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Systematic, phylogenetic and pollination studies of Specklinia (Orchidaceae)

Karremans, Adam Philip

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Chapter 3

The glandulous *Specklinia*: morphological convergence versus phylogenetic divergence

Adam P. Karremans
Diego Bogarín
Franco Pupulin
Carlyle A. Luer
Barbara Gravendeel

The present paper focuses on the systematics of the *Specklinia glandulosa* species complex. Traditionally, *S. glandulosa* has been considered a widely distributed and variable species, ranging from Mexico to the Guiana Shield. Here it is treated as one of at least six different, albeit closely related, species. Of these species, *S. pertenuis* and *S. vittariifolia*, are recognized as distinct species and removed from the synonymy of *S. glandulosa*, and *S. alajuelensis* and *S. gersonii* are described and illustrated as new to science. *Specklinia chontalensis* is described and illustrated from living, Costa Rican material. *Specklinia alajuelensis* is compared with *S. glandulosa* and *S. vittariifolia*, from which it differs in its broader leaves, multi-flowered, lax inflorescence that surpasses the leaves, and smaller petals and sepals. *Specklinia gersonii* is compared with S. glandulosa, from which it differs in the smaller leaves, and the smaller, orange flowers.

Keywords: Orchidaceae, Pleurothallidinae, *Specklinia*, *S. alajuelensis*, *S. chontalensis*, *S. gersonii*, *S. glandulosa*, *S. vittariifolia*

Introduction

Frequently, when a few outstanding morphological features are shared by a number of similar specimens authors tend to accept them as variations of a single species. In such cases the similarities amongst the group of specimens appear much larger than their individual differences. However, this can be misleading and such variations may not always represent the variation of a single taxon. A larger sampling of the alleged variable species might show that those supposedly unique morphological features are actually diagnostic to a whole lineage of well established species. Long, flattened inflorescences bearing large, bright reddish-orange flowers, led authors to believe that *Specklinia endotrachys* (Rchb.f.) Pridgeon & Chase, *S. pfavii* (Rchb.f.) Pupulin & Karremans, *S. remotiflora* Pupulin & Karremans and *S. spectabilis* (Ames & C.Schweinf.) Pupulin & Karremans, were all a single variable species despite their obvious morphological differences and completely different ecological preferences (Pupulin *et al.* 2012). The *Specklinia condylata* complex was another such example (Bogarín *et al.* 2014). Similarly a high morphological variation has been traditionally accepted in *Specklinia glandulosa* (Ames) Pridgeon & Chase, a name used for classifying any *Specklinia* specimen with orange flowers and fully glandular, single-flowered inflorescences (Luer 2006). However, when considering additional evidence it becomes evident that *S. glandulosa* is actually a species complex in need of disentanglement.

August Endrés was the first to collect and illustrate a member of the glandulous *Specklinia* species around 1867. The origin of his material was Costa Rica without any precise locality, but the illustrations and descriptions are still kept at Reichenbach's herbarium in Vienna. Nevertheless, the first name applicable to this group of species appeared much later. *Pleurothallis glandulosa* was described by Oakes Ames from a plant collected by Powell in central Panama in 1923. The fully glandular pedicel, rachis, peduncle, ovary and external surface of sepals, which prompted its name, were a unique combination of features amongst its known relatives at the time. The same year, Rudolf Schlechter described *Pleurothallis vittariifolia* Schltr. from a plant collected by Wercklé in San Jerónimo,

Costa Rica. A third name appeared a bit more than a decade later when *Pleurothallis pertenuis* C.Schweinf.) was published based on material from Guyana. Due to their very particular bright yellow-orange flowers, glandular inflorescences and thin leaves, the three were regarded as synonymous (Luer 2006).

Nevertheless, besides many conspicuous similarities we encounter several unique differences among specimens identified as *S. glandulosa* along its unusually broad distribution (Fig. 27). Therefore we conducted a morphological and genetic study of those specimens from their entire geographical range and present our findings here.

Materials and methods

This study was conducted at Jardín Botánico Lankester (JBL) of the Universidad de Costa Rica and Naturalis Biodiversity Center-Leiden University, from 2012 to 2015. Plants were collected under the scientific permits handed by the Costa Rican Ministry of Environment (MINAE) to researchers at JBL. Individual plants were photographed, illustrated and preserved as DNA samples, herbarium specimens and spirit specimens in FAA (53% ethanol, 37% water, 5% formaldehyde and 5% glycerol). Specimens were deposited at JBL-spirit and L-spirit and in the DNA bank of Naturalis Biodiversity Center.

Scanning Electron Microscopy (SEM): Tissue samples of floral parts were prepared for SEM observation by harvesting tissue from the flowers up to 48 h after the beginning of anthesis, fixing in FAA (ethanol 50%, acetic acid, formalin at a proportion of 18:1:1 v/v), and dehydration through a series of ethanol steps and critical-point drying using liquid CO2. Dried samples were mounted and sputter-coated with gold and observed with a JEOL JSM-5300 scanning electron microscope, at an accelerating voltage of 5 to 10 kV. All images were processed digitally.

Macrophotography: Color illustrations of plants and flowers were made using a Nikon® D5100, D5300 or D7100 digital camera, a DFC295 Leica® digital microscope color camera with Leica FireCam version 3.4.1 software, and an Epson® V370 Photo Scanner. Adobe Photoshop® was used for editing images and stacking whenever necessary.

Phylogenetic analysis: The data matrix included DNA sequences of 50 individuals (Table 3). Fresh leaf and flower cuttings of approximately 1 cm2 were dried with silica gel. Samples (20 mg) were pulverized and extraction performed following the DNEasy procedure (Qiagen). The nuclear ribosomal internal transcribed spacer (nrITS) region was amplified using the methods and primers for sequencing and amplification described by Sun *et al.* (1994), and Sanger sequencing was done commercially by Macrogen on a 96-capillary 3730xl DNA Analyzer automated sequencer (Applied Biosystems, Inc.) using standard dye-terminator chemistry (Macrogen, Inc.).

The Staden *et al.* (2003) package was used for editing of the sequences. Contigs were exported as .fas files and opened in Mesquite v2.72 (Maddison & Maddison 2007), where they were visually checked for base calling errors. Edited contigged sequences were aligned manually. The ends of each data set were trimmed to eliminate possible erroneous data, and gaps were regarded as missing data (filled with Ns). *Phloeophila peperomioides* (Ames) Garay was used as outgroup, as it was found to be one of the most distantly related of all included species in this phylogenetic analysis (Pridgeon *et al.* 2001). The trees were produced with an analysis of the nrITS dataset of 43 sequences using BEAST v1.6.0. (Drummond & Rambaut 2007). Parameters were set to preset, except for substitution model GTR with 10 categories, clock model uncorrelated lognormal, tree prior Yule process, and number of generations 20,000,000. The resulting trees were combined using TreeAnnotator v1.6.0., where the first 3000 trees were used as burn-in. FigTree v1.3.1. (Rambaut 2009) was used to edit the resulting tree. Posterior probabilities are given for each node in decimal form.

A pairwise comparison of the ITS sequence of analyzed glandulous *Specklinia* is presented in Table 4. Each different base was counted as an individual change, even when concurrent; insertions and deletions were counted as a single change regardless of length.

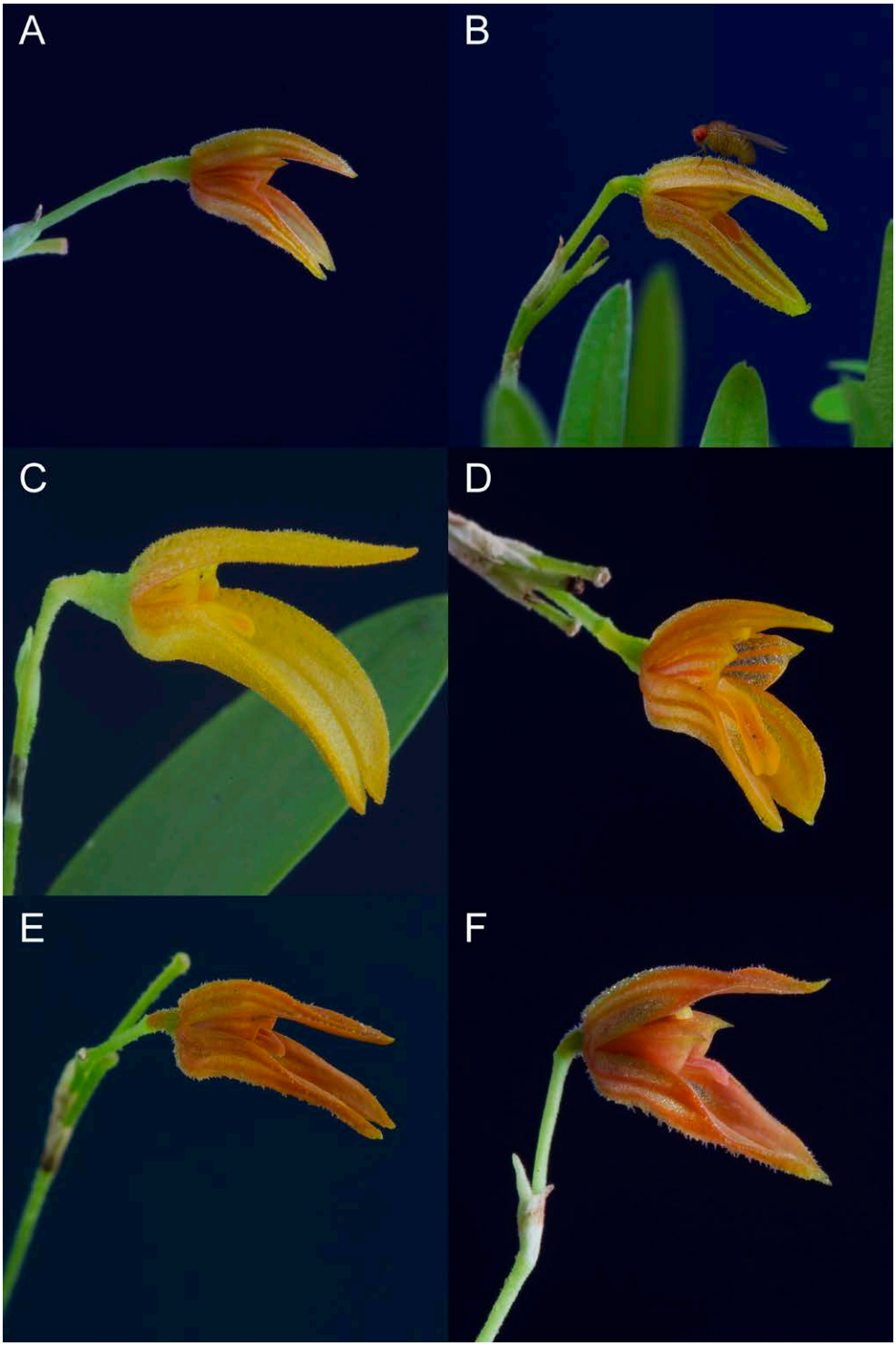

Figure 27. The glandulous *Specklinia* species. A. *S. alajuelensis* 1 (*Karremans 3265*). B. *S. alajuelensis* 2 (*Bogarín 2895*). C. *S. chontalensis* (*Pupulin 6543*). D. *S. gersonii* (*Karremans 6025*). E. *S. glandulosa* (*Karremans 6306*). F. *S. vittariifolia* (*Karremans 2945*). Photographs by A.P. Karremans.

Table 3. List of the 50 accessions used in the phylogenetic analysis. The vouchers, NCBI GenBank accession number and source are given.

Taxon	Sequence Voucher	GenBank Accession Number	Sequence Source
Dryadella simula (Rchb. f.) Luer	*Chase 1095*	AF262825	Pridgeon *et al.* (2001)
Dryadella susanae (Pabst) Luer	*Chiron 11240*	JQ306486	Chiron *et al.* (2012)
Phloeophila peperomioides (Ames) Garay	None	AF275690	Pridgeon *et al.* (2001)
Platystele compacta (Ames) Ames	*Chase 5637*	AF262822	Pridgeon *et al.* (2001)
Platystele misera (Lindl.) Garay	*Chase 5625*	AF262823	Pridgeon *et al.* (2001)
Platystele stenostachya (Rchb. f.) Garay	*Chase 5618*	AF262821	Pridgeon *et al.* (2001)
Scaphosepalum grande Kraenzl.	*Chase 1107*	AF262819	Pridgeon *et al.* (2001)
Scaphosepalum swertiifolium (Rchb. f.) Rolfe	*Chase 1383*	AF262818	Pridgeon *et al.* (2001)
Scaphosepalum verrucosum (Rchb. f.) Pfitzer	*Chase 1331*	AF262820	Pridgeon *et al.* (2001)
Specklinia absurda Bogarín, Karremans & Rincón	*Bogarín 8711*	KC425827	Bogarín *et al.* (2013b)
Specklinia alajuelensis Karremans & Pupulin 1 (a)	*Karremans 3268*	KP012455	Karremans *et al.* (unp.)
Specklinia alajuelensis Karremans & Pupulin 1 (b)	*Karremans 3265*	KC425791	Karremans *et al.* (unp.)
Specklinia alajuelensis Karremans & Pupulin 2 (a)	*Karremans 5501*	KC425792	Karremans *et al.* (unp.)
Specklinia alajuelensis Karremans & Pupulin 2 (b)	*Bogarín 2895*	KP012454	Karremans *et al.* (unp.)
Specklinia barbae (Schltr.) Luer (a)	*Karremans 4853*	KC425771	Karremans *et al.* (unp.)
Specklinia barbae (Schltr.) Luer (b)	*Karremans 3928*	KC425769	Karremans *et al.* (unp.)
Specklinia chontalensis (A.H.Heller & A.D.Hawkes) Luer (b)	*Pupulin 6543*	KC425776	Karremans *et al.* (unp.)
Specklinia chontalensis (A.H.Heller & A.D.Hawkes) Luer (b)	*Pupulin 6543*	KF747799	Karremans *et al.* (unp.)
Specklinia costaricensis (Rolfe) Pridgeon & M.W.Chase	*Chase 5612*	AF262862	Pridgeon *et al.* (2001)
Specklinia digitalis (Luer) Pridgeon & M.W.Chase	*Karremans 5737*	KF747806	Karremans *et al.* (2015a)
Specklinia endotrachys (Rchb.f.) Pridgeon & M.W.Chase (a)	*Blanco 961*	KC425784	Karremans *et al.* (unp.)
Specklinia endotrachys (Rchb.f.) Pridgeon & M.W.Chase (b)	*Blanco 961*	KF747810	Karremans *et al.* (unp.)
Specklinia fuegi (Rchb.f.) Solano & Soto Arenas	*Karremans 5600*	KC425786	Bogarín *et al.* (2013b)
Specklinia fulgens (Rchb.f.) Pridgeon & M.W.Chase	*Chase 5630*	AF262872	Pridgeon et al. (2001)
Specklinia gersonii Bogarín & Karremans	*Karremans 6025*	KP012457	Karremans *et al.* (unp.)
Specklinia grobyi (Bateman ex Lindl.) F.Barros	*Chiron 04524*	JQ306485	Chiron *et al.* (2012)
Specklinia lanceola (Sw.) Lindl. (a)	*Pridgeon s.n.*	KC425838	Bogarín et al. (2013)
Specklinia lanceola (Sw.) Lindl. (b)	*Chase 1433*	AF262861	Pridgeon *et al.* (2001)
Specklinia lentiginosa (F.Lehm. & Kraenzl.) Pridgeon & M.W.Chase		AF275692	Pridgeon *et al.* (2001)
Specklinia lugduno-batavae Karremans, Bogarín & Gravend.	*Pupulin 7709*	KC425824	Karremans *et al.* (2015a)
Specklinia montezumae (Luer) Luer (a)	Karremans 229	KC425811	Bogarín *et al.* (2013b)
Specklinia montezumae (Luer) Luer (b)	*Karremans 5751*	KF747816	Karremans *et al.* (unp.)
Specklinia picta (Lindl.) Pridgeon & M.W.Chase	*Van Den Berg 2146*	JQ306384	Chiron *et al.* (2012)
Specklinia pissina (Luer) Solano & Soto Arenas (a)	*Karremans 4797*	KC425795	Karremans et al. (2015a)
Specklinia pissina (Luer) Solano & Soto Arenas (b)	*Karremans 4839*	KC425797	Karremans et al. (2015a)
Specklinia pfavii (Rchb.f.) Pupulin & Karremans (a)	*Karremans 4825*	KC425814	Karremans *et al.* (unp.)
Specklinia pfavii (Rchb.f.) Pupulin & Karremans (b)	*Karremans 3656*	KF747819	Karremans et al. (unp.)
Specklinia pfavii (Rchb.f.) Pupulin & Karremans (c)	*JBL-11086*	KF747820	Karremans et al. (unp.)
Specklinia aff. remotiflora Pupulin & Karremans	*Chase 1303*	AF262859	Pridgeon *et al.* (2001)
Specklinia remotiflora Pupulin & Karremans (a)	*Karremans 4798a*	KC425818	Karremans *et al.* (unp.)
Specklinia remotiflora Pupulin & Karremans (b)	*Karremans 4798b*	KC425819	Karremans *et al.* (unp.)
Specklinia remotiflora Pupulin & Karremans (c)	*Karremans 4854*	KC425820	Karremans *et al.* (unp.)
Specklinia sp.	*Karremans 5966*	KP012456	Karremans *et al.* (unp.)
Specklinia spectabilis (Ames & C.Schweinf.) Pupulin & Karremans (a)	*Bogarín 7401*	KP012457	This Study
Specklinia spectabilis (Ames & C.Schweinf.) Pupulin & Karremans (b)	*Karremans 5699*	KC425824	This Study
Specklinia subpicta (Schltr.) F.Barros	*Chiron 11046*	KC425830	This Study
Specklinia succulenta Bellone & Archila	*Bellone 680*	KC425828	This Study
Specklinia tribuloides (Sw.) Pridgeon & M.W.Chase	*Chase 5615*	JQ306389	Chiron *et al.* (2012)
Specklinia vittariifolia (Schltr.) Pridgeon & M.W.Chase (a)	*Karremans 2945*	JQ306383	Chiron *et al.* (2012)
Specklinia vittariifolia (Schltr.) Pridgeon & M.W.Chase (b)	*Karremans 5944*	AF262867	Pridgeon *et al.* (2001)

Table 4. Pairwise comparison of the number of single base differences amongst the nrITS sequences of *Specklinia alajuelensis*, *S. chontalensis*, *S. gersonii* and *S. vittariifolia*.

	S. alajuelensis	***S. chontalensis***	***S. gersonii***	***S. vittariifolia***
Specklinia alajuelensis	-	49–50	31–32	17–18
Specklinia chontalensis	49–50	-	44	45
Specklinia gersonii	31–32	44	-	26
Specklinia vittariifolia	17–18	45	26	-

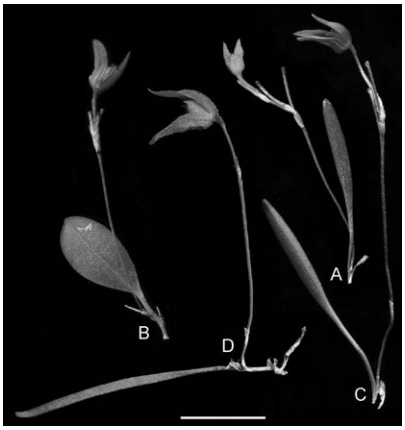

Figure 28. Comparison of the habits and flowers of species of the glandulous species of *Specklinia*. A. *S. alajuelensis* 1 (*Karremans 3265*). B. *S. gersonii* (*Karremans 6025*). C. *S. glandulosa* (*Karremans 6306*). D. *S. vittariifolia* (*Karremans 2945*). Scale bar = 1 cm. Photographs by A.P. Karremans.

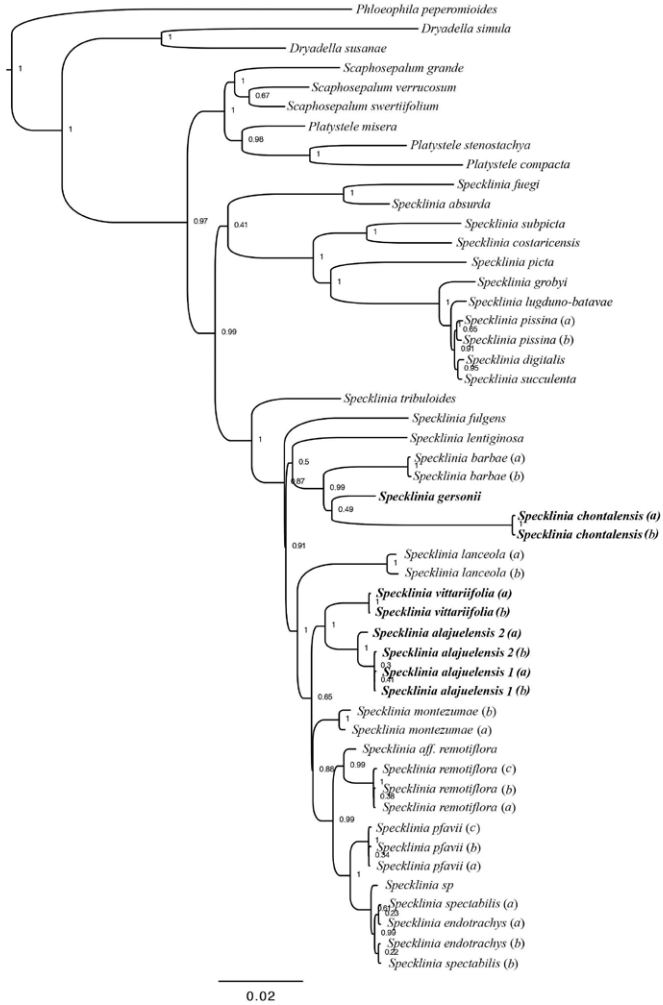

Figure 29. Phylogenetic relationship amongst the species of the glandulous *Specklinia*. The trees were produced with an analysis of a nrITS dataset of 50 sequences using BEAST v1.6.0. The resulting trees were combined using TreeAnnotator v1.6.0., where the first 3,000 trees were used as burn-in. Node values are posterior probabilities. The tree was edited using FigTree v.1.3.1. Branch lengths are relative to the relative number of changes. Names in bold correspond to species studied here.

Taxonomic Treatment

Phylogenetically, the glandulous *Specklinia* species are found in a clade, which includes *Specklinia lanceola* (Sw.) Lindl., the type species of the genus *Specklinia*. We recognize that at least 6 different *Specklinia* species share the small habit with a relatively long inflorescence, the single, bright yellow to orange flowers, flowering in succession, and a fully glandular pedicel, rachis, peduncle, ovary and external surface of the sepals (Fig. 28). These particular morphological features have evolved at least twice within the genus *Specklinia*, as the species treated here belong to two unrelated clades (Fig. 29). One clade includes *Specklinia chontalensis* (Heller & Hawkes) Luer, which is sister to *Specklinia barbae* (Schltr.) Luer. The second includes *Specklinia glandulosa*, which is sister to a clade that includes the species of the *Specklinia endotrachys* complex and *S. montezumae* (Luer) Luer.

Key to the glandulous species of Specklinia (as treated here)

1. Leaves elliptic to broadly elliptic, > 1 cm wide, peduncle lacking bracts, ovary trialate 2
- Leaves narrowly linear to ligulate, < 4 mm wide, peduncle with a single bract, ovary terete 3

2. Flowers orange, sepals < 8 mm long, dorsal sepal with no wart-like transparencies, petals 3-veined, lip apically bifid-emarginate ..... *S. gersonii*
- Flowers yellow, sepals > 10 mm long, dorsal sepal with conspicuous wart-like transparencies, petals 2-veined, lip apically obtuse ..... *S. chontalensis*

3. Inflorescence subequal to the leaf, arched to semi pendulous, flowers large, sepals exceeding 7.5 mm long and lip 4.5 mm long, lip with a pair of conspicuous sub-trapezoid lateral lobes ..... *S. vittariifolia*
- Inflorescence longer than the leaf, erect, flowers small, sepals between 4-6 mm long and lip 2.5-3.5 mm long, lip with a pair of relatively small triangular lateral lobes 4

4. Inflorescence distichous, frequently multi-flowered (up to 6 flowers) ..... *S. alajuelensis*
- Inflorescence sub-fascicled, few-flowered (frequently 1 or 2 flowers) 5

5. Inflorescence barely exceeding the leaf, flowers frequently cleistogamous, sepal ornamentation inconspicuous, petals narrow, oblong ..... *S. pertenuis*
- Inflorescence conspicuously exceeding the leaf, flowers not cleistogamous, sepal ornamentation conspicuous, petals falcate ..... *S. glandulosa*

6. *Specklinia alajuelensis* Karremans & Pupulin, Phytotaxa 218(2): 108. 2015.

> *The species is similar to Specklinia endotrachys but can be distinguished by the small habit, shorter leaves, smaller flowers, the flat, non-ascending dorsal sepal (vs. ascending), and the obtuse, shortly apiculate (vs. emarginate and long mucronate) petals.*

Type:—VENEZUELA. Alajuela: San Ramón, Piedades Sur, San Miguel (La Palma). Camino a San Bosco, a orillas y dentro de un pequeño bosque secundario, 10º07'18.8"N 84º31'13.1"W, 1,062 m, 21 december 2010, *A.P. Karremans, J.A.J. Karremans & M. Contreras Fernández 3265* (holotype, JBL-spirit, D4704!; Figs. 27a, 28a & 30).

Epiphytic, caespitose, ascending, erect herb to 2.0–3.0 cm tall (excluding the inflorescence). Roots fibrous, flexuous, glabrous. Stem abbreviated, terete, to 0.2–0.9 cm long, completely concealed by papyraceous, subancipitous, acute sheaths to 0.5 cm long. Leaf narrowly obovate to linear, up to 18–27 × 2.5–3.5 mm, minutely and irregularly emarginate at apex, the mid-vein protruding abaxially into a small apicule, gradually tapering toward the base into

a deeply conduplicate petiole, subcoriaceous. Inflorescence borne laterally from the apex of the stem, without an annulus, successively single flowered, up to 3.0–4.5 cm long, glandular; peduncle terete, to 4 cm long, with 1 distant, glandular, terete bract, 2–3 mm long. Floral bracts infundibuliform, glandular, broadly ovate, acute to subacuminate, 2 mm long. Pedicel terete, glandular, 13–15 mm long, persistent. Ovary subclavate, with low, irregularly crenulate crests, 1 mm long, green. Flowers up to 6 per inflorescence. Sepals fleshy, densely glandulose in the outer surface; dorsal sepal lanceolate-elliptic, 3-veined, acute, the base semi-hyaline, flushed with orange along the veins, the distal two thirds greenish, with reddish-orange veins, 5.0–6.0 × 1.5–2.0 mm; lateral sepals narrowly elliptic-oblanceolate, subfalcate, 3-veined, 5.0–6.0 × 2.5–3.5 mm, connate for about half their length, the base saccate, membranaceous-hyaline, the apex acute, the veins strongly carinate abaxially. Petals small, ligulate-falcate, acute, 2.0–2.5 × 1.0 mm, 2-veined. Lip reddish-orange, small, longitudinally arched-convex in natural position, thinly articulate with the column foot by a hyaline claw, the blade sagittate to sub-triangular when expanded, obtuse, 2.5 × 0.8 mm, provided with a pair of acute, triangular lateral lobes at about the middle of the blade, margin dentate-erose, especially apically. Column dark-red, arched, terete and slender at the base, 1.5 mm long without the foot, provided with membranous wings, serrulate along the margins, the apex prolonged into a deeply cucullate, lacerate clinandrium; column foot, stout, fleshy, 0.7 mm long. Anther cap deeply cucullate, ovate, 2-celled. Pollinia 2, obovate-complanate, minutely hooked at the base. *NOTE: Description based on *AK3265*, *AK3266* & *FP8470*.

Other material examined (morph 1):—COSTA RICA. Alajuela: San Ramón, Piedades Sur, San Miguel (La Palma). Camino a San Bosco, a orillas y dentro de un pequeño bosque secundario, 10º07’18.8”N 84º31’13.1”W, 1,062 m, 21 December 2010, *Karremans, Karremans & Contreras Fernández 3265* (JBL-spirit, D4704!); Idem, *Karremans et al. 3266* (JBL-spirit; D6078!, D5956!, D4721!); Idem, *Karremans et al. 3268* (JBL-spirit; D6074!). San Ramón, Santiago, road to Berlín, Balboa, 10º02’30”N 84º29’30”W, 1,230 m, premontane moist forest, epiphytic on trees along the roadside, 30 May 2013, *Pupulin, Bogarín, Díaz & Fernández 8469* (JBL-spirit); Idem, *Pupulin et al. 8470* (JBL-spirit; D6126!). Idem, *Pupulin et al. 8471* (JBL-spirit; D5873!). San Ramón, Santiago, camino a Balboa, 10°02’24.76”N 84°29’29.88”W, 1,222 m, epífitas en árboles aislados, bosque pluvial premontano, 30 May 2013, *Bogarín, Díaz, Fernández & Pupulin 10193* (JBL-spirit, D5867!). San Ramón, Piedades Sur, Potrerillos, 4 km E. of Piedades Sur, 1,235 m, 22 June 1969, *Lent 1762a* (CR!). San Ramón, Piedades, alt. 1,100 m, 21 June 1925, Brenes 1285 (78) (CR!). San Ramón, Piedades, alt. 1,100 m, 29 november 1925, *Brenes 1431 (244)* (CR!). San Ramón, camino de Piedades, alt. 1,025 m, 5 July 1924, *Brenes 2213 (32)* (CR!). San Ramón, el Socorro, alt. 1,050 m, 25 July 1924, *Brenes 2237 (84)* (CR!). Sine loc., ca. 1867, *Endrés 52* (W!).

Other material examined (morph 2):—COSTA RICA. Alajuela: Upala, Parque Nacional Rincón de la Vieja, road to Colonia Blanca by Quebrada Rancho Grande, 700 m, 7 July 1978, *Todzia 354* (CR!). San José: Vazquez de Coronado, Braulio Carrillo Nat. Park. Along sendero La Botella, 10º10’00”N 83º57’20”W, 750 m, 21 September 1990, *Ingram & Ferrell 558* (MO; CR!; SEL!). Limón: Pococí, Guápiles, 1 km después del puente sobre el Río Corinto en dirección a Guápiles, 10°12’40.9”N 83°52’38.5” W, 300 m, bosque muy húmedo tropical, epífitas en bosque secundario, 15 June 2006, *Bogarín, Dressler, Gómez-Laurito & Pupulin 2895* (JBL-spirit!; Fig. 27b & 31). Grecia, San Isidro, Coope Victoria, rio Rosales, del Puente 1 km al Sur, *Alfaro & Rodríguez 8* (Epidendra!). Guanacaste: Tilarán, Hno Jorge de la Cruz legit, *Karremans 5501* (JBL-spirit, D5148!). NICARAGUA. Rio San Juan: between Río Santa Cruz and Caño Santa Crucita, La Palma 11°02–04’N 84°24–26’W, elevation 40–60 m; tall evergreen forest, 30 November–2 December 1984, *Stevens, Montiel & Robleto 23460* (SEL!; MO!). Zelaya [Región Autónoma del Atlántico Sur]: along road to Colinia Yolaina, Colonia La Esperanza, etc., ca. 1.3 km SE of intersection with road between Nueva Guinea and Colonia Verdun, immediately upriver from bridge over Caño Sardina; ca. 11°40’N 84°26’W, elev. ca. 180–200 m; disturbed evergreen forest and river banks, 11–12 February 1978, *Stevens & Krukoff 6294* (MO!). Zelaya [Región Autónoma del Atlántico Norte]: 0.5–1.5 km from Plantel El Salto along road to Bonanza, slipe above Río Pis Pis; ca. 14°03’N 84°37’W, elevation ca. 140 m, tall evergreen forest on steep slopes and pastures, 16 December 1980, *Stevens & Krukoff 18814* (MO!).

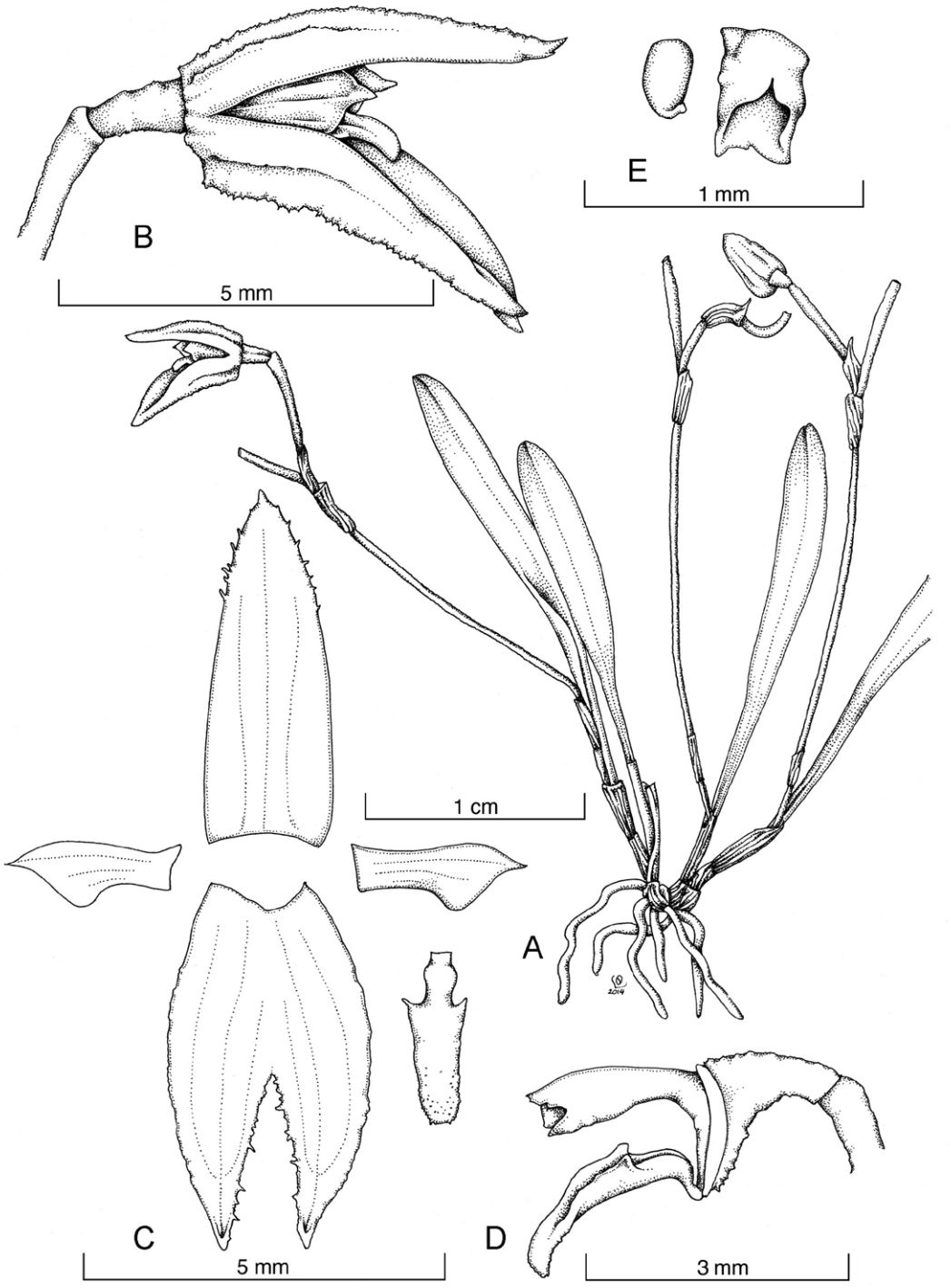

Figure 30. *Specklinia alajuelensis* Karremans & Pupulin. A: habit; B: flower; C: dissected perianth; D: column and lip, lateral view; E: anther and pollinaria. Drawn by A.P. Karremans & L. Oses from *A.P. Karremans 3265* (JBL-spirit).

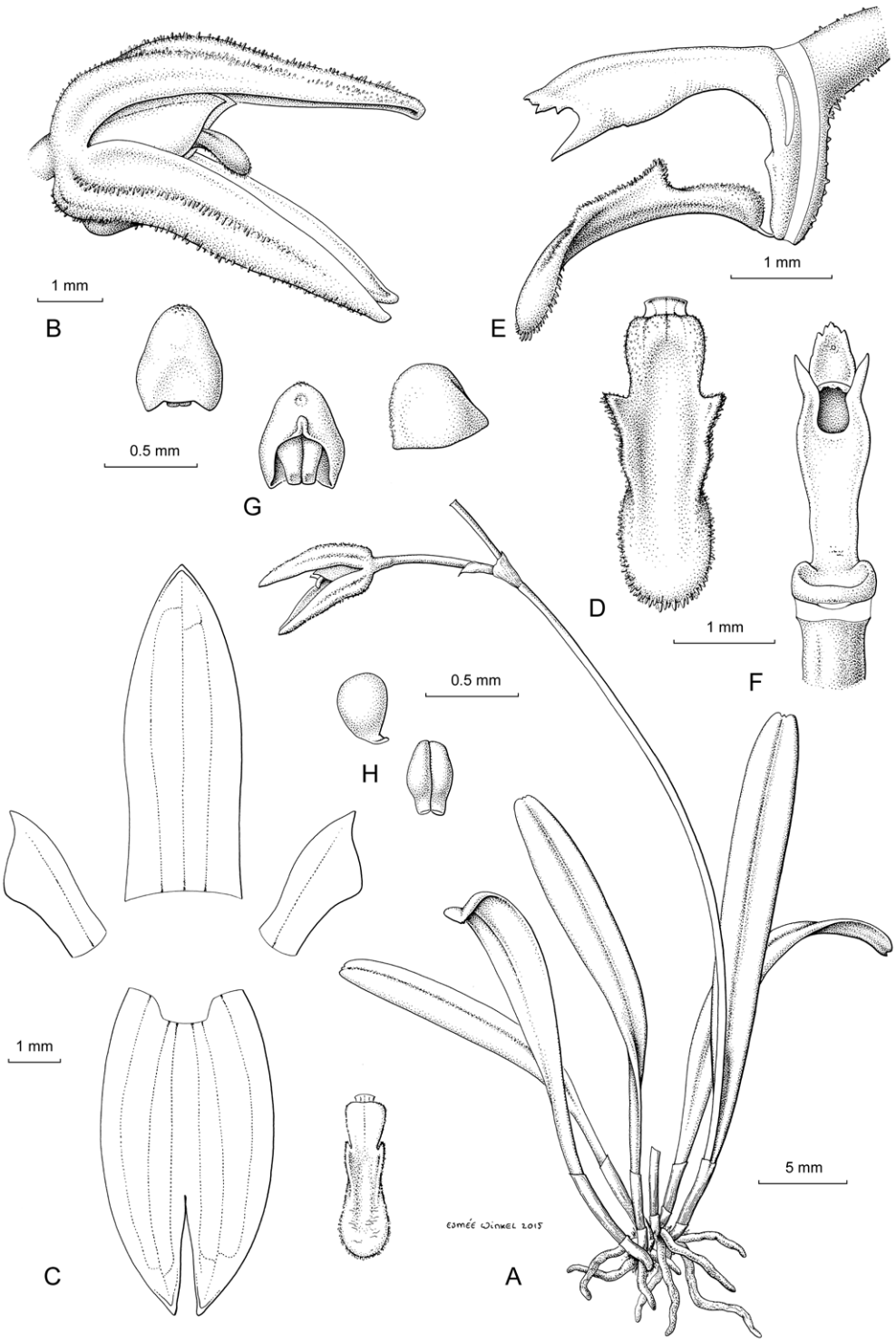

Figure 31. *Specklinia alajuelensis* Karremans & Pupulin. A: habit; B: flower; C: dissected perianth; D: lip; E: column and lip, lateral view; F: column, ventral view; G: anther with pollinaria; H: pollinaria. Drawn by E. Winkel from *D. Bogarín 2895* (JBL-spirit; L-spirit).

Etymology:—The name refers to the province of Alajuela in Costa Rica, where the type and most other specimens were collected.

Distribution:—Known only from Nicaragua and Costa Rica (Fig. 32), where it is found growing between 300–1,235 m in elevation.

Notes:—The first to collect this species was probably A. Endrés. *Endrés 52* was collected in Costa Rica, without a more specific locality. Nevertheless, a vast majority of his collections come from San Ramón, Alajuela, where this species is common. Luer also listed Endrés 46 under *Specklinia glandulosa*, however we believe that number 46 is actually *Specklinia acicularis* (Ames & C.Schweinf.) Pridgeon & M.W.Chase. The latter has similarly thin leaves but lacks the glandular ornamentation on the inflorescence and exterior of the sepals, and has a dark purplish to brownish coloration of the flower.

The typical form of this species (morph 1) has relatively short leaves, which are shorter than the multi-flowered inflorescence. The floral segments are typically not spreading. The species is common around San Ramón in Alajuela, at elevations between 1,025–1,235 m. Plants with similar characteristics (morph 2) are found in the Caribbean lowlands, at elevations between 300–750 m. Aside from the obvious ecological differences they can also be set aside morphologically, and could represent a different species. At this time we prefer to include them here until more evidence can be presented.

In Costa Rica, *S. alajuelensis* and *S. vittariifolia* have been confused with each other in herbaria. The first can be easily recognized from the second by the leaves that are less than 10 times as long as wide (while the second have extremely narrow leaves that can be more than 15 times longer than wide). The inflorescence of *S. alajuelensis* produces a lax inflorescence of an extremely slow succession, and always becomes longer than the leaf. The inflorescence of *S. vittariifolia* does not exceed the leaf length even though it can also produce several flowers over time; the flowers are born closely together making the inflorescence sub-fascicled.

7. *Specklinia chontalensis* (A.H.Heller & A.D.Hawkes) Luer.

Basionym: *Pleurothallis chontalensis* A.H.Heller & A.D.Hawkes. Type:—NICARAGUA. Chontales: Río Mico, epiphytic, alt. 1500 ft, Aug 1960, *A.H. Heller 3735* (holotype, AMES!).

Epiphytic, caespitose, ascending, erect herb to 6 cm tall (excluding the inflorescence). Roots fibrous, flexuous, glabrous. Stem abbreviated, terete, to 0.5–0.7 cm long, completely concealed by papyraceous, subancipitous, acute sheaths to 0.5 cm long. Leaf obovate-elliptic, up to 30–45 × 5–10 mm, minutely and irregularly emarginate at apex, gradually tapering toward the base into a deeply conduplicate petiole, subcoriaceous. Inflorescence borne laterally from the apex of the stem, without an annulus, successively single flowered, up to 4.0–5.0 cm long, glandular; peduncle terete, to 3.0–4.0 cm long, without bracts. Floral bracts infundibuliform, glandular, broadly ovate, acute, 1.0–1.5 mm long. Pedicel terete, glandular, 4–6 mm long, persistent. Ovary trialate, subclavate, 2–3 mm long, green. Flowers at least up to 5 per inflorescence, normally yellowish, rarely orange. Sepals fleshy, carinate, microscopically glandulose on both surfaces, and especially the margin; dorsal sepal lanceolate-elliptic, 3-veined, acute, the base semi-hyaline, conspicuously covered with inflated, wart-like transparencies, 10.5–11.0 × 3.0–3.2 mm; lateral sepals elliptic, 3-veined, 9.5–10.0 × 4.5 mm, connate for about three fourth of their length, the base saccate, membranaceous-hyaline, the apex acute, the veins strongly carinate abaxially. Petals small, ligulate-falcate, oblique, acute, 2.6–2.7 × 1.0 mm, 1 or 2-veined. Lip yellowish-orange, small, longitudinally arched-convex in natural position, thinly articulate with the column foot by a hyaline claw, ligulate when expanded, obtuse, 3.0 × 1.0–1.1 mm, fully papillose provided with a pair of acute, erect, triangular lateral lobes from just below to just above the middle, margin dentate-erose, especially apically. Column, arched, terete and slender at the base, 2.5–3.0 mm long without the foot, provided with membranous wings, serrulate along the margins, the apex prolonged into a deeply cucullate, lacerate clinandrium; column foot, stout, fleshy, 1.2–1.5 mm long. Anther cap deeply cucullate, ovate, 2-celled. Pollinia 2, obovate-complanate, minutely hooked at the base. *NOTE: Description based on *FP6543* and the original protologue.

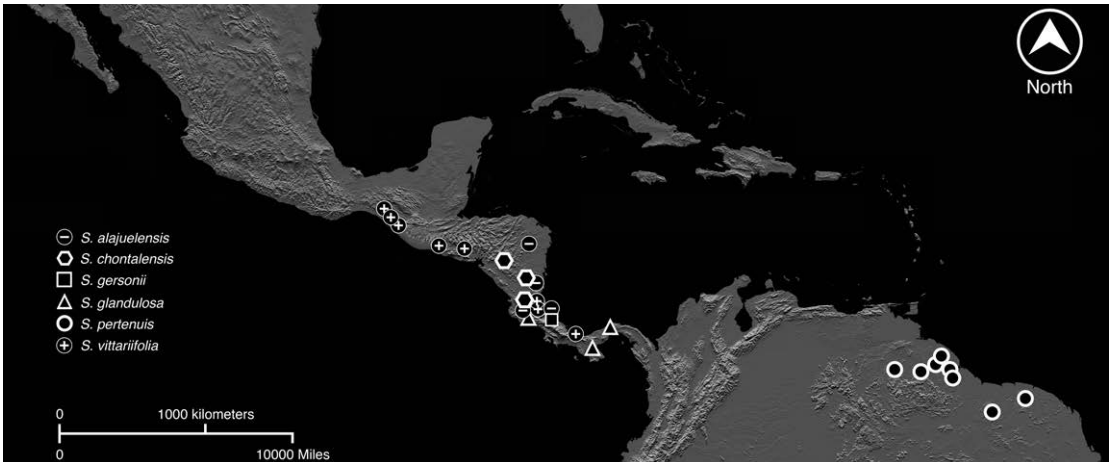

Figure 32. General distribution map of the glandulous species of *Specklinia*. Edited by D. Bogarín.

Other material examined:—COSTA RICA. Alajuela: Upala, road from Upala, ca. 3 km after Bijagua, turning toward Volcán Tenorio, northern slopes of Volcán Tenorio, Caribbean watershed, first bridge on the road, 10º45'52.2"N 85º01'04.4"W, 320 m, tropical moist forest, 28 March 2007, *F. Pupulin, D. Bogarín, S. Dalström, G. Gigot & M. Powell 6543* (JBL-spirit, D1926!, D2376!, D5150!; L-spirit!; Fig. 27c & 33). Upala, Aguas Claras, Colonia Blanca, camino entre Colonia Verde y Colonia Libertad hacia Buenos Aires, faldas al noreste del Volcán Rincón de La Vieja, 10°52'26.2"N 85°14'51.3"W, 550–600 m, bosque muy húmedo tropical, epífitas en potreros y árboles aislados, 4 febrero 2006, *D. Bogarín, J. Barrantes, R.L. Dressler, R. Gómez & A. Rojas 2557* (JBL-spirit, D0721!). Santa Maria National Park, primary forest, Caribbean slope, alt. 600 m, 8 Feb. 1978, *R. Liesner 5187* [MO; illustration by Luer (2006)!]. Guanacaste: Liberia, road from Potrerillos to Brasilia, proximity of Hacienda La Josefina, Pacific watershed of northern volcanic chain, 10º52'15.3"N 85º27'02.2"W, 620 m, tropical dry forest, 27 March 2007, *F. Pupulin, D. Bogarín, S. Dalström, G. Gigot & M. Powell 6521* (JBL-spirit, D3293!). NICARAGUA. Chontales: Río Mico, epiphytic, alt. 1400 ft, Aug 1960, *A.H. Heller 7827* (AMES). Cerro El Chamarro, La Liberta district, alt. 2,175 ft., *A.H. Heller 1036* (AMES).

Etymology:—The name refers to the department of Chontales, southern Nicaragua, where the type specimen was collected.

Distribution:—This species is only known from Nicaragua and Costa Rica (Fig. 32). It is found growing at elevations between 320–660 m.

Notes:—*Specklinia chontalensis* has been traditionally considered well distinguished from *S. glandulosa*. Of the species treated here this is probably the easiest to distinguish morphologically from the other members. The species does share some similarities in floral morphology, however it is mostly included here because of its glandular inflorescence and sepals, and it being sister to *S. gersonii.* The large yellow flowers with the dorsal sepal covered with inflated, wart-like transparencies set it aside immediately.

8. *Specklinia gersonii* Bogarín & Karremans, Phytotaxa 218(2): 112. 2015.

> *The species is similar to Specklinia glandulosa (Ames) Pridgeon & M.W.Chase, but can be easily distinguished by the wider and sub-orbicular (vs. linear) leaves, the lack of a bract on the peduncle, the trialate ovary (vs. terete), the wider dorsal sepal (2.5 vs 1.5 mm), and the widely rounded apical half of the sepals in natural position (vs. narrow and elongate).*

Type:—COSTA RICA. Limón: Guácimo, Pocora, La Argentina, camino a la catarata del río Dos Novillos, ca. 600 m, invenit Gerson Villalobos et Daniel Matamoros, floreció en cultivo en el Jardín Botánico Lankester, 12 abril 2012, *D. Bogarín 9565* (holotype, JBL-spirit, D5192!; isotype, JBL-spirit, D5197!; Fig. 34).

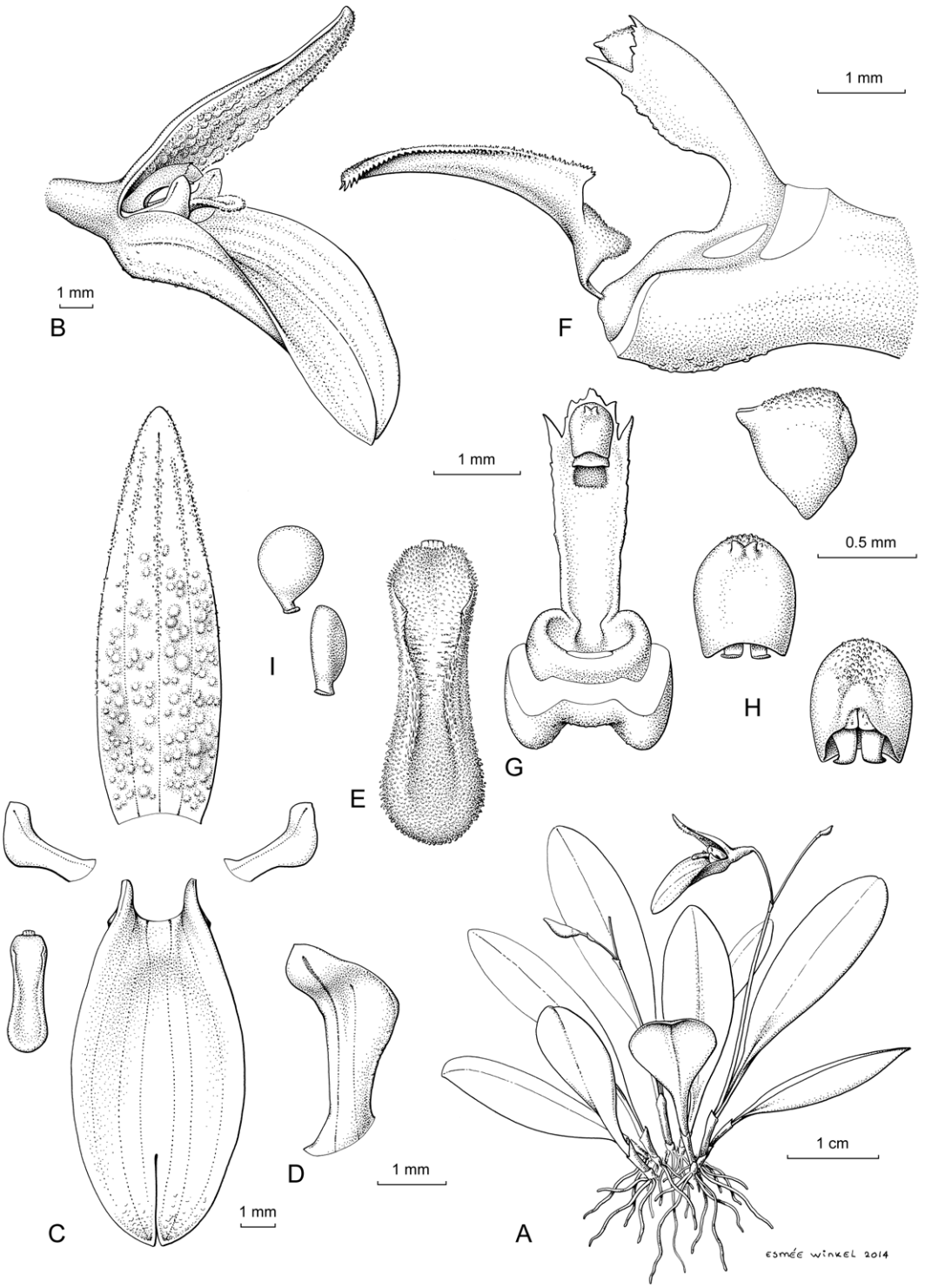

Figure 33. *Specklinia chontalensis* (A.H.Heller & A.D.Hawkes) Luer. A: habit; B: flower; C: dissected perianth; D: petal; E: lip; F: column and lip, lateral view; G: column, ventral view; H: anther with pollinaria; I: pollinaria. Drawn by E. Winkel from *F. Pupulin 6543* (JBL-spirit; L-spirit).

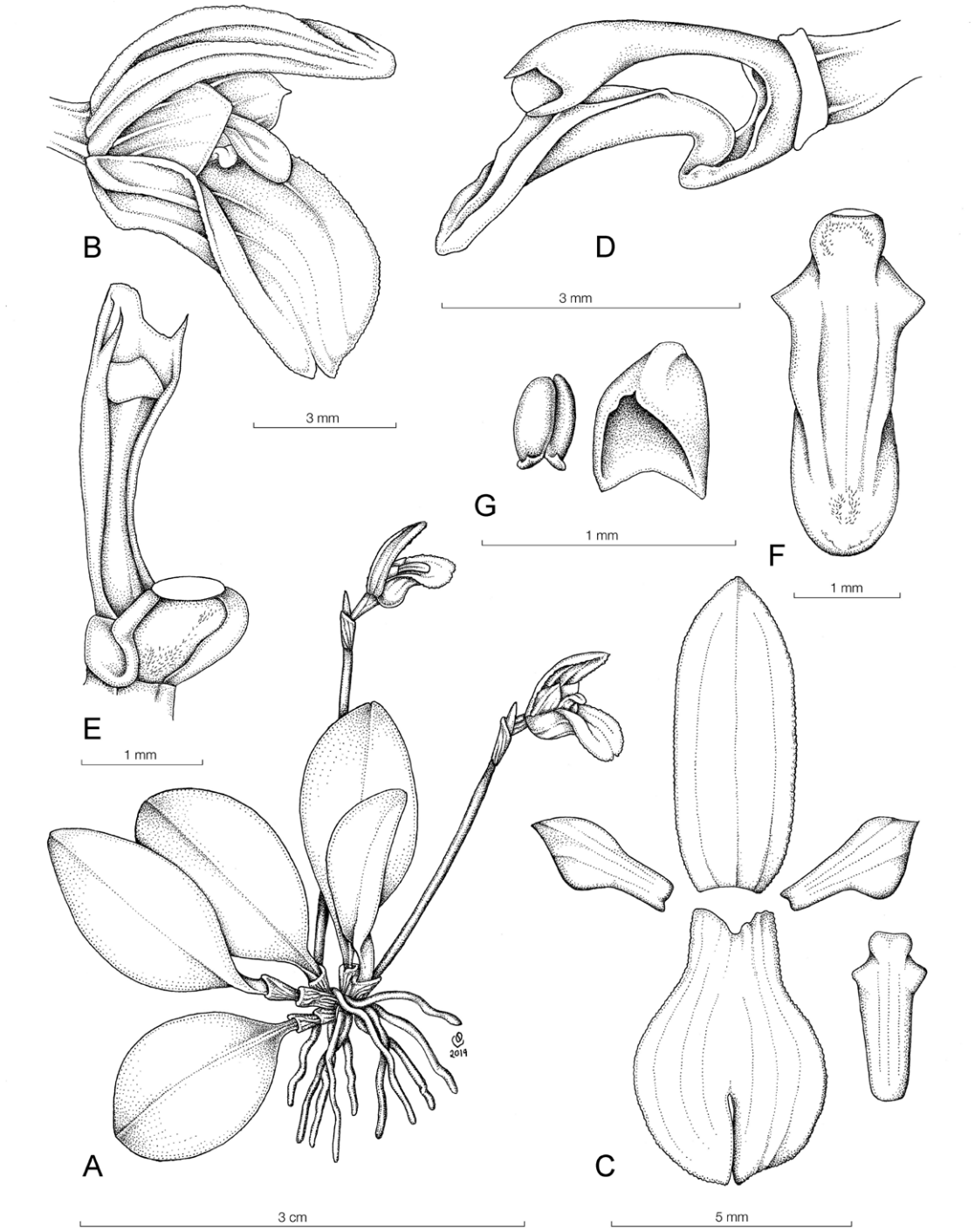

Figure 34. *Specklinia gersonii* Bogarín & Karremans. A: habit; B: flower; C: dissected perianth; D: column and lip, lateral view; E: column ventral view; F: lip; G: anther and pollinaria. Drawn by D. Bogarín & L. Oses from *Bogarín 9565* (JBL-spirit).

Epiphytic, caespitose, ascending, erect herb to 4.0 cm tall. Roots fibrous, flexuous, glabrous, to 1 mm in diameter. Stem abbreviated, terete, to 5 mm long, concealed by a papyraceous, subancipitous, acute sheath to 4 mm long. Leaf elliptic to broadly elliptic, up to 20 × 12 mm, minutely and irregularly emarginate at apex, the mid-vein protruding abaxially into a small apicule, gradually tapering toward the base into a deeply conduplicate petiole, subcoriaceous. Inflorescence borne laterally from the base of the leaf, without an annulus, successively single flowered, up to 3 cm long, glandular; peduncle terete, to 2 cm long, without bracts. Floral bracts infundibuliform, glandular, broadly ovate, acute to subacuminate, 4 mm. Pedicel terete, glandular, 3.5 mm long, persistent, appearing fascicled. Ovary trialate, subclavate, 2 mm long, greenish to orange. Flowers up to 4, only one developed at a time; with fruity fragrance around midday. Sepals fleshy, densely microscopically-glandulose on the outer surface; dorsal sepal narrowly-elliptic, 3-veined, acute, greenish orange, with bright orange-red, the margins microscopically glandulous, 7.0–8.0 × 2.5 mm; lateral sepals narrowly elliptic-oblanceolate, subfalcate, 3-veined, 6.5–7.5 × 4.0–5.0 mm, connate for about two thirds of their length, the midvein strongly carinate abaxially. Petals small, lanceolate-falcate, acute, 3.1–3.3 × 1.4–1.6 mm, 3-veined. Lip reddish-orange, small, longitudinally arched-convex in natural position, thinly articulate with the column foot by a hyaline claw, apically bifid-emarginate in natural position, sagittate to sub-triangular when expanded, obtuse, 3.5 × 1.4–1.5 mm, provided with a pair of sharp, triangular lateral lobes at the base. Column dark-red, arched, terete and slender at the base, 2.5 mm long without the foot, provided with membranous wings, the apex prolonged into a deeply cucullate, lacerate clinandrium; column foot, stout, fleshy, 1 mm long. Anther cap deeply cucullate, ovate, 2-celled. Pollinia 2, obovate-complanate, minutely hooked at the base. *NOTE: Description based on *DB9565* & *AK6025*.

Other material examined:—COSTA RICA. Limón: Guácimo, Pocora, La Argentina, camino a la catarata del río Dos Novillos, 10°06'07.71" N 83°39'28.74" W, 591 m, bosque muy húmedo tropical transición a premontano, 25 noviembre 2013, *A.P. Karremans, D. Bogarín & G. Villalobos 6025* (JBL-spirit!; Fig. 27d & 28b).

Etymology:—The name honors Gerson Villalobos, a Costa Rican orchid enthusiast who brought this species to our attention.

Distribution:—Known only from Costa Rica, growing at elevations around 600 m (Fig. 32).

Notes:—Despite its appealing bright orange flowers and easily recognizable broadly elliptic leaves it seems that *Specklinia gersonii* Bogarín & Karremans had eluded botanists so far. The species is as far as we know very rare; in fact we are aware only of a handful of plants, all from a single population on a trail along the Dos Novillos river in Limón.

9. *Specklinia glandulosa* (Ames) Pridgeon & M.W.Chase.

Basionym: *Pleurothallis glandulosa* Ames. Type:—PANAMA. Juan Grande range, sea level, *C.W. Powell 306* (holotype, AMES!; isotypes, AMES!, MO!; Fig. 35).

Epiphytic, caespitose, ascending, erect herb to 2.5 cm tall (excluding the inflorescence). Roots fibrous, flexuous, glabrous. Stem abbreviated, terete, to 5 mm long, completely concealed by papyraceous, subancipitous, acute sheaths. Leaf narrowly linear, up to 18–21 × 1.5–2.0 mm, gradually tapering toward the base into a deeply conduplicate petiole, subcoriaceous. Inflorescence borne laterally from the apex of the stem, without an annulus, successively single flowered, up to 3.5 cm long, glandular; peduncle terete, with 1 distant, glandular, terete bract. Floral bracts infundibuliform, glandular, broadly ovate, acute. Pedicel terete, glandular, 4 mm long, persistent. Ovary terete. Flowers 1 (probably up to a few with time) per inflorescence, Pompeian red. Sepals fleshy, densely glandulose in the outer surface; dorsal sepal narrowly lanceolate, 3-veined, acute, 8.0 × 1.5 mm; lateral sepals linear-lanceolate, subfalcate, 3-veined, 8.0 × 1.0 mm, connate to below the middle, the base saccate, the apex acute, the veins strongly carinate abaxially. Petals small, ligulate-falcate, acute, 3 × 1.5 mm, 2-veined. Lip small, longitudinally arched-convex in natural position, thinly articulate with the column foot by a hyaline claw, subpandurate from a cordate-sagittate base when expanded, obtuse, 3.5 × 1 mm, provided with a pair of acute, triangular lateral lobes from just below to just above the middle, margin dentate-erose, especially apically. Column arched, terete and slender at the

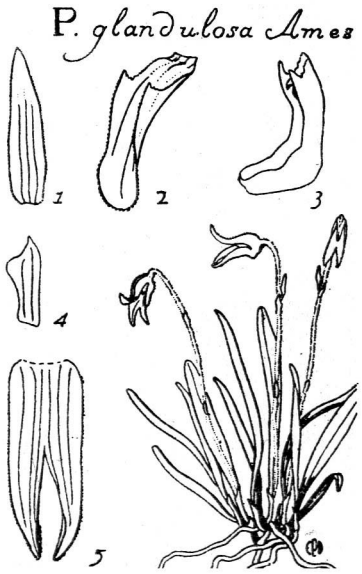

Figure 35. Type illustration of *Specklinia glandulosa* (Ames) Pridgeon & M.W.Chase, published in Ames (1923). Reproduced with the kind permission of the Orchid Herbarium of Oakes Ames, the Harvard University Herbaria.

base, 2 mm long without the foot, provided with membranous wings, margins irregular, the apex prolonged into a deeply cucullate, dentate clinandrium; column foot, stout, fleshy. *NOTE: Description adapted from the protologue.

Other material examined:—COSTA RICA. Puntarenas: Along N fork (known locally as "Quebrada Mona") of Quebrada Bonita, Carara reserve. 9º47'N 84º36'W, elev. 35–40 m. Epiphytic on branch of large fallen tree in primary forest. 31 August 1985, *Michael H. Grayum, R. Warner, P. Sleeper & S. Phelps 5939* (MO!). Without specific collection data, cultivated by Gerson Villalobos, flowered 29 August 2014, *A.P. Karremans 6306* (JBL-spirit!; Fig. 27e, 28c & 36). PANAMA. Herrera: Distrito de Las Minas, alrededor del primer Ciclo de Chepo, ca. 900 m, 7º43'N 80º50'O, bosque nuboso. 29 de septiembre de 1994, *C. Galdames, E. Montenegro, C. Chung & E. Valdez 1758* (PMA!). Chepo de las Minas, *K.S. Walter 78-1518*, flowered in cultivation at SEL, 29 Apr. 1980, C.A. Luer 5237 [SEL!; illustration by Luer (2006)!]. 18 km W of Las Minas, N slope of Cerro Alto Higo; 2400–3000 ft. (known locally as el Montoso); 6 Aug. 1978, *B. Hammel 4289* (MO!). Veraguas: Coiba. Parque Nacional Coiba, afluente del río Santa Clara, orilla del río, 24 julio 2005, *A. Ibáñez & C. Núñez 4342* (PMA!). Panama: Cerro Azul, near Goofy Lake, 24 Aug. 1960, *J.E. Ebinger 984* (MO!). Los Santos: Loma Prieta, Cerro Grande, alt. 2400–2800 ft. Cloud forest and disturbed margins, 8 June 1967, *W.H. Lewis, R.K. Baker, B. MacBryde & R.L. Oliver 2214* (MO!).

Etymology:—The name comes from the Latin *glandula* meaning "diminutive of gland", referring to the conspicuous presence of small glands covering most floral parts and inflorescence.

Distribution:—Known only from Costa Rica and Panama, from around sea level to up to 900 m (Fig. 13).

Notes:—The name *Specklinia glandulosa* has been applied to most of the species treated here at some point. Nevertheless, it can be recognized by the extremely long inflorescence in relation to the leaf (close to twice the length). The sepals are relatively long and narrow in comparison with *S. alajuelensis*, *S. pertenuis* and *S. vittariifolia*. Although it can produce more than a single flower per inflorescence with time, these are closely placed (sub-fascicled), and the species normally appear to have a single flowered inflorescence.

In Costa Rica this species seems to be restricted to the lowlands of the Central and South Pacific, and it is apparently seen very rarely. Most known specimens are from Central Panama.

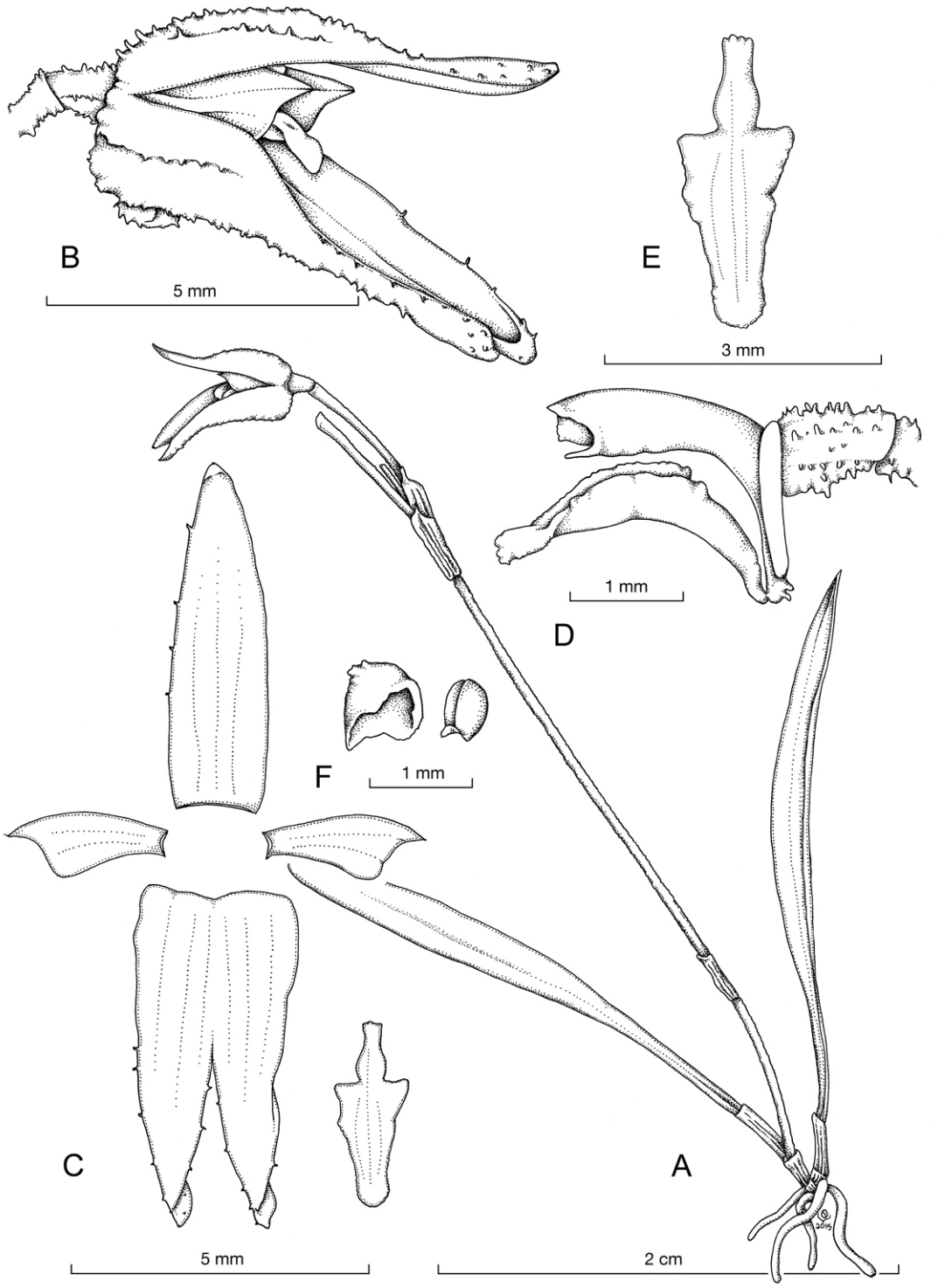

Figure 36. *Specklinia glandulosa* (Ames) Pridgeon & M.W.Chase. A: habit; B: flower; C: dissected perianth; D: column and lip, lateral view; E: lip; F: anther and pollinaria. Drawn by A.P. Karremans & L. Oses from *Karremans 6306* (JBL-spirit).

10. *Specklinia pertenuis* (C. Schweinf.) Karremans & Gravend., Phytotaxa 218(2): 116. 2015.
Basionym: *Pleurothallis pertenuis* C.Schweinf. Type:—GUYANA. Essequibo River, Moraballi Creek, near Bartica, nearly at sea-level. 15 Sept 1929, *N.Y. Sandwith 304* (holotype, K!; isotype, AMES; illustration of type, AMES!).

Epiphytic, caespitose, ascending, erect herb. Roots fibrous, flexuous, glabrous, to 1 mm in diameter. Stem abbreviated, terete, to 3.7 mm long, completely concealed by two papyraceous, subancipitous, acute sheaths. Leaf narrowly linear or oblanceolate-linear, coriaceous, fleshy, up to 22 × 1.7 mm, minutely and irregularly emarginate at apex, the mid-vein protruding abaxially into a small apicule, gradually tapering toward the base into a deeply conduplicate petiole, subcoriaceous. Inflorescence slender, successively single flowered, in anthesis shortly surpassing the leaves, minutely puberulent. Floral bracts infundibuliform, puberulent. Pedicel conspicuously protruding beyond the floral bract. Ovary slenderly terete, muricate. Flower buds brownish orange. Dorsal sepal lanceolate, 3-veined, acute, concave, 4 × 1.8 mm; lateral sepals elliptic-ovate, 3-veined, 4.1 × 2.2 mm, connate for about half of their length. Petals asymmetrical, oblong-spatulate, 2.7 × 1 mm, 1-veined. Lip sagittate-oblong, with acute, spreading angles just below the middle, 3 × 1.4 mm, rounded at the apex, finely papillose on the upper surface. Column stout, 2 mm long, narrowly winged on each side. *NOTE: Description is adapted from the original protologue.

Other material examined:—BRAZIL. Estado do Para, Municipio de Sao Felix do Xingu, vila Canaa, fazenda do Sr. Josue, 4 Jan. 1997, *J.B.F. da Silva 630* (MG!). GUYANA. Roriabo, 7 Nov. 1894, *E.F. im Thurn 84* (K; photograph of type, AMES!); Aruka, June 1897, *E.F. im Thurn 84* (K; photograph of type, AMES!); B.-B. [Barima-Barama] Road. Nov. 1896, *E.F. im Thurn 84* (K; photograph of type, AMES!) between Mazaruni Station and Labbakabra Creek, 27 Apr. 1937, *N.Y. Sandwith 1225* (K); Pomeroon River, Mar. 1884, *G.S. Jenman 1996* (K); Upper Mazaruni District, adjacent to Eboropu Mountain, alt. 470 m, 8 Apr. 1979, *P.J. Edwards 1188* (K). SURINAME. Brownsberg Mazaroni top, 16 April 1981, *R. Determann 148* (SEL!). Wilhelmina Mts., 15 July 1981, R. Determann 81-2168, flowered in cultivation 14 Feb. 1982, *C.A. Luer 6829* (illustration, SEL!). Lely Mountains, distr. Marowikne, 1 June 1976, *M. & P. Teunissen 1631* (SEL!). VENEZUELA. 113 km. south of El Dorado, in fairly dense forest at about 600 m, *G.C.K. Dunsterville 430* (illustration, AMES!; Fig. 37).

Etymology:—The name comes from the Latin *tenuis* meaning "thin or fine", referring to the "very slender" plants.

Distribution:—Known from Venezuela, Guyana, Suriname and Brazil, where it is typically found growing at low elevations, from around sea level to up to 600 m (Fig. 32).

Notes:—When describing *Specklinia pertenuis* (as *Pleurothallis pertenuis*), Schweinfurth recognized it closely resembled *P. vittariifolia* (= *Specklinia vittariifolia*). He distinguished the two species apart on the basis of the glabrous sepals of the first, which are characteristic of the second. Illustrations by Dunsterville and Luer of material from Venezuela and Suriname, respectively, show flowers with less conspicuous ornamentation than observed in *S. glandulosa* and *S. vittariifolia*, but nonetheless present. It is possible that the inconspicuous ornamentation of Schweinfurth's plants was even more difficult to observe in herbarium material. The disposition of the floral parts in the illustration and the statement in the protologue that "bud brownish orange", suggests that the type illustration was prepared from a cleistogamous flower. In fact, ovaries are swollen in many flowers of the herbarium specimens and illustrations.

Material from Brazil, Guyana, Surinam and Venezuela is therefore recognized a distinct species under the name Specklinia pertenuis. It can be recognized by the inflorescence that barely exceeds the leaf, and is rarely multi-flowered, the frequently bears cleistogamous flowers, with inconspicuous sepal ornamentation, very narrow sepals and petals, and a lip with sharp-triangular spreading angles just below the middle.

The plant illustrated by Silva & Silva (1997) of Brazilian origin (*Silva 369*; MG!) shows perianth parts typical of the *S. glandulosa* group, and comparable to those of *S. pertenuis* particularly. Nevertheless the leaves are much broader and have a different shape. Another Brazilian collection (*Silva 630*; MG!) does overlap well with *S. pertenuis*. Both specimens come from Sao Felix do Xingu, and at first glance do not seem to be the same species. Without more material it is difficult to determine them with certainty.

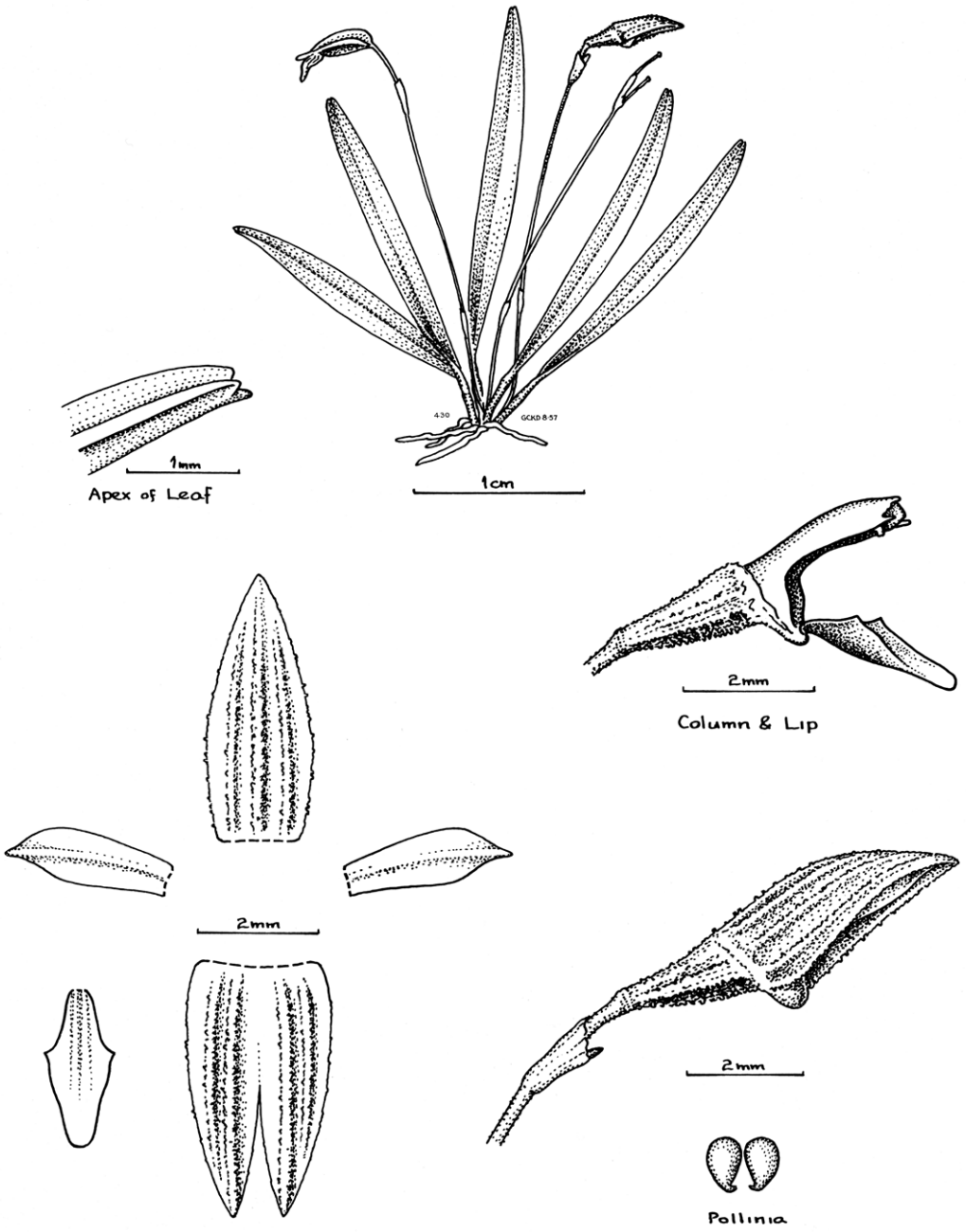

Figure 37. Illustration of *Specklinia pertenuis* (C.Schweinf.) Karremans & Gravend. by G.C.K. Dunsterville, based on *Dunsterville 430* (AMES) from Venezuela. Reproduced with the kind permission of the Orchid Herbarium of Oakes Ames, the Harvard University Herbaria.

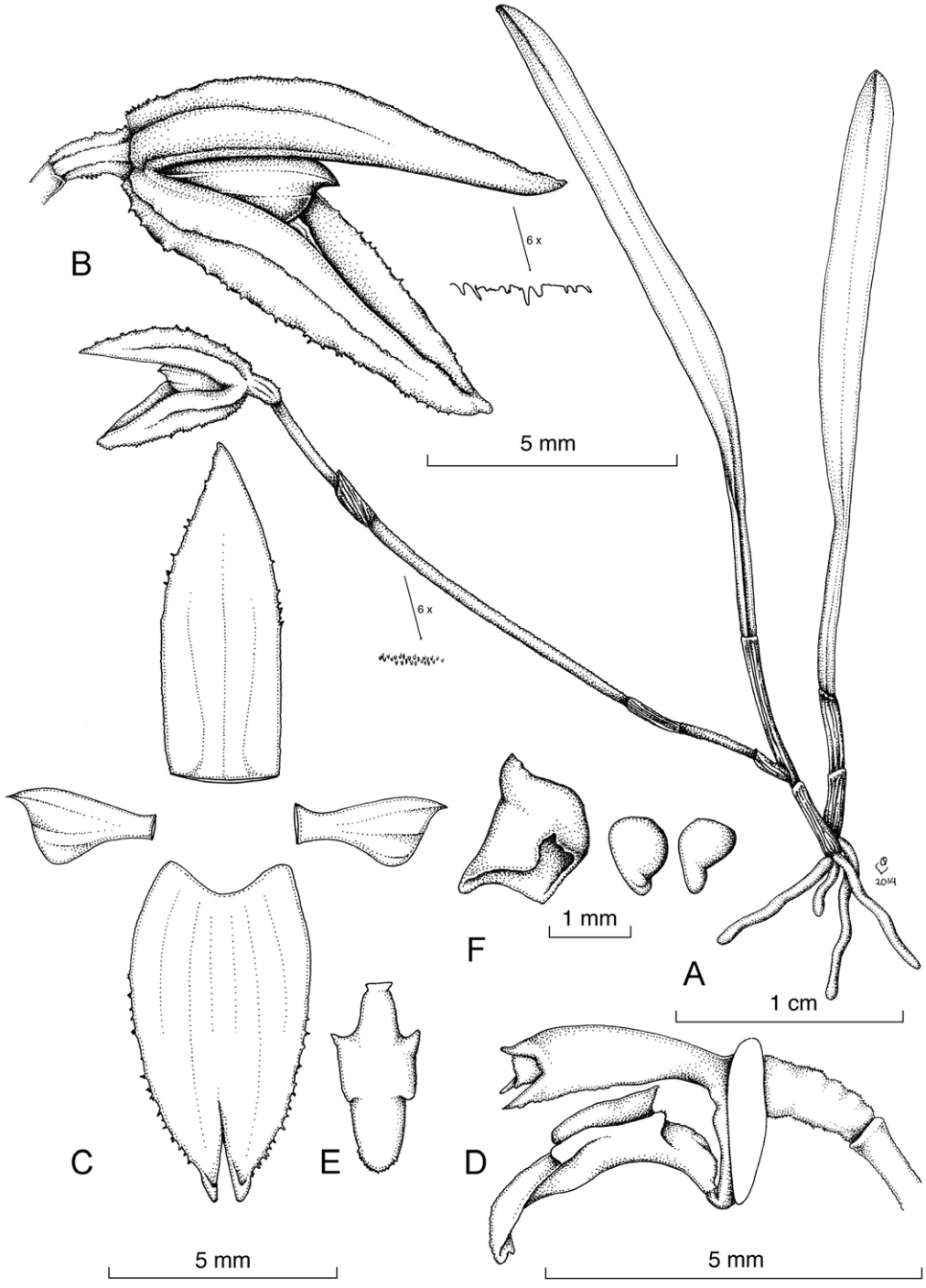

Figure 38. *Specklinia vittariifolia* (Schltr.) Pridgeon & M.W.Chase. A: habit; B: flower; C: dissected perianth; D: column and lip, lateral view; E: lip; F: anther and pollinaria. Drawn by A.P. Karremans & L. Oses from *Karremans 2945* (JBL-spirit).

11. *Specklinia vittariifolia* (Schltr.) Pridgeon & M.W.Chase.

Basionym: *Pleurothallis vittariifolia* Schltr. Type:—COSTA RICA. San Jerónimo. 1350 m. Flowered June 1921, *C. Wercklé no. 117* (holotype, B, destroyed; lectotype, AMES 28807!, selected by Pupulin (2010); illustration of type, AMES 28807!)

Epiphytic, caespitose, ascending, erect herb to 4.5 cm tall. Roots fibrous, flexuous, glabrous, to 1 mm in diameter. Stem abbreviated, terete, to 3.5–9.0 mm long, completely concealed by a papyraceous, subancipitous, acute sheaths to 3 mm long. Leaf narrowly linear, up to 35 × 1.5–3.0 mm, minutely and irregularly emarginate at apex, the mid-vein protruding abaxially into a small apicule, gradually tapering toward the base into a deeply conduplicate petiole, subcoriaceous. Inflorescence borne laterally from the base of the leaf, without an annulus, successively single flowered, up to 4.0–4.5 cm long, glandular; peduncle terete, to 3.0 cm long, with 1 distant, glandular, terete bract, 3 mm long. Floral bracts infundibuliform, glandular, broadly ovate, acute to subacuminate, 2.5 mm. Pedicel terete, glandular, 5 mm long, persistent. Ovary subclavate, with low, irregularly crenulate crests, 1.5–2.0 mm long, green. Flowers up to 4, reddish-orange, developed in succession. Sepals fleshy, densely glandulose on the outer surface; dorsal sepal lanceolate-elliptic, 3-veined, acute, the base semi-hyaline, flushed with orange along the veins, the distal two thirds reddish-orange with occasional transparent spots, 7.5–9.0 × 2.0–3.0 mm; lateral sepals narrowly elliptic-oblanceolate, subfalcate, 3-veined, 7.5–9.0 × 3.5–4.5 mm, connate for about three quarters of their length, the base saccate, membranaceous-hyaline, the apex acute. Petals reddish-orange, small, ligulate-falcate, 3.5–4.0 × 1.7–1.9 mm, 2-veined. Lip reddish-orange, small, longitudinally arched-convex in natural position, thinly articulate with the column foot by a hyaline claw, sagittate to oblong when expanded, obtuse, 4.5 × 1.0 mm, provided with a pair of acute, sub-trapezoid lateral lobes from just below to just above the middle, margin dentate-erose, especially apically. Column dark-red, arched, terete and slender at the base, 3.5 mm long without the foot, provided with membranous wings serrulate along the margins, the apex prolonged into a deeply cucullate, lacerate clinandrium; column foot, stout, fleshy, 1.0 mm long. Anther cap deeply cucullate, ovate, crested, 2-celled. Pollinia 2, obovate-complanate, minutely hooked at the base. *NOTE: Description based on *AK2945* and *IC1111*.

Other material examined:—COSTA RICA. San José: Vázquez de Coronado, Jesús, Parque Nacional Braulio Carrillo, Sendero La Botella, 10°09’33.9”N 83°57’14.8”W, 702 m, bosque muy húmedo tropical transición a premontano, epífitas en bosque secundario y primario, *A.P. Karremans, D. Bogarín & M. Fernández 2943* (JBL-spirit, D6069!). Idem. *A.P. Karremans, D. Bogarín & M. Fernández 2945* (JBL-spirit, D4898!, D5959!; Fig. 1f, 2d & 12). Limón: Pococí, Guápiles, Buenos Aires. Cuenca río Santa Clara, faldas del Volcán Turrialba, 10°05’25,96”N 83°45’39,33”W, 1190 m, 1 de octubre 2013, *I. Chinchilla 1111* (JBL-spirit!). Pococí, Guápiles, Cariari, Gerson Villalobos legit, *A.P. Karremans 5944* (JBL-spirit, D6100!). Limón: Guápiles, Río Corinto, sendero paralelo al Río Corinto y riberas del mismo, 10°19’09”N 83°56’10”W, 500 m, *C. Chávez 52* (MO!). Guácimo, Pocora, La Argentina, camino a la catarata del río Dos Novillos, 10°06’07.71” N 83°39’28.74” W, 591 m, bosque muy húmedo tropical transición a premontano, 25 noviembre 2013, *A.P. Karremans, D. Bogarín & G. Villalobos 6026* (JBL-spirit!). Heredia: La Selva, 1 Oct. 1985, *J.T. Atwood 85-74* (USJ!; SEL!). La Selva, on tree fall on SSE, 2 Oct. 1985, *J.T. Atwood 85-81* (SEL!). La Selva, on cacao along SOC of Annex, 4 Oct. 1985, *J.T. Atwood 85-103* (SEL!). La Selva, on tree fall on SSE, 5 Oct. 1985, *J.T. Atwood 85-123* (SEL!). La Selva, 6 Oct. 1985, *J.T. Atwood 85-127* (USJ!; SEL!). San José: Zona Protectora La Cangreja. Santa Rosa de Puriscal. Bosque primario en la márgenes del Río Negro, 09°42’28”N 84°23’35”W, 400 m. 20 Oct. 1992, *J.F. Morales & Q. Jiménez 891* (CR!). Costa Rica, without specific locality, *R. Lent 1762b* (CR!; SEL!). EL SALVADOR. Departamento Chalatenango, entre Dulce Nombre de María y San Fernando, km 12, a 1200 m. *H. Cl. Clason sub. Hamer 309* (SEL!; illustration by Hamer (1974)!). Cerro Campana, behind Ahuachapan-Ataco, alt. 1400 m, 12 June 1975 (SEL!). MEXICO: Chiapas, Municipio Acacoyagua, Mt. Madre Vieja, 15.450401 N 92.877612 W, 1000 m, *E. Matuda 2532* (MEXU; SEL!). Municipio Escuintla, Mt. Ovando, 15.39083 N 92.6025 W, 935 m, *E. Matuda 28541* (MEXU; AMO, illustration!). Municipio La Concordia, Finca Custepec, trail NW from Finca, 1–3 km along trail, 15.73333 N 92.73333 W, cloud forest, 1180 m, *R. J. Hamshire 1244* (MEXU). PANAMA: Bocas del Toro road, Los Gutiérrez to [Cerro] Pinola. Cultivated at Selby Botanical Gardens, SEL 78-455 ex N. Williams, Aug. 1985, *E.A. Christenson 1326* (SEL!).

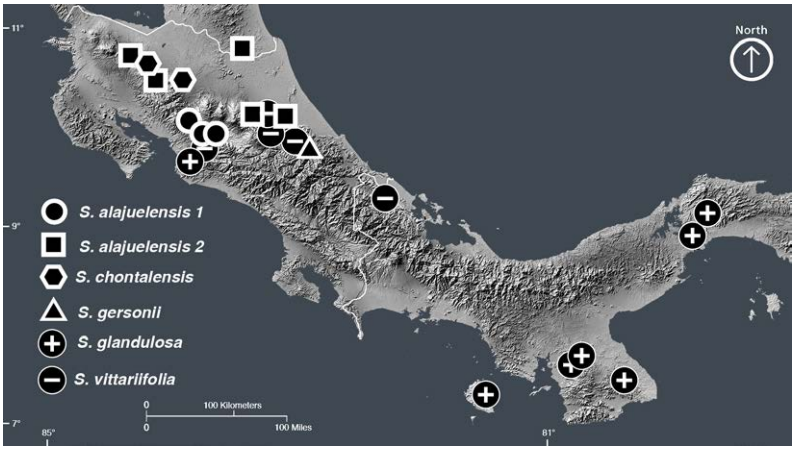

Figure 39. Extract of the distribution map of the glandulous species of *Specklinia*, with emphasis on Nicaragua, Costa Rica and Panama. Edited by D. Bogarín.

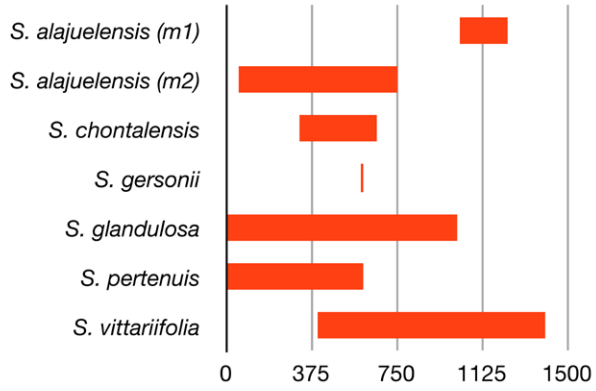

Figure 40. Known elevation distribution of the glandulous species of *Specklinia*. Based on the studied specimens cited. On the X-axis the elevations in meters are depicted.

Figure 41. Intra-specific variation of flower morphology of diverse individuals of two species of glandulous *Specklinia*. A: *S. alajuelensis* 1. B: *S. vittariifolia*. Scale bar = 1 cm. Photographs by A.P. Karremans.

Etymology:—The name alludes to the very long, thin leaves, which is reminiscent of species of the fern genus *Vittaria*.

Distribution:—Known from Mexico, El Salvador, Costa Rica and Panama. In Costa Rica and Panama it is found mostly in the Caribbean lowlands, from 400 to 1190 m elevation. In Mexico and El Salvador it is found at higher elevations, from 1000 to 1400 m (Fig. 32).

Notes:—Aside from a sterile fragment of the plant and an accompanying sketch of the type kept at AMES, nothing else remains of the type material of *Specklinia vittariifolia*. The specimen was supposedly collected in San Jerónimo, Moravia, Costa Rica. We were unable to locate any such plants in the area during a series of field trips, and doubt it did indeed come from there. It is more likely that Wercklé actually collected this plant a few km North-East along the same road, where this species is abundant. There are more collections from Wercklé that, like this species, are typically found on the warm and humid Caribbean watershed, but were allegedly collected in San Jerónimo, a dryer and colder locality in the Central Valley (Pupulin 2010). The illustration of the type and description are not very specific to any of the species of this group; however, the plant fragment and illustration clearly depict a species with long and narrow leaves and an inflorescence that barely reaches the length of the leaf.

Specklinia vittariifolia is locally abundant in certain areas in the Costa Rican Caribbean at mid to low elevations. It has been confused with the similar *S. glandulosa* in herbaria and living collections, however, it can be easily distinguished by the long leaves and relatively short inflorescences which in living material rarely exceed the leaf. The flower is conspicuously downward twisted, and its segments noticeably spreading. Although frequently appearing single flowered, the species can produce up to 4 flowers in tight succession on a single inflorescence, however only one is developed at a time. The flowers are relatively large, with sepals exceeding 7.5 mm long and a lip of 4 mm long, with a pair of conspicuous sub-trapezoid lateral lobes.

The herbarium sheet of Roy Lent's number *1762* kept at CR represents a mix of both *S. alajuelensis* and *S. vittariifolia*. We cannot be certain if both were collected together or if they come from different localities. However, the locality corresponds perfectly with that of other material of *S. alajuelensis*, and we have therefore chosen to give that material the number *Lent 1762a*. The two CR specimens with long, narrow leaves, and all of those kept at SEL are *S. vittariifolia*, and are given the number *Lent 1762b*, with unknown locality.

Discussion and conclusions

Heller & Hawkes (1966) were probably the first to note the phylogenetic relatedness of *Specklinia barbae*, *S. chontalensis*, *S. glandulosa*, *S. pertenuis* and *S. vittariifolia*, and coined the term "*S. glandulosa* alliance" for this species' group. Luer (2006) placed all of them in genus *Sarcinula* Luer, considering that they were not closely related to *Specklinia lanceola*, the type species of the latter genus. Here we have shown that the glandulous species of *Specklinia* include at least 6 species, that they do not form a monophyletic group, and that they are phylogenetically closely allied to the type species of *Specklinia* (Fig. 29).

This particular group ranges from Mexico to Venezuela and is apparently absent in the Antilles and the Andes (Fig. 32). The highest species diversity can be found in Nicaragua, Costa Rica and Panama (Fig. 39). Ecologically these species occupy similar niches and can be found growing sympatrically, which is apparently not rare for several well distinguished species of *Specklinia*. The here studied *Specklinia alajuelensis* (2), *S. gersonii* and *S. vittariifolia*, in addition to the close relatives, *S. luis-diegoi* (Luer) Luer, *S. microphylla* (Rich. & Galeotti) Pridgeon & M.W.Chase and *S. tribuloides* (Sw.) Pridgeon & M.W.Chase, were all found growing in a single locality along the Dos Novillos river in Costa Rica. Similarly, at the type locality of *S. alajuelensis* (1) in La Palma, San Ramón we have also collected *S. calyptrostele* (Schltr.) Pridgeon & M.W.Chase, *S. corniculata* (Sw.) Steudel, *S. fulgens* (Rchb.f.) Pridgeon & M.W.Chase, *S. grobyi* (Bateman ex Lindl.) Barros, *S. lanceola* and *S. tribuloides* in a single patch of a few dozen trees. The glandulous *Specklinia* have a notorious preference for mid to low elevations (Fig. 40). They can be found growing from sea level to up to about 1400 m, with all the studied species overlapping at 600 m in elevation.

The glandulous *Specklinia* share a "standard" morphological pattern, and the differences between them are not as conspicuous as their similarities (Fig. 28). Nevertheless, their intra-specific variation is low and populations are

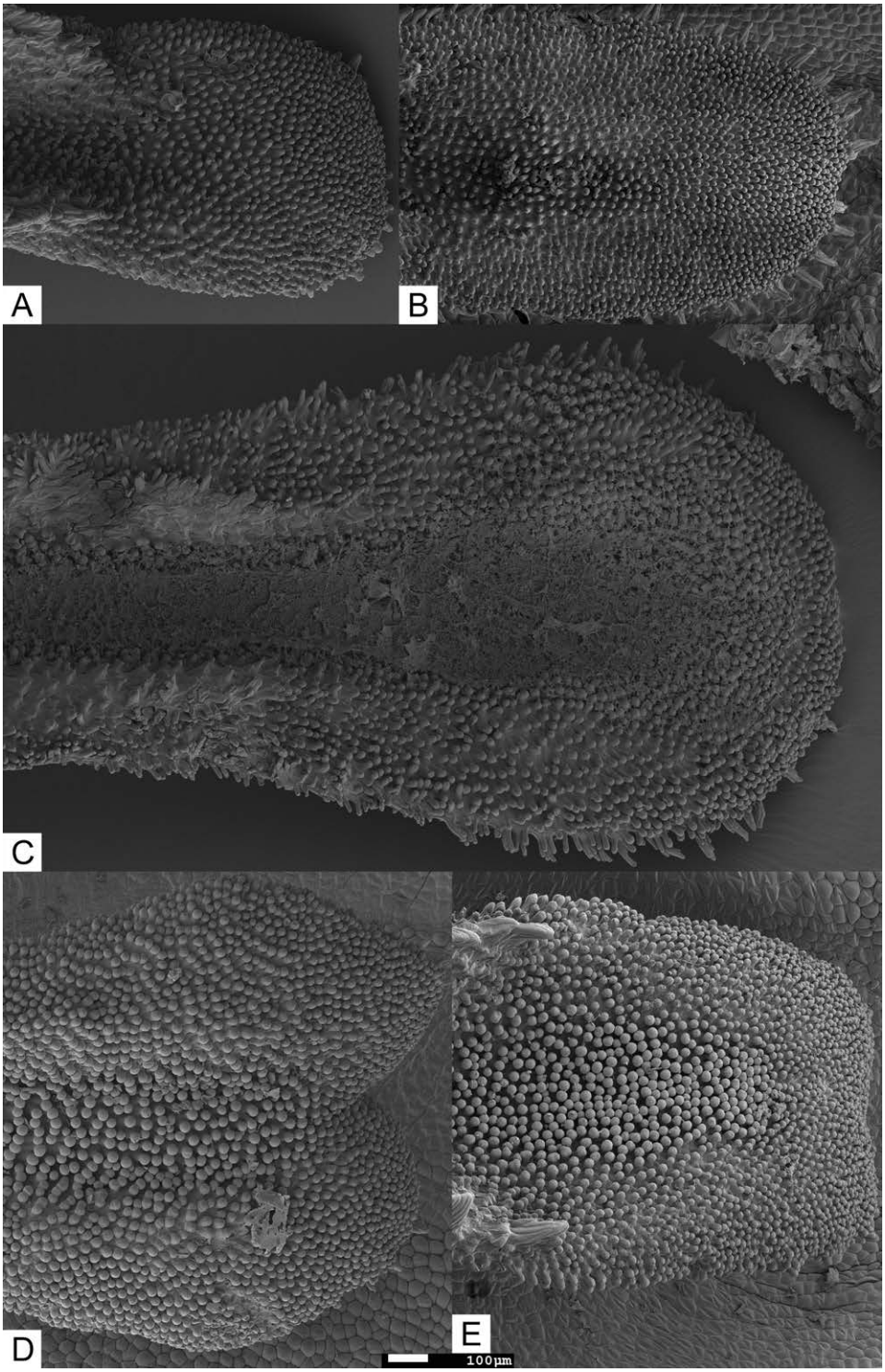

Figure 42. Micrographs of the lip apices of *Specklinia* species. A: *Specklinia alajuelensis* 1 (*Pupulin 8470*); B: *Specklinia alajuelensis* 2 (*Karremans 6460*); C: *Specklinia chontalensis* (*Pupulin 6543*); D: *Specklinia gersonii* (*Karremans 6025*); E: *Specklinia vittariifolia* (*Chinchilla 1111*). Photographs by A.P. Karremans.

morphologically stable (Fig. 41). Genetically they are not only a non monophyletic group, but are also highly differentiated (Table 4), with the nrITS sequence divergence between each species varying between 2.2% (between *S. alajuelensis* and *S. vittariifolia*) and 6.2% (between *S. alajuelensis* and *S. chontalensis*). If studied in detail, morphological differences become apparent as well. The tiny lips of species of this group are extremely delicate and deform easily with manipulation. In most illustrations they look quite similar to each other, sharing a comparable shape. They are all fully glandular and longitudinally depressed in the middle, where the glands are denser and residues are visible (Fig. 42). This common pattern is probably due to a similar pollination system in which the pollinator, following the nectar guides and steered by the lip lobes, is led to the base of the column/lip cavity. Nevertheless, they can be quite different from each other in size, shape, ornamentation, and even color. The lips of the sister species *S. alajuelensis* and *S. vittariifolia* for example are easily distinguished with micro-photography (Fig. 43).

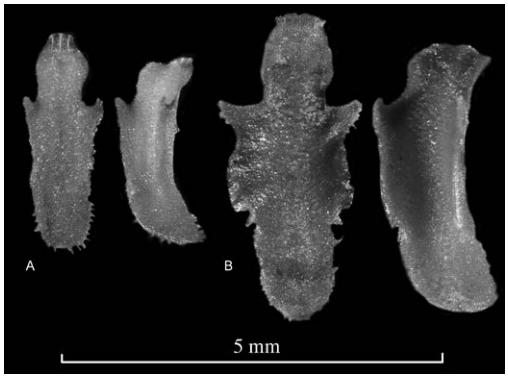

Figure 43. Comparison of the lip size, shape, ornamentation and color of two species of glandulous *Specklinia*, in natural position (right) and extended (left). A: *S. alajuelensis* 1 (*Pupulin 8470*). B: *S. vittariifolia* (*Chinchilla 1111*). Scale bar = 5 mm. Photographs by A.P. Karremans.

Sepal size, shape and color although similar also differs (Fig. 27). Even though all sepals are externally glandular, they are so in varying pattern and degrees (Fig. 44). The glands are variable in length between the different species, and are mostly conical or obconical in shape, but not capitate. The glands are placed mostly along the veins and margins, where also occasional stomata are found in all species. Those stomata are similar to those found on the inner surface of the sepals of species of the *Specklinia endotrachys* complex (Chapter 8). Additionally, and probably as in all Pleurothallidinae, sunken trichomes can be frequently observed on the outer surface of the sepals (Chapter 8).

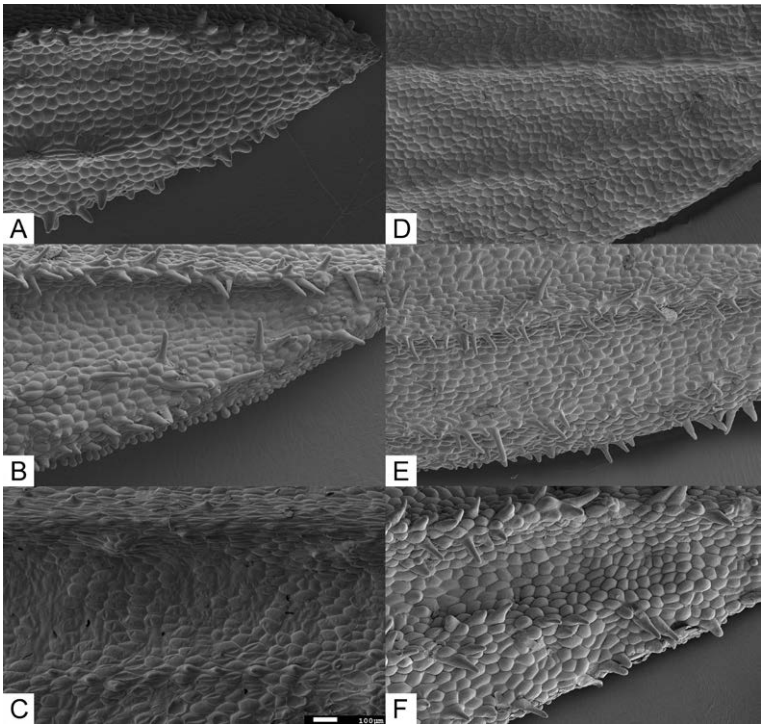

Figure 44. Micrographs of the outer surface of the sepals of *Specklinia* species. A: *Specklinia alajuelensis* 1 (*Pupulin 8470*); B: *Specklinia alajuelensis* 2 (*Karremans 6460*); C: *Specklinia chontalensis* (*Pupulin 6543*); D: *Specklinia gersonii* (*Karremans 6025*); E: *Specklinia glandulosa* (*Karremans 6306*) F: *Specklinia vittariifolia* (*Chinchilla 1111*). Photographs by A.P. Karremans.