

NOVELTIES IN BOLIVIAN *FOSTERELLA* (BROMELIACEAE)

PIERRE L. IBISCH*

Fundación Amigos de la Naturaleza (FAN-Bolivia), Casilla 2241, Santa Cruz, Bolivia, and
Institute of Botany, University of Bonn, Germany.
E-mail: pibisch@fan-bo.org

ROBERTO VÁSQUEZ

Fundación Amigos de la Naturaleza (FAN-Bolivia), Sociedad Boliviana de Botánica,
Casilla 2241, Santa Cruz, Bolivia.

ELVIRA GROSS

Institute of Botany, University of Bonn, Meckenheimer Allee 170, D-53115 Bonn, Germany.

THORSTEN KRÖMER

Albrecht-von-Haller-Institute for Plant Sciences, Dpt. Systematic Botany, University of Göttingen,
Untere Karspüle 2, D-37073 Göttingen, Germany.

MARTINA REX

Plants Systematics and Morphology, University of Kassel, Heinrich-Plett-Str. 40,
D-34132 Kassel, Germany.

ABSTRACT: Four new *Fosterella* species from Bolivia are described and illustrated: *F. fuentesii*, *F. nowickii*, *F. rexiae* (Andes), and *F. yuvinkae* (eastern lowlands, Chiquitano mountains). *Fosterella petiolata*, *F. weberbaueri* (re-established), and *F. windischii* are recorded as new species for Bolivia. *Fosterella graminea* and *F. heterophylla* are recorded for the first time since the type collection. Additional information on morphological variation and distribution of other species is provided. The number of described Bolivian *Fosterella* species rises to 27. Thus, *Fosterella* now ranks third in Bolivia (after *Tillandsia* and *Puya*) in total number of species and percentage of endemic species of Bromeliaceae within Bolivia.

Key words: Bromeliaceae, *Fosterella*, taxonomy, biogeography, Bolivia

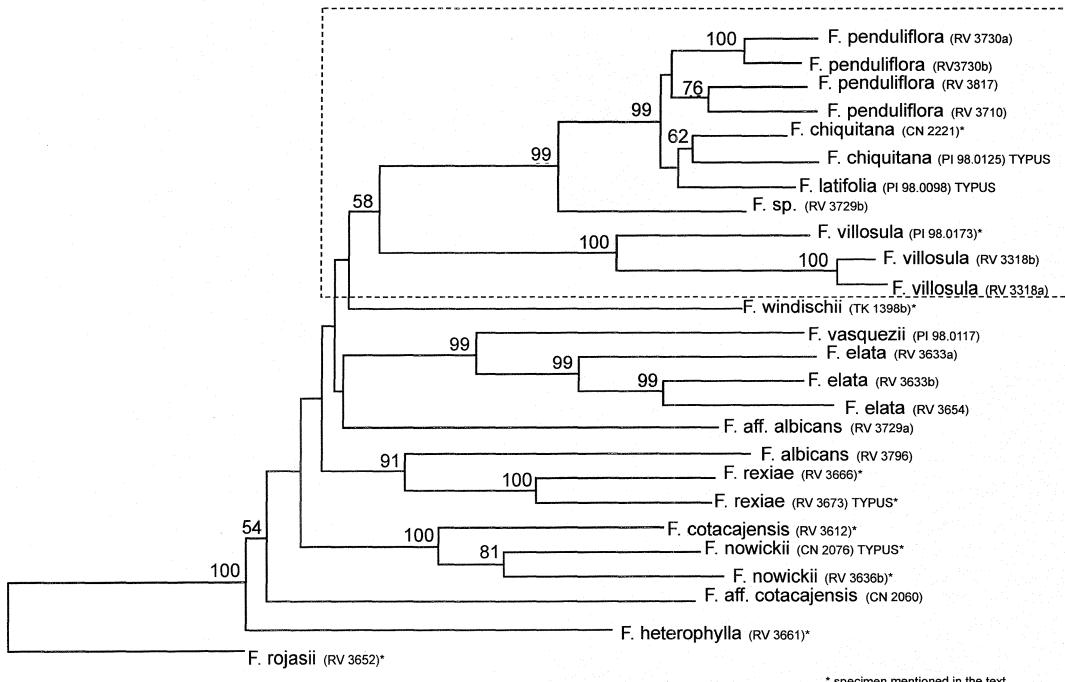
INTRODUCTION

Based on the many descriptions of new species or new records, *Fosterella* clearly belongs to the most speciose bromeliad genera with diversity centers in Bolivia (after *Tillandsia* and *Puya*; Ibisch et al. 2001). In the framework of an enhanced inventory of Bolivian bromeliads and especially of *Fosterella*, several taxa previously unknown to the country or to science have appeared in recent years. Additionally, *Fosterella* has been chosen as a model group for applying modern molecular methods to detect interspecific relationships and support traditional taxonomic research. Preliminary information based on the random amplified polymorphic DNA (RAPD) technique is facilitating the taxonomic assessment of the genus (Rex 2001, Rex et al. 2001). Molecular characters are especially useful, as *Fosterella* is an otherwise rather character-poor group. By joining taxonomic, ecolog-

ical, biogeographic, and molecular study efforts, we seek conclusions regarding the mechanisms of speciation and diversity generation within this genus. We also seek a conservation application by interpreting the beta-diversity patterns relevant to identifying distinctive biodiversity areas.

The most recent species were described in 1999 (Kessler et al. 1999, Ibisch et al. 1999). A recent checklist (Krömer et al. 1999) listed 20 species with 15 of those endemic to Bolivia. Here we present new data on the known species, the re-establishment of a species, three new records for Bolivia and the description of four new species. Considering these findings, we now know 27 *Fosterella* species from Bolivia. Most of all known species of the genus have been recorded in Bolivia (except *F. micrantha* from Central America, *F. hatschbachii* from Brazil, and *F. aletroides* from Peru, a new species to be described from Amazonian Brazil). Bolivia, as a whole, is the diversity center of the genus, with the northeastern Andean slopes being especially diverse. Types, for other than the new species

* Corresponding author.



* specimen mentioned in the text

FIGURE 1. Phenogram of a neighbor-joining analysis of 26 *Fosterella* specimens from Bolivia based on a distance matrix (Dice index) derived from 197 random amplified polymorphic DNA (RAPD) and 117 microsatellite-primed polymerase chain reaction (MP-PCR) characters (modified after Rex 2001, Rex et al. 2001). The tree was arbitrarily rooted with *F. rojasii*, which proved to be most distant to all other specimens. Accession numbers are given in parentheses. Bootstrap values above the branches are based on 200 replicates. Nodes without assigned values have a bootstrap support < 50. The dotted box encircles the group of species that do not present strongly recoiled petals.

when seen for this study, are marked with an asterisk.

NOTES AND NEW SPECIES

Fosterella chaparensis Ibisch, Vásquez & Gross, Rev. Soc. Boliviana Bot. 2(2): 118. 1999. TYPE: Bolivia. R. Vasquez & M.I. Vásquez 2792 (Holotype: LPB!; Isotypes: FR!, USZ!).

This recently described species from the very humid Cochabamba rain forests, at an altitude of 600–1550 m (Ibisch et al. 1999), now has been recorded in the adjacent department of La Paz, at an altitude of 1400–1550 m. Although the plants are much more robust and larger than the type plants, they should belong to the same species.

Specimens examined: BOLIVIA. Dpto. La Paz: Prov. Nor Yungas, valley of the Huarinillas river towards Chairo, 16°12'S, 67°52'W, 1400 m, 17 Sep. 1995, S.G. Beck 22617 (LPB); ibid.: Cotapata National Park, 16°12'S, 67°51'W, 1550 m, 24 Aug. 1999, T. Krömer & A. Acebey 730

(GOET, LPB); Cotapata National Park, trails around Estación Biológica de Tunquini, 16°11'S, 67°52'W, 1550 m, 13 Sep. 2000, T. Krömer & A. Acebey 1230 (GOET, LPB).

Fosterella chiquitana Ibisch, Vásquez & Gross, Rev. Soc. Boliviana Bot. 2(2): 118. 1999. TYPE: Bolivia. P. Ibisch 98.0125 (Holotype: LPB!; Isotype: USZ!).

Preliminary molecular data suggest that *Fosterella chiquitana* is related to *F. penduliflora* and *F. latifolia*, together forming a well-supported group in a neighbor joining analysis (Rex 2001, Rex et al. 2001, see FIGURE 1). A plant collected nearby the type locality by C. Nowicki differed morphologically (e.g., shorter floral bracts, plants less lepidote), but preliminary molecular data suggest that this plant is close to the type of *F. chiquitana*.

Specimen examined: BOLIVIA. Dpto. Santa Cruz: between San Javier and Concepción, on granitic rocks, 22 Apr. 2000, C. Nowicki 2221 (LPB).

The small, white, and not conspicuously fra-

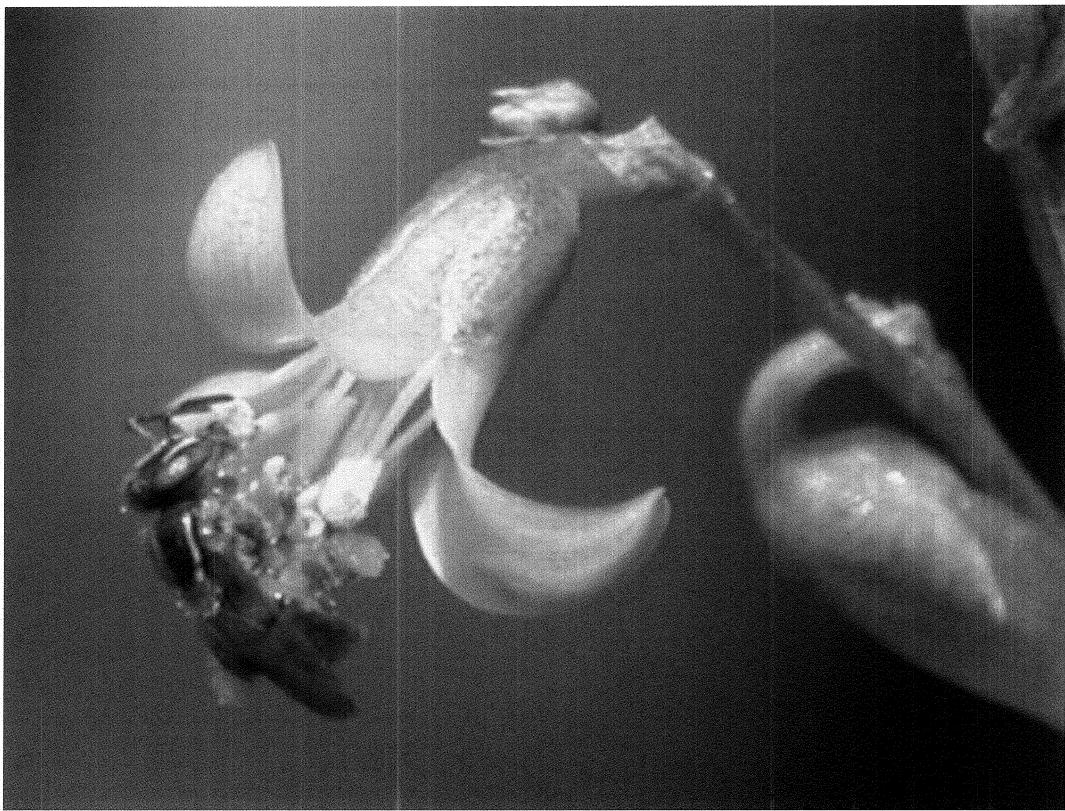


FIGURE 2. *Fosterella chiquitana*. Visitation by a small bee (photo of C. Nowicki 222, LPB, by P.L. Ibisch, Santa Cruz de la Sierra).

grant *Fosterella* flowers have made it difficult to determine the pollinators. Small flies have been observed on flowers (Ibisch et al. 1999), and fly pollination may still be possible with some species. More recently, however, we observed regular and frequent visitation by an unidentified species of a small bee (FIGURE 2) on a cultivated specimen of the above-cited collection, at Santa Cruz de la Sierra (not far from the wild populations). This may be the first documentation of bee-visitation in *Fosterella*. Krömer (1997) concluded from *F. micrantha* nectar analysis that because of the high relative hexose importance, small bees could be pollinators.

Fosterella cotacajensis Kessler, Ibisch & Gross, Rev. Soc. Boliviana Bot. 2(2): 111. 1999.
TYPE: Bolivia. Kessler et al. 9620 (Holotype: LPB!; Isotype: SEL).

This species, published some years ago (Kessler et al. 1999), was observed again in the Cotacajes valley. New localities extend the range of the species to lower elevations (1300 m) than originally observed (1650–2300 m).

Specimens examined: BOLIVIA. Dpto. Co-

chabamba: Prov. Ayopaya, between Pujiuni and Cotacajes, 16°44'S, 66°44'W, 1370 m, 20 Jun. 2001, R. Vásquez, G. Navarro, M. Fernández, F. Miranda & H. Rocha 4127 (VASQ); between Cotacajes and Atispaya, 16°40'S, 66°44'W, 1300 m, 21 Jun. 2001, R. Vásquez, G. Navarro, M. Fernández, F. Miranda & H. Rocha 4145 (VASQ); Dpto. La Paz: Prov. Inquisivi, 11 km from Inquisivi toward Circuata, 2170 m, 16°53'S, 67°08'W, 11 Feb. 2000, R. Vásquez, G. Gerlach, & L.R. Moreno 3612 (VASQ).

Fosterella floridensis Ibisch, Vásquez & Gross, Rev. Soc. Boliviana Bot. 2(2): 120. 1999.
TYPE: Bolivia. Ibisch & Ibisch 97.83 (Holotype: LPB!; Isotypes: FR!, USZ!).

There has been some confusion in the literature regarding the specimen *M. Kessler et al. 10189* (GOET, LPB, SEL) from Dpto. La Paz: Prov. Bautista Saavedra, Pauyi-Yuyo, between Apolo and Charazani. Ibisch et al. (1999) erroneously assigned the specimen to *Fosterella floridensis* instead of *F. latifolia*. The error was clarified in the attached 'Errata' of the Revista de la Sociedad Boliviana de Botánica, however

we now conclude that *F. latifolia* identification was wrong as a result of a specimen mix-up. Instead Kessler et al. 10189 is a collection of *F. petiolata* (see below). Both *F. floridensis* and *F. latifolia* are still known exclusively from restricted ranges in the semihumid Santa Cruz Andes.

Fosterella fuentesii Ibisch, Vásquez & Gross, sp. nov. TYPE: Bolivia. Dpto. Santa Cruz: Prov. Florida, Municipio de Pampagrande, Manzanillares, east of Valle Hermoso, 17°53'59.1"S, 64°10'13.6"W, 1820 m, 10 Aug. 2001, A. Fuentes, A. Araúz & I. Riberia 3176 (Holotype: LPB; Isotypes: FR, SEL). FIGURE 3.

Similis est *Fosterella petiolata* (Mez) L.B. Smith sed foliis prope basin serratis bracteis florum sepalisque lepidotis et sepalis petalique longioribus differt.

Plant stemless, flowering up to >1 m high. **Leaves** erect, to about 55 cm long, petiolate. **Sheaths** triangular, to 1.5–2 cm high, to 25 mm wide, brownish when dry, glabrescent, entire. **Petioles** up to 25 cm long, to about 4 mm wide, serrate with few spines above the sheath. **Blades** broadly ovate-lanceolate, long-cuneate, to 30 mm wide, to >25 cm long, entire, abaxially villous-lepidote, adaxially glabrous. **Scape** erect, to 85 cm long, 2–3 mm wide, villous-lepidote to glabrescent. **Scape bracts** erect, narrowly triangular-lanceolate, acuminate, entire, the upper ones to 5–6 cm long, all longer than the internodes, villous-lepidote abaxially. **Inflorescence** laxly tripinnate, erect, ca. 20 cm long, <10 cm wide, villous-lepidote. **Primary bracts** large, acuminate, generally longer than the sterile base of the branches to enveloping the short lower branches, lower ones to >5 cm long, upper ones to <2 cm long, ca. 7–10 mm wide. **Branches** (sub-)erect, usually shorter than 10 cm. **Floral bracts** ca. 4–6 mm long, always longer than the pedicels, to 4 mm wide, broadly ovate, apiculate, villous-lepidote, somewhat dry papyraceous when dry. **Flowers** laxly arranged, secund or spreading (sometimes too crowded to determine), subsessile. **Sepals** 3–4 mm long, 1.5 mm wide, oblong, obtuse, lepidote. **Petals** greenish yellow (observation of the collector), ca. 7–8 mm long, ca. 1.5 mm wide, obtuse, strongly recurved during and after anthesis (observed by authors but not easily visible in specimen, due to insect-caused destruction of petals in herbarium). **Stamens** ca. 8 mm long. **Anthers** 2–3 mm long. **Ovary** ca. 4 mm long, longer than style, ca. 1.5 mm wide.

This new species is clearly similar to *Fosterella petiolata* (see below) but differs by having serrate petioles and villous-lepidote floral bracts and sepals, as well as longer sepals and petals.

This terrestrial herb has been found on shaded rocks in an inter-Andean dry valley with a subhumid to dry forest with *Parapiptadenia excelsa*, *Schinopsis haenkeana*, and Myrtaceae (observation of the collectors). Thus its locality is ecologically distinct from the sites of *F. petiolata* from the humid Yungas forests of the north-eastern Andean slopes in northern Bolivia and Peru.

Fosterella graminea (L.B. Smith) L.B. Smith, Phytologia 7: 171. 1960. Basionym: *Lindmania graminea* L.B. Sm., Lilloa 14: 93. 1948. TYPE: Bolivia. Buchtien 417 (Holotype: US).

This species was known from the type locality only (San Carlos, region of Mapiri, 700 m, Buchtien 417; see Smith & Downs 1974). Now it has been re-collected by Robert Müller et al., who undertook an expedition to an inaccessible area not far from the type locality: BOLIVIA. Dpto. La Paz: Prov. Larecaja, between Chima and Llipi, 15°35"S, 68°09'W, 850 m, 9 Jan. 2001, R. Müller, I. Schürkes & J.C. Montero 7 (LPB), ibid: R. Müller, I. Schürkes & J.C. Montero 22 (USZ), ibid: below Chusi, 15°37"S, 68°15'W, 1200 m, 14 Jan. 2001, R. Müller, I. Schürkes & J.C. Montero 216 (SEL). The specimens perfectly coincide with the original description presenting the narrowly linear, grass-like leaves serrate above the sheath, and tripinnate inflorescences with nutant flowers with a pedicel much longer than the floral bracts. The species does not appear to be rare in the area characterized by rather humid montane forest.

Fosterella heterophylla Rauh, Trop. Subtrop. Pflanzenwelt 60: 24. 1987. TYPE: Bolivia. W. Rauh 40583A (Holotype: HEID!).

This caulescent and branched species was known from the type only, and the type locality was not well specified (Yungas, La Paz, 1000 m; Rauh 1987; colored photographs of the type in Ibisch & Vásquez 2000). Now we have found a plant in the La Paz Yungas that should represent this species, although it is less petiolate than described by Rauh. Thus a specific locality is known: Prov. Caranavi, 34 km from Caranavi to Yucumo, 15°41'S, 67°29'W, 1600 m, 14 Feb. 2000, R. Vásquez & G. Gerlach 3661 (LPB). FIGURE 4.

Fosterella latifolia Ibisch, Vásquez & Gross, Vasquez & Gross, Rev. Soc. Bol. Bot. 2(2): 123. 1999. TYPE: Bolivia. P. Ibisch 98.0098 (Holotype: LPB!; Isotypes: FR!, USZ!).

Comparing living plants of several species, we have observed that *Fosterella latifolia*, as a sterile plant, is quite similar to *F. villosula*. The

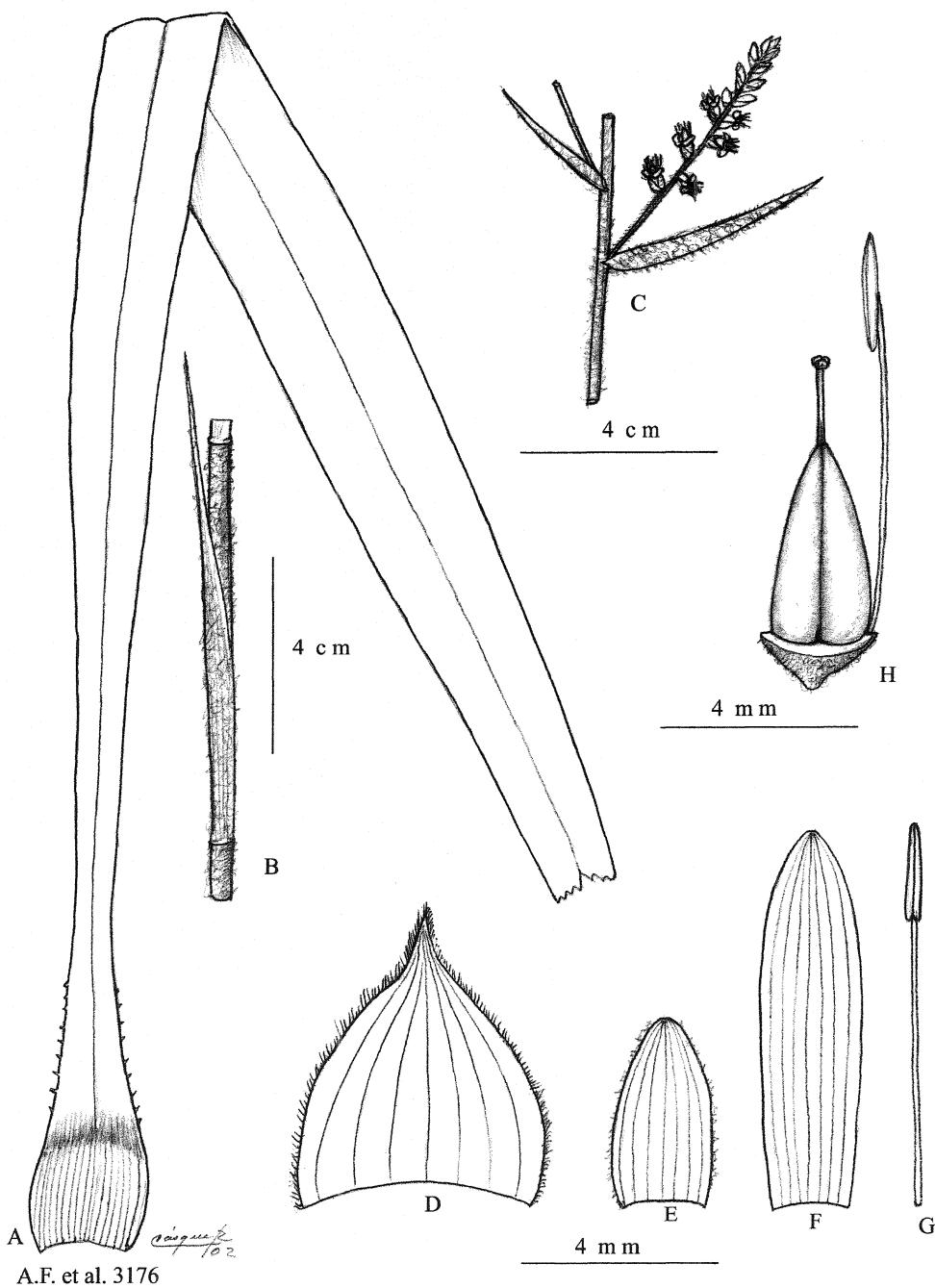


FIGURE 3. *Fosterella fuentesii*. A. Leaf. B. Scape bract. C. Inflorescence branch and primary bracts. D. Floral bract. E. Sepal. F. Petal. G. Stamen. H. Gynoecium and stamen. (drawing of A. Fuentes et al. 3176, LPB, by R. Vásquez).

latter can develop wide leaves (>5 cm), nearly as wide as *F. latifolia*. Both have entire leaves somewhat constricted at the base and can be reddish beneath (in *F. villosula* purely green leaves

may be more common). They are distinct, however; the differentiation is important, especially in Santa Cruz, where both occur. The petals of *F. latifolia* are larger, 8 mm \times 2–3 mm, oblong-

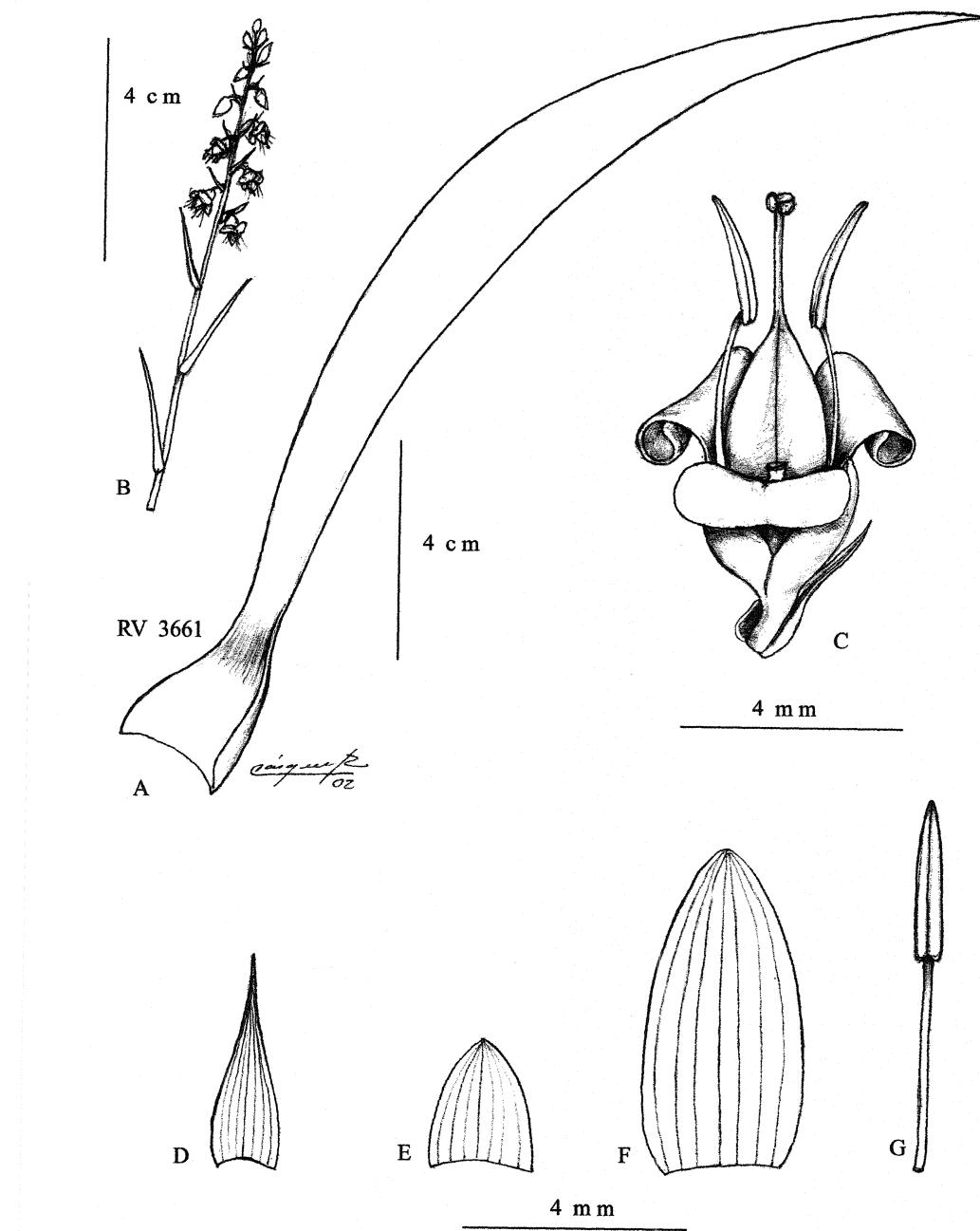


FIGURE 4. *Fosterella heterophylla*. A. Leaf. B. Inflorescence detail. C. Flower. D. Floral bract. E. Sepal. F. Petal. G. Stamen (drawing of R. Vásquez 3661, LPB, by R. Vásquez).

obovate, and not $7\text{ mm} \times 1\text{--}2\text{ mm}$, lanceolate, as in *F. villosula*. The sepals of *F. latifolia* are dark-green to somewhat reddish and glabrous, and not clear-green and lepidote. The floral bract is papyraceous and glabrous and not green and lepidote. The leaves are not so visibly channeled

as in *F. villosula*, and the axis of the inflorescence is glaucous-glabrous (epicuticular waxes) and not lepidote. *Fosterella villosula* seems to prefer humid forests, and *F. latifolia* semihumid forests.

Although *Fosterella latifolia* morphologically

differs from *F. penduliflora*, preliminary molecular data suggest they are close relatives (Rex 2001, Rex et al. 2001; FIGURE 1). A closer look at the *F. penduliflora* group, which may either represent only one very variable species or several closely related species, is needed.

Fosterella nowickii Ibisch, Vásquez & Gross, sp. nov. TYPE: Bolivia. Dpto. La Paz: Prov. Sud Yungas, nearby Irupana, 16°26'S, 67°28'W, 1200 m, 20 Feb. 2000 (cultivated specimen flowered in Oct. 2001), C. Nowicki & R. Müller 2076 (Holotype: LPB). FIGURE 5.

Similis est *Fosterella cotacajensis* Kessler, Ibisch & Gross sed foliis latioribus squamis laminae maioribus bracteis scapi glabris serratisque floribus non solum nutantibus bracteis florum multo magis longioribus sepalis petalisque brevioribus.

Plant caulescent, flowering to ca. 150 cm high, branched. **Leaves** numerous, arcuate, to 50 cm long. **Sheaths** to ca. 3 cm high, to 5 cm wide, brownish, serrate, glabrous. **Blades** somewhat constricted at base but not petiolate, narrowly lanceolate, to 27 mm wide, to ca. 50 cm long, abaxially densely white-lanate, adaxially glabrous, serrate with white antorse spines, to 2 mm long, regularly spined to about half of the blade, few spines toward apex. **Scape** erect, to 70–80 cm long, at base to 10 mm wide, green, glabrous, almost completely covered by bracts. **Scape bracts** erect, triangular, acuminate, upper ones 12–13 mm wide, ca. 4 cm long, at least lower ones serrate, longer than the internodes, glabrescent to glabrous. **Inflorescence** tripinnate, erect, ca. 40 cm long, glabrous. **Primary bracts** lower ones to 6 cm long, normally exceeding the sterile base of the branches, green. **Branches** numerous, 14–15 cm long. **Floral bracts** triangular, 3.5–5 mm long, ca. 0.8 mm wide, always exceeding the sepals. **Flowers** nutant or erect, ca. 8 mm long. **Pedicels** 1–3 mm long. **Sepals** broadly ovate, obtuse, to 2–3 mm long, 1.5 mm wide, glabrous. **Petals** greenish, to 5 mm long, to 2–3 mm wide, strongly recurved during and after anthesis. **Stamens** to 6 mm long. **Anthers** ca. 3 mm long, yellow, recurring when old. **Ovary** ca. 3 mm long. **Style** 2 mm long.

Paratype: BOLIVIA. Dpto. La Paz: Prov. Sud Yungas, 10 km from Irupana to Chulumani, 16°26'S, 67°28'W, 1400 m, 12 Feb. 2000, R. Vásquez, G. Gerlach, & L.R. Moreno 3636a (VASQ).

This new species resembles *Fosterella cotacajensis* but differs by broader and arcuate, (not angled at base) leaves, smaller scales in the blades, glabrous and serrate scape bracts, green primary bracts, erect flowers (not all nutant), much shorter floral bracts not exceeding the se-

pals, and shorter sepals and petals. As with *F. cotacajensis*, this new species lives in a dry valley (possibly somewhat less arid). Preliminary molecular data indicate that the species is most closely related to *F. cotacajensis* (Rex 2001, Rex et al. 2001; FIGURE 1). The species, which lives in a dry inter-Andean valley habitat, is dedicated to our colleague and friend Christoph Nowicki, German botanist who is working on the diversity of the Bolivian flora.

Fosterella petiolata (Mez) L.B. Smith, Phytologia 7: 172. 1960. TYPE: Peru. Weberbauer 1210 (Holotype: B).

Several collections of clearly petiolate plants made by T. Krömer and A. Acebey in the mid-altitudes of the humid La Paz Yungas montane rain forests caused confusion; some of them, at first glance, seemed similar to *Fosterella petiolata*, but then somewhat different with all of them differing from each other. After careful revision of the material, we place the plants with *F. petiolata*, suggesting a certain variability of this taxon. It makes sense ecologically that the plants belong to a single species that appears typical of a certain altitudinal belt in the La Paz Yungas. In that area, the species appears to be quite abundant, even at disturbed sites, e.g., in Cotopata National Park where large populations have been observed.

We provide the following description of a plant from La Paz and propose it as *Fosterella petiolata*, which thus is no longer endemic to Peru:

Plant stemless, flowering up to 1 m high, propagating by suckers. **Leaves** erect, to more than 50 cm long, long-petiolate. **Sheaths** triangular, 1.5–2 cm high, to 2 cm wide, brown-castaneous at the base, glabrous, entire. **Petioles** to 25 cm long, to 4 mm wide, entire. **Blades** broadly ovate-lanceolate, acute, to 33 mm wide, to 27 cm long, entire, abaxially densely white-lanate, adaxially glabrous. **Scape** erect, to 65 cm long, glabrous. **Scape bracts** erect, narrowly triangular, acuminate, entire, the lower ones to 1 cm wide, 10 cm long, longer than the internodes, lanate, the upper ones to 3 mm wide, 25 mm long, shorter than the internodes, glabrous to glabrescent. **Inflorescence** laxly paniculate, erect, 40 cm long, ca. 10 cm wide, glabrous. **Primary bracts** narrowly triangular, acuminate, generally shorter than the sterile base of the branches, lower ones to 2 cm long, 3 mm wide. **Branches** (sub-)erect, usually shorter than 10 cm. **Floral bracts** diminute, ca. 1.5 mm long, shorter, equaling or longer than the pedicels, ca. 1 mm wide, glabrous. **Flowers** laxly arranged, suberect to secund, nutant. **Pedicels** slender, 2–3 mm long. **Sepals** oblong-obtuse, 1–1.5 mm

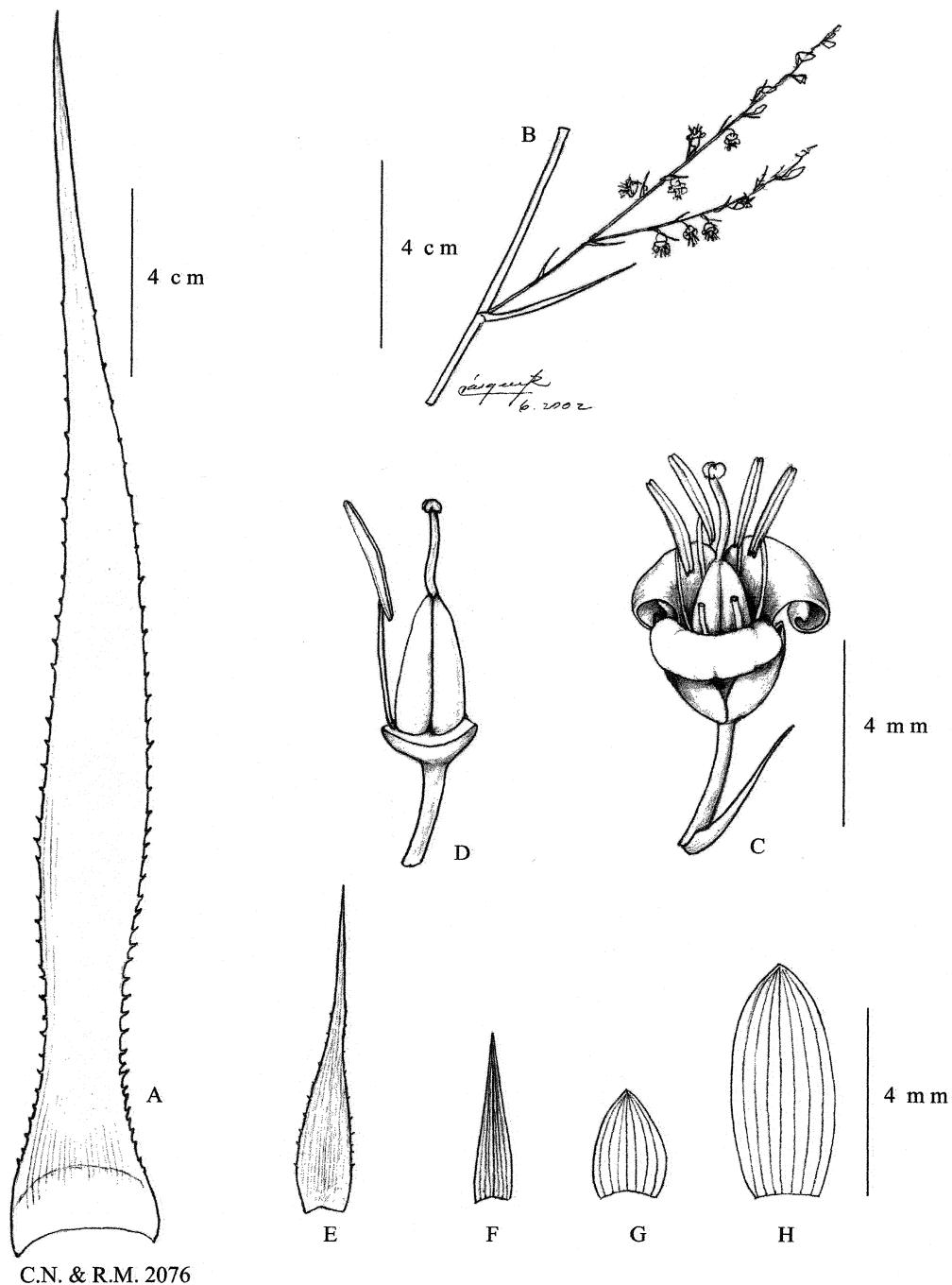


FIGURE 5. *Fosterella nowickii*. **A.** Leaf. **B.** Inflorescence branch and primary bract. **C.** Flower. **D.** Gynoecium and stamen. **E.** Scape bract. **F.** Floral bract. **G.** Sepal. **H.** Petal (drawing of C. Nowicki 2076, LPB, by R. Vásquez).

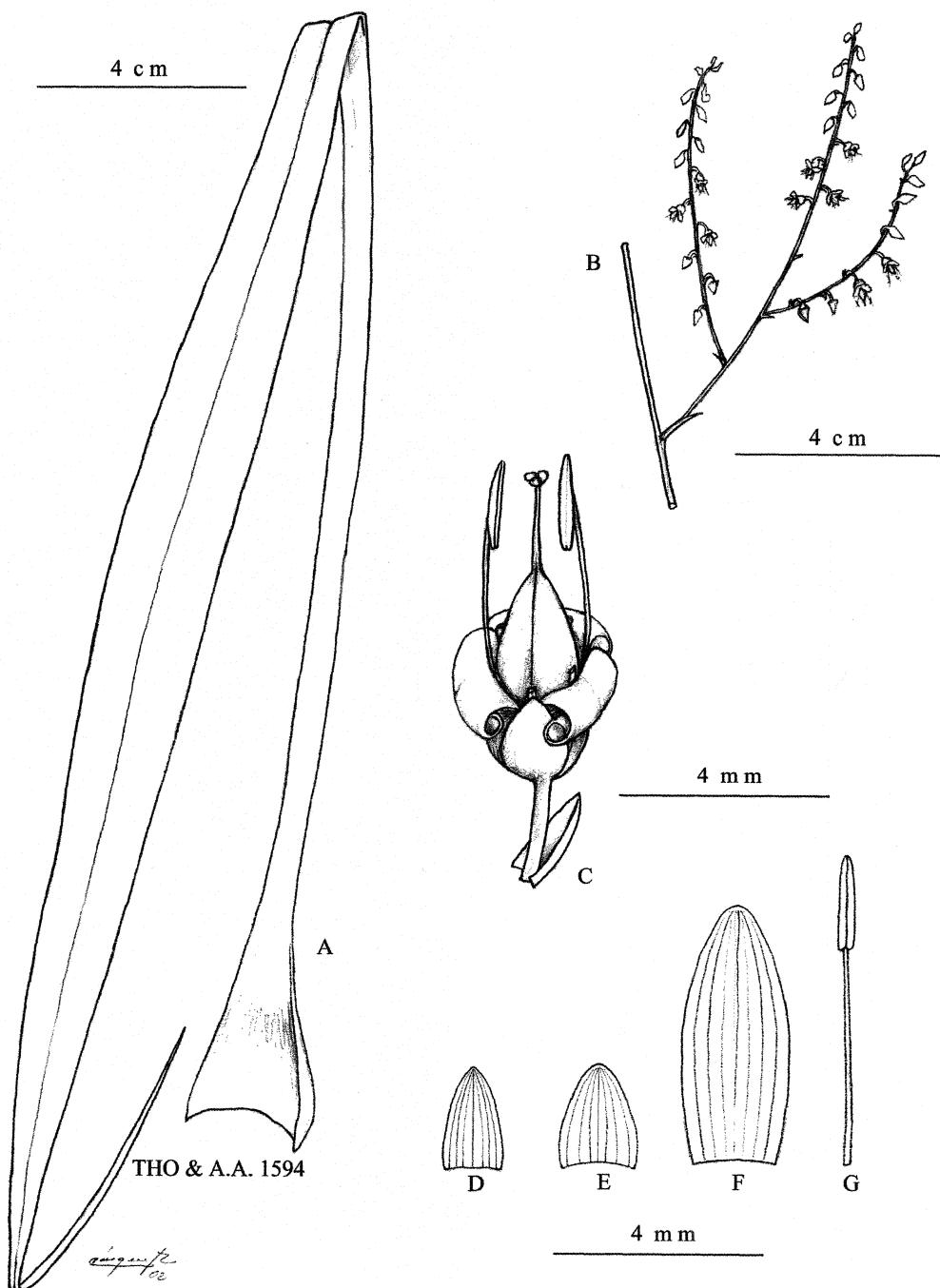


FIGURE 6. *Fosterella petiolata*. A. Leaf. B. Inflorescence branch and primary bract. C. Flower. D. Floral bract. E. Sepal. F. Petal. G. Stamen (drawing of Krömer & A. Acebey 1594, LPB, by R. Vásquez).

long, 1–1.5 mm wide, glabrous. **Petals** white, 4–5 mm long, to 2 mm wide, strongly recurved during and after anthesis. **Stamens** to 5–6 mm long. **Anthers** 2 mm long, elongate, slightly re-

curved, bright yellow. **Ovary** ca. 1.5 mm long. **Style** to 2 mm long. **Fruit** 3–5 mm long, 3–4 mm wide.

This plant differs from *Fosterella petiolata* as

described by Smith and Downs (1974) by the diminute floral bracts (not exceeding the pedicels, not broadly ovate) and the shorter sepals (1.5 mm not 2.5 mm). We await future molecular studies to decide if this plant and the specimens mentioned below all belong to the Peruvian *F. etiolata*, or if some differentiation on the specific or subspecific level is justified.

Specimens examined: BOLIVIA. Dpto. La Paz: Prov. Nor Yungas, Cotapata National Park, trails around Estación Biológica de Tunquini, 16°11'S, 67°53', 1650 m, 22 Sep. 2000, T. Krömer & A. Acebey 1594 (GOET, LPB, USZ). FIGURE 6; ibid.: 16°12S, 67°51'W, 1550 m, 25 Aug. 1999, T. Krömer & A. Acebey 763 (GOET, LPB) (flowers first suberect, later nutant, primary bracts larger than in the specimen *T. Krömer & A. Acebey 1594*, pedicels rather long, pedicels shorter than floral bracts, fruits higher than wide, 5 × 3 mm); ibid.: 16°12S, 67°50'W, 1300 m, 5 Oct. 1999, T. Krömer & A. Acebey 902 (GOET, LPB); ibid.: Prov. Caranavi, road from Caranavi to Sapecho, near summit of Serranía Bella Vista, 15°41'S, 67°29'W, 1500 m, 5 Aug. 2000, T. Krömer & A. Acebey 1398a (GOET, LPB, USZ) (similar to specimen *T. Krömer & A. Acebey 1594*, fruits also higher than wide); Prov. Bautista Saavedra, Pauyi-Yuyo, between Apolo and Charazani, 15°03'S, 68°29'W, 900 m, 15 Jun. 1997, M. Kessler et al. 10189 (GOET, LPB, SEL) (floral bracts as long or longer than the pedicels); ibid.: Prov. Nor Yungas, 15.2 km road from Chusipata to Yolosa, 16°17'S, 67°48'W, 1800 m, 26 Sep. 1999, T. Krömer & A. Acebey 891 (GOET, LPB) (flowers larger than in the specimen *T. Krömer & A. Acebey 1594*, primary bracts quite short, flowers spreading to suberect, fruits more bulky than in the specimen *T. Krömer & A. Acebey 1594*, shorter than wide, 3 × 4 mm); ibid.: Prov. Nor Yungas, 27 km road from Chusipata to Yolosa, 16°17'S, 67°48'W, 1250 m, 26 Sep. 1999, T. Krömer & A. Acebey 893 (GOET, LPB) (similar to previous collection).

Fosterella rexiae Ibisch, Vásquez & Gross, sp. nov. TYPE: Bolivia. Dpto. La Paz: Prov. Caranavi, 25 km from Caranavi to Yolosa, 15°57'S, 67°34'W, 830 m, 15 Feb. 2000 (cultivated specimen flowered in September 2001), R. Vásquez & G. Gerlach 3673 (Holotype: LPB). FIGURE 7.

Similis est *Fosterella albicans* (Grisebach) L.B. Smith sed inflorescentia laxiore ramis inflorescentiae longioribus gracilioribusque bracteis florum brevioribus sepalis petalisque brevioribus differt. Ab *Fosterella pearcei* (Baker) L.B. Smith foliis latioribus inflorescentia lepidote vel glabrescentia non tomentosa bracteis primariis longioribus quam basi sterile ramorum differt.

Plant stemless, flowering up to 90 cm high. **Leaves** erect to arching, linear to narrowly lanceolate, somewhat constricted at base but not petiolate. **Sheaths** triangular, to 1.5 cm high, to 2.5 cm wide, white, glabrous, entire. **Blades** green, quite stiff, lanceolate, acute, to 17 mm wide, to 30 cm long, serrate at base, green antorse spines, to 1 mm long, abaxially densely white-lepidote, adaxially sparsely lepidote, especially towards base. **Scape** erect, to 50 cm long, 3 mm wide, greenish or brownish-reddish, lanate to sparsely lepidote/glabrescent. **Scape bracts** erect, narrowly triangular, acuminate, entire, longer than the internodes or equaling, the lower ones ca. 7 mm long, lanate to glabrescent, dry-papyraceous. **Inflorescence** laxly tripinnate, erect, ca. 50 cm long, ca. 15 cm wide, brownish-reddish, lanate to glabrescent. **Primary bracts** narrowly triangular, acuminate, always longer than the sterile base of the branches, lower ones to 3 cm long. **Branches** (sub-)erect, usually shorter than 10 cm, green to brownish-reddish, glabrescent. **Floral bracts** small, ca. 1.5 mm long, broadly ovate, apiculate, dry papyraceous, lepidote. **Flowers** sessile, laxly arranged, erect to spreading, 6–7 mm long. **Sepals** triangular, 3 mm long, 1 mm wide, sparsely lepidote to glabrescent, green to reddish. **Petals** white, to 5 mm long, to 2 mm wide, recurved during and after anthesis. **Stamens** to 5 mm long. **Ovary** ca. 4 mm long. **Style** to 5 mm long.

This new species is rather similar to *Fosterella albicans* but differs by having laxer, less densely flowered inflorescences with longer and more slender branches, shorter floral bracts (to 1.5 mm long, not to 4–5 mm), shorter sepals (2 mm, not 4 mm) and petals (shorter than 5 mm). Preliminary molecular data have shown that the species is closely related to, but distinct from *F. albicans* plants collected further south in Santa Cruz and Chuquisaca; these are geographically less distant from the northern Argentine type of *F. albicans* than is *F. rexiae*. *Fosterella albicans* may be a species of semihumid forests, while *F. rexiae* sp. nov. may be limited to humid montane rain forest sites.

Paratype: BOLIVIA. La Paz: Prov. Caranavi, road from Caranavi to Yucumo, between the summit and Sapecho, 13°10'S 67°29'W, 1310 m, 14 Feb. 2000, R. Vásquez & G. Gerlach 3666 (USZ).

Fosterella rojasii (L.B. Sm.) L.B. Smith, Revista Argent. Agron. 7: 162. 1940. TYPE: Paraguay. Rojas 6771 (Holotype: GH).

This originally Paraguayan species was recorded in Bolivia (Santa Cruz) in a recent bromeliad checklist (Krömer et al. 1999). More recently, plants have been collected in the humid

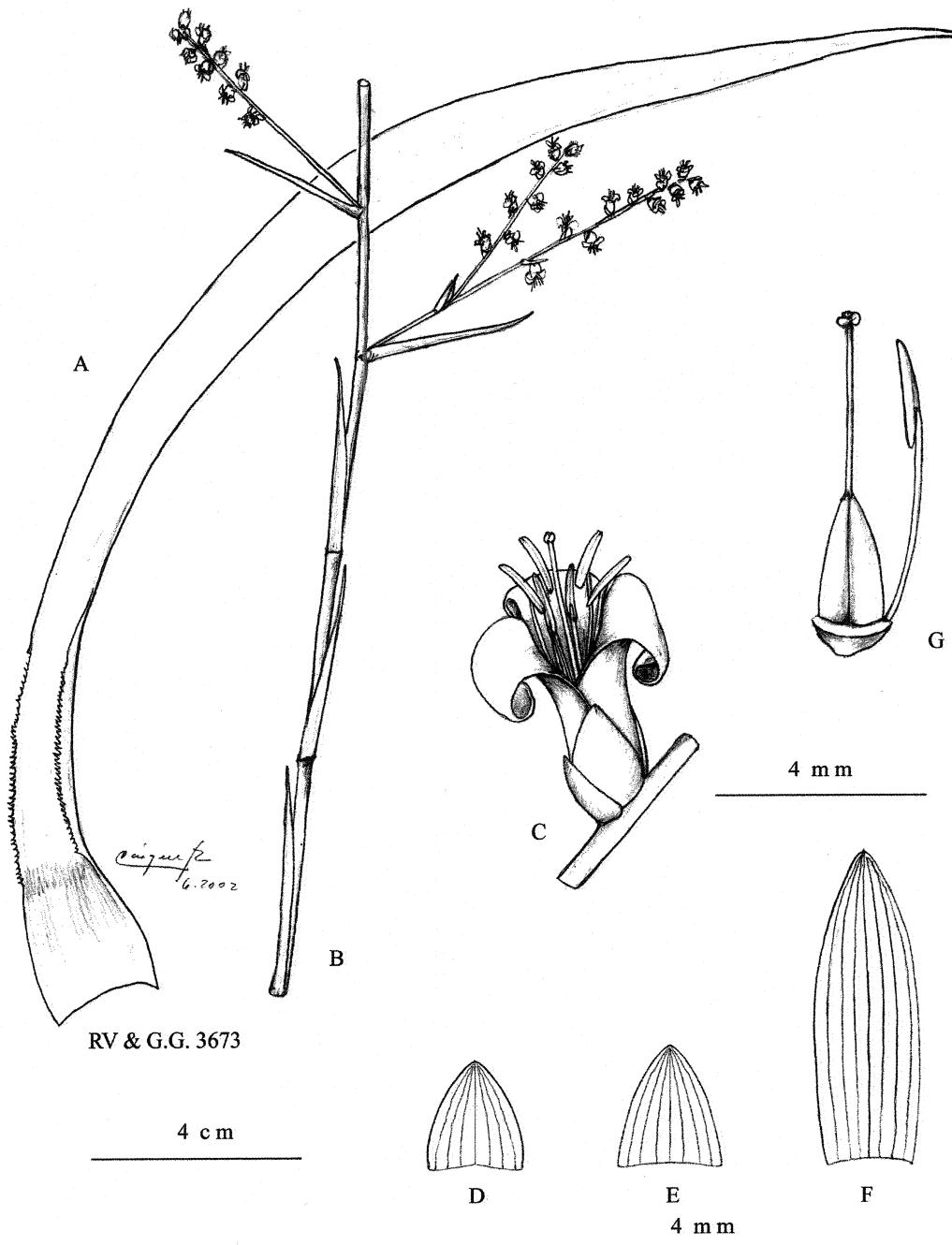


FIGURE 7. *Fosterella rexiae*. **A.** Leaf. **B.** Scape, scape bracts, primary bracts and branches. **C.** Flower. **D.** Floral bract. **E.** Sepal. **F.** Petal. **G.** Gynoecium and stamen (drawing of R. Vásquez & G. Gerlach 3673, LPB, by R. Vásquez).

montane forests of the La Paz department and are also morphologically referable to *F. rojasii*. Despite ecological and some morphological differences, we prefer to await more data be-

fore making a taxonomic decision on these populations.

Specimens examined: BOLIVIA. Dpto. La Paz: Prov. Nor Yungas, 25 km from Caranavi to

Yolosa, 15°57'S 67°34'W, 830 m, 15 Feb. 2000, R. Vásquez & G. Gerlach 3674 (VASQ); ibid. between Chusipata and Yolosa, 16°13'S, 67°44'W, 1970 m, 15 Feb. 2000, R. Vásquez & G. Gerlach 3652 (VASQ); Dpto. Cochabamba: Prov. Ayopaya, Atispaya, 1330 m, 16°36'S, 66°43'W, 22 Jun. 2001, R. Vásquez, G. Navarro, M. Fernández F. Miranda & H. Rocha 4177 (VASQ).

Fosterella villosula (Harms) L.B. Smith, Phytologia 7: 172. 1960. TYPE: Bolivia. Werdemann 2120 (Holotype: B).

This species is more variable than earlier thought; it can even resemble *Fosterella latifolia*. Erroneously, we classified some specimens as *F. latifolia* (Ibisch et al. 1999): Province A. Ibáñez: Arubay, property of G. Coimbra nearby Terebintho, in understory of semihumid forest, 17°44'S, 63°23'W, 450 m, 16 Nov. 1998, P. Ibisch & C. Nowicki 98.0173 (USZ); ibid., 4 Oct. 1998, R. Vásquez 2994 (VASQ). Preliminary molecular data support the designation of this specimen as *F. villosula* but also indicate that it is distinct from the *F. villosula* accessions R. Vásquez et al. 3318a (VASQ) and 3318b (VASQ) from the Chapare region in Cochabamba (Rex 2001, Rex et al. 2001; FIGURE 1).

In the Chapare region (not far from the type locality but at lower altitude), we collected a plant that differs in some characters from *Fosterella villosula*: Dpto. Cochabamba, Prov. Chapare, between the rivers Huayruruni and Correo Huañuska, 440 m, 2 Sep. 1999, R. Vásquez 3322 (VASQ). This may be a manifestation of some natural morphological and ecological variability of the species. The following is a description of the specimen.

Plant flowering to 50 cm. **Leaves** numerous forming a flat rosette. **Sheaths** to 15 mm wide, white, glabrous. **Blades** to 22 cm long, to 30 mm wide, entire, green, glabrous adaxially with only a few scales towards the bases, white lepidote abaxially, green, narrowed above sheath but not petiolate. **Scape** 22 cm long, 3 mm thick, lanate-lepidote, green. **Scape bracts** lower ones to 40 mm long, upper ones to 30 mm long, always longer than the internodes, dry papyraceous, triangular-lanceolate, long attenuate with a filiform tip. **Inflorescence** bi- to tri-pinnate, to 30 cm long, green, lanate-lepidote. **Primary bracts** to 25–30 mm long, to 7 mm wide, dry papyraceous, lepidote glabrescent, attenuate. **Branches** to 6 cm long, green, lanate-lepidote, rarely branched. **Flowers** 8–9 mm long, not very dense, pendent or nutant. Pedicel 1–2 mm long, green, sparsely lepidote. **Floral bracts** 4 mm long, 1.5 mm wide, longer than the pedicel. **Se-pals** 3 mm long, 1.5 mm wide, green, sparsely

lepidote, glabrescent. **Petals** 5 mm long, to 2 mm wide, white, somewhat recurved at anthesis but straight after anthesis. **Stamens** 3 mm long. **Ovary** to 6 mm long. **Style** 3–4 mm long.

This plant differs from the description as documented by Smith and Downs (1974) in the following characters: inflorescence not densely flocculose-villous. Floral bracts not villous and to 7 mm long. Petals not 7 mm long. Apparently, green and reddish plants (especially lower surface of leaves) of *Fosterella villosula* are found.

Fosterella weberbaueri (Mez) L.B. Smith, Phytologia 7: 172. 1960. TYPE: Peru. Weberbauer 33635 (Holotype: E).

This species was originally described as *Lindmania weberbaueri* by Mez, transferred to *Fosterella* by L.B. Smith and then classified as a synonym of *F. schidosperma* (Smith & Downs 1974). We here propose to reinstate *F. weberbaueri* as a valid species, and report a collection from Bolivia that expands the range southward from Peru. Although *F. schidosperma* and *F. weberbaueri* are astonishingly similar, as pointed out by R. Read (unpubl.) there is one important difference between these two groups of *Fosterella*. One group has petals that are recoiled as watch-springs and stay so even after anthesis (e.g., *F. schidosperma*); the other group is characterized by straight or more or less recoiled petals that become straight again after anthesis (e.g., *F. weberbaueri*). Preliminary molecular data support the distinctiveness of these two groups and hence the systematic relevance of this petal character (Rex 2001, Rex et al. 2001). Thus, we conclude that *F. schidosperma* and *F. weberbaueri* are distinct species.

We present the following description of the plant found in the sub-Andean rain forests of the Chapare region, which we conclude to represent *F. weberbaueri*: BOLIVIA. Dpto. Cochabamba: Prov. Chapare, between San Rafael and El Palmar, 590 m, 17°05'S, 65°29'W, 8 Feb. 2000, R. Vásquez, G. Gerlach, & L.R. Moreno 3570a (VASQ).

Plant flowering to 45 cm high. **Leaves** numerous forming a flat rosette. **Sheaths** to 25 mm wide, to 20 mm high, white, glabrous. **Blades** to 35 cm long, to 45 mm wide, entire, green, glabrous, green, ovally attenuate, narrowed above sheath but not petiolate. **Scape** 20 cm long, 2–3 mm thick, glabrous, green. **Scape bracts** lower ones 25–30 mm long, upper ones to 15 mm long, only the lower ones longer than the internodes, dry papyraceous, triangular-lanceolate, long attenuate. **Inflorescence** bi-pinnate, to 25 cm long, green, glabrous. **Primary bracts** to 10 mm long, dry papyraceous, attenuate. **Branches** to 6 cm long, green, glabrous, not branched.

Flowers 8–9 mm long, relatively dense, spreading, erect and nutant. Pedicels 1.5–2 mm long, green, glabrous. **Floral bracts** small, as long or longer than the pedicel, dry papyraceous. **Sepals** 2 mm long, green, glabrous. **Petals** 4–5 mm long, to 2 mm wide, white, recurved/recoiled like watch springs at anthesis but straight after anthesis. **Stamens** 4 mm long. Anthers yellow. **Gynoecium** to 6 mm long with a style 3 mm long and a white stigma.

Fosterella windischii L.B. Smith & R.W. Read, Bradea 6(15): 134. 1992. TYPE: Brazil. P.G. Windisch 2044 (Holotype: US; Isotype: HB).

This species was originally described from Brazil, from the Ricardo Franco mountain chain (15°S, 60°W, 450–500 m; Smith & Read 1992), near the Bolivian border. Not surprisingly, this species has now been collected from the neighboring Noel Kempff National Park in Bolivia, which has similar climatic and geological conditions. As the original description of the species is rather short and as we observe some differences, a detailed description of the Bolivian plant is provided.

Specimen examined: BOLIVIA. Dpto. Santa Cruz: Prov. Velasco, Parque Nacional Noel Kempff, Lago Caimán, 13°36'54"S, 60°54'31"W, 300 m, rock outcrops in dry forest ("Ladera con afloramientos rocosos y de fuerte pendiente. Bosque seco con *Callisthene* cf. *microphylla*, *Copaifera* sp., *Terminalia* sp."), 2 Oct. 1995, Israel Vargas, R. Foster, M. Peña, A. Fuentes, N. Paniagua, A. Goncalves, J. Baliviezo, E. Anibarro, M. Velasco, M. Toledo & R. Guillén 4001 (USZ).

Plant stemless, flowering up to 60 cm high, propagating by suckers. **Leaves** erect, ca. 50 cm long, constricted at base. **Sheaths** ovate, to 1 cm high, to 1.5 cm wide, white, glabrous, entire. **Blades** narrowly lanceolate, acuminate, to 12 mm wide, to 50 cm long, entire or some inconspicuous spines at the base, abaxially densely white-lanate, adaxially glabrous. **Scape** erect, to 27 cm long, glabrous, dark when dry. **Scape bracts** erect, narrowly triangular, cuneate, entire, glabrous, all longer than the internodes, the lower ones 5 cm long. **Inflorescence** laxly paniculate, erect, to 25 cm long, ca. 10 cm wide, glabrous. **Primary bracts** narrowly triangular acuminate, generally shorter than the sterile base of the branches, lower ones to 1 cm long. **Branches** ca. 10 or more, suberect, to 11 cm long. **Floral bracts** diminute, ca. 1–1.5 mm long, always shorter than the pedicels, ovate-acuminate, dry papyraceous. **Flowers** more or less laxly arranged, nutant, 6–7 mm long, glabrous. **Pedicels** slender, 2–3 mm long. **Sepals** to 2 mm long, 1.7

mm wide, glabrous. **Petals** cream (fide collector), to 4 mm long, 1.5 mm wide, strongly recurved during and after anthesis. **Stamens** 3–4 mm long. **Anthers** 1.5–2 mm long, elongate, not recurved, (but unclear if they stay so after anthesis). **Ovary** about to 2 mm long. **Style** to 2 mm long. **Stigma** compact. **Fruit** to 5 mm long, 2–2.5 mm wide.

The type specimen has longer floral bracts than the Bolivian collection (3 mm vs. 1 mm, and longer than the pedicels vs. shorter) and small differences in leaf blade width and petal length. This may indicate some genetic difference among the populations; however, considering the geographical and ecological coincidence, it should not justify the establishment of a new taxon. Together with *Fosterella vasquezii* (Ibisch et al. 1997), *F. windischii* is the second species of the genus known from the Noel Kempff National Park and surroundings.

A confusingly similar plant has been collected in the humid montane forests of the La Paz Andes: Dpto. La Paz: Prov. Caranavi, road from Caranavi to Sapecho, near the summit of the Serranía Bella Vista, 15°41'S, 67°29'W, 1500 m, T. Krömer & A. Acebey 1398b (USZ). Considering the geographical distance to the Noel Kempff National Park and the ecological differences, it is unlikely that the La Paz plant belongs to the same species. The morphological differences are not very marked, however, and without molecular evidence, we propose that the La Paz plant is *Fosterella windischii*. The following description highlights the characters that differ slightly from the now-recorded Bolivian *F. windischii*. All other characters are more or less identical.

Leaves ca. 40 cm long. **Sheaths** broadly ovate, to 2 cm high, to 3 cm wide, white. **Blades** to 22 mm wide, to 40 cm long, entire. **Scape** to 35 cm long, glabrous, green. **Scape bracts** entire, lepidote, not always longer than the internodes, the lower ones 4–5 cm long. **Inflorescence** bipinnate. **Branches** ca. 20, to 5 cm long. **Floral bracts** ca. 1–2 mm long, longer than the pedicels or equaling. **Pedicels** 1–2 mm long. **Sepals** 1–1.5 mm wide. **Petals** white, 4–5 mm long. **Anthers** 1.5–2 mm long, possibly during and after anthesis recurved.

Fosterella yuvinkae Ibisch, Vásquez, Gross & Reichle, sp. nov. TYPE: Bolivia. Prov. Chiquitos, Santiago de Chiquitos, 18°20'108"S, 59°34'301"W, Aug. 2001, S. Reichle P-SR1 (Holotype: LPB). FIGURE 8.

Similis est *Fosterella penduliflora* (C.H. Wright) L.B. Smith sed foliis dense lanatis cum trichomatibus longis petalis angustioribus differt.

Plant stemless, flowering up to 40 cm high.

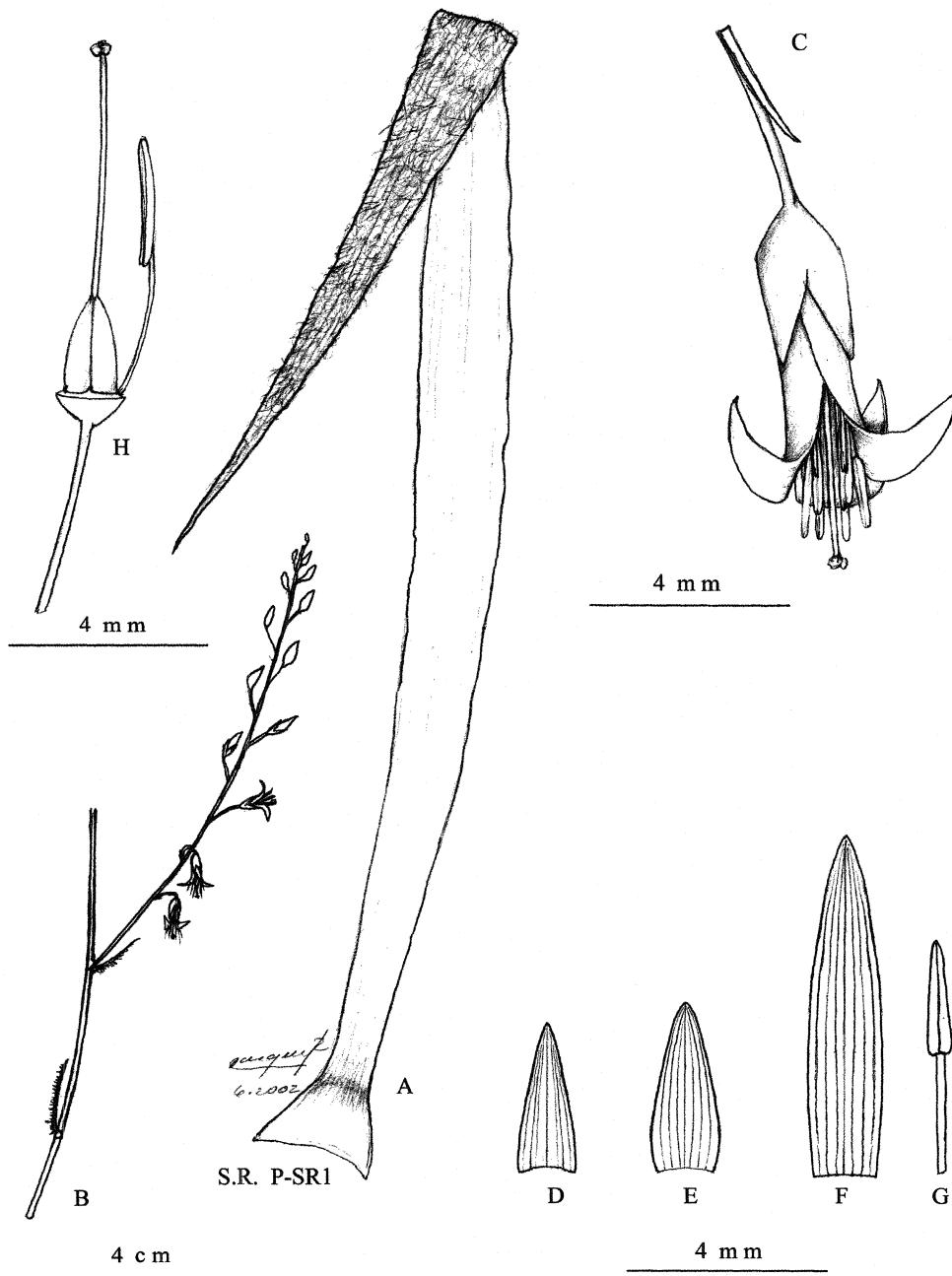


FIGURE 8. *Fosterella yuvinkae*. A. Leaf. B. Inflorescence branch and primary bract. C. Flower. D. Floral bract. E. Sepal. F. Petal. G. Stamen. H. Gynoecium and stamen (drawing of *S. Reichle P-SR1*, LPB, by R. Vásquez).

Leaves flatly rosulate, ca. 35 cm long. **Sheaths** ovate, to 1 cm high, to 2 cm wide, white, glabrous above, white-lanate beneath and at margins, entire. **Blades** linear-lanceolate, acuminate, somewhat narrowed at base but not petiolate, to

20 mm wide, to more than 30 cm long, entire, abaxially densely white-lanate with conspicuous, long trichomes, adaxially glabrous. **Scape** erect, to 30 cm long, glabrous, green. **Scape bracts** erect, narrowly triangular, entire, lanate,

dry papyraceous, at least lower ones longer than the internodes, ca. 2 cm long. **Inflorescence** bi-pinnate, pendent, to 15 cm long, glabrous. **Primary bracts** narrowly triangular, lower ones lanate, all shorter than the sterile base of the branches. **Branches** few, rather short. **Floral bracts** 3 mm long, 1 mm wide, always shorter than the pedicels, triangular, glabrous. **Flowers** more or less laxly arranged, secund, nutant, to 15 mm long, glabrous. **Pedicels** slender, 3–4 mm long, green. **Sepals** to 3.5 mm long, ca. 1 mm wide, glabrous. **Petals** white, to 7(9) mm long, 1.5 mm wide, strongly recurved during and after anthesis. **Stamens** 4–5 mm long. **Anthers** ca. 2.5 mm long, elongate, not recurved. **Ovary** ca. to 2–3 mm long. **Style** to 5 mm long, white.

Although this species is thought to belong to the *Fosterella penduliflora* group, no molecular data are available yet in support of this assumption. The group is characterized by, among other characters, having rather long petals (9 mm and more) that are not recoiled. It differs from *F. penduliflora* by having densely lanate leaves with long trichomes (vs. sparingly scurfy beneath), very narrowly lanceolate, 1.5 mm wide petals (vs. lanceolate-oblong and more than 2 mm wide). It should resemble the geographically close *F. chiquitana*, but differs by having 1–2 mm long floral bracts that do not exceed the pedicels (vs. 8–11 mm and exceeding the pedicels), glabrous floral bracts and sepals, much longer trichomes on the abaxial side of the leaves than in *F. chiquitana*, leaves somewhat constricted at the base and the style that is much longer than the ovary (vs. style about equaling ovary).

The type collection was made on steep slopes beside rocky rivulets in riverine forest of the Santiago mountain chain within the Chiquitano Dry Forest ecoregion, where plants either grew on rocks or directly on the ground. The diameter of adult plants varied significantly in different light situations. Flowering plants growing in permanent dark shade had a diameter of ca. 30 cm, and adult plants in areas of more light had diameters of up to approximately 100 cm. The plants flower in the dry season, at least from July to August, which may vary with different precipitation values in different years. Mean precipitation is ca. 1100 mm/year with a rainy season from October to February and the driest months in July and August (Villarpando et al. 2002). The riverine forests in some places consist only of one row of trees and are replaced by Cerrado forest about 5 m from the stream. In canyon-like valleys, the forest-belts are broader and may fill some small valleys (belts of up to 50–60 m wide). The Precambrian mountain chain is biogeographically important by being

rather isolated from other similar structures and by providing azonal climate. The Santiago mountains are floristically special as they represent humid forest remnants within a dry forest region (see Guillén et al. 2002). Typically, tree ferns are part of the riverine vegetation. Along with other areas, the rock outcrops on the top of the mountains are the habitat for the virtually *Puya*-like *Pitcairnia platystemon* (stiff and spiny leaves, petals somewhat twisted together after anthesis) which is endemic to the type locality.

The name *Fosterella yuvinkae* honors Yuvinka Gareca for her ongoing ecological research in the area of Santiago de Chiquitos.

COMMENT ON INFRAGENERIC RELATIONSHIPS

Preliminary molecular data resulted in phenetic trees that correspond fairly well to systematic relationships deduced from morphological criteria (FIGURE 1). In some cases, morphologically similar but ecologically distinct species, such as *Fosterella elata* and *F. vasquezii* (Ibisch et al. 1997), seem to be distinct but closely related sister species. In other cases, additional molecular data will help in deciding if morphological differences justify a differentiation at the specific or the subspecific level (e.g., within the *F. penduliflora* group, consisting of *F. penduliflora*, *F. chiquitana*, *F. latifolia* and possibly others). Robert W. Read discovered an important morphological difference that distinguishes two subgroups of *Fosterella*: one characterized by strongly recoiled petals that stay so even after anthesis; and the second with straight or somewhat recurved petals that become straight again after anthesis. He suggested that this character may be valuable in establishing subgenera but never published his ideas. The molecular data are fully consistent with Read's observations and indicate that at least the group with unrecoiled petals could be monophyletic (FIGURE 1). We prefer to wait, however, for more molecular data before deciding on taxonomic consequences.

ACKNOWLEDGMENTS

The senior author is an Integrated Expert supported by the Center for International Migration and Development (CIM)-program of the German government for the Fundación Amigos de la Naturaleza (FAN). We acknowledge the support of the FAN staff, especially Fabiola Pérez, who is responsible for the living plant collection. We thank R.W. Read for developing a key (unpubl.) that he sent us several years ago, which facilitated our *Fosterella* research. Our study

was conducted under the botanical research program of the Science Department of Fundación Amigos de la Naturaleza Noel Kempff—Bolivia, in the framework of the FAN project, “Floristic Diversity of Bolivia-From Collection to Cognition and Conservation”, as part of the International Biodiversity Observation Year (IBOY) satellite projects (DIVERSITAS initiative IBOY, 2001–2002). We thank Kurt Weising, University of Kassel, for a critical revision of a first draft of this article. We appreciated the valuable comments made by Harry Luther and Robert Read, and the careful revision and editorial guidance provided by Bruce Holst.

LITERATURE CITED

- Guillén, R., P.L. Ibisch and S. Reichle. 2002. Flora. Pp. 48–57 in P.L. Ibisch, K. Columba and S. Reichle, eds. Plan de Conservación y Desarrollo Sostenible para el Bosque Seco Chiquitano, Cerrado y Pantanal Boliviano. Editorial FAN, Santa Cruz, Bolivia.
- Ibisch, P.L., E. Gross, G. Rauer and D. Rudolph. 1997. On the diversity and biogeography of the genus *Fosterella* L.B. Smith (Bromeliaceae) with the description of a new species from Eastern Bolivia. J. Bromeliad Soc. 47(5): 211–217.
- Ibisch, P.L., C. Nowicki and R. Vásquez. 2001. Towards an understanding of diversity patterns and conservation requirements of the Bolivian Bromeliaceae. J. Bromeliad Soc. 51(3): 99–113.
- Ibisch, P.L., R. Vásquez and E. Gross. 1999. More novelties of *Fosterella* L.B. Smith (Bromeliaceae) from Bolivia. Rev. Soc. Boliviana Bot. 2(2): 117–132.
- Kessler, M., P.L. Ibisch and E. Gross. 1999. *Fosterella cotacajensis*, una nueva especie de Bromeliaceae de los valles secos andinos de Bolivia. Rev. Soc. Boliviana Bot. 2(2), 111–116.
- Krömer, T. “Untersuchungen zur Verbreitung, Ökologie und Nektarzusammensetzung von Bromeliaceen.” Thesis, University of Göttingen, 1997.
- Krömer, T., M. Kessler, B.K. Holst, H.E. Luther, E.J. Gouda, P.L. Ibisch, W. Till and R. Vásquez. 1999. Checklist of Bolivian Bromeliaceae with notes on species distribution and levels of endemism. Selbyana 20(2): 201–223.
- Rauh, W. 1987. *Fosterella heterophylla*. Trop. Subtrop. Pflanzenwelt 60: 24.
- Rex, M. “Molekulare Analyse von Verwandtschaftsbeziehungen in ausgewählten Gattungen der Pitcairnoideae (Bromeliaceae).” Thesis, University of Kassel (Fachbereich 19 Biologie/Chemie), 2001.
- Rex, M., R. Horres, G. Zizka, P.L. Ibisch and K. Weising. 2001. Molecular systematics of *Fosterella* (Bromeliaceae). P. 139 in T.H. Stützel, ed. Proceedings International Symposium “Biodiversität und Evolutionsbiologie” (23–28 Sep. 2001, Bochum). Bochum.
- Smith, L.B. and R.J. Downs. 1974. Flora Neotropica Monograph 14 (Pitcairnioideae, Bromeliaceae). Haefner Press, New York.
- Smith, L.B. and R.W. Read. 1992. Flora Neotropica Monograph 14(1), Supplement No. 3. Bradea 15: 134–140.
- Villarpando, R., S. Reichle and M. Bertzky. 2002. Clima. Pp. II.1–II.12 in P.L. Ibisch, K. Columba and S. Reichle, eds. Plan de Conservación y Desarrollo Sostenible para el Bosque Seco Chiquitano, Cerrado y Pantanal Boliviano. Editorial FAN, Santa Cruz, Bolivia.