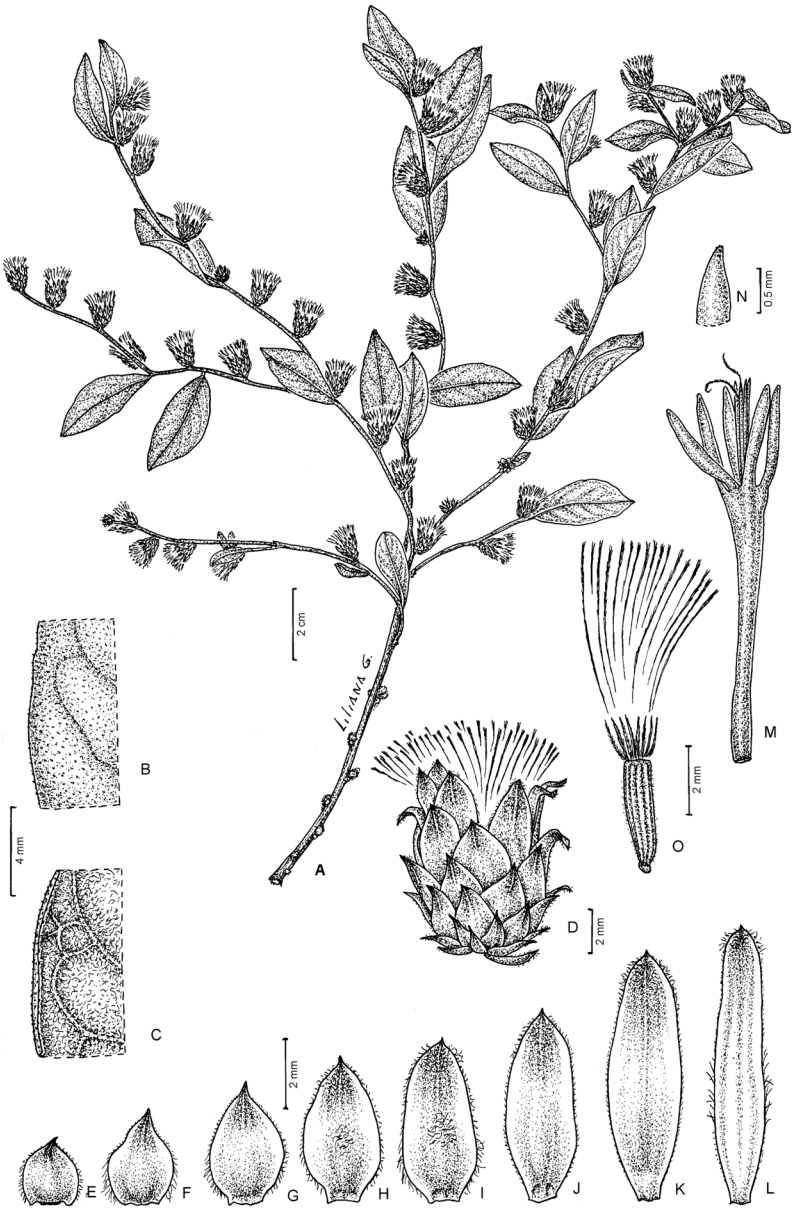

Fig. 4. *Lessingianthus coriarius* (from the holotype). — **A**: Habit. — **B**: Adaxial surface of leaf margin.— **C**: Abaxial surface of leaf margin. — **D**: Involucre. — **E**–**G**: Outer phyllaries. — **H**–**J**: Middle phyllaries. — **K** and **L**: Inner phyllaries. — **M**: Corolla showing anthers and style. — **N**: Dorsal view of lobes apex of corolla. — **O**: Cypsela with pappus.

la Universidad Nacional del Nordeste (SGCyT-UNNE) and the Myndel Botanica Foundation.

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