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A new species, four new combinations, a lectotypification, phylogenetic analysis, and a key to the species in *Funkiella* (Orchidaceae, Cranichideae, Spiranthinae)

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Abstract

A new species of the genus *Funkiella* from the region of the Área de Protección de Flora y Fauna Sierra de Álvarez, San Luis Potosí, Mexico, is described and illustrated as *F. garciaperezii* Salazar, Fortanelli & Cast.-Lara. Our phylogenetic analysis of nuclear (nrITS) and plastid DNA sequences (*matK-trnK*, *trnL-trnF*) recovered it as the sister of a clade consisting of all the species of *Funkiella* analyzed excepting *F. rubrocalosa*, which occupies the earliest-diverging position of the genus. Morphologically, *F. garciaperezii* is similar to *F. faucisanguinea* (Dod) Salazar (*comb. nov.*), but differs from the latter in the glabrous peduncle, rachis, ovary, and outer surface of the sepals (*vs.* sparsely glandular-pubescent); the dull brownish thickened area on the labellum hypochile (*vs.* bright red thickened area); the prominent digitiform papillae on the ventral surface of the column (*vs.* short digitiform papillae); and the proportionately shorter, parallel pollinia (*vs.* long linear, divergent pollinia). New combinations in *Funkiella* are provided for *Ecuadoria intagana*, *Galeottiella constricta*, *Spiranthes faucisanguinea*, and *Spiranthes muscicola*, and *Spiranthes porphyricola* is lectotypified. An identification key to the 14 accepted species of *Funkiella* is provided.

Key words: *Ecuadoria*, *Funkiella garciaperezii*, lectotypification, molecular phylogenetics, morphology, San Luis Potosí, *Stalkya*

Introduction

As originally proposed, the genus *Funkiella* Schlechter (1920: 430) included a single species, *F. hyemalis* (Richard & Galeotti 1845: 32) Schlechter (1920: 431), which was stated to be similar to *Schiedeella transversalis* (Richard & Galeotti 1845: 32) Schlechter (1920: 381), the type species of the genus *Schiedeella* Schlechter (1920: 379), but distinguished by a "non-cartilaginous" rostellum remnant (i.e. what remains of the rostellum after removal of the pollinarium), the small plants not surpassing 12 cm tall, and the large flowers about 2.5 cm long. The concept of *Funkiella* held by subsequent taxonomists varied noticeably; for instance, Balogh (1981, also as Burns-Balogh 1986) treated *Funkiella* as a synonym of *Schiedeella*, whereas Garay (1982) accepted *Funkiella* as a distinct genus and transferred to it two additional species, namely *F. congestiflora* (Williams 1946: 227) Garay (1982: 320) and *F. stolonifera* (Ames & Correll 1942: 63) Garay (1982: 320). Szlachetko (1993) increased the number of species included in *Funkiella* to four by the inclusion of *F. durangensis* (Ames & Schweinfurth 1935: 128) Szlachetko (1991c: 20), treating the former *Deiregyne confusa* Garay (1982: 283) and *Schiedeella tenella* (Williams 1946: 235) Balogh (1981: 40) as subspecies of the latter and soon after describing an additional species (*F. versiformis* Szlachetko 1994: 435). All such taxonomic treatments were based on intuitive weighing of a few floral attributes, which were not explicitly contrasted with those of other genera.

Salazar (2003a) followed the concept of *Funkiella* of Szlachetko (1993) except for excluding *F. congestiflora*, which he placed in *Svenkoeltzia* Burns-Balogh (1989a: 12) according to the molecular phylogenetic analysis of

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Salazar *et al.* (2003). In that study, analysis of one nuclear (ITS) and three plastid DNA genes or regions (*matK-trnK*, *rbcL*, and *trnL-trnF*) for 24 species of 20 genera of Spiranthinae showed that *Svenkoeltzia congestiflora* (Williams 1946: 227) Burns-Balogh (1989a: 12) was strongly supported as sister to a clade comprising *Aulosepalum tenuiflorum* (Greenman 1900: 308) Garay (1982: 298) and *Beloglottis costaricensis* (Reichenbach 1855: 214) Schlechter (1920: 365). *Funkiella hyemalis* was, in turn, strongly supported as the sister of "*Schiedeella parasitica*" (Richard & Galeotti 1845: 32) Schlechter (1920: 381; a misidentification for *Funkiella faucisanguinea* [Dod] Salazar in the present work; see later), with *Microthelys minutiflora* (Richard & Galeotti 1845: 32) Garay (1982: 337) as their collective sister (Salazar *et al.* 2003: Figure 7). Szlachetko (1991a, b) placed *M. minutiflora* and most other species that we include here in *Funkiella* (except *F. hyemalis*) in his polyphyletic concept of *Galeottiella* Schlechter (1920: 360), subsequently changing his mind and accepting *Microthelys* (see, e.g., Szlachetko *et al.* 1996, 2005).

The most inclusive molecular phylogenetic study of the Spiranthinae conducted to date (Salazar *et al.* 2018) analyzed nuclear ITS and plastid *matK-trnK* and *trnL-trnF* nucleotide sequences of about one-third (182 of ca. 520) of the species and 36 out of the 41 genera belonging in Spiranthinae sensu Chase *et al.* (2015). Such study confirmed previous results showing that *Funkiella hyemalis* is nested among species formerly assigned to *Schiedeella* [*S. faucisanguinea* (Dod 1978: 60) Burns-Balogh ex Espejo & López-Ferrari (1998: 74), as "*S. parasitica*," *S. valerioi* (Ames & Schweinfurth 1930: 8) Szlachetko & Sheviak (1990: 16)], *Microthelys* Garay (1982: 336) [*M. minutiflora*, *M. nutantiflora* (Schlechter 1906a: 131) Garay (1982: 338), *M. rubrocalosa* (Robinson & Greenman 1895: 165) Garay (1982: 338)], and *Funkiella porphyricola* (Schlechter 1906b: 18) Salazar & Soto Arenas in Solano *et al.* (2011: 52; see Salazar *et al.* 2018: Figure 3). Our concept of *Funkiella* directly reflects such relationships, and it includes *Microthelys*, *Stalkya* Garay (1982: 371), and *Ecuadoria* Dodson & Dressler in Dodson (1994: 133) as its synonyms (see also Salazar 2003a, b, Solano *et al.* 2011). Thus delimited, *Funkiella* includes about 14 described species inhabiting montane forests from the southern USA (Arizona, New Mexico, Texas; Larocque & Catling 1994) through the highlands of Mexico, the Greater Antilles (Dominican Republic), and Central America (Guatemala, Costa Rica), to Andean South America (Colombia, Ecuador, Venezuela). Mexico is the center of diversity of *Funkiella*, with ten species recorded so far, of which five are endemic to this country (Solano *et al.* 2019, Espejo 2012). However, much taxonomic work remains to be done on this genus, including the description or clarification of several recent collections of *Funkiella* from South America, such as a plant from the Colombian Andes reported as *Cyclopogon* cf. *peruvianus* (Presl 1827: 93) Schlechter (1930: 393) by Betancur *et al.* (2018: 252) and several unidentified Ecuadorian collections (G.A. Salazar, unpublished data).

As a result of our previous work aimed at inventorying the diversity of Orchidaceae of the state of San Luis Potosí, northeastern Mexico, an additional, undescribed species morphologically similar to *F. faucisanguinea* was discovered, but at the time we were not able to fully document its vegetative and floral characteristics (Fortanelli-Martínez *et al.* 2022). Subsequently we had the opportunity to re-visit the locale and obtain detailed photographic records and additional information on the morphology and habitat of the undescribed species. In the following, we describe and illustrate it, explore its phylogenetic relationships analyzing nucleotide sequences of one nuclear (ITS) and two plastid DNA regions (*matK-trnL*, *trnL-trnF*), and compare it with *F. faucisanguinea*, the morphologically most similar species. We also transfer the latter, as well as *Ecuadoria intagana* Dodson & Dressler in Dodson (1994: 133), *Galeottiella constricta* Szlachetko (1994: 427), and *Spiranthes muscicola* Garay & Dunsterville (1966: 280) to *Funkiella,* and lectotypify *Spiranthes porphyricola* Schlechter (1906b: 18).

Material and methods

Study area:—The new species was discovered near the southern border of the Sierra de Álvarez, a mountainous formation located east and southeast of the city of San Luis Potosí included in April 1981 in Mexico's National System of Protected Areas under the category of "Area of Protection of Flora and Fauna." The protected area covers 16,900 ha of the municipalities of Armadillo de Los Infante, San Nicolás Tolentino, and Zaragoza (CONANP continuously updated). The Sierra consists of limestones and mudstones from the Cretaceous in its central and northern parts, and of Cenozoic extrusive igneous rocks such as rhyolites and latites in its southern portion. The climate is semi-dry with summer rains. Soil consists predominantly of lithosols, and the area is dominated by oak- and pine-oak forests, although towards the margins there are chaparral and xerophilous scrub (García & Aguirre 2011). The new species was located near the town of Ranchito de Juárez, municipio of Zaragoza (see below), outside the protected area.

Morphological observations:—A specimen of the new species, consisting of two pressed plants collected and deposited previously in SPLM (herbarium acronyms according to Thiers continuously updated) was designated as the

holotype. An additional specimen from the same population was collected in March 2023, flowers were preserved in 70% ethanol, detailed photographic records were made, and a small fragment of leaf tissue for DNA study was obtained. Live plants and flowers were photographed with a digital camera (Nikon 7100; Nikon Corporation, Tokyo, Japan) provided with an 85 mm AF-S Micro Nikkor lens (Nikon). The morphological description was based on examination of fresh plants and flowers. Floral parts of alcohol-preserved flowers were measured with an electronic caliper and photographed under a stereomicroscope (Stemi SV 6, Carl Zeiss Mikroskopie, Jena, Germany). Plate preparation and image processing was carried out with Adobe Photoshop v. 25.12.0 (Adobe Systems Inc., San José, USA).

We studied the specimens of *Funkiella* and other Spiranthinae housed in the following herbaria: AMES, AMO, ANDES, ARIZ, ASU, BM, BR, CAS, CHAPA, COL, CORU, ENCB, F, FCME, GH, HB, HOXA, IBUG, IEB, JBSD, K, KUELAP, LL, M, MBM, MEXU, MG, MHES, MO, NY, P, PMA, QCA, QCNE, QMEX, R, RB, SEL, SERO, SLPM, SP, SPF, TEX, UAMIZ, US, USJ, USM, UVAL, VEN, W, and XAL, as well as digital images available from the following web portals: Harvard University Herbaria and Libraries (https://kiki.huh.harvard.edu/databases/), Instituto de Biología, Universidad Nacional Autónoma de México's IBdata 4 (https://www.ibdatav4pgsql.virtualhalls.net/web/), JSTOR Global Plants (https://plants.jstor.org/), Missouri Botanical Garden's Tropicos© (https://tropicos.org/home?langid=66), Virtual Herbaria *JACQ* (https://herbarium.univie.ac.at/database/collections.htm), Muséum National d'Histoire Naturelle databases (https://science.mnhn.fr/institution/mnhn/search), and SEINet Portal Network (https://swbiodiversity.org/seinet/checklists/index.php). Our material of the new species was also compared with the original descriptions and illustrations (if they exist) of all species and synonyms assignable to *Funkiella*. An identification key to the 14 hitherto known species of *Funkiella* was prepared.

Molecular analysis:—We analyzed DNA sequences of 47 terminals that represent 39 of the 43 genera of Spiranthinae currently recognized (sensu Chase *et al.* 2015, Salazar *et al.* 2018, 2019). Each of thirty-eight genera was represented by a single species, but we included nine species of *Funkiella* to determine the phylogenetic position of the new species (Table 1).

Genomic DNA of the new species was extracted form silica gel-dried leaf tissue of a plant from the type locality (*Fortanelli-Martínez & Castillo-Lara 852*). DNA extraction, amplification (PCR), and sequencing were carried out using standard methods and primers described in Salazar *et al.* (2019). The PCR products were sent for bidirectional capillary (Sanger) sequencing to the Laboratorio de Biología Molecular of the Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City.

The chromatograms were assembled and edited with Geneious Prime® 2025.0.3 (https://www.geneious.com/). The newly generated contigs of each DNA region were aligned with additional sequences from our previous analyses, which are available from GenBank (Table 1). Alignment of the ITS, *matK-trnK*, and *trnL-trnF* regions was carried out separately with default settings of the online version of the program MAFFT v. 7 (Katoh & Standley 2013), with minor manual adjustment in Mesquite v. 3.81 (build 955; Maddison & Maddison 2023). All characters were treated as unordered and the individual gap positions were treated as missing data. We could not obtain sequences of the *trnL-trnF* region for two species, and the corresponding positions were treated as missing data (representing 1.6% of the positions in the concatenated matrix).

TABLE 1. Taxa studied, voucher information, and GenBank accessions.

Taxon	Voucher	GenBank accession		
		matK-trnK	***trnL-trnF***	**ITS**
Aulosepalum tenuiflorum (Greenm.) Garay	Mexico, *Salazar et al. 6150*, MEXU	AM884249	AJ544474	AJ539591
Beloglottis costaricensis (Rchb.f.) Schltr.	Mexico, *Soto & Cibrián 8129*, MEXU	AJ543920	AJ544475	AJ539492
Brachystele camporum (Lindl.) Schltr.	Argentina, *Radins s.n.*, MEXU (spirit)	MG755102	MG582314	MF464955
Buchtienia ecuadorensis Garay	Peru, *Simpson s.n.*, FLAS	MG755107	MG582297	MF464938
Coccineorchis cernua (Lindl.) Garay	Panama, *Salazar 6249*, MEXU (spirit)	AJ543930	AJ544485	AJ539502
Cotylolabium lutzii (Pabst) Garay	Brazil, *Martins da Costa 326*, BHCB	HG425363	HG425367	HG425360
Cyclopogon ovalifolius C.Presl	Peru, *Morón s.n.*, MEXU (spirit)	MG755118	MG582356	MF464999
Deiregyne eriophora (Robins. & Greenm.) Garay	Mexico, *Salazar et al. 6104*, MEXU	HE575499	FN641885	FN641873
Dichromanthus cinnabarinus (Lex.) Garay	Mexico, *Linares 4469*, MEXU	AJ543914	AJ544469	AJ539486
Eltroplectris calcarata (Sw.) Garay & H.R.Sweet	Brazil, *Soares s.n.*, MEXU (photograph)	AJ519450	AJ519452	AJ519448
Eurystyles cornu-bovis Szlach.	Panama, *Maduro 230*, FLAS	FN556172	FN556167	FN556162
Funkiella constricta (Szlach.) Salazar	Mexico, *Soto s.n.*, MEXU	AM902108	-	AM778173

.....continued on the next page

TABLE 1. (Continued)

Taxon	Voucher	GenBank accession		
		matK-trnK	***trnL-trnF***	**ITS**
Funkiella faucisanguinea (Dod) Salazar	Mexico, *Jiménez s.n.* (AMO)	AJ543924	AJ544479	AJ539496
Funkiella garciaperezii Salazar, Fortanelli & Cast.-Lara	Mexico, *Fortanelli & Castillo-Lara et al. 852*, MEXU	PV592022	PV592024	PV590873
Funkiella hyemalis (A.Rich. & Galeotti) Schltr.	Mexico, *Salazar et al. 6128*, MEXU	AJ543923	AJ544478	AJ539495
Funkiella markowskiana (Szlach.) Salazar & Soto Arenas	Mexico, *Reyes 5515*, MEXU	PV592023	PV592025	PV590874
Funkiella minutiflora (A.Rich. & Galeotti) Salazar & Soto Arenas	Mexico, *Salazar et al. 6129*, MEXU	AJ543922	AJ544477	AJ539494
Funkiella nutantiflora (Schltr.) Salazar & Soto Arenas	Mexico, *Suárez 2494*, MEXU (spirit)	MG755126	MG582364	-
	Mexico, *Salazar 7340*, MEXU	-	-	PV590872
Funkiella rubrocalosa (Schltr.) Salazar & Soto Arenas	Mexico, *Castillejos 385*, MEXU	MG755127	MG582365	MF465010
Funkiella valerioi (Ames & C.Schweinf.) Salazar & Soto Arenas	Costa Rica, *Blanco 2536*, USJ	MG755128	-	MF465009
Greenwoodiella wercklei (Schltr.) Salazar & R.Jiménez	Mexico, *Pérez-Bravo 100*, MEXU	LT600884	LT600901	LT600866
Hapalorchis aff. *lineatus* (Lindl.) Schltr.	Guatemala, *Salazar et al. 7699*, MEXU (spirit)	HE575502	HE575525	HE575515
Kionophyton sawyeri (Standl. & L.O.Williams) Garay	Mexico, *Salazar 7252*, MEXU	LT600873	LT600891	LT600856
Lankesterella gnoma (Kraenzl.) Hoehne	Brazil, *Warren s.n.*, K (spirit)	FN556173	FN556168	FN556163
Lyroglossa grisebachii (Cogn.) Schltr.	Brazil, *Batista et al. 3050*, BHCB	MG460449	MG460416	MG460384
Mesadenella cuspidata (Lindl.) Garay	Argentina, *Penz s.n.*, MEXU (photograph)	MF179019	MG582306	MF464946
Espinhassoa glaziovii (Cogn.) Salazar & J.A.N.Bat.	Brazil, *Batista et al. 3158*, BHCB	MG460450	MG460417	MG460385
Mesadenus polyanthus (Rchb.f.) Schltr.	Mexico, *Salazar 6370*, MEXU	AM902109	LT600902	AM778175
Nothostele acianthiformis (Rchb.f. & Warm.) Garay	Brazil, *Viana 767*, BHCB	FN868833	FN868836	FN868838
Odontorrhynchus variablis Garay	Chile, *Wallace 130/85*, CANB	AJ543926	AJ544481	AJ539498
Pelexia adnata (Sw.) Poit. ex Spreng.	Mexico, *Salazar 6012*, MEXU	AJ543929	AJ544484	AJ539501
Pachygenium orthosepalum (Rchb.f. & Warm.) Szlach., R.González & Rutk.	Brazil, *Smidt 768*, HUEFS	MG755145	MG582318	MF464961
Physogyne gonzalesii (L.O.Williams) Garay	Mexico, *Soto & Salazar10557*, AMO	LT600872	LT600890	LT600855
Pseudogoodyera wrightii (Rchb.f.) Schltr.	Cuba, *Mújica 4*, MEXU (photograph)	MG755148	MG582376	MF465021
Pteroglossa macrantha (Rchb.f.) Schltr. 1	Argentina, *Flachsland s.n.*, MEXU (photograph)	MF179016	MG582303	MF464943
Quechua glabrescens (T.Hashim.) Salazar & Jost	Ecuador, *Jost 7916*, QCA	HE575503	HE575526	HE575516
Sacoila lanceolata (Aubl.) Garay	Argentina, *Salazar et al. 9917*, MEXU (spirit)	MG755150	MG582307	MF464947
Sarcoglottis acaulis (J.E.Sm.) Schltr.	Trinidad, *Salazar 6346*, K (spirit)	AJ543928	AJ544483	AJ539500
Sauroglossum corymbosum (Lindl.) Garay	Peru, *Weigend et al. 5650*, M	MG755168	MG582312	MF464953
Sauroglossum elatum Lindl.	Argentina, *Cabassi s.n.* MEXU (spirit)	HG425365	HG425368	HG425361
Schiedeella transversalis (A.Rich. & Galeotti) Schltr.	Mexico, *Salazar 6073*, MEXU	-	AJ544470	-
	Mexico, *Salazar et al. 6105*, MEXU	AJ543915	-	AJ539487
Skeptrostachys paraguayensis (Rchb.f.) Garay	Argentina, *Radins s.n.*, MEXU (photograph)	MG755170	MG582309	MF464949
Sotoa confusa (Garay) Salazar	Mexico, *Hernández 3320*, MEXU	HE575506	FN641876	FN641865
Spiranthes spiralis (L.) Cheval.	U.K., *Bateman s.n.*, K (spirit)	AJ543918	AJ544473	AJ539490
Stenorrhynchos speciosum (Jacq.) Rich. ex Spreng.	Virgin Islands, *Salazar 7661*, MEXU (spirit)	HG425364	FN996959	FN996947
Svenkoeltzia congestiflora (L.O.Williams) Burns-Bal.	Mexico, *Salazar 6143*, MEXU	AJ543921	AJ544476	AJ539493
Thelyschista ghillanyi (Pabst) Garay	Brazil, *van den Berg 1435*, HUEFS	MG755181	MG582296	MF464937

We conducted a parsimony analysis of all the concatenated data, which has been shown to maximize resolution and support in our previous phylogenetic analyses of subtribe Spiranthinae of the same markers (Salazar *et al.* 2018 and references therein). The concatenated matrix consisted in 47 terminals and 4388 characters. The analysis was conducted with the package PAUP* (Swofford 2003) and consisted of 1000 replicates of random sequence addition

with tree bisection-reconnection (TBR) branch swapping and with the MULTREES option activated, saving up to 20 most- parsimonious trees per replicate to reduce the time spent swapping on large islands. Clade support was assessed with 500 bootstrap replicates (Felsenstein 1985), conducting heuristic searches as explained above. *Cotylolabium lutzii* was used as prime outgroup to root the Spiranthinae tree following prior molecular phylogenetic analyses of this subtribe (Salazar *et al.* 2016, 2018, 2019).

Results

Phylogenetic analysis:—Of the 4388 aligned characters, 669 were potentially informative to parsimony. The analyses found 8 equally most-parsimonious trees with a length of 3020 steps, Consistency Index excluding uninformative characters of 0.48 and Retention Index of 0.68. The strict consensus of the 8 trees, on which bootstrap percentages (BP) greater than 50 (from the bootstrap analysis) are indicated, is shown in Figure 1. All major clades found in previous molecular phylogenetic analyses of Spiranthinae were recovered, including *Cotylolabium lutzii* as the sole sister species of the remaining Spiranthinae, and the *Pelexia*, *Stenorrhynchos*, *Eurystyles* and *Spiranthes* clades. Overall relationships in Spiranthinae have been discussed in detail elsewhere (e.g. Salazar *et al.* 2003, 2016, 2018, 2019) and here we focus solely on the phylogenetic relationships in *Funkiella*.

Our analysis strongly supports the monophyly of *Funkiella* sensu Salazar *et al.* (2018), including *Microthelys* (BP 100), as well as its position as the sister of the clade [[*Aulosepalum—Beloglottis*]—[*Sotoa—Svenkoeltzia*]]. Within *Funkiella*, *F. rubrocalosa*, *F. garciaperezii* and *F. minutiflora* are the successive sisters of the rest, which form a strongly supported clade (BP 100) with two subclades: [*F. faucisanguinea—F. valerioi*] and [*F. hyemalis*—[*F. markowskiana*—[*F. constricta—F. nutantiflora*]]] (Figure 1).

Taxonomy

Funkiella garciaperezii Salazar, Fortanelli & Cast.-Lara, *sp. nov*. (Figures 2−4)

Type:—MEXICO. San Luis Potosí: Municipio Zaragoza, Sierra de Álvarez, montañas al sur del Ranchito de Juárez, 21°57’10.4” lat. N, 100°36’22.5” lon. W, 2050 m, herbácea perenne de 15 cm de alto, flores de color blanco con el labelo de color verdoso, frecuente localmente, 14 April 2016, *P. Castillo-Lara et al. 1049* (holotype: SLPM 053386!).

Similar to *Funkiella faucisanguinea* (Dod) Salazar, differing in the glabrous peduncle, rachis, ovary, and outer surface of the sepals; the dull brownish thickened area on the labellum hypochile; the prominent digitiform papillae on the ventral surface of the column; and the proportionately shorter, parallel pollinia.

Description:—Acaulescent herb 13−34 cm tall from the surface of the ground including the inflorescence. Roots 1−3, tuberoid, fasciculate, fusiform, obtuse, sometimes somewhat irregular, dull yellow, glabrous, 10−40 × 7−12 mm. Leaves deciduous, absent at flowering time, when present 1 or less commonly 2 per plant, slightly fleshy, shortly petiolate; petiole pale green, channeled, 5−20 × 1−2 mm; blade grayish green, lustrous, irregularly bullate, ovate-elliptic, acute, (10)25−53 × (7)10−35 mm. Inflorescence arising from the tip of the fascicle of roots, erect, 13−34 cm long, long-pedunculate; peduncle 10−24 cm long, 0.6−1.6 mm in diameter, glabrous, covered at base by a scarious, appressed, dark brown, obtuse to acute bract 11−23 mm long, remaining peduncle partially covered by 4−7 dull white to pale green, appressed, acute bracts 10−18 mm long; raceme more or less one-sided, 3.8−10.0 cm long, with 5−13 flowers opening in succession, with about 3 flowers open at a time, rachis glabrous, 0.2−0.4 mm in diameter. Floral bracts pale green, sometimes with brownish midvein, glabrous, clasping the ovaries and slightly shorter than them, ovate, acuminate, 1-veined, 4.5−6.2 × 1.8−2.8 mm. Flowers resupinate, horizontal upon anthesis but pointing upwards as the perianth withers, without perceptible fragrance. Dorsal sepal glabrous, lanceolate-oblong, acute, 3-veined, 4−5 × 1.0−1.2 mm. Lateral sepals glabrous, obliquely lanceolate-oblong, obliquely rounded to shallowly emarginate, 2-veined, 5.9−6.3 × 1.3−1.4 mm, decurrent on the ovary for about 1.5 mm to form a nectar chamber, which is barely visible from outside except when seen against the light. Petals with the upper margin adherent to the dorsal sepal and long-decurrent (about 2 mm) to the column foot, free portions obliquely oblanceolate-spathulate, rounded, 1-veined, slightly twisted and shallowly channeled on the basal one-half, the margin free from the dorsal

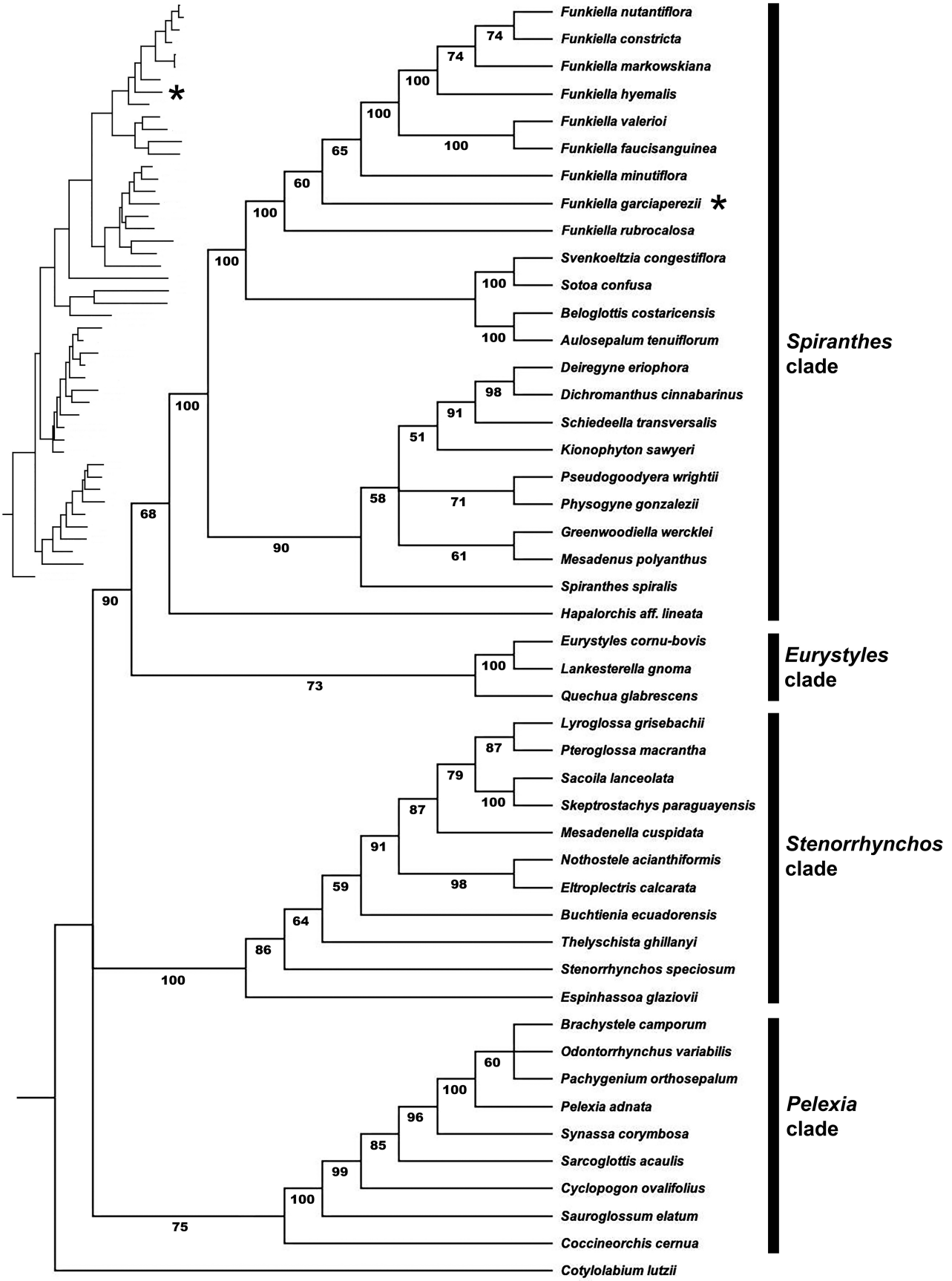

FIGURE 1. Phylogenetic relationships in *Funkiella* and other Spiranthinae. The main tree is the strict consensus of the eight equally most-parsimonious trees of the analysis of concatenated nrITS, *matK-trnK* and *trnL-trnF* DNA sequences. Numbers under the branches are bootstrap percentages (> 50). The inset on the upper left-hand is one of the eight most-parsimonious trees drawn with branch lengths proportional to the number of changes. An asterisk (*) indicates the position of *Funkiella garciaperezii*.

sepal protruding slightly and broadly rounded, apex recurved in natural position, free portion 3.5−4.2 × 0.8−1.3 mm. Labellum sessile, pandurate, with a papillose, slightly retrorse, semiorbicular thickening (nectar gland) at each side of the base, 3.8−4.3 mm total length, with 7 main veins from the base, which branch slightly towards the sides above the middle of the hypochile, veins not reaching the margins; hypochile widely cuneate towards the base, expanded above to each side into a broadly rounded lobe with crenulate margin which in natural position adheres to the sides of the column, provided with 2 oblong-elliptic dorsal thickenings, internally pubescent especially along the center, 2.4−2.6 mm long, ca. 1.8 mm wide at the base, 2.2−3.0 mm wide between the marginal lobes; epichile transversely elliptic, margins undulate, crenate and papillose (papillae conical), apex truncate, inner surface pilose, the hairs digitiform, single-celled, translucent, longest centrally and gradually reduced to conical papillae towards the margins, ca. 1.4 × 2.1−2.8 mm. Column subclavate, papillose ventrally, the papillae finger-shaped, somewhat retrorse, apex with a triangular, membranaceous lobe at each side of the clinandrium, 2.0−2.5 × 0.9−1 mm, base projected into a column foot ca. 1.5 mm long that becomes gradually glabrous towards the base. Anther accounting for most of the length of the column, concave by the lateral margins curved downwards, when spread out suborbicular, obtuse at apex, cordate at base, shallowly 2-celled, 1.5−1.8 mm long and wide. Rostellum shortly and widely triangular, obscurely apiculate upon removal of the pollinarium. Pollinarium oblong, made up of two pale yellow, longitudinally cleft, shortly linear pollinia parallel throughout their lenght, ca. 2 mm long, with a semi-ellipsoid, ventral viscidium ca 0.4 mm long. Stigma ovate, flat, ca. 0.6 mm long. Ovary subcylindrical-fusiform, arcuate on the distal 1/3, slightly twisted, glabrous, 4.3−6.0 × 0.7−1.25 mm. Capsule not seen.

Distribution and habitat:—*Funkiella garciaperezii* is known so far from a single population located near the town Ranchito de Juárez, W of La Salitrera, municipio of Zaragoza, San Luis Potosí, Mexico. The plants live on rocks covered with mosses and lichens on a NNE-facing, 30−45° slope at 2014 m elev. The overall substrate is made up of rhyolites with grayish brown leptosols. The vegetation consists of *Pinus cembroides* Zuccarini (1832: 392) woodland mingled with oak forest with *Quercus eduardi* Trelease in Standley (1922: 121), *Q. grisea* Liebmann (1854: 171), and *Q. potosina* Trelease (1924: 84). Other conspicuous floristic elements in the area are *Juniperus flaccida* Schlechtendal (1838: 495), *Dodonaea viscosa* Jacquin (1760: 19), *Mimosa biuncifera* Bentham (1839: 12), *Agave salmiana* Otto ex Salm-Dyck (1859: 88), *A. filifera* Salm-Dyck (1834: 309), *Opuntia robusta* Wendland ex Pfeiffer (1837: 165), *O. megacantha* Salm-Dyck (1834: 363), *O. engelmannii* Salm-Dyck ex Engelmann in Gray (1850: 207), *O. tomentosa* Salm-Dyck (1822: 8), *Ferocactus histrix* (De Candolle 1828: 115) Lindsay (1955: 171), *Pittocaulon praecox* (Cavanilles 1794: 23) Robinson & Brettell (1973: 453), *Pachyphytum* Link, Klotzsch & Otto (1841: 9) *sp.*, *Echeveria agavoides* Lemaire (1863: 78), *Sedum palmeri* Watson (1882: 355), *S. furfuraceum* Moran (1961: 103), *Ponthieva schaffneri* (Reichenbach 1855: 238) Greenwood (1990: 56), *Tillandsia recurvata* (Linnaeus 1753: 287) Linnaeus (1762: 410), and *T. usneoides* (Linnaeus 1753: 287) Linnaeus (1762: 411). Leaves present only during the rainy season and shortly after, from August to November. Flowering in March and April. Fruits were not observed.

Etymology:—Named after our friend and colleague, José García Pérez, botanist and former Curator of the herbaria CHAPA (Colegio de Postgraduados, Montecillos) and SLPM (Universidad Autónoma de San Luis Potosí), who during his nearly 60 years of professional life collaborated closely with other outstanding Mexican botanists, such as Jerzy Rzedowski and Efraím Hernández Xolocotzi.

Conservation status:—The new species is known so far from a single population consisting of about 20−25 plants growing on several mossy rocks. The area is subjected to considerable anthropogenic disturbance, including forest clearing and cattle grazing, but living on rocks affords some protection to the observed individuals. The plants are very inconspicuous and easily go unnoticed if not searched for specifically, which, together with the fact that there are large expanses of unexplored areas in the neighboring Sierra de Álvarez with potentially suitable habitats for this species, suggests that the species might be less uncommon than the available information indicates. The category of Data Deficient (DD) is suggested, pending further field studies aimed at determining objectively its conservation status (see IUCN Standards and Petitions Committee 2024).

Additional specimen examined (paratype):—**MEXICO.** San Luis Potosí, Ranchito de Juárez, piñonar con algunos rodales de encinar, *Pinus cembroides*, *Quercus eduardii*, *Q. grisea*, *Q. potosina*, *Juniperus flaccida*, *Dodonaea viscosa*, *Mimosa aculeaticarpa*, *Agave salmiana*, *Opuntia robusta*, ladera con exposición NNO, pendiente de 30° a 45°, suelo pardo grisáceo, riolitas, 2040 m, hierba de 15 cm de altura, flores blancas con tintes rosados, labelo blanco con tres líneas verdes, 20 March 2024, *J. Fortanelli-Martínez & P. Castillo-Lara 852* (MEXU!).

Taxonomic discussion:—Our phylogenetic analysis recovered *F. garciaperezii* in a relatively early-diverging position within the genus, as the sister of a clade including all the other *Funkiella* species analyzed excepting *F. rubrocalosa* (Figure 1). Morphologically, *F. garciaperezii* is most similar to *F. faucisanguinea* (Figure 5) in that both have 1−3 fusiform, tuberous roots, 1 (uncommonly 2) ovate-elliptic, shortly petiolate leaf present only during the rainy

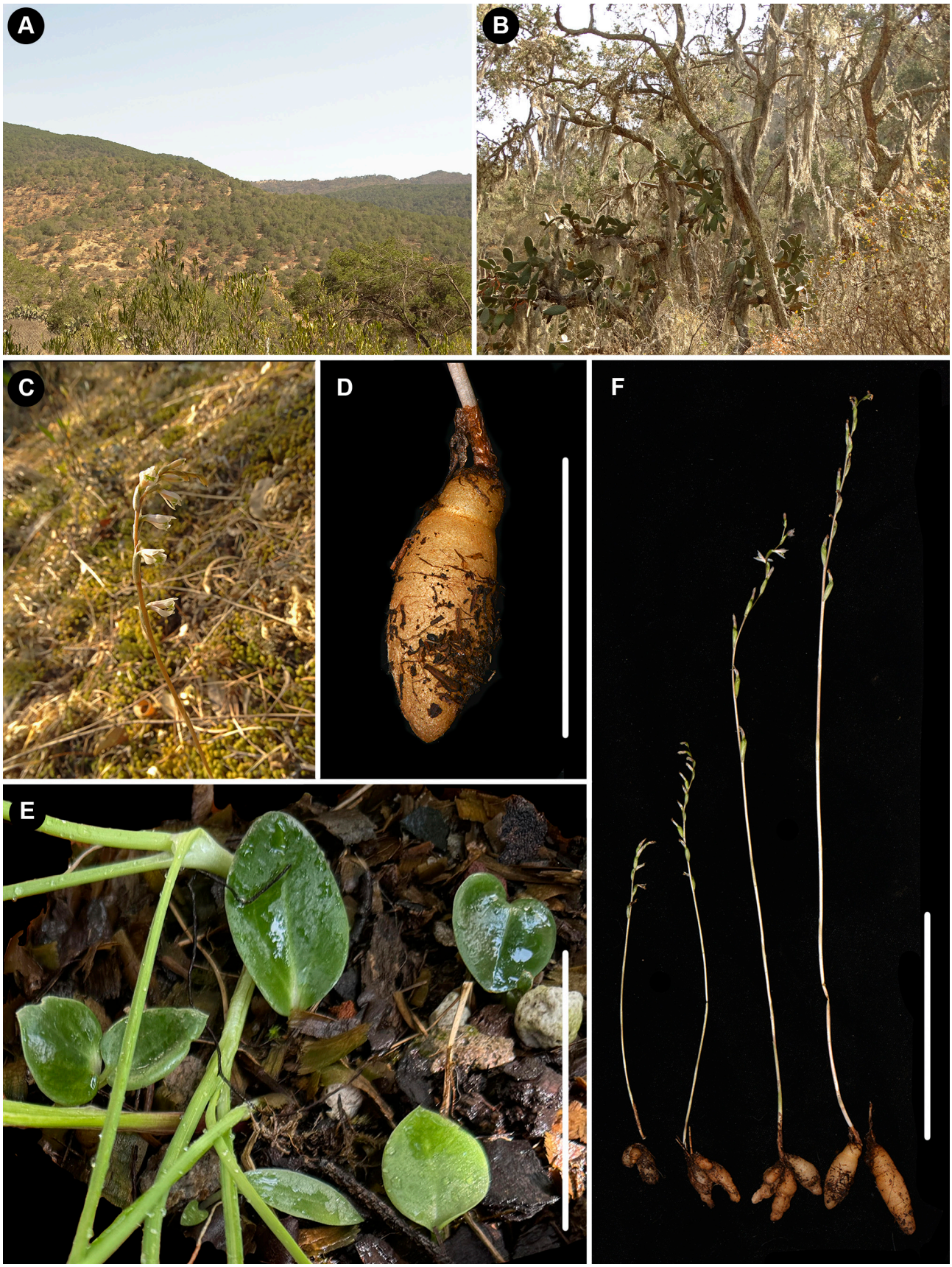

FIGURE 2. *Funkiella garciaperezsii*. **A.** Overview of the habitat. **B.** Detail of the oak forest with *Opuntia tomentosa* and *Tillandsia usneoides*. **C.** Plant flowering *in situ* during the dry season after shedding the leaves. **D.** Root. E. Group of plants with functional leaves during the rainy season. F. Several flowering individuals showing variation in plant size. Scale bars: D, E = 4 cm; F = 10 cm. (A–C from *Castillo-Lara et al. 1049*, D–F from *Fortanelli-Martínez & Castillo-Lara et al. 852.*). Photographers: Javier Fortanelli-Martínez (A–C) and Gerardo A. Salazar (D–F).

season, more or less one-sided raceme with each flower subtended by a prominent, herbaceous bract, short campanulate, predominantly white flowers, and a pandurate, prominently papillose labellum with a marginally thickened, somewhat retrorse, rounded nectar gland at each side of the base, and a transverse epichile with crenate margins and green veins (Figures 3F, 4, 5C). However, *F. garciaperezii* has glabrous peduncle, rachis, ovary, and outer surface of the sepals (Figure 3A; *vs*. sparsely glandular-pubescent, including the bases of the sepals, in *F. faucisanguinea*, Figure 5A); the thickened area of the labellum hypochile is pale dull brownish (Figures 3E, F, *vs*. bright red, Figures 5C, E); the veins of the hypochile are bright green and branched (Figures 3A, C, F, *vs.* dull green and unbranched, Figures 5A, B); the ventral surface of the column is densely covered by somewhat retrorse, digitiform papillae (Figures 4D, E, *vs.* shortly digitiform, Figure 5F); and the pollinia are shortly linear and parallel throughout their length (Figure 3I, *vs*. long linear pollinia that diverge from each other from below the middle, Figure 5D; see also McVaugh 1985: Figure 106).

Funkiella constricta (Szlach.) Salazar, *comb. nov. Galeottiella constricta* Szlachetko (1994: 427). *Microthelys constricta* (Szlachetko) Szlachetko (1996: 852).

Type:—MEXICO. Valle de Mexico: Tacubaya, June 1866, [*E.*] *Bourgeau 243b* (holotype: P, not seen; analysis of a flower from the holotype in Szlachetko 1994: 428!).

Taxonomic discussion:—See the clarification of the identity of an accession included as "*F. rubrocalosa*" in previous molecular phylogenetic analyses by Salazar *et al.* (2018) but corrected here to *F. constricta* in the Taxonomic discussion section of *F. rubrocalosa*, below.

Funkiella faucisanguinea (Dod) Salazar, *comb. nov. Spiranthes faucisanguinea* Dod (1978: 60). *Schiedeella faucisanguinea* [sic] (Dod) Burns-Bal. (1989: 171), without basionym year. *Schiedeella faucisanguinea* (Dod) Burns-Bal. ex Espejo & López-Ferrari (1998: 74). (Figure 4).

Type:—DOMINICAN REPUBLIC. San José de Ocoa: Valle Nuevo, creciendo terrestre entre plantas de *Baccharis myrsinites* Persoon (1807: 424) entre hojas de pino en un pinar, no lejos de la pirámide, 2200 m, 23 January 1973, *D. Dod 618* (holotype: SDM; isotypes AMES 00104442!, NY, SEL, US).

= *Schiedeella arizonica* Brown en Brown & Coleman (2000: 3). Type:—U.S.A. Arizona: Pima County, Marshal Gulch, Santa Catalina Mountains, June 1906, *J.J. Thornber 5563* (holotype: ARIZ 12503!).

= *Schiedeella arizonica* P.M.Br. f. *virescens* Brown (2006: 10). Type:—U.S.A. Arizona: Cochise County, Coronado National Forest, along trail to Rustler's Park, 6 June 1998, *P.M. Brown s.n.* (holotype: Photograph in Figure 4 of Brown 2006: 11!).

Taxonomic discussion:—This species has been incorrectly referred to as *Spiranthes parasitica* Richard & Galeotti (e.g. Correll 1950, McVaugh 1985), *Schiedeella parasitica*, and *Funkiella parasitica* (Richard & Galeotti 1845: 32) Salazar & Soto Arenas in Solano *et al.* (2011: 52), but the type specimen of *Spiranthes parasitica* (Ciudad Real, 6800 [ft], *Linden 1221*, P, barcode P00345823, digital image!) lacks the bright red thickening of the labellum and differs in several floral morphological features, seemingly representing a genuine member of *Schiedeella* (Burns-Balogh 1989b, Szlachetko 1992: Figure 15).

Funkiella faucisanguinea has been included, either as *Schiedeella parasitica* or *Funkiella parasitica*, in several molecular phylogenetic analyses (e.g. Salazar *et al.* 2003, 2016, 2018). All such analyses have shown that it belongs in a clade that also includes *Funkiella hyemalis*, the type species of *Funkiella*, with which it shares the bright red thickening on the labellum hypochile (Salazar *et al.* 2018: Figure 2). The phylogenetic analysis conducted in the present work corroborates such a relationship (Figure 1), and the new combination in *Funkiella* is thus required.

We agree with Szlachetko (1992), Solano *et al.* (2011), and Catling (2024) in that *Schiedeella arizonica* Brown in Brown & Coleman (2000: 3) is conspecific with *F. faucisanguinea*, hence we list the former as a synonym of the latter. The plant described as *Schiedeella arizonica* f. *virescens* Brown (2006: 10) represents an albinistic form of *F. faucisanguinea* in which the thickened areas of the hypochile are yellow instead of bright red. It is worth noting that Brown's description was published one year in advance of the critical date of 1 January 2007, on and after which, according to Article 40.4 of the Shenzhen Code (Turland *et al.* 2018), the holotype of a new species or infraspecific taxon of extant plants must be specimen, not an illustration.

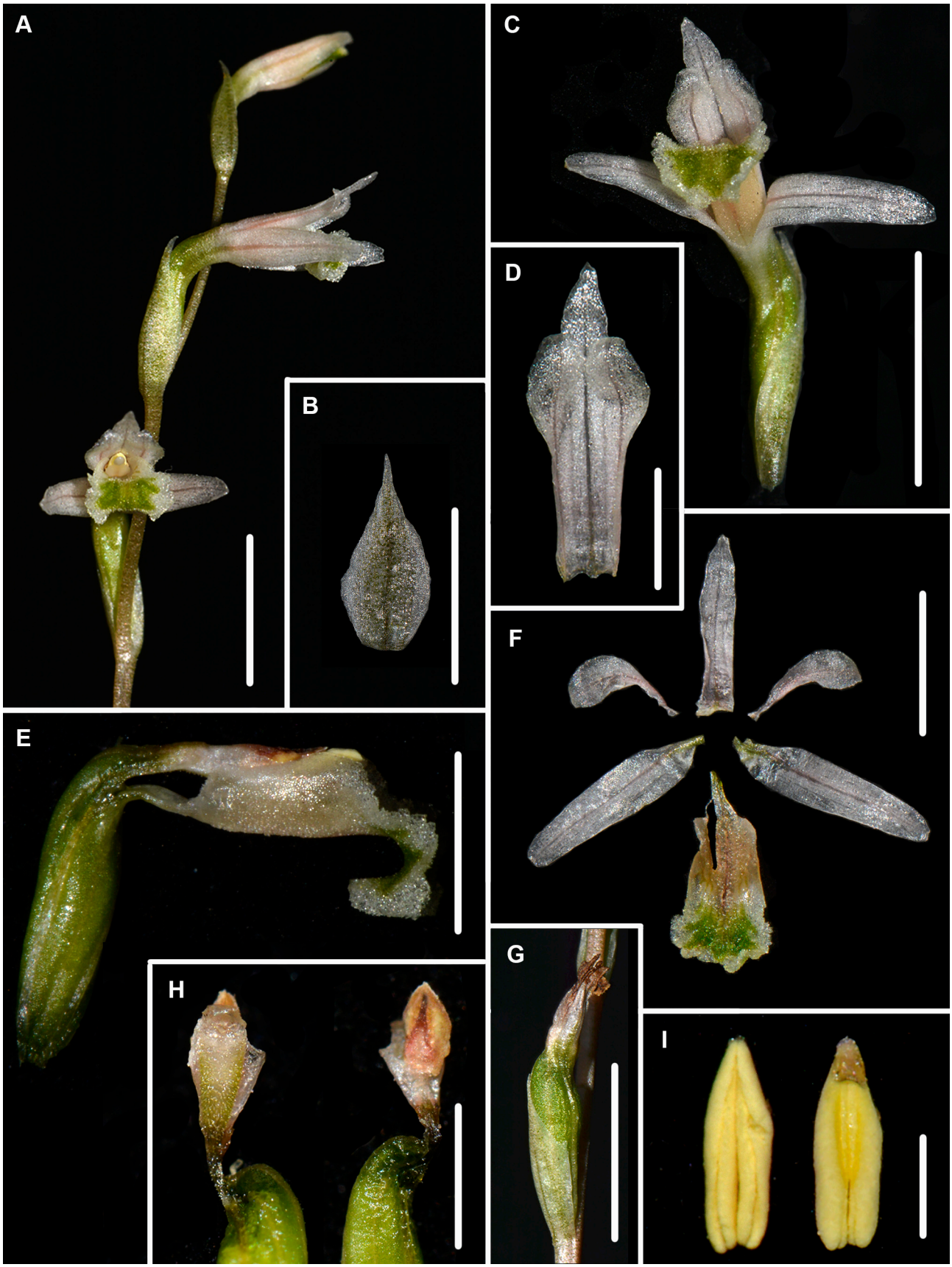

FIGURE 3. *Funkiella garciaperezii* (from *Fortanelli & Castillo-Lara et al. 852*). **A.** Raceme. **B.** Floral bract, spread out. **C.** Flower, oblique view from below. **D.** Dorsal sepal and petals in natural position. **E.** Flower from side with the sepals and petals excised, showing the position of labellum and column. **F.** Perianth dissection. **G.** Old flower pointing upward. **H.** Column from below (left) and above (right). **I.** Pollinarium from above (left) and below (right). Scale bars: A–C, G = 5 mm, D, H = 2 mm, E = 3 mm, F = 4 mm, I = 1 mm. Photographer: Gerardo A. Salazar.

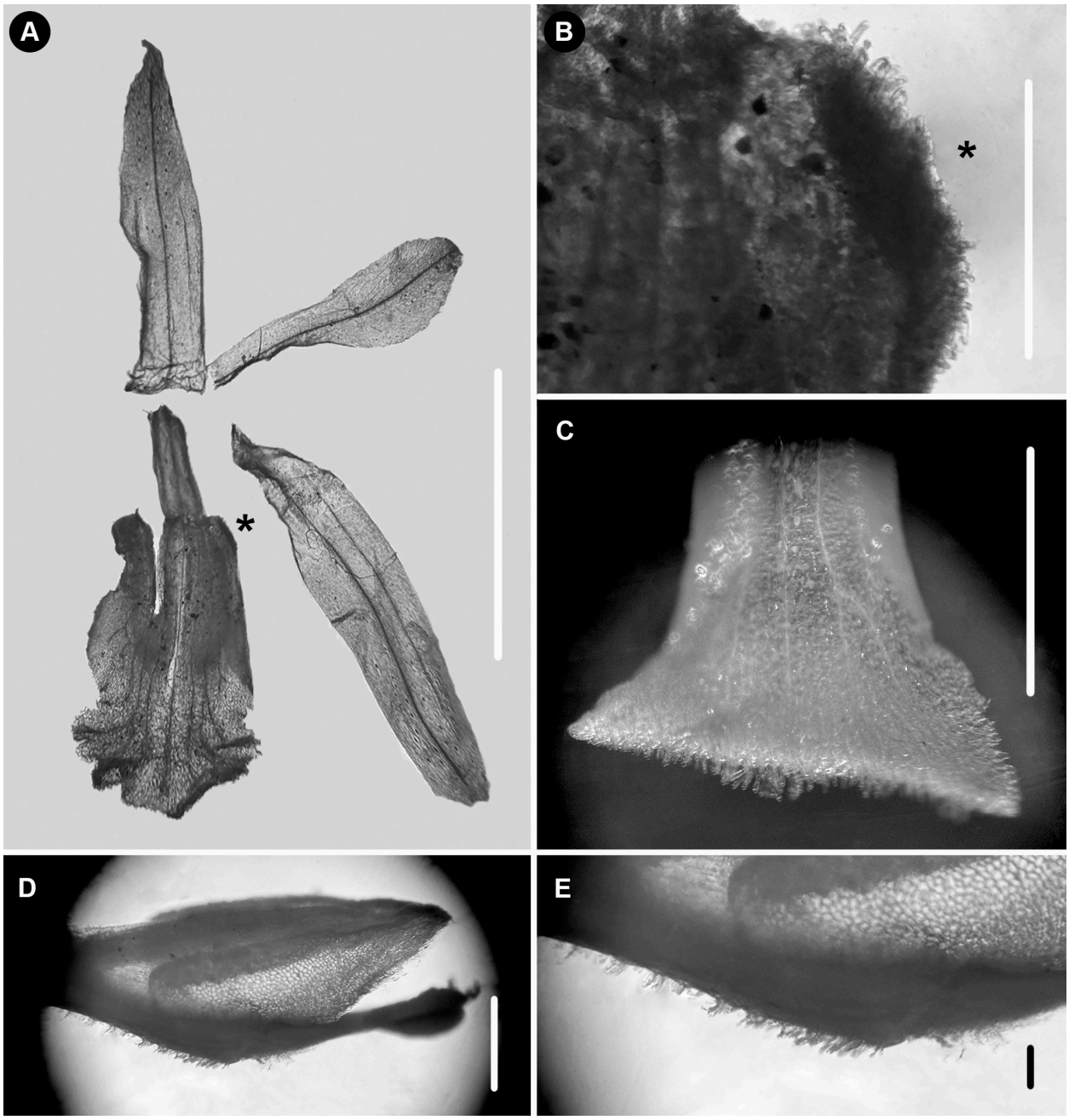

FIGURE 4. *Funkiella garciaperezii* (from *Fortanelli & Castillo-Lara et al. 852*). **A.** Dissection of the perianth illuminated from behind. **B.** Nectar gland of the labellum (marked with * in A). **C.** Labellum epichile with the distal one-half folded backwards to show the elongated papillae on its inner surface. **D.** Column illuminated from behind showing the digitiform ventral papillae. **E.** Detail of D. Scale bars: A = 4 mm, B, D = 0.5 mm, C = 2 mm, E = 0.1 mm. Photographer: Gerardo A. Salazar.

Funkiella intagana (Dodson & Dressler) Salazar, *comb. nov*. *Ecuadoria intagana* Dodson & Dressler in Dodson (1994: 133). *Microthelys intagana* (Dodson & Dressler) Szlachetko (1996 : 853).

Type:—ECUADOR: Imbabura: Road from Otovalo [Otavalo] to Intag via Lago Cuicocha, km 46, 2900 m, *C.H. Dodson & A. Hirtz 16413* (holotype: MO ex RPSC No. 0003101, digital image!).

Taxonomic discussion:—The line drawing published in the protologue of *Ecuadoria intagana* (Dodson 1994: 133) is inaccurate in depicting the roots as thin and cylindrical, whereas the holotype bears tuberous, fusiform roots characteristic of *Funkiella*. It is worth noting that the holotype, as all of Dodson's specimens of Orchidaceae originally housed at the Rio Palenque Science Center in central-western Ecuador (RPSC), were transferred to MO (Thiers continuously updated).

FIGURE 5. *Funkiella faucisanguinea* (from *Soto & Soto 10902*). **A.** Inflorescence. **B.** Another view of inflorescence. **C.** Labellum. **D.** Pollinarium from above. **E.** Flower from side with the lateral sepals excised. **F.** Column from side showing the short ventral papillae (from a flower preserved in ethanol). Scale bars: A, B, E = 3 mm, C = 2 mm, D, F = 1 mm. Photographer: Gerardo A. Salazar.

Funkiella muscicola (Garay & Dunst.) Salazar, *comb. nov*. *Spiranthes muscicola* Garay & Dunsterville (1966: 280). *Schiedeella muscicola* (Garay & Dunsterville) Garay & Dunsterville (1979: 915). *Stalkya muscicola* (Garay & Dunsterville) Garay (1982: 372).

Type:—VENEZUELA: Mérida: Pregonero road above Bailadores, epiphytic among mosses on tree trunk at about 10,000 ft, *L.A. Garay s.n.* (holotype: AMES, flower in spirit; illustration based on the original collection in Garay & Dunsterville 1966: 281!).

Taxonomic discussion:—This species shows the distinguishing features of *Funkiella* as understood here, including the high-elevation habitat, tuberous root, and shortly tubular flowers with centrally thickened, papillose labellum. Salazar (2003c) noticed the similarities between monospecific *Stalkya* and *Microthelys*, which we consider a synonym of *Funkiella*.

Funkiella rubrocalosa (Robinson & Greenman) Salazar & Soto Arenas in Solano *et al.* (2011: 52). *Spiranthes rubrocalosa* Robinson & Greenman (1895: 165). *Schiedeella rubrocalosa* (Robinson & Greenman) Balogh (1981: 39). *Microthelys rubrocalosa* (Robinson & Greenman) Garay (1982: 338). *Galeottiella rubrocalosa* (Robinson & Greenman) Szlachetko (1991a: 64).

Lectotype (designated by Williams 1951):—Mexico. [Estado de México:] In dry ledges under firs, Sierra de las Crucis [Cruces], 20 August, 1892, *Pringle 5326* (GH 1752!).

= *Spiranthes porphyricola* Schlechter (1906: 18). *Funkiella porphyricola* (Schlechter) Salazar & Soto Arenas in Solano *et al.* (2011: 52).

Lectotype (first step lectotype designated by Szlachetko & Rutkowski in Rutkowski *et al.* 2008: 137; second step designated here):—MEXICO. Chihuahua: Im külhem Porphyrgeröl, besonders unter *Arbutus*, auf der Sierra Madre, blühend und fruchtend im Oktober 1887, *Pringle 1373* (US 814858!; isolectotypes: AMES 71824!; NDG 012312, digital image!; VT UVMVT024233, digital image!; US 42138!).

Taxonomic discussion:—In describing *Spiranthes rubrocalosa*, Robinson & Greenman (1895) cited two different collections (i.e., syntypes): "Collected by C.G. Pringle, chiefly under *Arbutus*, in cool porphyritic gravel, Sierra Madre, Chihuahua, October 1887 (*No. 1373*); and on dry ledges under firs, Sierra de las Crucis [sic], 20 August, 1892 (*No. 5326*)." Williams (1951: 56) noted that "Robinson and Greenman did not indicate which of two Pringle collections cited they considered to be the type. Number 1373, which Ames apparently considered to be the type, is a specimen well advanced in fruit while the other specimen, number 5326 is in better condition. Perhaps, for this reason, the latter should be considered the type even though it is the second specimen cited. It is quite obvious that both specimens were carefully considered in preparing the original description." We concur with McVaugh (1985: 333) in considering that Williams (1951) carried out the lectotypification of *S. rubrocalosa* with specimen *Pringle 5326* (GH 1752). Szlachetko & Rutkowski (in Rutkowski *et al.* 2008) attempted to lectotypify *S. rubrocalosa*, apparently unaware both of Williams' (1951) proposal and of the fact that two different collections were involved, as they indicated only *Pringle 1373* as the type collection of *S. rubrocalosa*. In any event, the earlier lectotypification by Williams (1951) makes their purported lectotypification superfluous. Szlachetko & Rutkowski (in Rutkowski *et al.* 2008) also intended to lectotypify *S. porphyricola* with a duplicate of *Pringle 1373* housed at US, but they failed to specify which one of the two duplicates of that collection found there would be the lectotype (both specimens bear handwritten annotations by Szlachetko dated 9 September 1990, so he was aware of their existence). Here we select the specimen *Pringle 1373* with catalog number US 814858 as lectotype of *S. porphyricola*.

Salazar & Soto Arenas (in Solano *et al.* 2011) transferred both concepts, *Spiranthes rubrocalosa* and *S. porphyricola*, to *Funkiella* considering that the two (syn)type collections represented two different species. Subsequent examination of specimens throughout the distribution range of the species failed to substantiate that belief, and *F. porphyricola* is here considered as a synonym of *S. rubrocalosa*. The accession included in the analyses of Salazar *et al.* (2018) as "*Funkiella porphyricola*" is corrected in the present analysis to *F. rubrocalosa*, whereas the accession referred there to as "*F. rubrocalosa*" actually represents the species described as *Galeottiella constricta* Szlachetko (1994: 427). The latter is deeply nested in *Funkiella* and is transferred here to that genus to achieve monophyly (Figure 1; see transfer above).

Key to the species of *Funkiella*

1. Colored areas of the hypochile of the labellum orange or bright red 2
- Colored areas of the hypochile of the labellum yellow or brownish 10
2. Floral segments ≥ 10 mm long 3
- Floral segments ≤ 8 mm long 5
3. Leaves present at flowering time; sepals and petals acuminate ..... *F. hyemalis* (A.Rich. & Galeotti) Schltr.
- Leaves absent at flowering time; sepals and petals obtuse to acute 4
4. Plants with conspicuous stolons; labellum constricted above the middle, ≥ 18 mm long ..... *F. stolonifera* (Ames & Correll) Garay
- Plants without stolons; labellum not constricted or obscurely so above the middle, 10-11 mm long ..... *F. versiformis* Szlach.
5. Floral segments ≤ 3 mm long; labellum apically trilobulate, the central lobule acute ..... *F. minutiflora* (A.Rich. & Galeotti) Salazar & Soto Arenas
- Floral segments ≥ 4 mm long; labellum not trilobulate apically 6
6. Labellum subrectangular below, abruptly expanded above into a transverse epichile ..... *F. faucisanguinea* (Dod) Salazar
- Labellum variously shaped but never expanded above into a transverse epichile 7
7. Flowers nutant; labellum constricted on the apical 1/4 into an epichile distinctly narrower that the hypochile ..... *F. nutantiflora* (Schltr.) Salazar & Soto Arenas
- Flowers horizontal, ascending or facing upwards vertically; labellum not constricted on the apical 1/4 into an epichile distinctly

narrower than the hypochile 8
8. Flowers facing upwards vertically ..... *F. markowskiana* (Szlach.) Salazar & Soto Arenas
- Flowers horizontal or ascending 9
9. Flowers horizontal; labellum not constricted in the apical 1/3 into an epichile as wide as the hypochile ..... *F. rubrocalosa* (B.L.Rob. & Greenm.) Salazar & Soto Arenas
- Flowers ascending; labellum constricted in the apical 1/3 into an epichile as wide as the hypochile ..... *F. valerioi* (Ames & C.Schweinf.) Salazar & Soto Arenas
10. Labellum subrectangular below and abruptly expanded above into a transverse epichile ..... *F. garciaperezii* Salazar, Fortanelli & Cast.-Lara
- Labellum variously shaped but never expanded above into a transverse epichile 11
11. Labellum oblong, twice as long as wide or longer 12
- Labellum elliptic-ovate to obovate, less than twice as long 13
12. Labellum conspicuously constricted near the middle ..... *F. constricta* (Szlach.) Salazar
- Labellum not constricted near the middle ..... *F. laxispica* (Catling) Salazar & Soto Arenas
13. Roots 2 or more; floral segments green, labellum without green veins; labellum obovate ..... *F. intagana* (Dodson & Dressler) Salazar
- Root single; floral segments cream with green bases, labellum with green veins; labellum elliptic-ovate ..... *F. muscicola* (Garay & Dunst.) Salazar

Conclusion

This study provided additional support to previous ones in which the genus *Funkiella*, including *Microthelys*, is recovered as a strongly supported natural (i.e., monophyletic) assemblage of species specialized to live in montane habitats throughout the Neotropics, which, in spite of variation in floral size and details of the rostellum, are diagnosed by the possession of thickened areas on the labellum hypochile that can be orange to bright red (e.g., *F. faucisanguinea*, *F. hyemalis*) or not (e.g., *F. garciaperezii*, *F. valerioi*). Future phylogenetic work should focus on broadening the taxonomic sampling to include Andean representatives of the genus, which have not been available for molecular studies. Moreover, additional field work is required to attain an objective picture of the conservation status of seemingly uncommon taxa like the new species formally described here as *Funkiella garciaperezii*.

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