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Source: Systematic Botany, 37(2):339-346. 2012.

Published By: The American Society of Plant Taxonomists

URL: <http://www.bioone.org/doi/full/10.1600/036364412X635395>

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Galactodenia, a New Genus of Grammitid Ferns Segregated from *Terpsichore* (Polypodiaceae)

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Communicating Editor: Thomas L. P. Couvreur

Abstract—Polyphyly among genera of grammitid ferns has necessitated several nomenclatural innovations. The genus *Galactodenia* is here described to accommodate two species that were previously placed in *Terpsichore*, *G. delicatula* and *G. subscabra*, and three new species that are here described, *G. pumila*, *G. parriseae*, and *G. vareschii*. In recent phylogenetic studies, the two previously described species form a clade sister to the clade of *Lellingeria*, *Melpomene*, and *Stenogrammitis*, and are not closely related to either *Terpsichore* or *Alansmia*, two genera that they have been previously considered close to. *Galactodenia* can be diagnosed by having concolorous rhizome scales, monomorphic fronds with non-calcareous hydathodes, and hairs that are simple and 2-celled or 1-furcate and 3-celled with large translucent clavate glands that produce a viscid exudate. Most species of *Galactodenia* are found in montane forests from southern Mexico and the West Indies to Bolivia, from 2,000–4,000 m. One exception to this is *G. pumila*, which is known only from isolated granite inselbergs at 1,500 m, in southwestern Venezuela. All five species are illustrated, and a distribution map and a key are provided.

Keywords—Epiphyte, inselberg, montane, morphology, Neotropical, taxonomy.

Systematics of Neotropical grammitids have undergone numerous changes following a series of molecular phylogenetic studies (Ranker et al. 2004; Labiak et al. 2010a, 2010b; Sundue et al. 2010; Hirai et al. 2011) demonstrating the polyphyly of three prominent genera: *Lellingeria* A. R. Sm. & R. C. Moran (sensu Smith et al. 1991), *Micropolypodium* Hayata (sensu Smith 1992), and *Terpsichore* A. R. Sm. (sensu Smith 1993). Together, these genera account for ca. 60% of the Neotropical grammitid flora. Consequently, numerous nomenclatural innovations have been proposed, including the establishment of *Leucotrichum* Labiak and *Stenogrammitis* Labiak to accommodate portions of the former *Lellingeria*, *Moranopteris* R. Y. Hirai & J. Prado to accommodate the Neotropical species of the former *Micropolypodium*, and *Alansmia* M. Kessler & Moguel and *Ascogrammitis* Sundue to accommodate portions of the former *Terpsichore*. These new genera are sufficient to house most of the Neotropical species in need of new placement; however ca. 35 species, currently residing under *Terpsichore*, are still pending placement in suitable genera.

Here, we establish *Galactodenia* to accommodate *Terpsichore delicatula* (M. Martens & Galeotti) A. R. Sm., *T. subscabra* (Klotzsch) B. León & A. R. Sm., and three new species (described below) that have been discovered as a result of our recent efforts to revise the Neotropical grammitid flora (León and Smith 2003; Sundue and Kessler 2008; Sundue 2010a; Labiak et al. 2010a; Labiak 2011; Kessler et al. 2011; Rouhan et al. 2012).

The two previously described species treated here (*Terpsichore delicatula* and *T. subscabra*) were included by Smith (1993) under “group 3” of his informal infrageneric classification for *Terpsichore*. This group was based upon *Terpsichore lanigera* (Desv.) A. R. Sm., and was recently recognized as a new genus, *Alansmia*, by Kessler et al. (2011). Molecular phylogenetic analyses, however, indicate that both *Terpsichore* s. s. and

Alansmia are distantly related to *T. delicatula* and *T. subscabra*, which are instead supported as sister to the clade that includes *Lellingeria*, *Melpomene* A. R. Sm. & R. C. Moran, and *Stenogrammitis* (Ranker et al. 2004; Lehnert et al. 2009; Labiak et al. 2010b; Sundue et al. 2010).

Sundue et al. (2010) diagnosed the clade of *Terpsichore delicatula* and *T. subscabra*, and distinguished it from related genera by having dorsiventral rhizomes with ventral root insertion, concolorous rhizome scales with glandular margins, monomorphic fronds with non-calcareous hydathodes, and hairs that are simple and 2-celled or 1-furcate and 3-celled, with large translucent clavate glands that produce a viscid exudate (see op. cit. for additional characters). We maintain most of those characters here; however, we expand the description of the rhizome to include radially symmetrical plants with radial root insertion, and the rhizome scales to include non-glandular margins.

The characters of the glandular hairs alone are sufficient to distinguish *Galactodenia* from nearly all other grammitid ferns, the one exception being *Chrysogrammitis* Parris, a genus of two species from southeastern Asia (Parris 1998, 2009). Glandular hairs of *Chrysogrammitis* are superficially similar to those of *Galactodenia*, but differ by being more deeply orange, shinier, and by their more enlarged terminal cell. *Chrysogrammitis* can further be distinguished by lacking hydathodes. Phylogenetic analyses of cpDNA sequences (Ranker et al. 2004; Sundue et al. 2010) do not support a close relationship between the two genera; thus their similarity is interpreted as an example of the striking convergent morphological patterns found among the grammitid ferns.

Given the topology of current phylogenetic hypotheses and abundant diagnostic character data, we choose to provide a new name for the clade that includes *Terpsichore delicatula*, *T. subscabra*, and the three species described below. We believe that alternate nomenclatural solutions, such as

combining these five species along with *Lellingeria* (49 species), *Melpomene* (29 species), and *Stenogrammitis* (25 species) into a single genus (*Lellingeria* is the oldest name) would be counter-productive because it would replace several moderately-sized, morphologically uniform and diagnosable genera with a large heterogeneous genus that could not easily be diagnosed by morphological characters alone.

MATERIALS AND METHODS

Selected specimens were examined from the following herbaria: BM, BR, COL, DS, F, IEB, K, LPB, MERF, MEXU, MICH, MO, NY, PMA, PORT, UC, US, VEN, VT, and XAL. We cite a single specimen per political administrative division. Detailed description of how morphological characters and phylogenetic relationships are interpreted can be found in Ranker et al. (2004), and Sundue (2010a, 2010b). The dot-distribution map was generated from coordinates reported on specimen labels, or georeferenced as accurately as possible from locality data when coordinates were not reported.

RESULTS

Galactodenia Sundue & Labiak, gen. nov.—TYPE: *Galactodenia delicatula* (M. Martens & Galeotti) Sundue & Labiak, based on *Polypodium delicatulum* M. Martens & Galeotti

Differt a *Terpsichore* foliis squamisque rhizomatum pilis simplicibus et unifurcatis glandulosis praeditis.

Plants epiphytic, sometimes epipetric; rhizomes short-creeping, with or without apparent lateral branch buds, radially symmetrical, with radial root insertion and radial frond arrangement, or bilaterally symmetrical with ventral root insertion and dorsal frond arrangement, provided with scales and sometimes glandular hairs, the scales concolorous, non-clathrate, orange, golden-brown or castaneous, lanceolate or oblong, the cells turgid in *G. delicatula*, otherwise flattened (or not conspicuously turgid), the margins entire, provided with papillate glandular cells or not; fronds determinate but frequently seen with immature blade apices (delayed maturation), pendent (arching to pendent in one species), monomorphic,

with or without setae, provided throughout with glandular hairs, these simple and 2-celled, or 1-furcate and 3-celled, the glandular cells clavate, hyaline, milky-white to gray or golden brown; petioles with a single vascular bundle, blackish; laminae membranaceous or chartaceous, 1-pinnatisect to 1-pinnate-pinnatisect; rachises blackish, visible on both sides of the laminae; pinnae with blackish costae, these often visible on both sides of the laminae; veins simple, free, not blackish, and not visible without transmitted light; hydathodes present, reddish, non-cretaceous, sometimes poorly developed and difficult to see; sori round, with or without paraphyses, the paraphyses simple glandular hairs similar to those of the lamina; sporangia glabrous, or, when young, bearing glands similar to those found on the lamina; spores green, trilete.

Etymology—The name *Galactodenia* refers to the milky-white glandular hairs characteristic of these plants [Gr. galacto = milk, aden- = gland].

Habitat and Distribution—This genus is found in montane forests from southern Mexico and the West Indies to Bolivia, 2,000–4,000 m, except one species (*G. pumila*) at 1,500 m in southwestern Venezuela.

Notes—In addition to the characters cited above and in Sundue et al. (2010), diagnostic characters of *Galactodenia* include the thin-textured and pendent fronds, and weakly developed hydathodes. The absence of setae in all species except *G. delicatula* is also helpful. Although setae are present in most other Neotropical grammitid genera, they are absent in *Cochlidium*, *Lellingeria*, and *Stenogrammitis* (Bishop 1978; Smith et al. 1991; Labiak et al. 2010b; Sundue 2010b). In the Neotropics, *Galactodenia* could be most easily confused with *Ceradenia* (Bishop 1988) or *Alansmia* (Kessler et al. 2011). Species of *Ceradenia* also bear hairs with glands on the laminae, but in this genus the hairs are 3-furcate, bearing three rounded glandular cells that produce an opaque wax-like exudate. *Alansmia* can be distinguished from *Galactodenia* by the presence of stellate or clustered setae on the petioles and laminae (at least in most species), as well as by its frequently ciliate sporangia.

KEY TO THE SPECIES OF GALACTODENIA

1. Laminae 1-pinnate-pinnatisect, the laminar tissue always incised nearly to the pinna costa *G. vareschii*
1. Laminae 1-pinnatisect to 1-pinnate-pinnatifid, the laminar tissue incised one third of the way to the pinna costa or less 2
2. Setae present throughout laminae, the setae spreading, reddish *G. delicatula*
2. Setae absent 3
3. Fronds 3–6 × 0.35–0.52 cm; pinnae 1.5–3 × 1 mm, oblong, with a lobe on the acroscopic side (pinnae gibbous); one sorus per pinna; margins of rhizome scales non-glandular *G. pumila*
3. Fronds 10–30 × 0.6–4.0 cm; pinnae 3.5–20 × 1.5–3 mm, narrowly deltate to oblong, lacking an acroscopic lobe; 2 or more sori per pinna; margins of rhizome scales glandular 4
4. Laminae membranaceous, moderately glandular, (pinnatisect–)1-pinnate to 1-pinnate-pinnatifid; pinnae 6–20 mm long; rhizome scales orange *G. subscabra*
4. Laminae chartaceous, densely glandular, pinnatisect; pinnae 3.5–6 mm long; rhizome scales castaneous *G. parrisiae*

TAXONOMIC TREATMENT

Galactodenia delicatula (M. Martens & Galeotti) Sundue & Labiak, comb. nov., *Polypodium delicatulum* M. Martens & Galeotti, Nouv. Mém. Acad. Roy. Sci. Bruxelles 15(5): 35, pl. 7, f. 1. 1842. *Ctenopteris delicatula* (M. Martens & Galeotti) J. Sm., Bot. Voy. Herald: 227. 1854. *Grammitis delicatula* (M. Martens & Galeotti) Proctor, Fern Gaz. 9:

219. 1965. *Terpsichore delicatula* (M. Martens & Galeotti) A. R. Sm., Novon 3: 486. 1993. —TYPE: MEXICO. Oaxaca, Llano Verde, H. G. Galeotti 6378 (holotype: BR!, numbered “6328,” photo US!; isotypes: BR!–2 sheets, K, frag. US!).

Polypodium heterotrichum Baker, in Jenman, J. Bot. 17: 262. 1879. —TYPE: JAMAICA. on trees around Blue Mtn. Peak, 1878, *Jenman 24* (holotype: K; isotype: NY!).

Plants usually epiphytic, sometimes epipetric; rhizomes ca. 1–2 mm wide, dorsiventral, with fronds inserted upon the dorsal side, and roots inserted ventrally, bearing scales and glandular hairs, the scales 0.5–1 × 0.2–0.4 mm, oblong, turgid, concolorous, orange, viscid, the margins glandular; fronds 10–30 × 1.2–2 cm, apparently determinate, but most fronds terminating in undeveloped crosiers and therefore appearing indeterminate, pendent; oblong, provided throughout with setae and minute branched glandular hairs, the setae 0.5–1.8 mm long, reddish, spreading, the hairs ca. 0.1–0.2 mm long, simple and 2-celled, or 1-furcate and 3-celled, translucent to whitish, appearing whitish en masse; petioles obsolete to 15 × 0.2–0.3 mm, blackish; laminae membranaceous, pinnatisect or 1-pinnate, with 25–60 pairs of pinnae, the proximal pinnae reduced; pinnae 5–10 × 1–2 mm, narrowly deltate to oblong, the bases decurrent onto the rachis, the margins entire, the apices acute; pinna costae blackish, the color visible abaxially, not usually visible adaxially; veins free, pinnate, not visible without transmitted light; sori round, 4–5 pairs per pinna, without paraphyses; sporangia bearing glands when young, the glands like those elsewhere on the fronds. Figures 1A–B, D; 2A–D; 4.

Habitat and Distribution—This species is found in humid montane forests of southern Mexico, Guatemala, Honduras, and Jamaica, 1,900–4,000 m.

Notes—The combination of setae and pinnatisect or 1-pinnate laminae distinguish *G. delicatula* from its congeners. The combination of setae and the glandular hairs, typical of *Galactodenia*, distinguish *G. delicatula* from all other grammitid species known to us.

Representative Specimens Examined—MEXICO. Chiapas: Municipio Motozintla de Mendoza, Cerro Mozotal, rd. from Huixtla to El Porvenir and Siltepec, 3,000 m, 20 Sep 1976, *Breedlove 40450* (DS, MEXU, MICH, MO); Municipio Unión Juárez, Mt. Tacaná, 2,000–4,038 m, Aug 1938, *Matuda 2379* (US); Guerrero: F. Lorea 4208 (IEB). Hidalgo: Barranca Trinidad, 10 May 1904, *Pringle 13494* (US); Oaxaca: Depto. Ixtlán, trail from San Pedro Nolasco N to the Llano Verde, 5 Oct 1969, *Mickel & Hellwig 3826* (MICH, NY, UC, US); Cerro Pelón, Carretera 175, 33 m N of the mirador at highest point on road, 17°35.095'N, 96°30.934'W, 2,980 m, 20 Jan 2009, *Sundue & Martin 2123* (NY, VT); Veracruz: *Bohs et al. 1777* (XAL).

GUATEMALA. Chimaltenango: Sta. Elena, 2,400–2,700 m, Nov–Dec 1930, *Skutch 96b* (US); Huehuetenango: Sierra de los Cuchumatanes, at Km 36, ca. 3,300 m, 31 Dec 1940, *Standley 81629* (US); San Marcos: Mountains along rd. between San Marcos and Serchill, 2,700–3,150 m, 30 Jan 1941, *Standley 85393* (F); Sololá: Volcán Atitlán, north-facing slopes, 2,600–3,700 m, 12 June 1942, *Steyermark 47524* (F).

HONDURAS. Lempira: Montaña de Celaque, SE part of massif, canyon of the Quebrada El Naranjo, 14°33'N, 88°39'W, 1,800–1,900 m, 24 May 1991, *Davidse & Zúñiga 34688* (MO); Santa Bárbara: 7 km N of El Mochito, on E slopes of Mt. Santa Bárbara, 14°55'N, 88°07'W, 2,200–2,500 m, 23 Nov 1991, *Moran 5681* (MO).

JAMAICA. St. Thomas: Blue Mtn. Peak, summit area, ca. 7,350 ft., 11 Feb 1951, *Proctor 5428* (MO).

Galactodenia subscabra (Klotzsch) Sundue & Labiak, comb. nov., *Polypodium subscabrum* Klotzsch, *Linnaea* 20: 377. 1847. *Xiphopteris subscabra* (Klotzsch) Crabbe, *Brit. Fern Gaz.* 9: 319. 1967. *Grammitis subscabra* (Klotzsch) C. V. Morton, *Phytologia* 22: 80. 1971. *Terpsichore subscabra* (Klotzsch) B. León & A. R. Sm., *Amer. Fern J.* 93: 87. 2003.—TYPE: VENEZUELA. Mérida, J. W. K. Moritz 332 (holotype: B; isotypes: F!, K!, LL, photos BM).

Polypodium jamesonioides Fée, *Mém. Foug.* 7: 59. 1857. *Ctenopteris jamesonioides* (Fée) Copel., *Philipp. J. Sci.* 84: 416. 1955. *Grammitis jamesonioides* (Fée) C. V. Morton, *Contr. U.S. Natl. Herb.* 38: 108. 1967. *Terpsichore jamesonioides* (Fée) A. R. Sm., *Novon* 3: 487. 1993.—TYPE: COLUMBIA. Depto.

Norte de Santander, Prov. de Ocaña, L. J. Schlim 399 (lectotype, designated by R. G. Stolze, in Tryon and Stolze 1993: L, photos: F, NY!, UC!, US).

Ctenopteris nudipes Copel., *Philipp. J. Sci.* 84: 405–406. 1956.—TYPE: PANAMA. Distrito Boquete, Volcán Chiriquí, 10,400 ft, 18 Jul 1938, M. E. Davidson 1022 (holotype: US!; isotype: MO!).

Plants epiphytic; rhizomes ca. 1.5–2 mm wide, dorsiventral, with fronds inserted upon the dorsal side, and with roots inserted ventrally, bearing scales and glandular hairs, the scales 0.5–0.7 × 0.2–0.3 mm, oblong, concolorous, orange, viscid, the margins glandular, branch buds not observed; fronds 15–30 × 1–4 cm, apparently determinate, but most fronds terminating in undeveloped crosiers and therefore appearing indeterminate, pendent, laminae oblong, lacking setae, provided throughout with minute branched glandular hairs, the hairs ca. 0.1–0.3 mm long, simple and 2-celled, or 1-furcate and 3-celled, translucent, appearing whitish en masse; petioles 5–20 × 0.3–0.4 mm, blackish; laminae membranaceous, rarely pinnatisect, usually 1-pinnate to 1-pinnate-pinnatifid, with 25–70 pairs of pinnae, the proximal pinnae reduced; pinnae 6–20 × 1.5–3 mm, narrowly deltate to oblong, the bases decurrent onto the rachis, the margins entire or incised 1/3 of the way to the pinna costa, the apices acute; pinna costae blackish, the color visible abaxially, not usually adaxially; veins pinnate, not visible without transmitted light; sori round, 3–22 per pinna, without paraphyses; sporangia bearing glands when young, the glands like those elsewhere on the fronds. Figures 1C, J–L; 2E–H; 3A–C; 4.

Habitat and Distribution—This species is found in humid montane forests of Costa Rica, Panama, Haiti, Colombia, Venezuela, Ecuador, Peru, and Bolivia, 2,200–4,000 m.

Notes—*Galactodenia subscabra* can be distinguished by its usually 1-pinnate to 1-pinnate-pinnatifid laminae that lack setae. It is a common species in the northern Andes and mountains of Costa Rica and Panama. *Galactodenia delicatula*, to the north and in Jamaica, can be distinguished by its setose laminae. In Panama, *G. subscabra* is sympatric with *G. parrisiae*, which differs by its thicker textured (chartaceous vs. membranaceous) and more densely glandular laminae, smaller segments (3.5–6 vs. 6–20 mm long), and castaneous (vs. orange) rhizome scales. In Venezuela, *G. subscabra* is sympatric with *G. vareschii*, which differs by its 1-pinnate-pinnatisect laminae.

The pendent, 1-pinnate laminae of *Ceradenia dendrodoxa* L. E. Bishop are similar and could be confused with those of *Galactodenia subscabra*. *Ceradenia* can be distinguished by lacking hydathodes, bearing setae, and by their hairs that usually exude an opaque whitish and wax-like exudate rather than the translucent and viscid glands of *Galactodenia*.

Representative Material Examined—COSTA RICA. Cartago: Cerro de la Muerte, 1 km N of Villa Mills on Interamerican Hwy, behind hotel La Georgina, 2,900 m, 8 Aug 1967, *Mickel 3204* (NY); Limón: Limón-Puntarenas border, Cordillera de Talamanca, Cerro Kasir, on the continental divide, 09°12'N, 83°03'W, 2,950 m, 20 Sep 1984, *Davidse & Herrera 29383* (MO, UC); Puntarenas: Cantón de Buenos Aires, P. N. La Amistad, Tararira, sendero a Cerro Kámuk, 9°12'00"N, 83°3'30"W, 2,900–3,050 m, 8 Nov 1996, *Rojas 3211* (MO, NY); San José: Cantón de Perez Zeledón, P. N. Chirripó, cordillera de Talamanca, 9°27'25"N, 83°32'55"W, 1,900–2,500 m, 26 Jul 1996, *Rojas 2826* (MO).

PANAMA. Bocas del Toro: Parque Internacional La Amistad, Cerro Itamut, 9°6'N, 82°52'W, 3,265 m, 12 Mar 2003, *Klitgaard et al. 766* (NY); Chiriquí: Volcán Baru, 2,800–3,400 m, 23 Oct 1977, *Folsom & Page 6078* (MO).

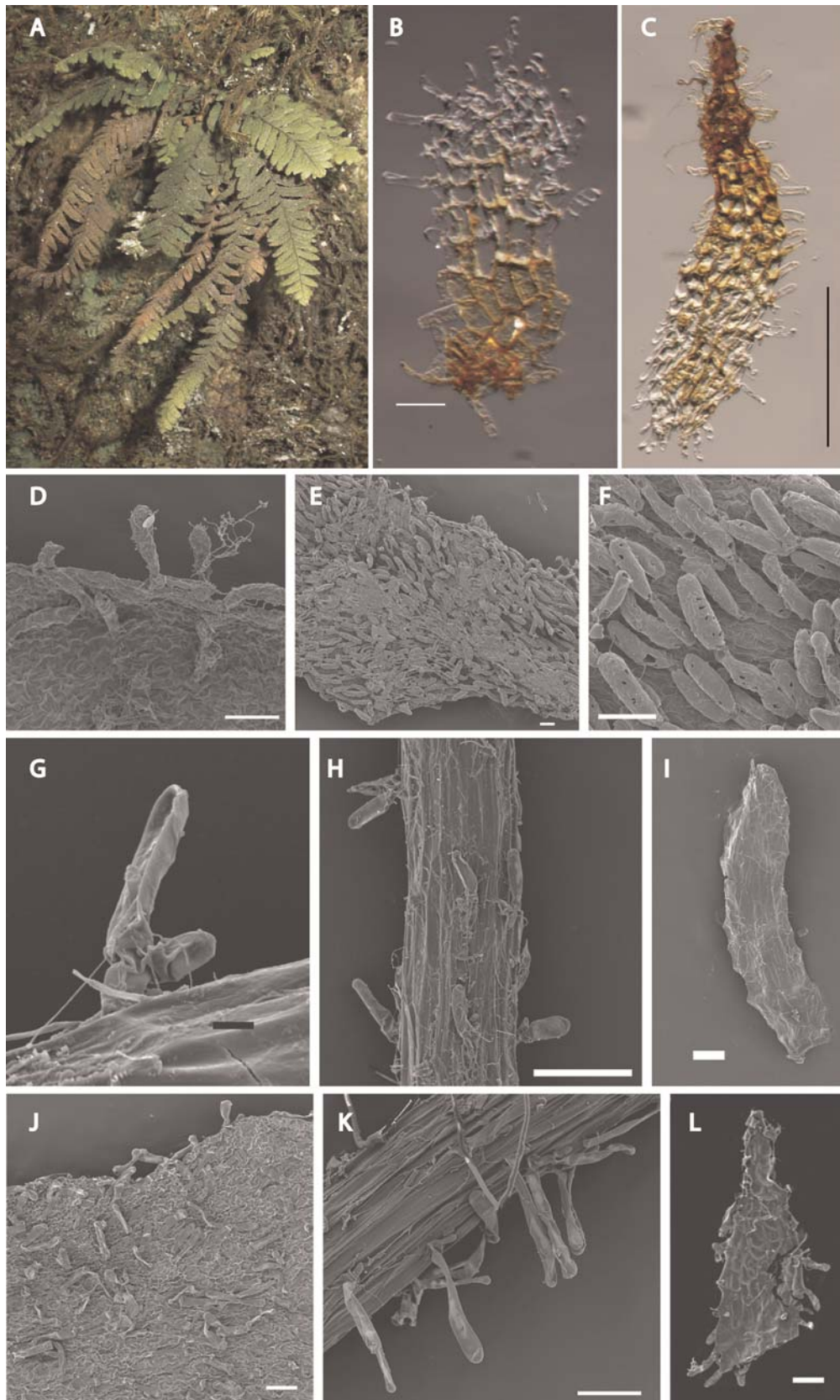


FIG. 1. A–B. *Galactodenia delicatula*. A. habit (Sundue & Martin 2123, VT). B. Rhizome scale, scale bar = 100 μm (Mickel 5292, NY). C. *Galactodenia subscabra*, rhizome scale, scale bar = 500 μm (Mickel 3204, NY). D. *Galactodenia delicatula*, abaxial lamina (Sundue 2123, NY). E–F. *Galactodenia parrisiae*, scale bars = 100 μm (Monro & Knapp 5272, MO). E. Abaxial lamina. F. Detail of glandular hairs on abaxial lamina. G–I. *Galactodenia pumila* (Fernández et al. 6032, MO). G. Branched glandular hair from the petiole, scale bar = 10 μm . H. Detail of the hairs upon the petiole, scale bar = 100 μm . I. Detail of rhizome scale, scale bar = 100 μm . J–L. *Galactodenia subscabra* (Mickel 3204, NY), scale bars = 100 μm . J. Abaxial lamina. K. Detail of the hairs upon the petiole. L. Detail of rhizome scale.

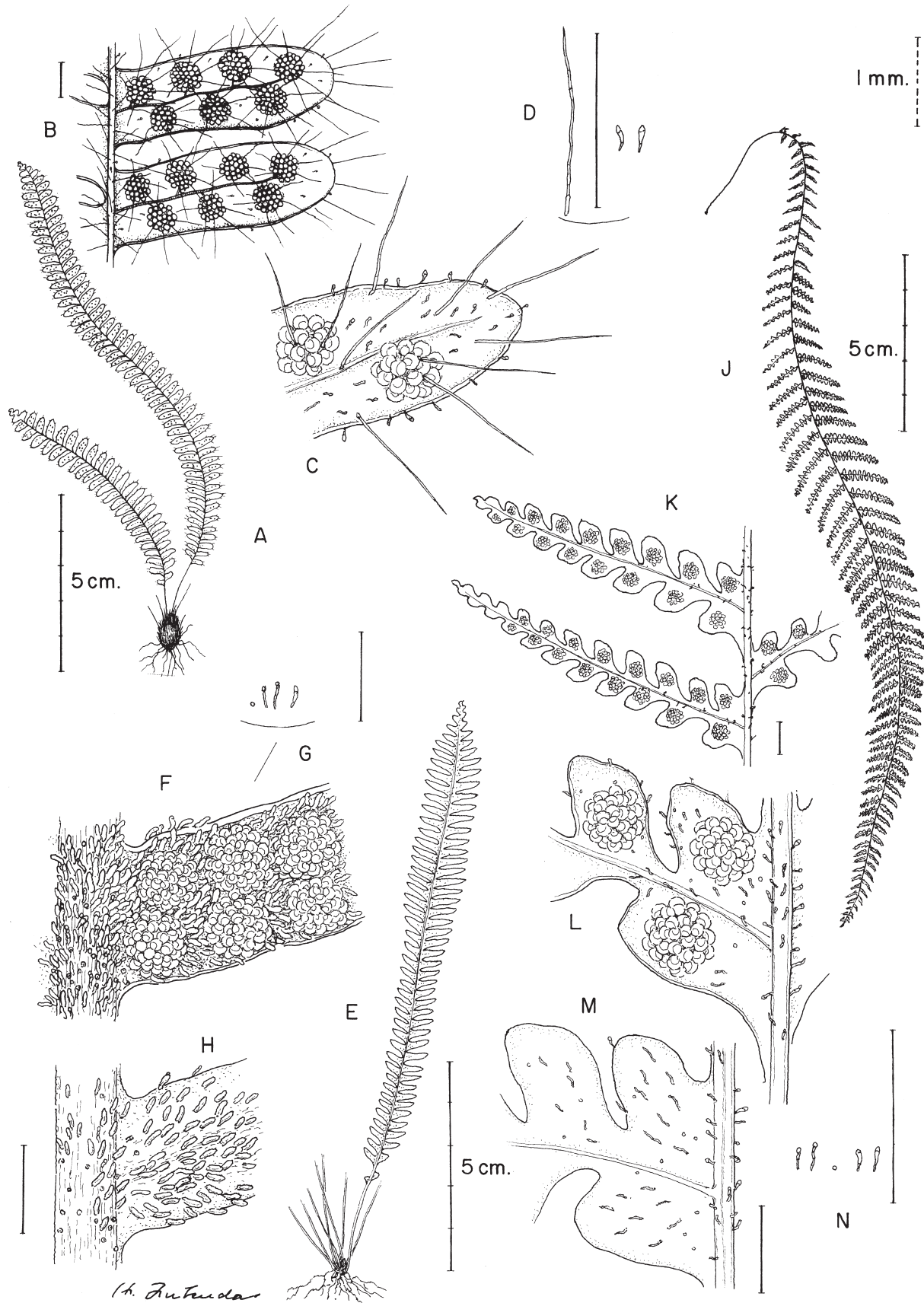


FIG. 2. A–D. *Galactodenia delicatula*, Mexico, Oaxaca, Dto. Ixtlán, 27 Oct 1969, Mickel 4275 (NY). A. habit. B. Abaxial lamina. C. Detail of abaxial lamina. D. Detail of setae and hairs. E–H. *Galactodenia subscabra*, Costa Rica, San José, 25 Jun 2002, Boyle 6328 (NY). E. Habit. F. Abaxial lamina. G. Detail of hairs. H. Adaxial lamina. J–N. *Galactodenia vareschii*, Vareschi 5412 (VEN). J. Frond. K. Abaxial lamina. L. Detail of abaxial lamina. M. Adaxial lamina. N. Detail of hairs.

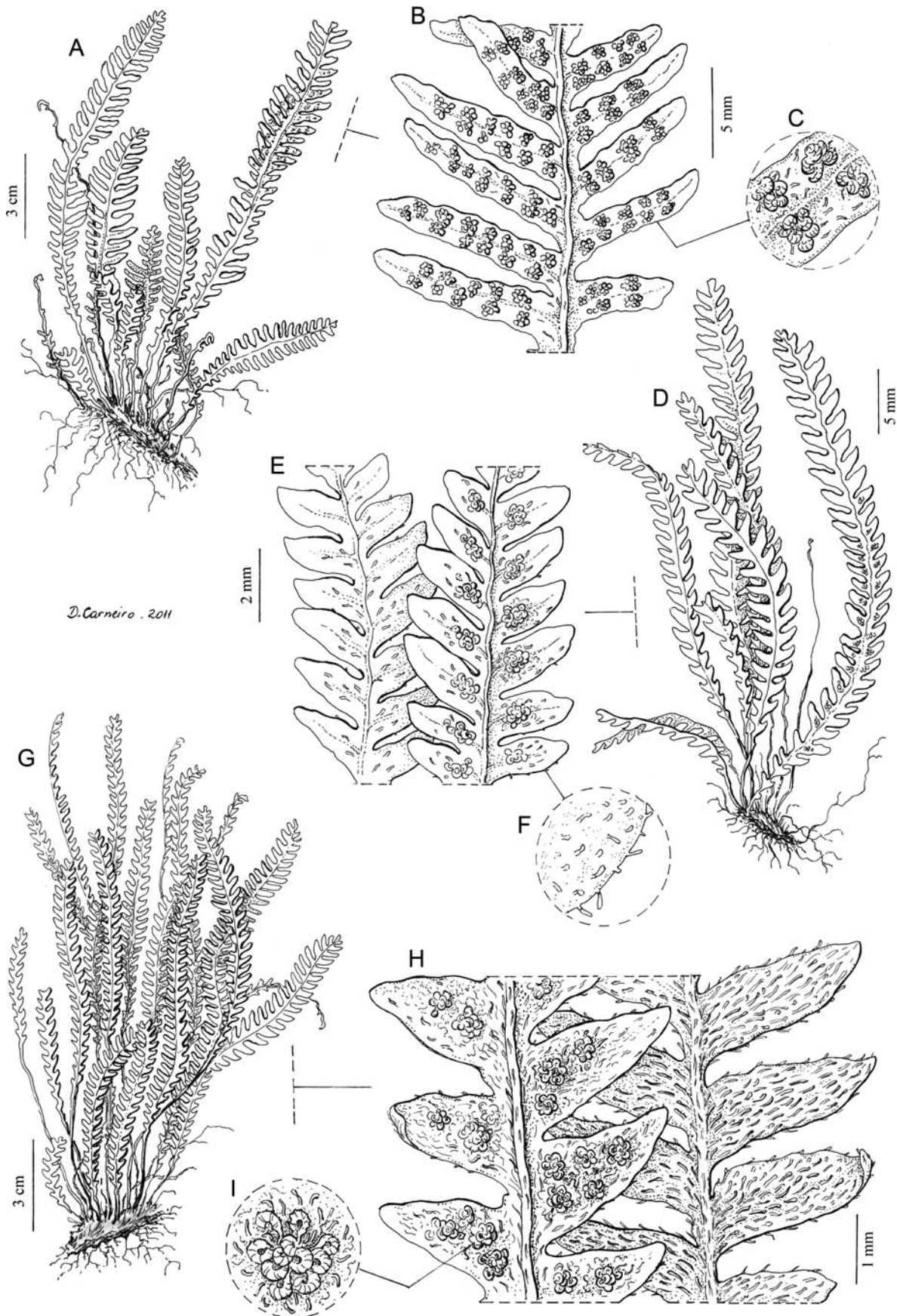


FIG. 3. A–C. *Galactodenia subsabra* (Riviero & Rondón 1681, UC). A. Habit. B. Detail of the abaxial lamina. C. Detail of the segments showing the sori and hairs. D–F. *G. pumila* (Fernández et al. 6032, MO). D. Habit. E. Detail of the adaxial and abaxial lamina. F. Margin of a segment showing the hairs. G–I. *G. parrisiae* (Monro & Knapp 5272, MO). G. Habit. H. Detail of the abaxial and adaxial side of the lamina. I. Detail of a sorus.

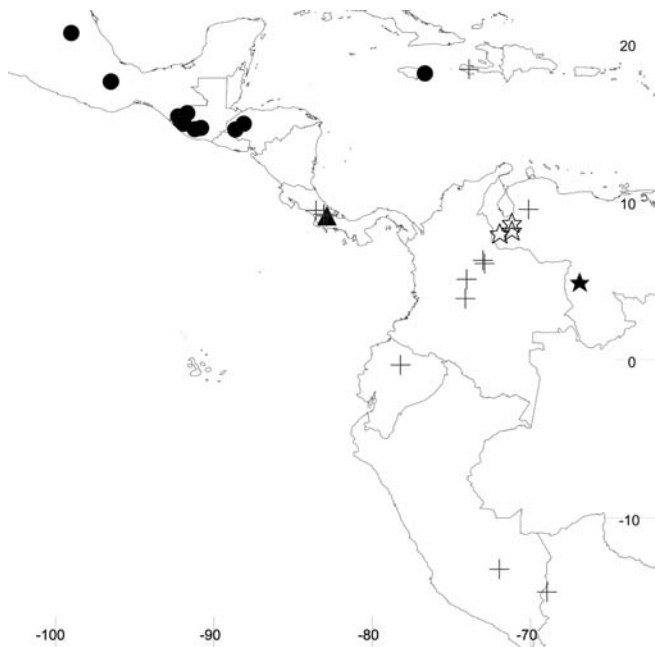


FIG. 4. Distribution of *Galactodenia* species. *Galactodenia delicatula* (circle), *G. parrisiae* (triangle), *G. pumila* (solid star), *G. subscabra* (plus sign), *G. vareschii* (open star).

HAITI. Grand'Anse: Massif de la Hotte, western group, Les Roseaux, Morne La Hotte, 2,375 m, 13 Sep 1928, *Ekman 10635* (NY).

VENEZUELA. Mérida: Sierra Nevada, 3,500 m, 4 Feb 1939, *Alston 6907* (NY); Trujillo: Dtto. Carache, Entre los Páramos El Jabón y Cende, 9°31'N, 70°07'W, 3,300–3,500 m, *Rivero & Rondón 1681* (PORT, UC).

COLOMBIA. Boyacá: Páramos al NW de Belén, cabeceras Quebrada Minas, 3,820 m, 28 Feb 1972, *Cleef 1959* (COL). Cundinamarca: Río Colorado, 5 km al sur de la laguna de Chisacá, 3,600 m, 1 May 1959, *Bischler 2367* (COL); Meta: Páramo de Sumapaz, Hoya El Nevado, Lagunas El Sorbadero, y El Nevado, SE de la Laguna El Nevado, 3,470 m, 12 Jan 1973, *Cleef 7726* (COL); Santander: Mun. Coromoro, Laguna de la Jiguera, páramo de las Carnicerías, fuentes de la quebrada Coromoro, 3,850 m, 29 Nov 1967, *Jaramillo & van der Hammen 4357* (COL).

ECUADOR. Pichincha: At pass of Quito-Papallacta road, 4,000 m, 14 July 1991, *van der Werff & Gray 12352* (UC).

PERU. Cuzco: Mollepeta, Hac. Pincopata, 11,000 ft, 27 Jan 1976, *Bishop 2520* (UC).

BOLIVIA. La Paz: Prov. Franz Tamayo, P. N. Madidi, 14°41'S, 68°58'W, 3,690 m, 29 Apr 2003, *Jiménez 1808* (LPB).

***Galactodenia parrisiae* Sundue & Labiak, sp. nov.**—TYPE: PANAMA. Bocas del Toro, [Parque Internacional La Amistad], small stream leading W from Cerro Fábrega into the Valle del Silencio, 9°6'57.9" N, 82°52'76.9" W, 3,200 m, 11 March 2006, *A. K. Monro & S. K. Knapp 5272* (holotype: MO!; isotypes: BM, INB, MEXU, PMA).

A *G. subscabra* laminae chartaceis (vs. membranaceis), plus dense glandulosis, pinnis 3.5–6.0 mm longis, paleis rhizomatis castaneis differt.

Plants epiphytic; rhizomes ca. 2.5 mm wide, dorsiventral, with fronds inserted upon the dorsal side, and with roots apparently inserted ventrally, branch buds present, associated with frond bases, rhizomes bearing scales and glandular hairs, the scales 0.5–0.8 × 0.1–0.2 mm, oblong, concolorous, castaneous, viscid, the margins glandular; fronds 10–25 × 0.6–1.5 cm, determinate, pendent, oblong, lacking setae, provided throughout with minute branched glandular hairs, the hairs ca. 0.1–0.2 mm long, simple and 2-celled, or 1-furcate and 3-celled, translucent, appearing gray en masse; petioles 15–30 ×

0.3 mm, blackish; laminae chartaceous, pinnatisect, with 40–60 pairs of pinnae, the proximal pinnae reduced; pinnae 3.5–6 × 1.5–2 mm, narrowly deltate to oblong, the bases decurrent onto the rachis, the margins entire, the apices acute; veins free, pinnate, not visible without transmitted light; hydathodes poorly developed and easily overlooked; sori round, 6–8 per pinna, without paraphyses; sporangia bearing glands when young, the glands like those elsewhere on the fronds. Figures 1E–F; 3; 4G–I.

Habitat and Distribution—This species is known from the type and one other consecutive collection, made at 3,200 m near the summit of Cerro Fábrega in humid forest rich in *Quercus* and *Drimys* in the Cordillera Talamanca, Panama.

Notes—*Galactodenia parrisiae* appears most similar to *G. subscabra*, which was also collected at the same locality. It differs from *G. subscabra* by having a chartaceous lamina (vs. membranaceous) that is densely glandular (vs. moderately glandular), shorter segments (3.5–6 vs. 6–20 cm long), and castaneous rhizome scales (vs. orange).

Etymology—This species is named in honor of Barbara S. Parris, in recognition of her numerous contributions to the systematics of grammitid ferns.

Other Material Examined—PANAMA. Bocas del Toro, small stream leading W from Cerro Fábrega into the Valle del Silencio, 9°6'57.9" N, 82°52'76.9" W, 3,200 m, 11 March 2006, *Monro & Knapp 5271* (BM, PMA).

***Galactodenia pumila* Sundue & Labiak, sp. nov.**—TYPE:

VENEZUELA. Amazonas, Municipio Átures, lomas graníticas, Caño Piedra, 115 km al SE de Pto. Ayacucho, 4°54'N, 66°54'W, 1,500 m, Sep 1989, *A. T. Fernández, E. Sanoja, M. Yáñez 6032* (holotype: MO!; isotype: PORT).

A *G. subscabra* foliis 30–60 × 3.5–5.2 mm, pinnis oblongis 1.5–3 × 1 mm, unaquaque lobo acroscopico (gibboso) differt.

Plants epiphytic; rhizomes 0.5 mm wide, radially symmetrical, with radial frond arrangement, and with radial root insertion, the apex provided with scales, otherwise apparently glabrous, the scales 0.5–1.0 × 0.1–0.2 mm, oblong to lanceolate, concolorous, golden brown, translucent, the margins entire or slightly irregular, the apex entire with 1–2 apical or subapical glandular cells; fronds 3–6 × 0.35–0.52 cm, determinate, arching to pendent, oblong, lacking setae, provided throughout with minute branched glandular hairs, the hairs ca. 0.1 mm long, simple and 2-celled, or 1-furcate and 3-celled, translucent, golden brown, sometimes covered with an exudate the same color as the hairs; petioles 5–10 × 0.1 mm; laminae membranaceous, 1-pinnate with 20–40 pairs of pinnae, the proximal 3–4 pinna pairs reduced; pinnae 1.5–3 × 1 mm, oblong, with a gibbous lobe on the acroscopic side, the bases decurrent, the margins entire, the apices rounded, each provided with a single unbranched vein, the vein surrounded by blackish sclerenchyma, color visible with transmitted light, otherwise not readily visible; sori round, one per pinna, lacking paraphyses; sporangia glabrous. Figures 1G–I; 3; 4D–F.

Habitat and Distribution—This species is known only from the type collection, from a granite inselberg in southwestern Venezuela, 1,500 m. These inselbergs, known locally as "lajas," mark the edge of the Guayana Shield. Inselbergs, and those of Átures in particular, are known to harbor a flora rich in endemic species (Gröger and Barthlott 1996; Gröger and Huber 2007), but remain poorly collected. Other taxa described from the inselbergs of Átures include species of *Adenarake* (Ochnaceae; Sastre 1998), *Froesia* (Quiinaceae; Schneider and Zizka 1997), and *Peltula* (Peltulaceae; Schultz et al. 2000).

Notes—*Galactodenia pumila* is distinguished by its small size (3–6 × 0.35–0.52 cm), segments with a single vein and a gibbous acroscopic lobe. These characters are shared with some species of *Stenogrammitis* and *Moranopteris*, but those genera lack the conspicuous glandular indument found on fronds of *G. pumila*.

Etymology—*Galactodenia pumila* is named for its diminutive size [Latin *pumilus* = a dwarf].

Galactodenia vareschii A. R. Sm. & Mostacero, sp. nov.—

TYPE: VENEZUELA. Mérida, Distrito Campo Elías, Llano Compedero, arriba de la Piedra de Pirela, Páramo de Pozo Negro, un sector del gran Páramo de San José, 3,170 m, 18 Dec 1971, L. E. Ruiz-Terán & S. López-Palacios 6561a (holotype: MERF!, isotypes: NY!, UC!, US).

A *G. subscabra* laminae profunde pinnato-pinnatifidis differt.

Plants epiphytic; rhizomes 1.5–2 mm wide, dorsiventral, with fronds inserted upon the dorsal side, and with roots inserted ventrally, bearing scales, the scales 0.7–0.9 × 0.5 mm, oblong to lanceolate, concolorous, golden brown, dull, the margins glandular; fronds 9–30 × 1–2.5 cm, pendent, lacking setae, provided throughout with glandular hairs, the hairs hyaline, golden brown, simple and 2-celled or 1-furcate and 3- or 4-celled, the glandular cells clavate; petioles 1–5 cm long, ca. 0.3 mm wide; laminae membranaceous, deeply 1-pinnate-pinnatisect, with 20–60 pinna pairs, the proximal pinnae reduced; pinnae 5–25 × ca. 2 mm, sessile, each with 6–10 pinnule lobes; pinna costae blackish, visible on both sides of the lamina; veins free, pinnate, with a single vein per pinnule lobe, lacking blackish sclerenchyma and not visible without transmitted light; sori round, one per pinnule lobe, usually eight per pinna, sporangia glabrous. Figures 2J–N; 3.

Habitat and Distribution—This species is known only from sub-páramo woodlands of Mérida and Táchira, Venezuela, 3,000–3,350 m. These habitats have been threatened by development and agriculture. Despite recent field work by one of us (JM), *Galactodenia vareschii* has not been collected in forty years, and may be extinct.

Notes—The large and deeply 1-pinnate-pinnatisect fronds readily distinguish *Galactodenia vareschii* from its congeners. The laminar cutting is reminiscent of *Moranopteris longisetosa* (Hook.) R.Y. Hirai & J. Prado, or *Ceradenia mirabilis* L. E. Bishop. *Moranopteris* species can, however, be distinguished by abundant reddish setae that are absent from *G. subscabra*, and *Ceradenia* species can be distinguished by their hairs. *Ceradenias* usually exude an opaque whitish and wax-like exudate rather than the translucent and viscid glands of *Galactodenia*.

Etymology—*Galactodenia vareschii* is named in honor of Volkmar Vareschi (1906–1991), in recognition of his contributions to the taxonomy of Venezuelan ferns and lycophytes.

Other material examined—VENEZUELA. Mérida, Distrito Campo Elías, páramo de Pozo Negro, 3,170 m, 18 Dec 1971, Ruiz-Terán & López-Palacios 6560 (MERF); en la faja superior de la selva montana de la Mucuy, 3,000 m, 30 May 1952, Vareschi & Pannier 1423 (VEN); selva de *Podocarpus*, Páramo Monsalves, 3,190 m, 10 Nov 1952, Vareschi 2374 (VEN); Táchira, [Parque Nacional General Juan Pablo Peñaloza], Páramo El Batallón, [approx. 7°59'N, 71°57'W], selva de musgos, 3,100–3,350 m, 3 Oct 1956, Vareschi 5412 (VEN).

ACKNOWLEDGMENTS. We thank George Yatskievych (MO), Fernando Matos (NY), Alex Monro (BM), and Ángel Fernández (IVIC) for providing specimen information. We also thank Robbin C. Moran (NY) and Alejandra Vasco (NY) for their help with this study, and two anonymous reviewers for their helpful comments. The illustration in figure two was prepared by H. Fukuda. The illustration in figure four was prepared by Diana Carneiro. Paulo Labiak's research was funded by a grant from the

CNPq (Proc. n° 301997/2010-1). Michael Sundue's research was funded in part by NSF DEB-1119695.

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