THREE NEW SPECIES AND TWO NEW RECORDS OF GREIGIA REGEL (BROMELIACEAE) FROM BOLIVIA

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ABSTRACT. We describe three new endemic species of *Greigia* Regel (Bromeliaceae) from Bolivia: *Greigia acebeyi* B. Will, T. Krömer, M. Kessler, D. Karger and H. Luther, *Greigia marioae* B. Will, T. Krömer, M. Kessler, D. Karger and H. Luther, *Greigia membranacea* B. Will, T. Krömer, M. Kessler, D. Karger and H. Luther. *Greigia danielii* L.B.Smith and *G. stenolepis* L.B.Smith vel aff. are reported for the first time for Bolivia. A key to the eight Bolivian species of *Greigia* is provided.

Key words: Bolivia, Bromeliaceae, Greigia, new species

Introduction

The genus Greigia Regel comprises large, mostly terrestrial bromeliads occurring in disturbed vegetation along roadsides and trails as well as in the understory of upper montane forests from Mexico to the tropical Andes as well as in temperate rain forests of central and southern Chile (Will and Zizka 1999, Krömer 2000, Krömer et al. 2006). Greigia was first reported for Bolivia by Luther (1998a, 1998b) who described the three new species G. atrocastanea, G. cochabambae, and G. kessleri based on a limited number of herbarium collections. Subsequent collections, especially by T. Krömer and A. Acebey, have expanded the number of specimens available from Bolivia. These have been studied by B. Will in the scope of a revision of the genus. As a result of this work we here describe three further new species from Bolivia and list two species as first records for the country (Krömer et al. 1999). The number of Greigia species now known from Bolivia (eight) is striking considering that a decade ago this genus was unknown from this country. This reflects the reluctance of many botanists to collect these large and unspectacular plants as well as the lack of detailed studies on the genus until recently (e.g., Will and Zizka 1999). It is especially noteworthy that although some species are more widespread, all eight species have been recorded within an area of about 15 × 20 km in the Yungas of La Paz department. Such a high local species density is previously unreported in Greigia. We anticipate that additional species await discovery in Bolivia and elsewhere in the tropical Andes.

MATERIALS AND METHODS

Morphological studies of *Greigia* from Bolivia (19 herbarium collections, 29 specimens) and

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from Chile, Colombia, Costa Rica, Ecuador, Guatemala, Honduras, Mexico, Panama, Peru, and Venezuela (354 collections, 433 specimens) were undertaken by B. Will. In the descriptions, the following types of bracts were recognized: scape bracts (± spread out along the scape); outer primary bracts (outermost of the primary bracts); primary bracts (bracts directly encircling the flowers at the base of the flower head), and floral bracts (subtending individual flowers). The full length of the leaf sheath was measured from bottom up to the turning point from convex to concave.

KEY TO THE SPECIES OF *GREIGIA* IN BOLIVIA 1a. Leaf blades sparsely lepidote abaxially with very

	sma	all, brown scales 0.11–0.17 mm 2
	2a.	All primary bracts entire or some bracts entire
		and some with few 0.1-0.5 mm long teeth
		3a. Sepals 23–27 mm long; primary bracts
		completely dark brown, 51–55 mm long;
		leaf sheaths stramineus to light brown
		C attacastance
		G. atrocastanea
		3b. Sepals 13–17 mm long; primary bracts
		partially light brown or light castaneous
		with paler apex, 22-38 mm long; leaf
		sheaths distinctly castaneous proximally,
		paler distally G. danielii
	2b.	All primary bracts serrate or spinose at apex
		or up to upper half with 0.3-2.4 mm long
		spines 4
		spines
		cm long; primary bracts largely stramin-
		eus, castaneous towards base, 36–39 mm
		long; sepals 12–16 mm long
		G. marioae
		4b. Leaf sheaths stramineus, 10 cm long; pri-
		mary bracts largely dark castaneous, api-
		ces stramineus or light brown, 63 mm
		long; floral bracts 27 mm long; sepals 19–
11		20 mm long G. acebeyi
16.	Lea	of blades ± densely lepidote abaxially with 0.3–
	0.9	mm long \pm white to yellow scales 5
	Sa.	Primary bracts wholly stramineus
		G. cochabambae
	5b.	Primary bracts largely castaneous 6
		6a. Petals 17-23 mm long; sepals 15-20 mm
		long; primary bracts densely spinose in
		upper two thirds G. kessleri
		6b. Petals 36-48 mm long; sepals 23-24 mm
		long; primary bracts entire or spinulose
		only distally
		7a. Petals 41–48 mm long; leaf sheaths
		reddish brown; primary bracts 65-80
		mm long, with membraneous margins
		only at bases; most primary bracts
		entire, some finely spinulose apically,
		the spines 0.2–0.4 mm long
		C standaria val off
		G. stenolepis vel aff.
		7b. Petals 36 mm long; leaf sheaths
		mostly stramineus or light brown;
		primary bracts 80-90 mm long, with

NEW SPECIES

Greigia acebeyi B. Will, T. Krömer, M. Kessler, D. Karger and H. Luther, sp. nov. Type: Bolivia—Dept. La Paz: Prov. Nor Yungas, Carretera La Paz—Caranavi, near Unduavi 14 km down towards Yolosa, 2800 m, 24 Nov 1998, *T. Krömer and A. Acebey 181* (Holotype: GOET; Isotypes: LPB, SEL).

FIGURE 1.

Greigia squamis minutissimis (0.16 mm longis), brunneis, sparsis in pagina abaxiali laminarum praestans; vaginae foliorum usque 10 cm longae, stramineae; bracteae primariae usque 63 mm longae, atrocastaneae, apice pallide brunneae vel stramineae, seratis vel spinosis, spinis 0.7–1.6 mm longis; bracteae florales 27 mm longae; sepala 19–20 mm longa.

Plants terrestrial, caulescent, stems ca. 1m long, covered by leaves. Leaf sheaths 10×4.0 cm, ± distinct, ovate; spinose in upper third with triangular, castaneous, 1.6-1.8 mm long spines; straw-colored (concolorous with the blades) aband adaxially, sparsely lepidote ab- and adaxially with dark brown, small, appressed scales; thin coriaceous, distinctly finely nerved abaxially, finely adaxially, without membraneous margins. Leaf blades 95 × 2.5 cm, linear-attenuate, ensiform, slightly narrowed toward base, tip of the apex attenuate, dark brown, with very short mucro, margin revolute; laxly spinose toward base with narrowly triangular, 0.5-1.8 mm long spines, centrally entire, serrulate toward apex with antrorse, 0.6-0.8 mm long spines; stramineus; sparsely lepidote with very small (0.16 mm), individual, ± appressed, brown punctuate-lepidote abaxially, very sparsely lepidote with similar scales adaxially; thick papery, hardened and slightly vaulted toward base, finely nerved ab- and adaxially. Scapes visible (elongated, not hidden by bracts), flattened. Scape bracts not known. Inflorescences lateral, ca. 13 flowered, 6.5 (excluding petals) \times 7 cm, compound (with two-flowered branches). Outer primary bracts 6.3×2.6 cm, exceeding the sepals when in fruit; base slightly spoon-shaped, ovate-acuminate, with distinct 25 mm long apex, extending into a firm, dark tip plus a fine mucro; serrate at apex with 0.7-1.6 mm long, slightly antrorsely curved, castaneous spines; apex light brown to stramineus, rest dark castaneous and lustrous abaxially, apex stramineous, the rest light golden brown and lustrous adaxially; lepi-

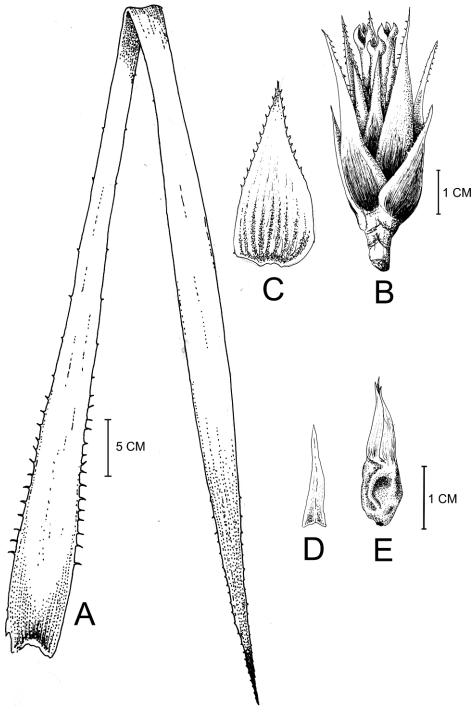


FIGURE 1. *Greigia acebeyi*: **A.** Leaf blade. **B.** Inflorescence. **C.** Primary bract. **D.** Floral bract. **E.** Fruit (drawing of T. Krömer & A. Acebey 181 by Dirk N. Karger).

dote with brown, appressed scales, densely and paler toward apex, glabrous at base abaxially, lepidote with brown fringed scales adaxially; thin crustaceous, (without membraneous margin), ecarinate, distinctly nerved toward apex abaxially, not nerved adaxially. *Floral bracts* 27 × 10 mm, exceeded by the sepals when in fruit, lanceolate, acute, with apical, retrorsely curved mucro; entire; light castaneous with paler margin, slightly lustrous abaxially, light golden brown and lustrous adaxially; sparsely lepidote with brown, appressed, fringed scales abaxially; papery, distinctly wide carinate (when in fruit), with 1.3 mm wide membraneous margin in lower two thirds, few fine nerves abaxially. Flowers purple. Sepals $19-20 \times 7$ mm, free, asymmetrical, entire; light golden brown, slightly lustrous ab- and adaxially (when in fruit base castaneous); sparsely brown, appressed lepidote becoming glabrous toward base abaxially, lepidote with similar scales adaxially; thin crustacious (without membraneous margin), distinctly carinate, inconspicuously to finely nerved ab- and adaxially. Petals, Anthers not known. Epigynous tube none. Ovaries, Styles, Stigmata not known. Fruits 18×9 mm (excluding persistent sepals), clavate-trigonous, dark castaneous. **Seeds** $2.0-2.2 \times 1.1-1.2$, \pm almond-shaped, distinctly reddish.

Comments. This species and G. marioae are both characterized by very small (0.11–0.17 mm long), brown, sparse scales abaxially on the leaf surfaces and by all primary bracts being serrate or spinose apically with 0.3–2.4 mm long spines. They differ from each other by the coloration and length of the leaf sheaths (stramineus, 10 cm long in G. acebeyi vs. reddish-brown, 2.5-3.5 cm long in G. marioae), the coloration and length of the primary bracts (largely dark castaneous, apically straw-colored or light brown, 63 mm long vs. largely stramineus, only castaneous towards base, 36-39 mm long), and the length of the sepals (19–20 mm vs. 12–16 mm). Greigia acebeyi is known only from the type collection made at 2800 m on a steep road bank through humid cloud forest.

We name this species after Bolivian botanist and specialist on the aroids of Bolivia Amparo Acebey who, together with T. Krömer, has collected the holotype material of all three species described here.

Greigia marioae B. Will, T. Krömer, M. Kessler, D. Karger and H. Luther, sp. nov. TYPE: Bolivia—Dept. La Paz: Prov. Nor Yungas, Parque Nacional Cotapata, camino principal desde la Estación Biológica Tunquini hacia la mina, 16°11′S, 67°52′W, 2500 m, 21 May

2000, *T. Krömer and A. Acebey 1164* (Holotype: GOET; Isotypes: LPB, SEL).

FIGURES 2, 4, 5.

Greigia squamis minutissimis (0.11–0.17 mm longis) brunneis in pagina abaxiali laminarum vaginisque foliorum fusco-brunneis praestans; bracteae stramineae, basin castaneae, 36–39 mm longae, apicibus serratis vel spinosis, spinis bractearum primariarum 0.3–2.4 mm longis; sepala 12–16 mm longa.

Plants terrestrial, caulescent; stems 11 mm thick, *Leaf sheaths* $2.5-3.5 \times 2.4-3.7$ cm, distinct, widely ovate, clasping the stem, distinctly spoon-shaped; entire or spinose toward apex with flat, triangular, castaneous, 0.6-1.5 mm long spines; reddish-castaneous, stramineus at apex abaxially, centrally light castaneous, the base and apex stramineus adaxially; sparsely lepidote ab- and adaxially with small, individual, light brown, appressed scales; thin coriaceous, finely nerved ab- and adaxially. Leaf blades 45- $75 \times 1.3-1.7$ cm, linear attenuate, only slightly narrowed toward base (± ensiform), tip of the apex attenuate into a thin, ± subulate-flattened, light brown tip (no mucro), margin revolute; spinose toward base with flat, narrow, triangular, castaneous, 0.6-3.4 mm long spines, elsewhere serrate with slightly antrorsely curved, dark tipped 0.4-1.4 mm long spines, becoming denser toward apex; stramineus to light brown aband adaxially; sparsely lepidote with very small (0.11-0.15 mm), light brown, appressed scales ab- and adaxially; papery, slightly hardened toward base, inconspicuously nerved ab- and adaxially. Scapes 1.3-2.6 cm long, visible (elongated, not hidden by bracts), flattened; castaneous, lustrous. Scape bracts $1.1-1.5 \times 0.6-1.0$ cm, widely triangular-ovate, cucullate, without distinction between base and blade, without a mucro, entire; castaneous ± lower ½, rest straw or light castaneous, dull or slightly lustrous aband adaxially; sparsely lepidote with light brown, appressed scales toward base abaxially, thin crustaceous, without membranous margin, wide carinate, few distinct nerves abaxially, finely nerved adaxially. *Inflorescences* lateral, at least 2 per plant, ca. 11 to 15 flowered, 3.5-3.9 \times 3–5 cm, compound (two-flowered branches). Outer primary bracts $3.6-3.9 \times 1.6-1.7$ cm, equalling the petals at anthesis, narrowly ovateacuminate, some with distinct, 20 mm long apex, some without distinction of base and blade, extended into a thin tip (no mucro); upper third to half spinose with 0.3-2.4 mm long, triangular or irregularly curved, dark castaneous spines; castaneous toward base, rest straw abaxially, light castaneous toward base, rest straw adaxially, dull or slightly lustrous ab- and adaxially; very sparsely lepidote in ca. upper half

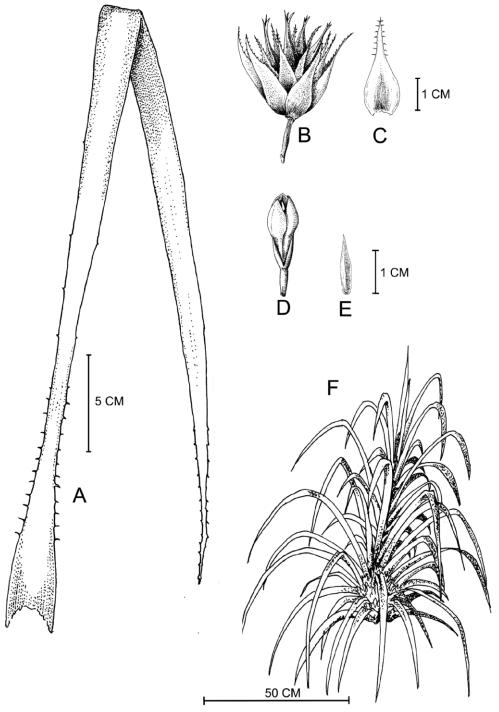


FIGURE 2. *Greigia marioae*: **A.** Leaf blade. **B.** Inflorescence. **C.** Primary bract. **D.** Flower. **E.** Floral bract. **F.** Habit (drawing of T. Krömer & A. Acebey 1164 by Dirk N. Karger).

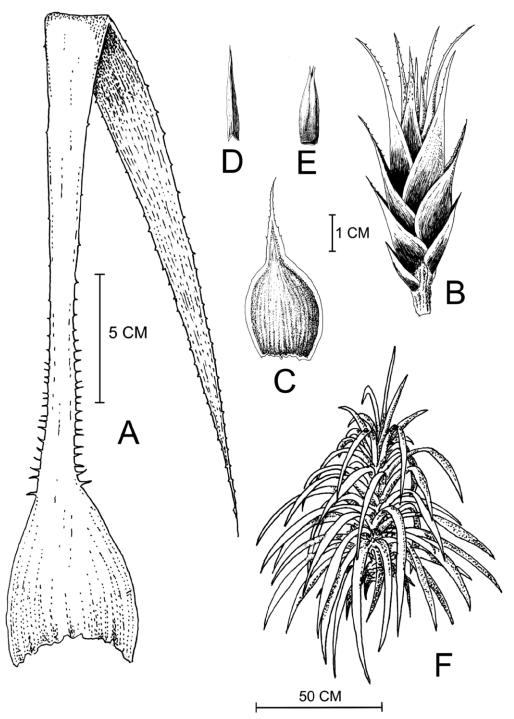


FIGURE 3. *Greigia membranacea*: **A.** Leaf blade. **B.** Inflorescence. **C.** Primary bract. **D.** Floral bract. **E.** Fruit. **F.** Habit (drawing of T. Krömer & A. Acebey 132 by Dirk N. Karger).



FIGURES 4–7. FIGURE 4. Habit of *Greigia marioae*. FIGURE 5. Rosette with inflorescences of *Greigia marioae*. FIGURE 6. Rosette with inflorescences of *Greigia membranacea*. FIGURE 7. Habit of *Greigia membranacea* (all photos by T. Krömer).

with small, yellow, appressed scales abaxially, lepidote with small, light brown, short fringed, appressed scales adaxially; thin crustacious, some with 0.4-0.8 mm wide membraneous margin toward base, ecarinate (outermost two finely carinate), very finely nerved abaxially, inconspicuously nerved adaxially. Floral bracts 15- $29 \times 5-10$ mm, lanceolate-long acuminate, slightly ensiform, sometimes asymmetric, some with fine, castaneous apical mucro, entire or with few 0.1-0.16 mm long spines; toward base and keel castaneous abaxially, rest straw and slightly lustrous ab- and adaxially; sparsely lepidote with light brown, appressed scales abaxially; papery, distinctly narrow carinate lower third, with 0.4-0.8 mm wide membraneous margin, inconspicuously nerved abaxially, not adaxially. **Flowers** sessile. **Sepals** $12-16 \times 4-6$ mm, free, triangular-ovate, mucro like floral bracts, entire; at base castaneous, rest straw, dull abaxially, similar but paler adaxially; very sparsely lepidote with small, yellow, short fringed scales ab- and adaxially; mostly papery, base thin crustacious (without membraneous margin), carinate toward base only, finely nerved ab- and adaxially. *Petals* 19 mm long, lobes $11 \times 5-7$ mm. Filaments 56 \times 1.1 mm. Anthers 2.8–3.4 \times 0.6-1.0 mm, dorsifixed. *Epigynous tubes* none. Ovaries $6-10 \times 4$ mm, distinctly clavate, stramineus, trigonous. *Fruits* $14-16 \times 6-7$ mm (excluding persistent sepals), ellipsoidal-trigonous; dark castaneous, slightly lustrous. Seeds 1.6–1.9 \times 0.8–1.2 mm, \pm almond-shaped, distinctly reddish-brown.

Paratype. Bolivia—Dept. La Paz, Prov. Nor Yungas, Parque Nacional Cotapata, camino principal hacia la mina, 16°11′S, 67°53′W, 2700 m, 21 Nov 2000, *T. Krömer and A. Acebey 1749* (LPB, GOET, SEL).

Comments. This species is closest to G. acebeyi. Their differentiation is discussed under the latter species. The paratype of G. marioae differs from the type collection in some important features: leaf sheath entire vs. spinose toward apices, primary bracts lacking membraneous margin and lacking distinction of blade and apex vs. membraneous margin toward base and distinct 20 mm long apex, floral bracts 20-29 × 6–10 mm vs. 15×5 mm. However, the remaining similarities especially the small leaf blade scales served as a basis for the decision to group these specimens together with G. marioae. This preliminary decision will have to be re-evaluated as a larger number of specimens might become available in the future.

Greigia marioae is known from two collections made at 2500–2700 m in humid montane forest above Tunquini Biological Station in Co-

tapata National Park, about 15 km across a valley from the type locality of *G. acebeyi*.

We take pleasure in naming this species after Dr. Mario Baudoin, past director of the Ecology Institute of the Universidad de San Andrés in La Paz and of the Dirección Nacional Conservación de Biodiversidad (DNCB), who was instrumental in the creation of Cotapata National Park and the Tunquini Biological Station.

Greigia membranacea B. Will, T. Krömer, M. Kessler, D. Karger and H. Luther, sp. nov. Type: Bolivia—Dept. La Paz, Prov. Nor Yungas, Carretera La Paz-Caranavi, near Unduavi 3 km down towards Yolosa, 16°18′S, 67°53′W, 3100 m, 20 Oct 1998, *T. Krömer and A. Acebey 132* (Holotype GOET; Isotypes LPB, SEL).

FIGURES 3, 6, 7.

A Greigia stenolepe L.B.Smith petalis brevioribus (36 mm vs. 41–48 mm longis), bracteis primariis longioribus (80–90 mm vs. 65–80 mm longis) cum marginibus membranaceis amplioribus spinisque 0.2–1.6 mm (vs. 0.2–0.4 mm) longis, vaginis stramineis vel pallide brunneis (vs. fusco-brunneis) differt.

Plants terrestrial, caulescent, stems ca. 1m long, covered by leaves. *Leaf sheaths* 11–14 × 4.8-6.5 cm, distinct, ± ovate; entire except sometimes with few triangular, dark tipped, 0.6-1.5 mm long spines toward apex; light brown, toward apex stramineus abaxially, mostly stramineus adaxially; densely lepidote with brown, short fringed appressed scales ab- and adaxially; thin coriaceous, distinctly nerved ab- and adaxially, (no membraneous margin). Leaf blades $54-113 \times 2.2-3.3$ cm, linear-attenuate, distinctly ensiform, distinctly narrowed toward base; tip of the apex attenuate with castaneous, very short mucro; margin flat or revolute; spinose toward base with triangular, dark-tipped, 0.9-2.9 mm long spines, the rest laxly serrulate, becoming denser toward apex with antrorse, brown-tipped, 0.5–1.0 mm long spines; greenish-stramineus or brown, mostly with paler median stripe; lepidote to densely lepidote with whitish, 0.5-0.78 mm long, ± overlapping scales with thick cellwalls abaxially, glabrous adaxially; thick papery, slightly hardened toward base; finely nerved aband adaxially. Scapes 2.5-4 mm long, visible (elongated, not hidden by bracts), flattened. Scape bracts $3.2-3.8 \times 1.4-1.9$ cm, triangular or ovate, acute, slightly cucullate; without a mucro, entire; castaneous and slightly lustrous, margin and apex paler abaxially, light golden brown and slightly lustrous adaxially; sparsely lepidote to lepidote with yellow, appressed scales abaxially, sparsely lepidote toward apex only adaxially; thin crustacious, some with 1.5-2 mm wide membranous margin in lower third, distinctly widely carinate, finely nerved ab- and adaxially. Inflorescences lateral, at least 2 per plant, 13-flowered, $8.5-10 \times 5-6$ cm, compound (6 branches with two flowers plus one terminal flower). *Primary bracts* $8.2-9.0 \times$ 2.6–3.8 cm, (much) exceeding the sepals at anthesis; outermost primary bracts ovate-attenuate, the inner ovate-acuminate with slightly spoonshaped base and distinct 33-45 mm long apex, extending into a firm, castaneous tip (some with a fine mucro); spinulose at apex with 0.28-1.6 mm long, ± triangular, straight, castaneous spines; apex stramineus (to light brown), the rest dark castaneous abaxially, similar but lighter adaxially; conspicuously, densely lepidote with yellow, appressed scales, at apex, becoming fewer proximally abaxially, similar but with fringed scales adaxially; thin coriaceous, toward base with 1.6-2.1 mm wide membraneous margin, ecarinate, finely nerved toward apex abaxially, not nerved adaxially. Floral bracts 35-41 \times 10-13 mm, exceeded by the sepals at anthesis, lanceolate, acute-acuminate; with castaneous mucro; entire or with few minute 0.1–0.2 mm spines at apex; apex darker than base ab- and adaxially (color varies); sparsely lepidote with yellow, appressed scales toward apex abaxially; papery to thin crustacious, distinctly narrow carinate, some with 1.4-2.0 mm wide membraneous margin in lower ½, finely nerved abaxially. *Flowers* $55-58 \times 7-9$ mm, sessile, purple. **Sepals** $23-24 \times 4-6$ mm, free, lanceolate, acute, entire; mostly straw, toward apex light brown ab- and adaxially; lepidote with light brown, appressed scales abaxially, with fringed scales adaxially; papery to thin crustacious, some with 0.9 mm membraneous margin toward base, slightly narrow carinate, inconspicuously nerved ab- and adaxially. Petals 36-40 mm long, lobes $16 \times 6-7$ mm, ovate-acute, pink sparsely appressed lepidote abaxially, with fringed scales adaxially; tube 20-24 mm long, distinctly broadening upwards. Filaments 0.7-0.8 mm wide. Anthers $5.5 \times 1.3-1.6$ mm, exceeded by the petals at anthesis, dorsifixed; apex acute, base obtuse. *Epigynous tubes* none. *Ovary* 15 \times 3–5 mm, tubular, light brown. Styles 32×0.3 mm. Stigmata $3.2-3.6 \times 0.3-0.6$ mm, the three stigmatic branches separately spiral. Fruits and Seeds not known.

Paratypes. Bolivia—Dept. La Paz, Prov. Nor Yungas, 1.1 km camino Chuspipata-Yolosa, 16°17'S, 67°48'W, 2750 m, 26 Sep 1999, *T. Krömer and A. Acebey 885* (LPB, GOET, SEL); Dept. La Paz, Prov. Nor Yungas, Trocha al Valle de Coscapa, Parque Nacional Cotapata, 3250 m, 11 Sep 1997, *M. Kessler, J. Gonzales, K. Bach and A. Portugal 11840* (LPB, GOET, SEL).

Comments. This new species, named for its conspicuous membranaceous primary bract margins, differs from *G. stenolepis* by its shorter petals (36 mm vs. 41–48 mm long), longer primary bracts (80–90 mm vs. 65–80 mm long) with more extensive membranaceous margins and 0.2–1.6 mm long spines on all primary bracts (vs. primary bracts entire to finely spinulose apically with spines 0.2–0.4 mm long), and straw-colored to light brown (vs. reddish brown) leaf sheaths. *Greigia membranacea* has been collected at 2750–3250 m in humid cloud forest and on steep roadsides near the type locality.

NEW RECORDS FOR BOLIVIA

Greigia danielii L.B.Smith

A single, sterile collection from Bolivia (Dept. La Paz, Prov. Nor Yungas, 10 km de Chuspipata a Coroico, 16°24'S, 67°47'W, 2500 m, 20 Sep 1997, M. Kessler 12135, LPB, GOET, SEL) is assigned to this species, otherwise only known from Colombia (Smith and Downs 1979), because of the similarity of leaf and scale characters. However, the Bolivian collection differs from Colombian specimens by its shorter leaf sheaths (2.8 cm vs. 4.9-8.5 cm long), and somewhat sparser and darker sheath and leaf surface scales, and fertile material is needed to corroborate the identification. Typically, G. danielii is characterized by sparsely lepidote leaves with very small scales, 22-38 mm long, mostly entire (some with few minute spines) primary bracts with pale apices, 13–17 mm long sepals, and leaf sheaths castaneous in lower half.

Greigia stenolepis L.B.Smith vel aff.

This species, previously only reported from Colombia (Smith and Downs 1979) but now also known from Ecuador, is taxonomically one of the most difficult in the genus, showing considerable variation. The current state of research portrays it as a species group possibly comprising several taxa. In Bolivia, this species is known from a single, fertile collection (Bolivia-Dept. La Paz, Prov. Nor Yungas, cerca de Cotapata, 16°17'S, 67°53'W, 3450 m, 09 Oct 1997, S.G. Beck 24400, LPB, GOET) characterized by densely lepidote leaf blades with thickened scales; reddish brown leaf sheaths; largely castaneous, 65–80 mm long, apically entire to finely spinulose primary bracts with distinct membraneous margins; and 41–48 mm long petals. These characters do not necessarily occur in other populations of G. stenolepis in the same combination.

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