



Article

A reconsideration of the empusellous species of *Specklinia* (Orchidaceae: Pleurothallidinae) in Costa Rica

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Abstract

This paper focuses on the systematics of the *Specklinia endotrachys* species complex in Costa Rica. Traditionally considered a variable species, *S. endotrachys* is here treated as one of at least four, albeit closely related, taxa. Of these species, *S. endotrachys*, *S. pfavii*, and *S. spectabilis* are described and illustrated from living material, and *S. remotiflora* is described and illustrated as new to science. *Specklinia remotiflora* is compared with *S. endotrachys* and *S. spectabilis*, from which it differs in the repent habit, lax inflorescence and campanulate flowers provided with convergent sepals and non-apiculate petals. New combinations are proposed for *Pleurothallis pfavii* and *P. spectabilis*. A lectotype is selected for *Pleurothallis endotrachys*. Observations on the pollination of *S. remotiflora* and *S. spectabilis* in cultivation are given.

Key words: Neotropical orchids, pollination, *Specklinia endotrachys* complex, *Specklinia remotiflora*

Introduction

Recircumscription of the generic limits of the mammoth genus *Pleurothallis* Brown (1813: 211) (Orchidaceae: Pleurothallidinae) as a result of molecular studies (Pridgeon *et al.* 2001, Pridgeon & Chase 2001) and the consequent creation of several more segregate genera (Pridgeon & Chase 2001, 2002, Luer 2004, 2005, 2006, 2007, 2010, 2011) has made the taxonomy of some concepts fluid. In particular, the paper by Pridgeon and Chase (2001) presented new evidence to re-establish *Specklinia* Lindley (1830: pl. 8), recognizing 86 species, most of which were transferred by the authors. Both in the bootstrap consensus trees of the *matK/trnL-F* dataset and the most parsimonious tree from the combined *matK/trnL-F/ITS* nrDNA dataset their “clade F” unites a morphologically highly heterogeneous set of taxa, including *Dryadella simula* (Rchb.f.) Luer (1978: 209), *Pleurothallis costaricensis* Rolfe (1917: 80), *P. lentiginosa* Lehmann & Kränzlin (in Kränzlin 1899: 446), *P. endotrachys* Reichenbach (1876: 95), *Acostaea costaricensis* Schlechter (1923a: 284), and species of the genera *Platystele* Schlechter (1910: 565) and *Scaphosepalum* Pfitzer (1889: 139). In one of the most parsimonious trees of the complete ITS nrDNA matrix, based on a larger sampling, clade F also includes other species of *Pleurothallis*, among which *P. lanceola* (Sw.) Sprengel (1826: 731)—the type species of the genus *Specklinia*—together with *P. endotrachys*, *P. fulgens* Reichenbach (1875b: 516), *P. lateritia* Endrés ex Reichenbach (1872: 731), *P. lentiginosa*, and *P. tribuloides* (Sw.) Lindley (1830: 6), form a distinct subclade treated by the authors as the “core” *Specklinia*. Even with the removal of the basal *Dryadella* Luer (1978: 207) and the derived *Platystele* and *Scaphosepalum* from clade F, the resulting circumscription of *Specklinia* is variable both in terms of vegetative and floral morphology.

Specklinia sensu Pridgeon & Chase (2001) is difficult to characterize on the basis of a particular set of distinguishing morphological features, which has promoted the creation of several new genera, expressly

designed to fit one or more morphologically aberrant species of *Specklinia* (Luer 2004, 2006). Due to the different interpretations of the circumscription of *Specklinia*, it is difficult to estimate the actual number of species of this genus, but Barros and Trettel Rodrigues (2009) recently accounted for 420 binomials (Barros 2004, 2006, Barros & Trettel Rodrigues 2009, Luer 2004, 2007), more than twice the number originally included by Pridgeon (2005).

Among segregates from *Specklinia*, we focus here on the species of the supposedly monotypic genus *Empusella* (Luer) Luer (2004: 258), elevated to generic rank and based on *Pleurothallis* subgen. *Empusella* Luer (1986: 41) to accommodate *Pleurothallis endotrachys* [syn. *Specklinia endotrachys* (Rchb.f.) Pridgeon & M.W.Chase, 2001: 257] (Luer 2004). According to Luer (1986), *Pleurothallis* subgen. *Empusella* may be recognized by the caespitose habit with short stems (“ramicauls”), an inflorescence born from an annulus near the base of the ramicaul, and a laterally compressed peduncle. The name is derived from the Latin *empusella*, a little hobgoblin, in allusion to the fancied appearance of the flower (Luer 2007). In his diagrammatic representation of possible relationships between groups of *Pleurothallis*, Luer (1986) placed subgen. *Empusella* as a derived member of the “affinity *Specklinia*”, close to *Masdevallia* Ruiz & Pavón (1794: 122) and *Scaphosepalum*. He considered the “bizarre” *Pleurothallis endotrachys* as the only member of the subgenus, “without close relatives”, noting how other names for the species (which he considered synonyms) had been placed in four genera in the past. Luer formally transferred *P. endotrachys* to *Empusella* Luer (2004: 258), without rationale either for creation of the new genus or its phylogenetic relationships. In his later treatment of *Specklinia* and other vegetatively similar genera, Luer (2006) did not include *Empusella* in the discussion, possibly considering it only distantly related to his concept of *Specklinia*.

The results of nuclear (ITS) and plastid DNA (*trnL-F*, *matK*) sequencing for 185 taxa of the Pleurothallidinae (Pridgeon *et al.* 2001) showed, however, that *Pleurothallis* subgen. *Empusella* is placed in a clade sister to the *Scaphosepalum-Platystele* clade, which comprises several sections of *Pleurothallis* subgen. *Specklinia* (Lindl.) Garay (1974: 121–123; including the type of the genus, *S. lanceola*) and *Pleurothallis lentiginosa* Lehm. & Kraenzl. (in Kränzlin 1899: 446), the last previously treated as the monotypic genus *Pseudoctomeria* Kränzlin (1925) on the basis of its highly divergent floral morphology. Due to the absence of reliable morphological characters to interpret as synapomorphies and the strong support provided by the genetic evidence, Pridgeon and Chase (2001) resurrected and redefined *Specklinia* as sister to the *Scaphosepalum-Platystele* clade. The recircumscribed *Specklinia* included species of *Pleurothallis* subgenera *Specklinia* [*P.* sects. *Hymenodanthae* Barbosa Rodrigues (1892:9), *Tribuloides* Luer (1986: 91), *Muscariae* Luer (1986: 89)], *Empusella* and *Pseudoctomeria*, and *Acostaea* Schlechter (1923a: 22, 102), showing low levels of sequence divergence. Among the morphological features useful to define *Specklinia*, the authors indicated the usually small plants provided with an abbreviated stem with an annulus, the variously connate sepals, and the hinged lip; the sepals and petals of *Specklinia* are mostly membranous, and the column is provided with a toothed apex, and ventral anther and stigma.

Our independent genetic analyses (unpubl.) confirm the phylogenetic placement of the empusellous species close to the core of *Specklinia*. Therefore, recognizing this small group of species as a separate genus would result in recognition of most of the segregate genera from *Specklinia*, including *Acostaea*, *Gerardoa* Luer (2006: 86), *Muscarella* Luer (2006: 94), *Pseudoctomeria*, *Sarcinula* Luer (2006: 201), and *Tribulago* Luer (2004: 265), but would also require creation of at least two additional genera, reducing *Specklinia sensu stricto* to just a few species.

The empusellous species of *Specklinia* belong to a clade that includes *Specklinia barbae* (Schltr.) Luer (2004: 259), *S. chontalensis* (A.H.Heller & A.D.Hawkes) Luer (2004: 259), *S. corniculata* (Sw.) Steudel (1840–1841: 489), *S. fulgens* (Rchb.f.) Pridgeon & M.W.Chase (2001: 257), *S. guanacastensis* (Ames & C.Schweinf.) Pridgeon & M.W.Chase (2001: 258), *S. glandulosa* (Ames) Pridgeon & M.W.Chase (2001: 257), *S. lanceola*, *S. lentiginosa*, *S. psichion* (Luer) Luer (2004: 263), and *S. tribuloides* (Sw.) Pridgeon & M.W.Chase (2001: 259). This singular group is comprised of morphologically heterogeneous species that have never before been presumed to be closely related, the only constant morphological character they seem to share is the color of the flowers. All species mentioned, except for *S. lentiginosa*, have intense bright

orange flowers with a fruity odor. What makes this clade unusual is not only the fact that more than a dozen species share a common color, but that the different bright orange shades are unique within *Specklinia*, uncommon in Pleurothallidinae, and not at all common among Orchidaceae in general. Whereas most orange-flowered orchid species appear to be members of a clade of hummingbird-pollinated within mainly non-orange, bee-pollinated group (i.e. *Elleanthus* Presl 1827: 97, *Ornithidium* Salisbury ex R. Brown 1813: 210, *Scaphyglottis* Poeppig & Endlicher 1836: 58), in this case the species of the *S. endotrachys* complex are pollinated by fruit flies, *Drosophila*, as it was early noted out by Endrés (in Reichenbach 1878) in the nineteenth century and confirmed by Chase (1985) with cultivated plants.

Therefore, we will treat here the species close to *Pleurothallis endotrachys* as members of *Specklinia*, making the necessary combinations.

Materials and Methods. This study was conducted at the Lankester Botanical Garden (JBL) of the University of Costa Rica and the Hortus Botanicus of Leiden University in The Netherlands between 2010 and 2012. Cited specimens belong to the *Specklinia endotrachys* complex and include vouchers kept mainly at CR, JBL, INB, L, MO and USJ. Phenological data were recorded in the field and from cultivated specimens or herbarium labels. Herbarium specimens were deposited at CR, JBL and L. Sketches of specimens were drawn with a Leica MZ 9.5 stereomicroscope with a drawing tube and conserved in the reference collections of JBL and L. The species were illustrated by composite line drawings from living specimens by Pupulin and Winkel. Descriptions were prepared from living specimens and herbarium material from JBL and L.

Key to the Costa Rican species of *Specklinia* close to *S. endotrachys*

1. Flowers yellow with red petals; lip acute, yellow, with a central red line; column wings broad, entire; clinandrium entire *S. pfavii*
- Flowers entirely orange; lip rounded to truncate, concolorous orange; column wings narrow, denticulate; clinandrium erose-dentate 2
2. Plant repent; inflorescence lax; flowers not spreading; petals not apiculate *S. remotiflora*
- Plant caespitose; inflorescence congested; flowers spreading; petals distinctly apiculate 3
3. Floral bracts subequal to the length of the pedicel; dorsal sepal lanceolate; petals retuse, densely and coarsely papillose, provided with a long mucron abruptly inserted within the sinus *S. endotrachys*
- Floral bracts much shorter than the length of the pedicel; dorsal sepal linear-triangular; petals acute, tapering, microscopically papillose, the mucron continuous with the apex *S. spectabilis*

Taxonomic treatment

1. *Specklinia endotrachys* (Rchb.f.) Pridgeon & M.W. Chase (2001: 257).

Basionym: *Pleurothallis endotrachys* Reichenbach (1876: 95). Type: COSTA RICA. Alajuela: San Ramón, along the Barranca River, Endrés 92 (lectotype, selected here, W 0021581; isoelectotypes, W 1889-003365, W 0020331, W 0020150, AMES 118500). Additional material associated with the type is recorded by Pupulin *et al.* 2011: 32.

Homotypic synonyms: *Humboltia endotrachys* (Rchb.f.) Kuntze (1891: 667). *Empusella endotrachys* (Rchb.f.) Luer (2004: 258). *Non Pleurothallis endotrachys* Lehm. & Kraenzl. (in Kränzlin 1899: 439), *nom. illeg.* [= *Pleurothallis lehmanniana* Schltr. (1920: 235)].

Epiphytic, caespitose, erect herbs to 16 cm tall. Roots fibrous, flexuous, glabrous, to 0.7 mm in diameter. Stem abbreviated, terete, slender, to 1.5 cm long, monophyllous, completely covered by a glumaceous, imbricating, acute sheath to 2 cm long, becoming dry-papyraceous with age. Leaf oblong-elliptic, obtuse, minutely retuse, the midvein protruding abaxially into a small apicule, 11.0–16.0×1.7–2.2 cm, gradually tapering toward the base into a deeply conduplicate-rounded petiole provided with ancipitous margins, subcoriaceous. Inflorescence produced laterally from the apex of the stem, without an annulus, and emerging from a short, spathaceous, acute, carinate bract ca. 2 mm long, a successively, many-flowered (to 19+), distichous,

congested raceme to 27 cm long; peduncle flattened, ancipitous, to 20 cm long, with 3 distant, imbricating-tubular, ancipitous, acute bracts, 9–10 mm long; rachis fractiflex, almost completely covered by the floral bracts. Floral bracts tubular-amplectent, strongly conduplicate-ancipitous, broadly ovate, acute, uncinata in lateral view, 8–10×8–9 mm. Pedicel cylindric, subclavate, glabrous, 8–10 mm long, persistent. Ovary linear, subtrigonus, 6 mm long, orange. Flowers with pale orange dorsal sepal, striped with darker orange, the lateral sepals, petals and lip bright orange, the column pale orange. Sepals densely papillose in the inner surface except at the base, the lateral ones fleshy and thickened along the external margin, the dorsal one thinner; dorsal sepal erect, elliptic-lanceolate, 5-veined, acuminate, geniculate at the middle, semi-hyaline, flushed with orange along the veins, 27×8 mm, the distal two thirds densely papillose, the papillae extending along the margins almost to the base; lateral sepals lanceolate, acuminate, ending into a filiform mucro, 3-veined, 24×5 mm, connate at the base ca. 4 mm to form a deeply saccate mentum in front to the column foot, membranous-hyaline at the base, then thick, papillose, with a prominent keel abaxially along the midvein, the margins slightly revolute-thickened. Petals small, linear-ligulate, falcate, subspathulate, retuse, provided with a filiform mucro in the sinus, 4.5×1.0 mm, univeined, the apex and the distal labellar margin papillose. Lip small, arched-convex in natural position, thinly articulate with the column foot by a hyaline claw, ligulate-spathulate when expanded, rounded-subretuse, 5.5×1.8 mm, the central portion provided with a pair of thin, elevated keels converging and running to the base of the apical lobe. Column arched, semi-terete, 5–6 mm long without the foot, margins of the stigma dilated into semi-rhombic, crenulate, obtuse, membranous wings, the clinandrium apically tridentate, flanked by a small tooth laterally; column foot forward-projecting, fleshy, incurved, ca. 2.0 mm long. Anther cap cucullate, ovate, strongly keeled above, the keel protruding into a small mucro, 2-celled. Pollinia 2, ligulate-obovate, semi-convex, the sub hyaline base flattened, minutely uncinata. Fruit not seen.

Other material examined:—COSTA RICA. Puntarenas: Monteverde: San Gerardo de Santa Elena, vertiente Atlántica de la Cordillera de Tilarán, ca. 1000 m, 23 Enero 1999, floreció en cultivo en el JBL el 11 Abril 2000, *Blanco 959 & Arias* (USJ!); Same locality and collection date, *Blanco 961* (JBL-Spirit!, CR!; Fig. 1, 5). Alajuela: Upala, Aguas Claras de Buenos Aires, Hotel Termas Azules, laderas del Volcán Rincón de La Vieja, 10°49'09" N - 85°16'04" W. 700–1000 m, 05 de Abril del 2004, *Karremans 218* (JBL-Spirit!). Without specific locality, *Endrés s.n.* (W!).

Distribution:—Endemic to Costa Rica, where it has been recorded from the Pacific watershed of the northern volcanic and Tilarán mountain chains, at 700–1100 m elevation (Fig. 2).

Notes:—*Pleurothallis endotrachys* was described by Reichenbach (1876) as a member of his *Pleurothallis* series *Sicariae* on the basis of a plant collected by Endrés (no. 92) in Costa Rica at San Ramón, along the Barranca River on the Pacific side of the Tilarán range. The sheet at W with the handwritten description by Reichenbach (W 0020331), which Luer annotated as lectotype (correction label, 1992), is sterile, as well as W 0020150, whereas flowers are present on W 0021581 (with a detailed description by Endrés), selected here as the lectotype, and W 1889-0033651 (all part of the same collection under *Endrés* 92). Another sheet with two fertile specimens from the same collection is conserved at AMES (118500). Two sheets at W include drawings prepared by Endrés of his collection number 92 (W 0020151, 0020152). On one of the drawings (W 0020152) Endrés wrote: "Inner surface of sepals slightly viscous? / much visited by a small fly!"; and in the description he stated: "Sepals scabrous in inner surface (exuding honey)" (W 0021581). This explains the intended name of "*Pleurothallis mellifera*", proposed by Endrés in the description he sent to Reichenbach. Endrés' note, translated in Latin by Reichenbach in 1878 ("*Flos intus viscidus a parva mosca quadam diligentissime visitatus*"), is probably one of the earliest (if not the first) published observations about pollination in *Pleurothallidinae*.

Chase (1985) reported on the pollination of Costa Rican populations of *S. spectabilis* (as *Pleurothallis endotrachys*) cultivated in Michigan (USA), observing that early in the day the flowers emit a faint rotten-fruit odor and that only fragrant flowers were of interest to the flies. The species of *Drosophila* observed, *D. immigrans*, has also been noted from Costa Rica and hence could be the natural pollinator (Chase 1985).

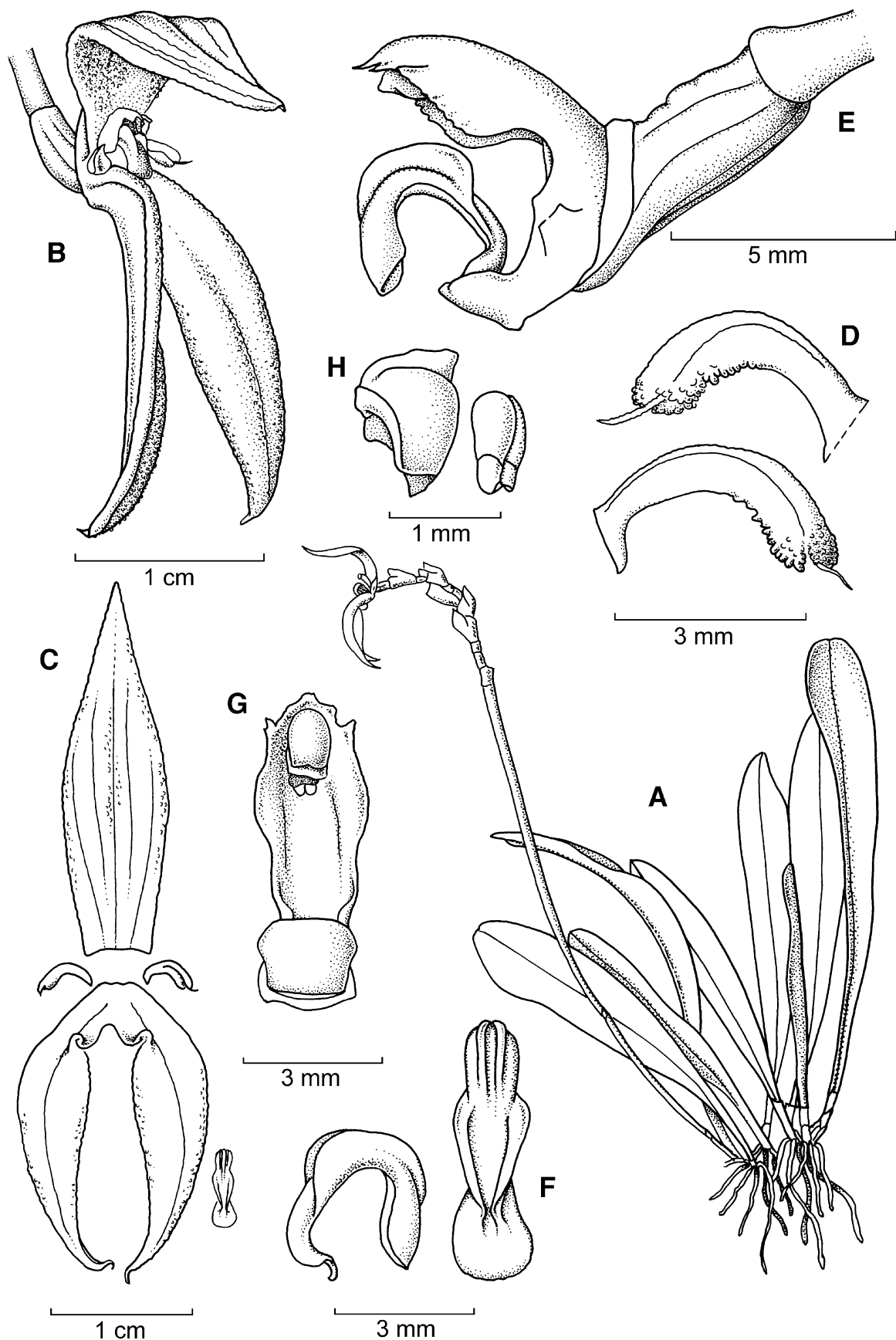


FIGURE 1. *Specklinia endotrachys* (Rchb.f.) Pridgeon & Chase. A. Habit. B. Flower. C. Dissected perianth. D. Petals. E. Column and lip, lateral view. F. Lip, front and side views. G. Column, ventral view. H. Anther and pollinia. Drawn by F. Pupulin & E. Winkel from Blanco 861 (JBL-spirit).

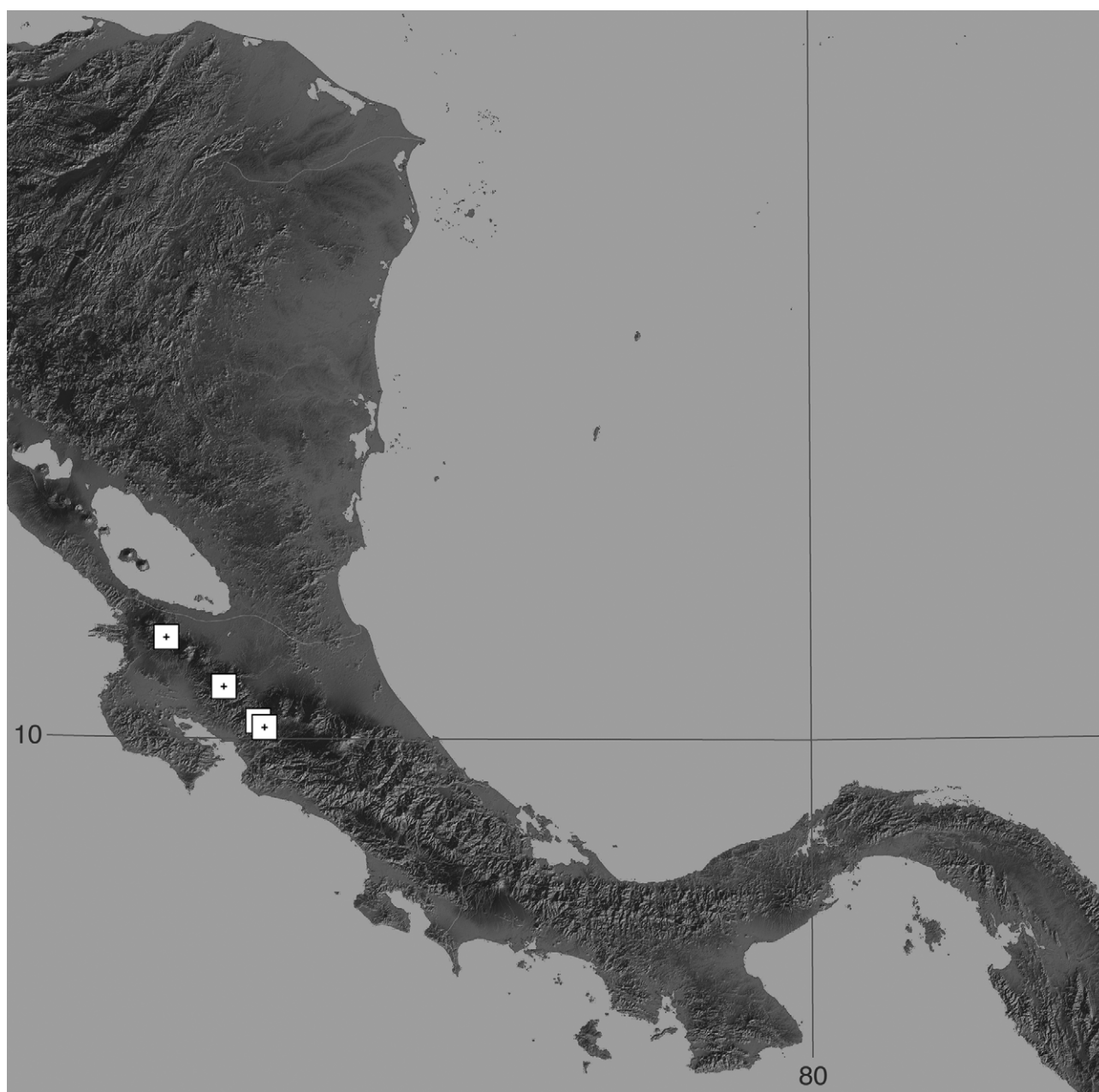


FIGURE 2. Distribution map of *S. endotrachys*.

In the research greenhouses of Lankester Botanical Garden, species of *S. endotrachys* group are frequently visited by small drosophiloid flies (Fig. 3). The visits extend over the whole day, but they are apparently more frequent in the hottest hours of the afternoon. Flies spend a long time on the flowers, exploring both the abaxial and adaxial sides of the sepals with their mouthparts, but mostly they walk around the inner base of the sepals and the lip. It is not uncommon to observe the flies resting immobile on the sepals for up to one hour. When the fly goes up along the strongly convex lip, its weight causes a shift in balance, provoking the blade to shift and to trap the fly against the column (Fig. 4). The column wings and porrect petals have a clear function in maintaining the body of the fly in the correct position to receive the pollinia on the underside of the scutellum, where they firmly adhere with their hooked apex (Fig. 3). We cannot confirm presence of any “meal” or nectar on the surface of the fresh flowers we examined, as suggested by Endrés. Also Chase (1985) observed no nectar on the flowers, nor did he observe the flies removing anything from the roughened areas of the sepals. Further ultrastructural and chemical studies aimed to understand the powerful attraction of these flowers on drosophilid flies are under way.

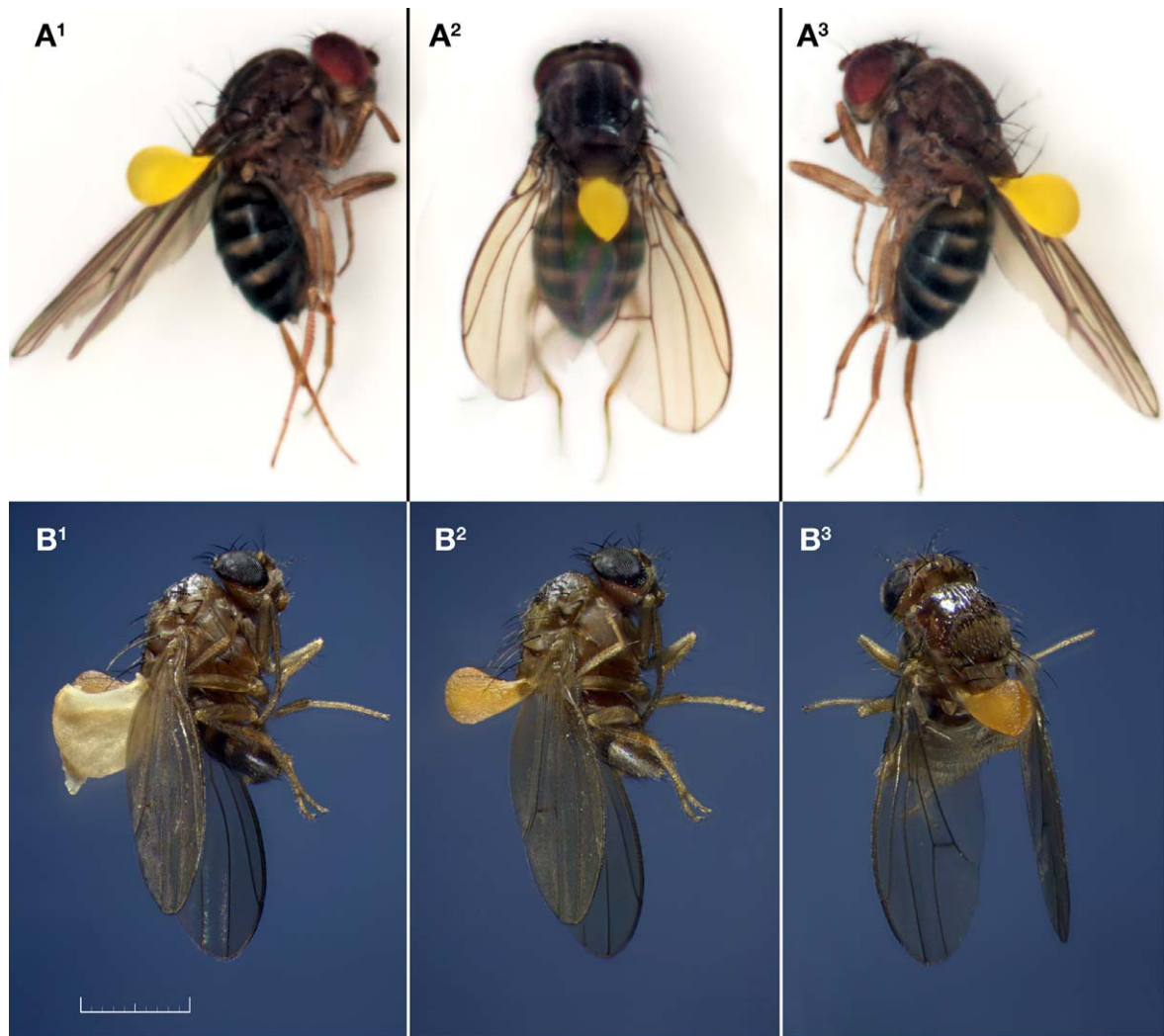


FIGURE 3. Pollinators of *Specklinia* species. A¹–A³. Drosophilideae species with pollinarium of *S. remotiflora* (Bogarín 8181). B¹–B³. Drosophilideae species with pollinarium of *S. spectabilis* (JBL-02643). In B¹ the pollinarium is still enclosed within the anther cap. Scale bar=1 mm.



FIGURE 4. Pollinator of *Specklinia spectabilis* (JBL-02643), trapped against the column of the flower. Sepals are removed. Scale bar = 5 mm.

In the protologue of *Pleurothallis endotrachys*, Reichenbach (1876) mentioned the uncinat floral bracts, longer than the subtended pedicels (“*bracteis [...] introrsum curcatis, ovariis pedicellatis multo longioribus*”), the retuse apex of the petals (“*tepalis linearibus retusiusculis*”), the triangular wings of the column and the denticulate clinandrium that are diagnostic of the species.

Among the species of this group, *S. endotrachys* is easily distinguished by the combination of caespitose habit, long floral bracts hiding the pedicels, orange flowers, twisted lateral sepals and distinctly retuse petals provided with a long mucron abruptly inserted within the sinus.

2. *Specklinia pfavii* (Rchb.f.) Pupulin & Karremans, *comb. nov.*

Basionym: *Pleurothallis pfavii* Reichenbach (1886: 555). Type: [COSTA RICA or PANAMA]. Chiriquí, *Pfau. s.n.* (holotype, W).

Heterotypic synonyms: *Masdevallia platyrachis* Rolfe (1888: 178–179). *Pleurothallis platyrachis* (Rolfe) Rolfe (1890: 136), *comb. inval.*; (Rolfe) Rolfe ex Hooker f. (1890: sub pl. 7129). *Kraenzlinella platyrachis* (Rolfe) Rolfe (1915: 326). TYPE: COSTA RICA: “The plant was imported from Costa Rica by Mr. Shuttleworth, and sent to Kew in 1884, in which year a scape was produced. It has now become fully established and is bearing several scapes, the first flower having recently expanded”, *E. Shuttleworth s.n.* (holotype, K).

Epiphytic, caespitose, erect herb to 17 cm tall. Roots fibrous, flexuous, glabrous, to 1.5 mm in diameter. Stem abbreviated, terete, to 1.5 cm long, monophyllous, completely concealed by 2 glumaceous, slightly loose, ancipitous, acute sheaths to 1.8 cm long, becoming brown-papyraceous with age. Leaf elliptic, 10.7–14.2×2.4–3.0 cm, minutely retuse, the midvein protruding abaxially into a small apicule, gradually tapering toward the base into a conduplicate petiole, the margins ancipitous, subcoriaceous. Inflorescence born laterally from the apex of the stem, without an annulus, an erect-subarching, congested, successively-flowered, distichous raceme to 35 cm long; the rachis strongly fractiflex, producing up to 30+ flowers; peduncle flattened, ancipitous, to 28 cm long, with 3–4 distant, tubular-ampectent, ancipitous, apically subuncinate, acute bracts, 6–7 mm long. Floral bracts infundibuliform, subuncinate laterally, ovate, abaxially ancipitous, subacuminate, 7×6 mm. Pedicel cylindric, glabrous, to 12 mm long, persistent. Ovary subclavate, subtrigonus, to 5 mm long, green. Flowers with bright yellow sepals and lip, lip with longitudinal orange stripes, petals dark red, column yellow. Sepals fleshy, densely papillose on the inner surface with the exception of the hyaline basal third, margins revolute, strongly keeled abaxially along veins; dorsal sepal lanceolate, triveined, acute, the base hyaline, flushed with yellow along veins, the distal two-thirds densely papillose, 24×8 mm; lateral sepals narrowly elliptic-subfalcate, 3-veined, 23.0×3.5 mm, connate at the base for about 3 mm into a deeply concave mentum, membranaceous-hyaline at the base, then densely papillose, margins slightly revolute. Petals small, ligulate-subfalcate, rounded, porrect, univeined, 12×3 mm, with a rounded keel abaxially along the vein, the apex thickened, minutely papillose inside, the labellar margin provided with low papillae in the basal half. Lip lanceolate, articulate with the apex of column foot by a hyaline claw, strongly arched-convex in natural position, triveined, subtrullate when expanded, obtuse to subacute, with a small, rounded apicule, the distal half provided with 2 thin, high keels converging toward the apex but not reaching it, the clawed base thickened, subquadrate; entire lip 18×8 mm. Column arched, semiterete, provided with a foot, 6.5 mm long without the foot, with 2 broad, thin, membranaceous, rounded wings in the middle portion, the apex rounded, deeply cucullate, the clinandrium shallow, entire; column foot forward-projecting, stout, fleshy, 4 mm long. Anther cap ovate, deeply cucullate, strongly keeled in the middle, 2-celled. Pollinia 2, obovate-complanate, hooked at attenuate base. Fruit not seen.

Other material examined:—COSTA RICA. Pérez Zeledón: without any additional collection data, cultivated by Wubben in The Netherlands, flowered in cultivation at the Hortus Botanicus in Leiden, 1 Dec 2011, *Karremans 4825* (L-Spirit!; Fig. 6). Without collecting data, flowered in cultivation at Lankester Botanical Garden, *JBL-11086* (JBL-Spirit!, CR!; Fig. 5).

Distribution:—Endemic to the lowlands of southern Costa Rica and western Panama, on the Pacific watershed of the Talamanca-Chiriquí range, at around 500 m elevation (Figure 7).



FIGURE 5. Comparison of flowers of species of the *Specklinia endotrachys* group. A. *Specklinia endotrachys* (Blanco 961). B. *Specklinia pfavii* (JBL-11086). C. *Specklinia remotiflora* (Bogarín 8181). D. *Specklinia spectabilis* (JBL-02641). All flowers shown in front, three-quarters side, and side views. Scale bar = 1 cm.

Reichenbach (1886b) described *Pleurothallis pfavii* on the basis of a living plant he received from Pfau, who collected it in “Chiriquí”. He precisely noted the colors of the perianth: “*Flores intense sulphurei pollicem longi. Tepalo pulcherrime cinnamomeo brunnea. Labellum flavum linea mediana rufa. Columna viridula*”. The exact locality of the original collection is unknown, and the region of Chiriquí (actually in Panama) was at the time shared by Panama and Costa Rica. The Swiss Rudolf Richard Pfau (?—1897) collected mostly in Costa Rica, where he eventually owned a nursery in San José. According to the protologue, *Pleurothallis pfavii* has falcate, obtuse petals provided with a thickened external margin and acute (“quasi sagittato”) lip (Reichenbach 1886b), a set of features that makes it unmistakable.

Originally described in the *Gardeners' Chronicle* in August 1888, *Masdevallia platyrachis* was illustrated shortly after in the *Botanical Magazine* (Hooker 1890: sub pl. 7129) under the name of *Pleurothallis platyrachis*. The original description of *Masdevallia platyrachis* was based a plant cultivated at Kew and received from Shuttleworth of Charlesworth & Co., where it was supposedly introduced from Costa Rica. Edward Shuttleworth (1829-1909) collected orchids in Colombia, but he never went to Costa Rica, and no records remain of the collectors employed by the commercial nursery of Charlesworth in Central America during the last decades of nineteenth century. This leaves the exact type locality of *M. platyrachis* unresolved. Rolfe (1890) transferred it to *Pleurothallis* in his reconsideration of *Scaphosepalum*, but as he did not expressly associate the epithet with the genus *Pleurothallis*, the combination is invalid according to art 33.1 of the ICBN. A valid combination was published that same year, when *Pleurothallis platyrachis* was first illustrated (Hooker 1890). The precise illustration by Fitch, showing the plant habit and details of the petals, lip, and column, leaves no doubts about the identity of *Pleurothallis platyrachis* as conspecific with *P. pfavii*.

The combination of bright yellow flowers with red petals, the yellow with a central red line, acute lip, and the rounded, not apiculate petals, distinguish *S. pfavii* from other members of the *S. endotrachys* complex.

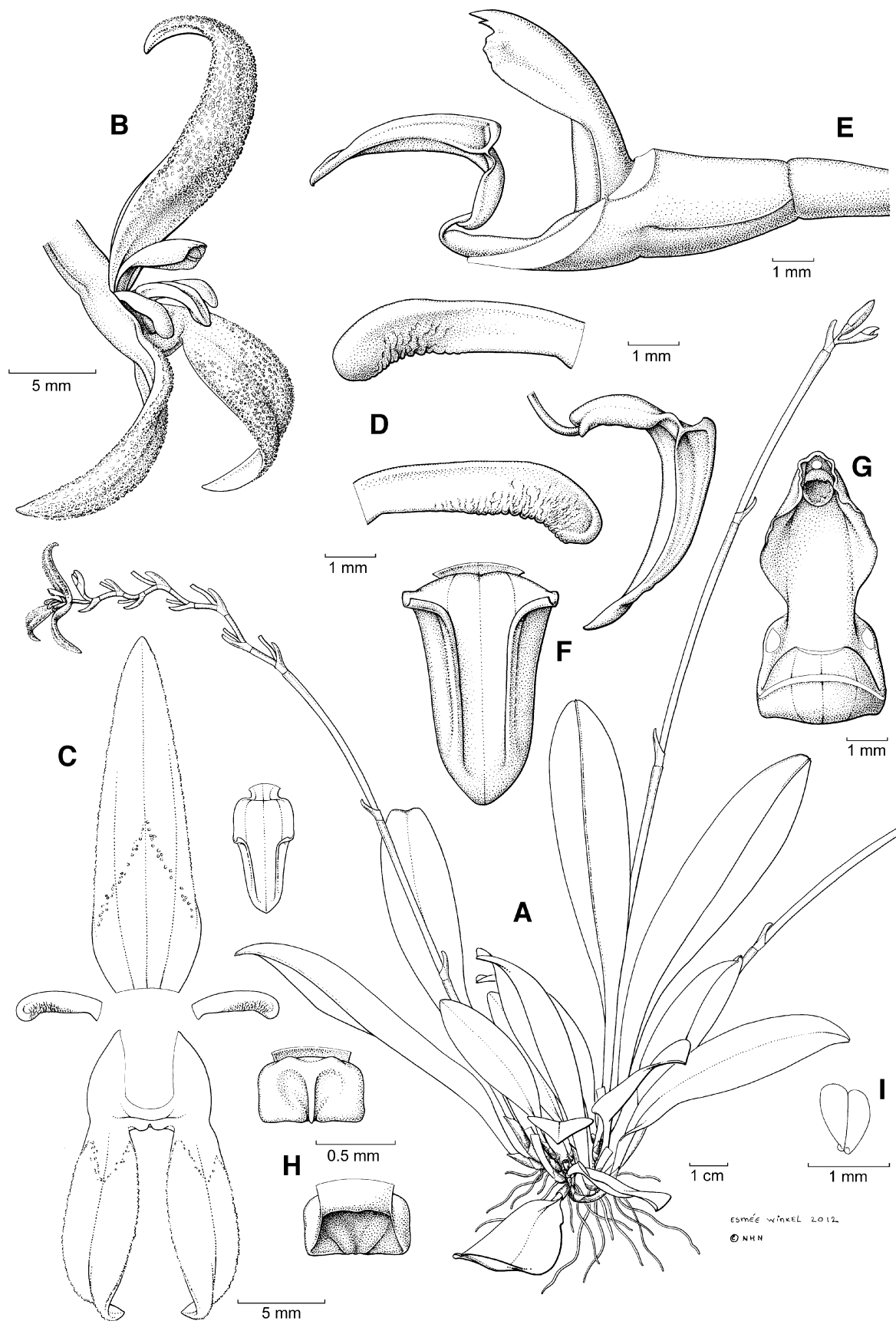


FIGURE 6. *Specklinia pfavii* (Rchb.f.) Pupulin & Karremans. A. Habit. B. Flower. C. Dissected perianth. D. Petals. E. Column and lip, side view. F. Lip, front and side views. G. Column, ventral view. H. Anther. I. Pollinia. Drawn by E. Winkel from Karremans 4825 (L-spirit).

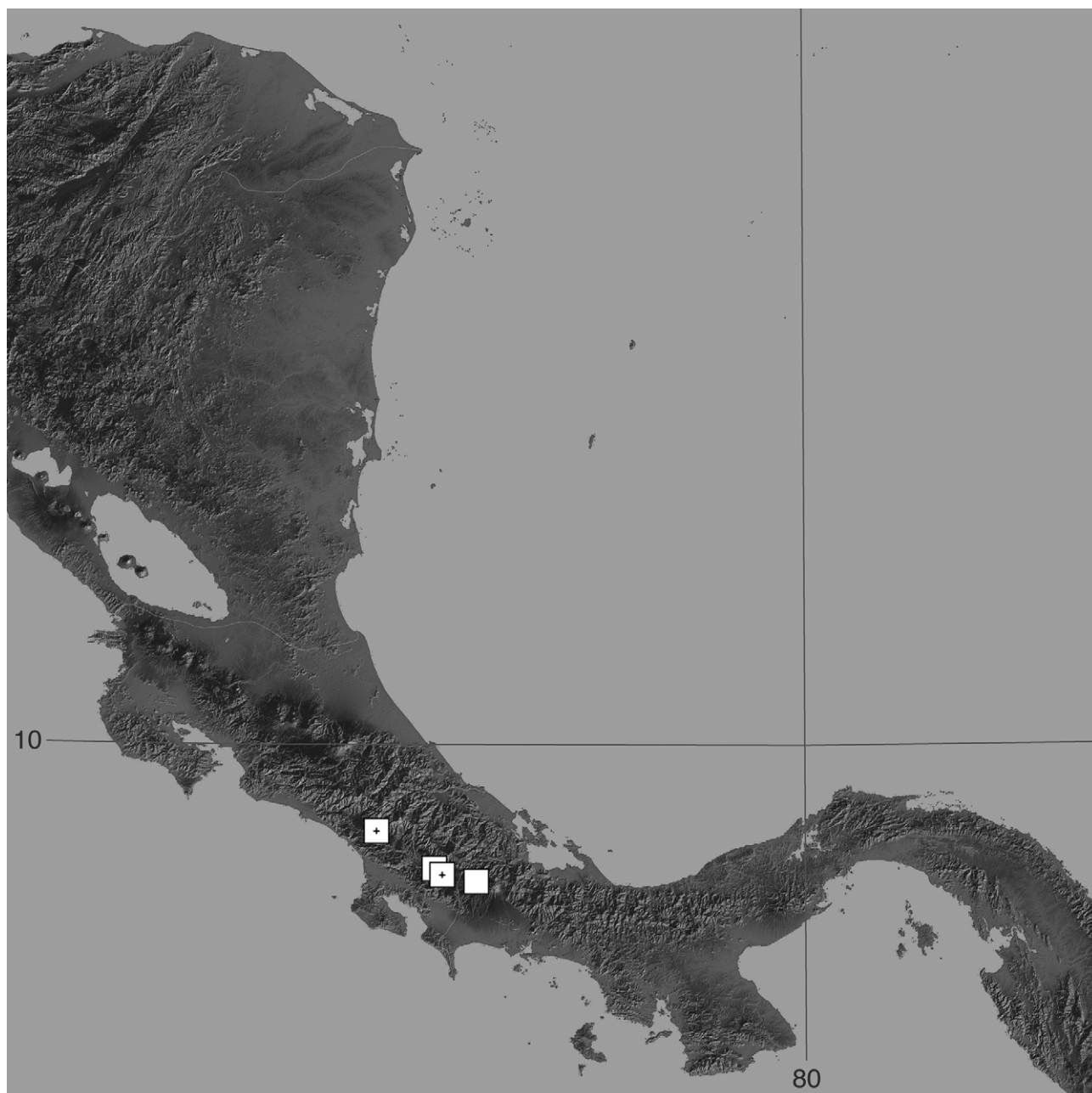


FIGURE 7. Distribution map of *Specklinia pfavii*.

Specklinia remotiflora* Pupulin & Karremans, *sp. nov.

A Pleurothallide endotrachyde Rchb.f. *similis*, *habitu repente*, *inflorescentia laxa*, *floribus subcampanulatis sepalibus convergentibus petalibusque truncatis nec apiculatis recedit.*

Type:—COSTA RICA. Coto Brus: Sabalito, Zona Protectora Las Tablas, 15 km al noreste de Lucha, Sitio Coto Brus, Finca de Miguel Sandí, bosque muy húmedo montano, *ad ager Sandiorum* “El Surá”, *crescenti epiphytica in sylvis humidis versus pascues prope flumen Surá*, 7 October 2010, Bogarín 8181, Dressler, Fernández & Pupulin (holotype, USJ; isotype, JBL-Spirit!). Fig. 5, 8.

Epiphytic, subrepent-ascending, erect herb to 30 cm tall. Roots fibrous, flexuous, glabrous, to 1.5 mm in diameter. Stem abbreviated, terete-cylindric, to 2.2 cm long, monophyllous, completely concealed by a papyraceous, subancipitous, acute sheath to 3.5 cm long, eventually disintegrating into fibrous remains. Leaf

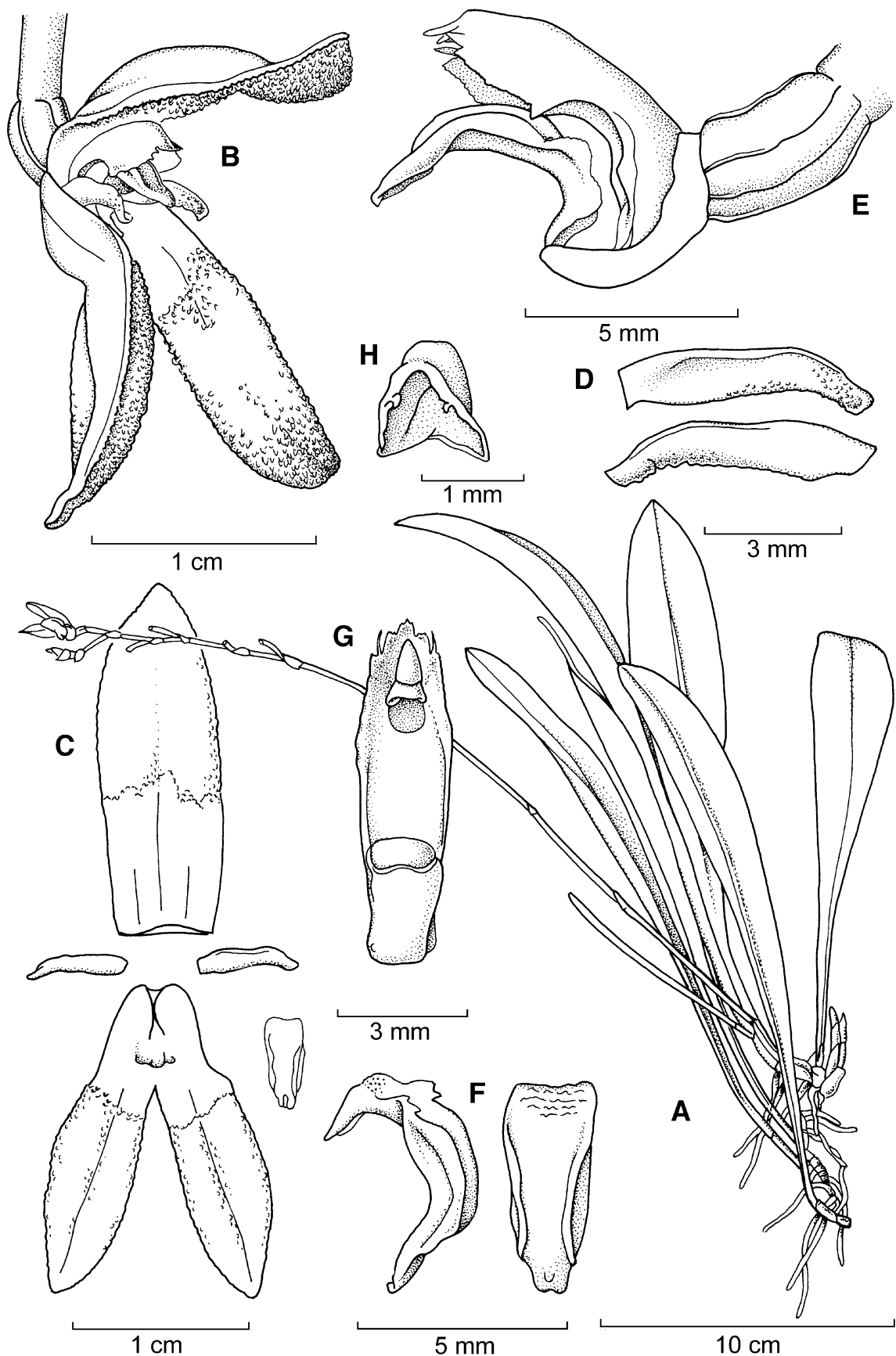


FIGURE 8. *Specklinia remotiflora* Pupulin & Karremans. A. Habit. B. Flower. C. Dissected perianth. D. Petals. E. Column and lip, side view. F. Lip, front and side views. G. Column, ventral view. H. Anther. Drawn by F. Pupulin & E. Winkel from *Bogarín 8181* (JBL-spirit).

narrowly obovate-oblongate, 17.0–29.0×3.2–3.9 cm, minutely and irregularly emarginate at apex, the midvein protruding abaxially into a small apicule, gradually tapering toward the base into a deeply conduplicate petiole with strongly ancipitous margins, subcoriaceous. Inflorescence born laterally from the apex of the stem, without an annulus, a lax, distichous, successively 4–7-flowered raceme, up to 40 cm long; peduncle flattened, ancipitous, to 30 cm long, with 4–5 distant, amplexant, ancipitous, subacute bracts, 7–8 mm long. Floral bracts infundibuliform, broadly ovate, abaxially ancipitous, acute to subacuminate, 10×8 mm. Pedicel cylindric, glabrous, 13–15 mm long, persistent. Ovary subclavate, with low, irregularly crenulate crests, 4–5 mm long, green. Flowers with dark orange-red sepals and petals, lip red, column yellow. Sepals fleshy, densely papillose on the inner surface except at base, margins thickened-revolute; dorsal sepal lanceolate-elliptic, triveined, acute, the base semi-hyaline, flushed with orange along veins, the distal two-thirds densely papillose, the revolute margins glabrous, 20×7 mm; lateral sepals narrowly elliptic-oblongate, subfalcate, triveined, 19–20×5 mm, connate for about one-quarter to one-third of their length, the base saccate, membranaceous-hyaline, the apex acute, gently deflexed at the middle, the midvein strongly carinate abaxially. Petals small, ligulate-falcate, truncate, correct, 6.0–7.0×1.0–1.5 mm, univeined, papillose-thickened toward the concave apex, the labellar margin provided with coarse papillae arranged in two rows, the outer margin thickened. Lip small, longitudinally arched-convex in natural position, thinly articulate with the column foot by a hyaline claw, narrowly elliptic-lanceolate when expanded, obtuse, the apex reflexed, appearing minutely retuse, the clawed base thickened, transversely minutely gibberose, 8.0–9.0×2.0–2.5 mm, provided with 2 slender keels, fringed-lacerate at the base, gently converging from the base of the lamina to near the apex, then spreading. Column arched, terete-slender at the base, 6.0–6.5 mm long without the foot, provided with broad membranous wings serrulate along the margins, at the apex forming a deeply cucullate, sharply lacerate clinandrium; column foot forward-projecting, stout, fleshy, incurved, 2.0–2.5 mm long. Anther cap deeply cucullate, ovate, 2-celled. Pollinia 2, obovate-complanate, minutely hooked at the base. Fruit not seen.

Other material examined:—COSTA RICA. Puntarenas: Coto Brus, Sabalito, Las Mellizas, siguiendo la línea divisoria entre Costa Rica y Panamá, entre Cerro Nubes y Cerro Pando, hito geográfico 340, camino de la Sierra, 08°55'18" N, 82°43'30" W, 2465m, 15 Aug. 1989, *Herrera 3411* (USJ!; INB!); Buenos Aires: P.N. La Amistad, Cuenca Térraba-Sierpe, sendero a Valle del Silencio, colectado a orilla de bosque, 9°04'51.0781" N -82°58'47.5188" W 2300 m, 18 Apr. 2001, *Alfaro 3646* (INB!); Coto Brus: Sabalito, Las Mellizas, siguiendo línea divisoria entre Costa Rica y Panamá, entre Cerro Nubes y Cerro Pando, hito geografico 340, camino de la Sierra, 8°55' N, -82°43' W, 2465 m, 21 Sept. 1996, *Navarro 476* (INB!); Coto Brus: Sabalito, Zona Protectora Las Tablas, 13 km al noreste de Lucha, Sitio Coto Brus, entre Río Surá y Quebrada Sutú, Finca de Miguel Sandí, 8°56'46.1" N 82°44'30.9" W, 1778 m, bosque pluvial montano bajo, epífitas en potreros arbolados, 6 Jun. 2010, *Bogarín 7773 & Karremans* (JBL-Spirit!). Same date and locality, *Karremans 2856 & Bogarin* (JBL-Spirit!); Coto Brus: Sabalito, Zona Protectora Las Tablas, 15 km al noreste de Lucha, Sitio Coto Brus, Finca de Miguel Sandí, bosque muy húmedo montano, *ad ager Sandiorum* "El Surá", *crescenti epiphytica in sylvis humidis versus pascues prope flumen Surá*, 7 Oct. 2010, *Bogarín 8180*, *Dressler, Fernández & Pupulin* (JBL-Spirit!); same locality and date *Bogarín 8183*, *Dressler, Fernández & Pupulin* (JBL-Spirit!); Coto Brus: Sabalito, Zona Protectora Las Tablas, 15 km al noreste de Lucha, Sitio Coto Brus, 8°56' N 82°44' W, 2000 m, finca de Miguel Sandí, en bordes de bosque subiendo por el margen del río Surá en el cerro al noroeste de la finca, bosque muy húmedo montano, 7 Oct. 2010, *Fernández 402*, *Dressler, Bogarín & Pupulin* (JBL-Spirit!). Limón: Talamanca, Bratsi, P.N. La Amistad, Atlantic slope, south side of unnamed cordillera between the Rio Terbi and Rio Sini, 2–4 airline km W of the Costa Rican-Panamanian border, 09°11' N, -82°58' W, 2300–2500m, 11/ Sept. 1984, *Davidse 28921*, *Herrera & Grayum* (INB!); Talamanca: P.N. La Amistad, Tararia, Valle del Silencio, Sendero el Alto, colectado en bosque. 9°06'02.6103" N -82°58'03" W, 1714 W 2440 m, 20/jun/2003, *Alfaro 4597*, *Alfaro & Alfaro* (INB!); Talamanca: Bratsi, P.N. La Amistad, Valle del Silencio, sector de acampar a los jardines, 9°07' N, -82°57' W, 2500 m, bosque primario, 14 Apr.1996, *Quesada 1481* (INB!); Talamanca: Bratsi, P.N. La Amistad, Sendero Valle del Silencio al Jardin Natural, 9°07' N, -82°57' W, 2400 m, 01 Jun. 1996, *Quesada 1574* (INB!). COSTA RICA—PANAMA. Puntarenas-Chiriquí: Coto Brus-Renacimiento, línea fronteriza hacia el Cerro Pando, después del mojón, N.338, 8°55'11.22" N 82°43'18.18" W, 2446 m, bosque muy húmedo montano bajo,

epífitas en bosque primario, *in sylvis virginis versus montium Pando in itinere ad summum Costa Rica austro-orientalis in finibus utrimque Costa Rica et Panama*, 19 Apr. 2011, *Karremans 4023, Bogarín & Jiménez* (JBL-Spirit!); same date and locality, *Karremans 4024, Bogarín & Jiménez* (JBL-Spirit!); Same date and locality, *Bogarín 8656, Karremans & Jiménez* (JBL-Spirit!, CR!). PANAMA. Chiriquí: NW of Cerro Punta, at INRENARE station in Parque Amistad; trail below station; forested slopes; collected with 08°54'N 082°35'W, 2100 m, 20 Oct. 1992, *McPherson & Richardson 15941* (MO!). COLOMBIA. Chocó: south of Cabo Marzo, Bahía del Aguacate, sea level, *Misas Urreta 291* (HPUJ). **Unknown country of origin**, cultivated by Wubben in The Netherlands, flowered in cultivation at the Hortus Botanicus in Leiden 1 Dec. 2011, *Karremans 4798* (L-spirit!); same data, *Karremans 4846* (L-spirit!); cultivated by Sijm in The Netherlands, flowered in cultivation, 9 Jan. 2012, *Karremans 4854* (L-spirit!).

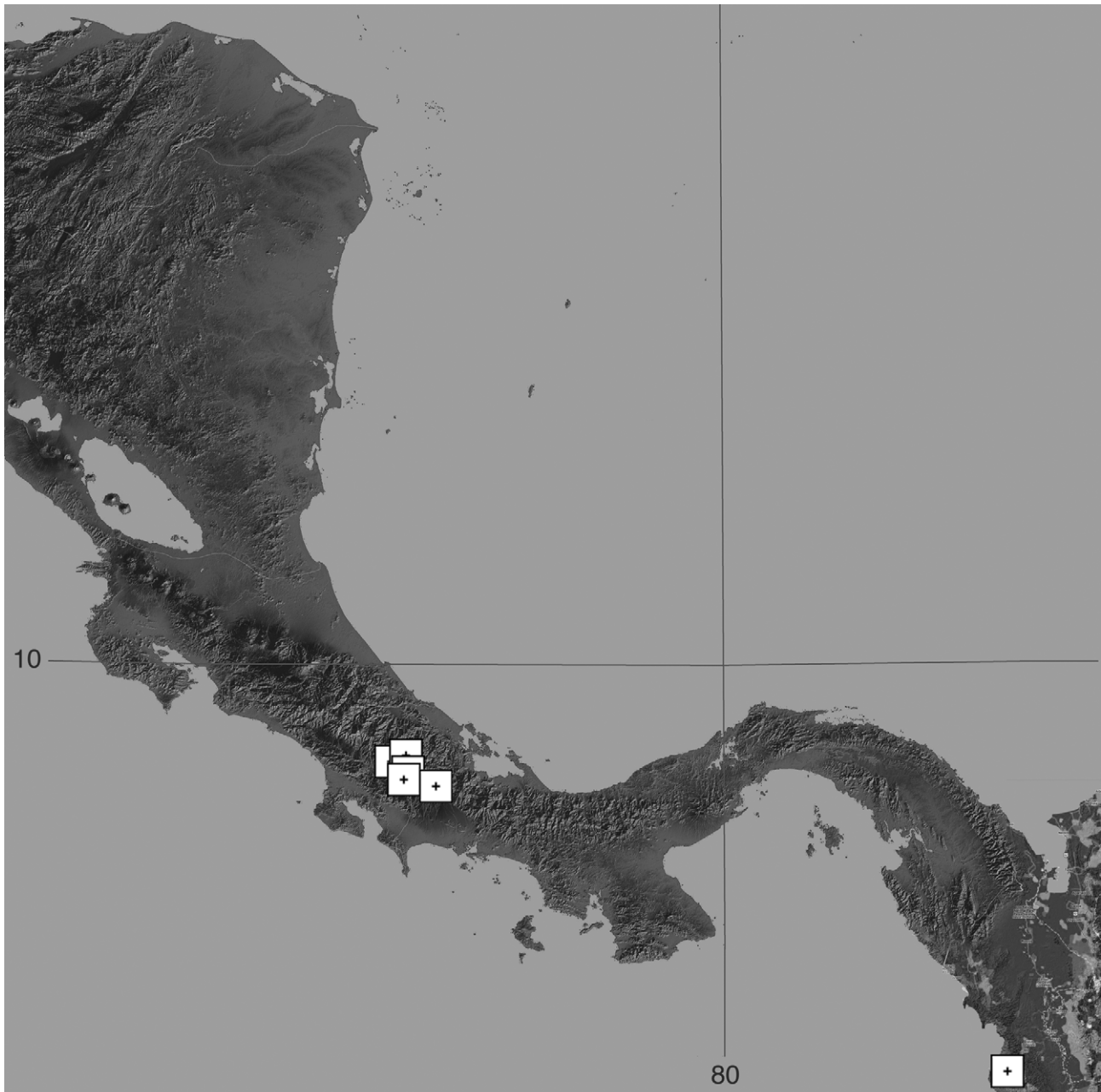


FIGURE 9. Distribution map of *Specklinia remotiflora*.

Distribution:—Relatively frequent in southern Costa Rica and western Panama, where it grows on the Talamanca-Chiriqui range, at 1750–2500 m. Also reported from the Colombian northern Pacific coast at sea level, perhaps ranging to Ecuador (Fig. 9).

Notes:—*Specklinia remotiflora* is apparently common along the Pacific watershed of southern Talamanca Mountains in Costa Rica and adjacent Panama. Even though we are not aware of any record in central and western Panama, the distribution of the species is likely continuous southward at least to the Pacific coastal range of Baudó in northern Colombia, where populations morphologically similar to *S. remotiflora* were documented by Misas Urreta (2006). It is noteworthy, however, that Colombian plants were found growing at sea level, whereas in Costa Rica and Panama *S. remotiflora* is exclusively known from submontane and montane wet forests at 1750–2500 m. Plants in cultivation at Ecuagenera (Pupulin, pers. obs. 2009), supposedly collected in Ecuador but without specific locality data, also correspond to this species.

The repent habit, lax inflorescence, and subcampanulate, orange flowers provided with obtuse, non-apiculate petals easily distinguish *S. remotiflora* from *S. endotrachys* and *S. spectabilis*, to which it is most similar. It has non-mucronate petals like *S. pfavii*, but the latter has a caespitose habit (vs. repent in *S. remotiflora*), congested inflorescence (vs. lax), yellow flowers with red petals (vs. orange), and oblong, entire column wings (vs. triangular, denticulate).

Specklinia spectabilis* (Ames & C.Schweinf.) Pupulin & Karremans, *comb. nov.

Basionym: *Pleurothallis spectabilis* Ames & Schweinfurth (1925: 34). Type: PANAMA. Veraguas: Santa Fé, Feb. 1924, 1500 ft, *Powell 382* (holotype, AMES!; isotype, MO; photo of type, AMES!).

Epiphytic, caespitose, erect herb to 18 cm tall. Roots fibrous, flexuous, glabrous, to 1 mm in diameter. Stem abbreviated, terete-subcomplanate, slender, monophyllous, 1.2–1.5 cm long, covered by a glumaceous, adpressed, obtuse sheath, becoming dry-papyraceous with age and eventually dissolving. Leaf narrowly oblanceolate, minutely retuse, subcoriaceous, 11.5–16.5×1.2–1.7 cm, the adaxial midvein protruding at apex into a small apicule, gradually tapering toward the base into a strongly conduplicate-channeled, ancipitous petiole to 3.5 cm long. Inflorescence produced laterally from the apex of the stem, with an annulus, born from a small, papyraceous, spathaceous bract to 4 mm long, erect to arching, distichous, congested, successively many-flowered (to 23+) raceme, to 36 cm long; peduncle flattened, ancipitous, to 28 cm long, provided with 3 distant, tubular-amplexant, ancipitous, acute bracts to 9 mm long; rachis complanate, gently fractiflex. Floral bracts broadly ovate, acute, strongly flattened, abaxially ancipitous, apically shortly recurved-subuncinate in lateral view, 10×6 mm. Pedicel cylindric, glabrous, to 11 mm long, persistent. Ovary cylindric-subclavate, 4 mm long, green. Flowers orange, sepals semi-hyaline at the base, tinged orange along the veins, column yellow. Sepals densely papillose adaxially except at the base, where they become semi-hyaline; dorsal sepal erect, triangular-lanceolate, acute, 5-veined, slightly concave at the base, inner surface densely papillose on the distal two-thirds, papillae extending almost to the base along the thickened margins, base semi-hyaline, the veins flushed with orange, 18.4–20.2×4.8–5.2 mm; lateral sepals semigeniculate, born subparallel and then twisted outwards, lanceolate-subfalcate, triveined, subacuminate, ending into a short mucro, margins slightly revolute, 18.0–18.4×3.6–4.1 mm, connate at the base for ca. 5 mm to form a deeply saccate mentum around the column foot, base hyaline, ribbed abaxially along veins, then densely papillose, the midvein strongly carinate externally. Petals ligulate-falcate, acute, porrect, papillose at the concave apex, abruptly contracting into a mucro, univeined, 4.1–4.5×0.8–1.0 mm. Lip longitudinally arched-convex in natural position, thinly articulate with the column foot by a hyaline claw, rectangular-subpandurate when expanded, truncate, with a small apicule, 4.9–5.2×1.5–1.6 mm, provided with a pair of thin, erect keels arising from the middle margin and gently converging close to the apex, central portion with a shallow groove between the keels. Column semiterete, arched, 4.5 mm long without the foot, central portion expanded into broad, membranaceous, semihyaline wings, upper margin denticulate, clinandrium deeply lacerate-dentate; column foot stout, forward-projecting, incurved, slightly grooved at the base, ca. 2.0 mm long. Anther cap ovate-subquadrate, deeply cucullate, 2-celled. Pollinia 2, obovate-complanate, the subhyaline base contracted into a small hook. Immature fruit a green capsule, narrowly obovate, glabrous, with six crests, three taller, thus appearing triangular, 18 mm long, 10 mm wide at its widest point, just below the apex.

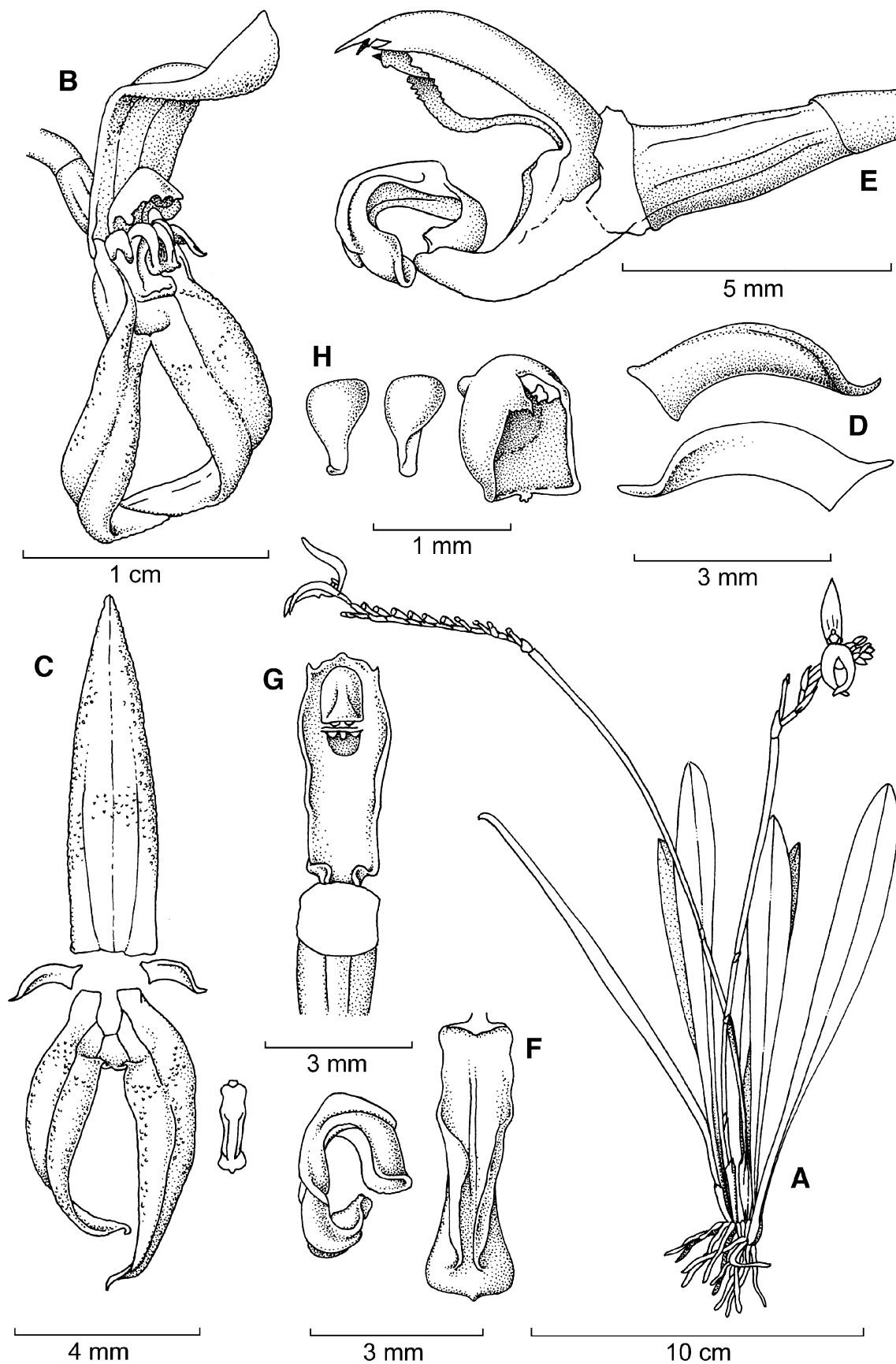


FIGURE 10. *Specklinia spectabilis* (Ames) Pupulin & Karremans. A. Habit. B. Flower. C. Dissected perianth. D. Petals. E. Column and lip, side view. F. Lip, front and side views. G. Column, ventral view. H. pollinaria and anther. Drawn by F. Pupulin & E. Winkel from JBL-02641 (JBL-spirit).

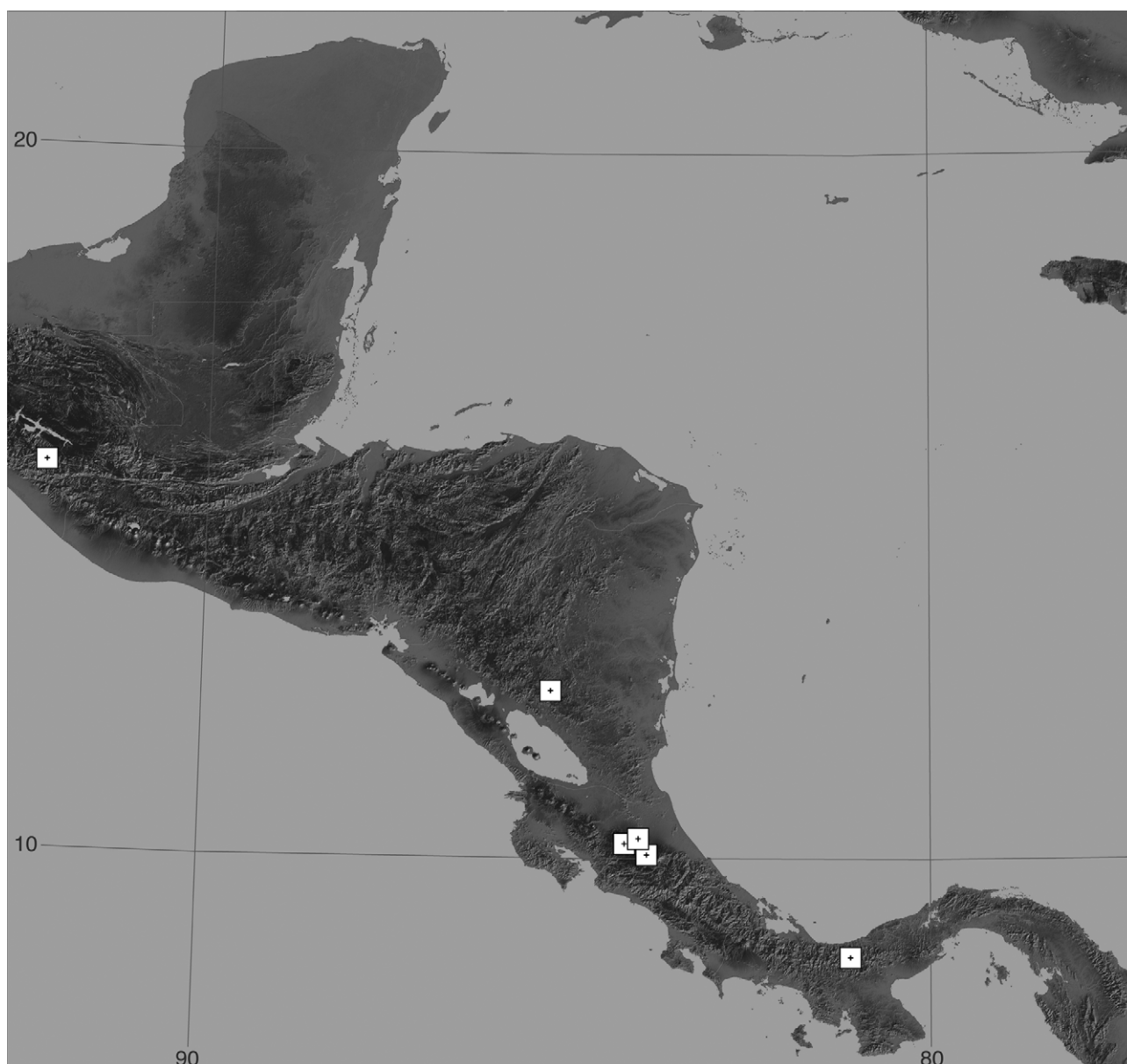


FIGURE 11. Distribution map of *Specklinia spectabilis*.

Other material examined:—MEXICO. Chiapas: Soto 9484 (AMO). NICARAGUA. Chontales: Cerro Oluma, lower to middle E slopes; moist forest in quebradas, 12°18'06"N 085°23'22"W, 500–700 m, 30 Jan. 2008, Stevens, Coronado, Montiel, Duarte 26820 (HULE; MO; photograph of flower, MO!). COSTA RICA. San José: trail up to water source for guard station in Parque Nacional Braulio Carrillo; humid forest, 700–750 m, 83°57' N - 10°06' W. 16/II/1984, Chase 84218 (CR-98483!; CR-98381!; K-spirit); Bajo de la Hondura: Parque Nacional Braulio Carrillo, floreció en el JBL 16-XII-1993, Mora s.n. (USJ!); Vasquez de Coronado: Parque Nacional Braulio Carrillo, Sendero la Botella, 10°10'00" N 83°57'20" W, 750m, 21 Sept. 1990, Ingram 559 & Ferrell (USJ!; INB!); Limón: Pococí, Guapiles, Reserva Teleférico del bosque lluvioso, parque atlántico, 10°10'24.5" N–83°54'48.3" W, 546 m, 14 Oct. 2008, Quesada 2729, Serrano & Volio (CR!); Heredia: Estación Carillo de 700 a 450 m. de la Fila Cañón del R. Sucio, bosque muy húmedo tropical-transición a premontano, 12/11/1983, Chacón 1716 & Herrera (CR-108241!); Parque Nacional Braulio Carrillo, Bajo de La Hondura, recolector desconocido, sin fecha, floreció en el JBL el 26 Oct. 2000, Blanco 1653 (USJ!); Parque Nacional Braulio Carrillo, Río Sucio, 1350 m, 10 Oct. 2001, Bosch s.n. (USJ!); Pococí: Parismina, recolectada por Gerson Villalobos, floreció en cultivo en el Jardín Botánico Lankester, 30 Octubre 2009, Bogarín 7401 (JBL-Spirit!); same locality and data, Bogarín 7403 (JBL-spirit!); Alajuela: Potrerillos,

Piedades de San Ramón, 1150m, 6/XII/1922, *Brenes* 495 (CR!); Piedades de San Ramón, 1100 m, 26/X/1925, *Brenes* 273(1458) (CR!); without collection data, flowered in cultivation at Lankester Botanical Garden, *JBL*-02643 (JBL-spirit!, CR!); flowered in cultivation at Lankester Botanical Garden, *JBL*-02641 (JBL-spirit!) (Fig. 5, 10); flowered in cultivation at Lankester Botanical Garden, *JBL*-02535 (JBL-spirit!); flowered in cultivation at Lankester Botanical Garden, *JBL*-02532 (JBL-spirit!).

Distribution:—Southern Mexico (Chiapas) to central Panama, mostly along the Caribbean watershed, at 450-1350 meters (Fig. 11).

Ames described *Pleurothallis spectabilis* from Central Panama, comparing it with *P. pfavii* and its synonym, *P. platyrachis*, and distinguishing it by the truncate-retuse lip, and dentate wing of the column (Ames & Schweinfurth 1925). The short rhizome, congested inflorescence with floral bracts shorter than pedicels, and apiculate-mucronate petals are diagnostic of the species.

We accept here populations from Nicaragua as belonging to *S. spectabilis*, even though the available material is scanty and illustrations somewhat confused. The plant illustrated by Hamer (1984) from Nicaragua and supposedly based on *Stevens & Hahn 18980* (MO) is actually a mix of that collection and the flower from a specimen from El Salvador, previously illustrated under *Hamer 482* in his series on orchids of El Salvador (Hamer 1981). Whereas the size of the caespitose plant, floral bracts shorter than pedicels, truncate lip and serrulate column-wings are apparently consistent with the concept treated here as *S. spectabilis*, the petals of both specimens illustrated from El Salvador and Nicaragua are not mucronate, but instead acute and rounded-involute, respectively. It may well be that populations from El Salvador on the Pacific watershed of Central America continental division represent a still undescribed taxon. On the other hand, photographs of flowers of *Stevens 26820* (MO), also from Nicaragua, are consistent with *S. spectabilis*. Finally, the presence in Mexico of *S. spectabilis* (Solano & Soto 2008) confirms that this taxon reaches the northernmost distribution for the group and strengthens our interpretation of intermediate populations as belonging to this species.

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References

- Ames, O. (1923) New or noteworthy orchids. *Schedulae orchidiana* 6: 60–61.
- Ames, O. & Schweinfurth, C. (1925) New or noteworthy species of orchids from the American tropics. *Schedulae orchidiana* 8: 1–84.
- Ames, O. & Schweinfurth, C. (1930) New or noteworthy orchids. *Schedulae orchidiana* 10: 1–112.
- Barbosa Rodrigues, J. (1892) *Genera et species orchidearum novarum* 2: 9.

- Barros, F. (2004) Taxonomic and nomenclatural notes on Brazilian Orchidaceae. pp. 7–22. In: Manilal, K. S. & Satish Kumar, C. (eds.) *Orchid memories: a tribute to Gunnar Seidenfaden*. Mentor Books, Kolkata.
- Barros, F. (2006) Seis novas combinações para orquídeas brasileiras. *Bradea* 11: 29–32.
- Barros, F. & Trettel Rodrigues, V. (2009) Nomenclatural notes and new combinations on *Acianthera* Scheidw. and *Specklinia* Lindl. (Orchidaceae). *Bradea* 14: 21–26.
- Brown, R. (1813) *Pleurothallis*. p. 211. In: Aiton, W. T. *Hortus Kewensis*, (2nd ed.) 5. Taylor, London.
- Chase, M.W. (1985) Pollination of *Pleurothallis endotrachys*. *American Orchid Society Bulletin* 54: 431–434.
- Garay, L.A. (1974) *Acostaea* y los géneros del complejo *Pleurothallis*. *Orquideología* 9: 103–124.
- Hamer, F. (1981) *Las orquídeas de El Salvador, III, suplemento*. The Marie Selby Botanical Gardens, Sarasota.
- Hamer, F. (1984) *Pleurothallis endotrachys*. Sub pl. 1096. In: Hamer F. *Orchids of Nicaragua, Icones plantarum tropicarum* 11.
- Hooker, J.D. (1890) *Pleurothallis platyrachis*. *Curtis' Botanical Magazine* 116: sub pl. 7129.
- Heller, A.H. & Hawkes, A.D. (1966) Nicaraguan orchid studies – 1. *Phytologia* 14: 1–35.
- Kränzlin, F.W.L. (1899) Orchidaceae Lehmannianae in Guatemala, Costa Rica, Columbia et Ecuador collectae, quas determinavit et descripsit. *Botanische Jahrbücher für Systematik* 26: 437–502.
- Kränzlin, F.W.L. (1925) New species of *Masdevallia* and allied genera. *Bulletin of Miscellaneous Information, Royal Botanic Gardens, Kew*, 1925: 97–117.
- Lindley, J. (1830) *The genera and species of orchidaceous plants* 8. Asher, London. xvii, 554 pp.
- Luer, C.A. (1978) *Dryadella*, a new genus in the Pleurothallidinae. *Selbyana* 2: 207–209.
- Luer, C.A. (1986) Systematics of *Pleurothallis* (Orchidaceae). Icones pleurothallidarum III. *Monographs in Systematic Botany from the Missouri Botanical Garden* 20.
- Luer, C.A. (1996) New species in the Pleurothallidinae (Orchidaceae) from Costa Rica. *Lindleyana* 11: 89.
- Luer, C.A. (2004) New genera and combinations in Pleurothallidinae. Icones pleurothallidarum XXVI. *Monographs in Systematic Botany from the Missouri Botanical Garden* 95.
- Luer, C.A. (2005) *Dryadella* and *Acronia* section *Macrophyllae-Fasciculatae*: addenda to *Acianthera*, *Andinia*, *Dracula*, *Dresslerella*, *Lepanthes* and *Masdevallia* new taxa, validation of taxa, errata. Icones pleurothallidarum XXVII. *Monographs in Systematic Botany from the Missouri Botanical Garden* 103.
- Luer, C.A. (2006) A reconsideration of *Masdevallia*. Systematics of *Specklinia* and vegetatively similar taxa (Orchidaceae). Icones pleurothallidarum XXVIII. *Monographs in Systematic Botany from the Missouri Botanical Garden* 105.
- Luer, C.A. (2007) A third century of *Stelis* of Ecuador. Systematics of *Apoda-Prorepentia*. Systematics of miscellaneous small genera. Addenda: new genera, species and combinations (Orchidaceae). Icones pleurothallidarum XXIX. *Monographs in Systematic Botany from the Missouri Botanical Garden* 112.
- Luer, C.A. (2010) *Lepanthes* of Bolivia. Systematics of *Octomeria* species north and west of Brazil. Addenda: new species of *Brachionidium*, *Lepanthes*, *Masdevallia*, *Octomeria*, *Playstele*, *Pleurothallopsis* and *Porroglossum*. Corrigenda. Icones pleurothallidarum 31. *Monographs in Systematic Botany from the Missouri Botanical Garden* 120.
- Luer, C.A. (2011) Miscellaneous new species in the Pleurothallidinae excluding species from Brasil. *Harvard Papers in Botany* 16: 311–360.
- Misas Urreta, G. (2006) Orquídeas de la Serranía del Baudó, Chocó, Colombia. Corporación Capitalina de Orquideología y Concreto. Medellín.
- Pfitzer, E.H.H. (1889) Monandrae-Pleurothallidinae. pp. 135–140. In: Pfitzer, E. H. H. *Natürlichen Pflanzenfamilien nebst ihren Gattungen und wichtigsten Arten, II. Teil*, 6. Abteilung (Orchidaceae).
- Poeppig, E.F. & Endlicher, S.L. (1836) *Nova genera ac species plantarum, quas in regno Chilensi Peruviano et in terra Amazonica: annis MDCCCXXVII ad MDCCCXXXII / legit Eduardus Poeppig et cum Stephano Endlicher descripsit iconibusque illustravit* 1: 58.
- Presl, C.B. (1827) Orchideae Juss. pp. 91–104. In: Haenke, T. *Reliquiae Haenkeanae seu Descriptiones et Icones Plantarum quas in America Meridionali et Boreali, in Insulis Phillipinis et Marianis Collegit. (Orchidaceae), fasciculus 2*. Calve, Prague.
- Pridgeon, A.M. (2005) 355. *Specklinia*. pp. 402–405. In: Pridgeon, A. M., Cribb, P. J., Chase, M. W. & Rasmussen, F. N. *Genera orchidacearum* Vol. IV. Oxford University Press, Oxford.
- Pridgeon, A.M. & Chase, M.W. (2001) A phylogenetic reclassification of Pleurothallidinae (Orchidaceae). *Lindleyana* 16: 235–271.
- Pridgeon, A.M. & Chase, M.W. (2002) Nomenclatural notes on Pleurothallidinae (Orchidaceae). *Lindleyana* 17: 98–101.
- Pridgeon, A.M., Solano, R. & Chase, M.W. (2001) Phylogenetic relationships in Pleurothallidinae (Orchidaceae): combined evidence from nuclear and plastid DNA sequences. *American Journal of Botany* 88: 2286–2308.
- Pupulin, F., Ossenbach, C., Jenny, R. & Vitek, E. (2011) Typi Orchidacearum ab Augusto R. Endresio in Costa Rica lecti. *Annalen Naturhistorisches Museums Wien, Ser. B, Botanik. Zoologie*. 112: 265–313.
- Reichenbach, H.G. (1872) New garden plants: *Odontoglossum ulopterum*, *Odontoglossum spilotanthum*, *Pleurothallis lateritia*. *Gardeners' Chronicle* 1872: 731.

- Reichenbach, H.G. (1875a) New garden plants: *Bollea patinii*, *Masdevallia simula*. *Gardeners' Chronicle*, n.s. 3: 8–9.
- Reichenbach, H.G. (1875b) New garden plants. *Gardeners' Chronicle*, n.s. 4: 516.
- Reichenbach, H.G. (1876) Orchidiographische Beiträge. *Linnaea* 41: 17–98.
- Reichenbach, H.G. (1878) Zu Tafel 210. *Pleurothallis endotrachys* Rchb. fil. *Xenia Orchidacea* 3(1): 16–17.
- Reichenbach, H.G. (1886a) Orchideae Wendlandianae. pp. 61–102. In: Reichenbach, H. G. (ed.). *Beiträge zu einer Orchideenkunde Central-Amerika's*.
- Reichenbach, H.G. (1886b) Orchideae describuntur. *Flora* 69: 547–562.
- Rolfe, R.A. (1888) New or noteworthy plants. *Gardeners' Chronicle* 4: 178–179 [18 August 1888].
- Rolfe, R.A. (1890) The genus *Scaphosepalum* Pfitzer. *Journal of Botany, British and Foreign* 28: 135–137.
- Rolfe, R.A. (1917) New orchids. Decade XLV. *Bulletin of Miscellaneous Information, Royal Botanic Gardens, Kew* 1917: 80–84.
- Ruiz, H. & Pavón, J. (1794) *Florae Peruvianaee, et Chilensis Prodrum*. Imprenta A. de Sancha, Madrid.
- Salisbury, R.A. (1812) *Transactions of the Horticultural Society of London* 1: 293.
- Schlechter, F.R.R. (1910) Orchidaceae novae et criticae. Decas XIV–XV. *Repertorium Specierum Novovarum Regni Vegetabilis* 8: 561.
- Schlechter, F.R.R. (1920) Orchideenfloren der Suedamerikanischen Kordillerenstaaten, II. Colombia (I. Allgemeines). *Repertorium Specierum Novarum Regni Vegetabilis, Beihefte* 7: 1–301.
- Schlechter, F.R.R. (1923a) Beiträge zur Orchideenkunde von Zentralamerika, II. Additamenta ad Orchideologiam Costaricensem, IV. Orchidaceae novae et rariores collectorum variorum in Costa Rica collectae. *Repertorium Specierum Novovarum Regni Vegetabilis Beihefte* 19: 270–307.
- Schlechter, F.R.R. (1923b) Beiträge zur Orchideenkunde von Zentralamerika, II. Additamenta ad Orchideologiam Costaricensem, II. Orchidaceae Bradeanae Costaricenses. *Repertorium Specierum Novovarum Regni Vegetabilis Beihefte* 19: 76–157.
- Solano, R. & Soto, M. (2008) *Specklinia endotrachys*. Sub pl. 1092. In: Hágsater, E. & Soto, M. (eds.). *Orchids of Mexico*, part 4. *Icones orchidacearum* 10: pl. 1001–1100.
- Sprengel, C.P.J. (1826) *Caroli Linnaei... systema vegetabilium. Editio decima sexta. Volumen III. Classis* 16–23. Sumtibus Librariae Dieterichianae. Gottingen. 936 pp.
- Steudel, E.T. (1840–1841) *Nomenclator botanicus seu synonyma plantarum universalis*. Cotta, Stuttgart and Tübingen.
- Swartz, O. (1788) *Nova genera species plantarum seu prodromus descriptionum vegetabilium maximam partem incognitorum quae sub itinere Indiam Occidentalem annis 1783–1787*. Acad. M. Swederi, Stockholm.