239-252

Illustrations and Studies in Neotropical Orchidaceae. 2. A note on *Pleurothallis luctuosa* (Pleurothallidinae), with a new species

F. Pupulin*, **, ***, D. Bogarín*, ** & M. Fernández*

Abstract

The identity of *Pleurothallis luctuosa*, its taxonomic history and geographic distribution are discussed, and the species is described and illustrated. A new species from Costa Rica, *P. neglecta*, is described and illustrated. *Pleurothallis neglecta* is compared with *P. luctuosa*, from which it differs by the distinct conduplicate leaves, different color of the flowers, triangular and smaller lip, falcate, erose petals, and the callus formed by two conspicuous, densely papillose keels.

Key words: Orchidaceae, Pleurothallidinae, *Pleurothallis, Acronia, Pleurothallis luctuosa, Pleurothallis neglecta*, Costa Rica, A.R. Endrés, new species.

Introduction

In 2008, the Lankester Botanical Garden (LBG) at the University of Costa Rica began a large project devoted to the reconstruction of the phylogenetic relationships and the assessment of the taxonomic identity of the species of subtribe Pleurothallidinae LINDL. (Orchidaceae) in Costa Rica. Pleurothallidinae represents the most diverse orchid group in the Neotropics, and the taxonomy of this large assemblage of species has been traditionally problematic, both under the profiles of generic circumscriptions and taxa identification. *Pleurothallis* subgen. *Pleurothallis* sect. *Pleurothallis* subsect. *Acroniae* (PRESL) LUER (= *Acronia* PRESL pro parte, LUER 2005) includes in Costa Rica a relatively small number of species. With some sixty described taxa, the subsect. *Acroniae* (sensu LUER 1998) is predominantly South American in distribution, with only six species recorded from Costa Rica. In revising specimens of this group in the living collection of LBG, we noted that the name *Pleurothallis luctuosa* RCHB.f. was apparently applied to two different taxa, one of which is still undescribed.

Taxonomic history of Pleurothallis luctuosa

The circumstances, under which A.R. Endrés died in Colombia, supposedly in the first months of 1875, have been traditionally unclear, until a recent article brought some light

^{*} Franco Pupulin, Diego Bogarin, Melania Fernandéz, Lankester Botanical Garden, University of Costa Rica, P.O. Box 302-7050 Cartago, Costa Rica.

^{**} Ángel Andreetta Andean Orchids Research Center, University Alfredo Pérez Guerrero, Gualaceo,

^{***} Harvard University Herbaria, Cambridge, MA, U.S.A. – franco.pupulin@ucr.ac.cr

on the crucial facts of his biography (OSSENBACH et al. 2010). Endrés left Costa Rica, the country where he spent the last eight years of his life, in the course of 1874, when he traveled to Europe and met Heinrich Gustav Reichenbach in Hamburg. According to REICHENBACH (1875), they had good days talking about orchids in the company of Benedikt Roezl (1823–1885), the Czech explorer, gardener and botanist, who was considered the greatest orchid collector of his time. By the end of the summer, Endrés crossed the Atlantic again, and in late August he was in New York. A few months later, he died of pleurisy in the Caribbean village of Dibulla, at the foot of the Sierra Nevada de Santa Marta mountains in Colombia. The prestigious Gardener's Chronicle presented the sad new of Endrés' death on May 8th, 1875, promising an obituary of the great orchidologist by Prof. REICHENBACH (ANONYMOUS 1875), but this text was never published, and likely it was never written.

By the time the destiny was driving Endrés to the date with his death in Dibulla, a new *Pleurothallis* flowered for the first time in the orchid collection of the Botanical Garden of the University of Hamburg, of which H.G. Reichenbach had been appointed director in 1862. In the original description of the new species published in Linnaea, REICHEN-BACH (1877) made no reference to Endrés and the origin of the plant, nor he gave any reasons to baptize the new *Pleurothallis* as "*luctuosa*", or mournful, just recording that he saw the living plant in the collection of the Hamburg Botanical Garden. Many years later, SCHLECHTER (1923) strongly protested for the lack of information associated with many of the new species that Reichenbach published in Linnaea. However, in 1878, Reichenbach augmented the description of *Pleurothallis luctuosa* and illustrated it in Xenia Orchidacea (Fig. 1) and here he credited Endrés as the discoverer of the new species, explaining that he was just examining the first opening, black-purple flowers, when he was surprised by the news of the death of his friend. "Hence the name" (REICHENBACH 1878).

According to the manuscript notes by Endrés which are now in Vienna, P. luctuosa had been found in Costa Rica ten years before, in 1867. In his meticulous style, Endrés prepared a detailed description and a set of drawings of his finding, including the habit of the plant and floral dissections, as well as a series of duplicate specimens under his number 50. It has to be noted that this number has not to be interpreted as a "collecting number" in the modern sense: instead, Endrés mostly used his numeration system to refer to taxa rather than to individual collections. Actually, only one of the sheets conserved in Vienna is labeled as *P. luctuosa* in Reichenbach's handwriting [W-Rchb. Orch. 53791!], and the mounted specimen was likely prepared from living material cultivated in Hamburg. The holotype sheet includes several inflorescences, ramicauls and detached leaves, all of them apparently prepared in Hamburg from the living collection accession N° 2537, plus sketches by Reichenbach himself and a pencil drawing by Endrés with a note about the color of the plant and the flowers, and a record of the date and altitude of the original collection (Endrés 50). Technically, there is no way to unequivocally associate the living plant accessed to the Hamburg Botanical Garden collection with Endrés' collection bearing his number 50, and we consider more correct to cite the holotype of *P. luctuosa* as Endrés sine numero, even though the plant flowered in Hamburg was likely part of the original collection made by Endrés at San Ramón.

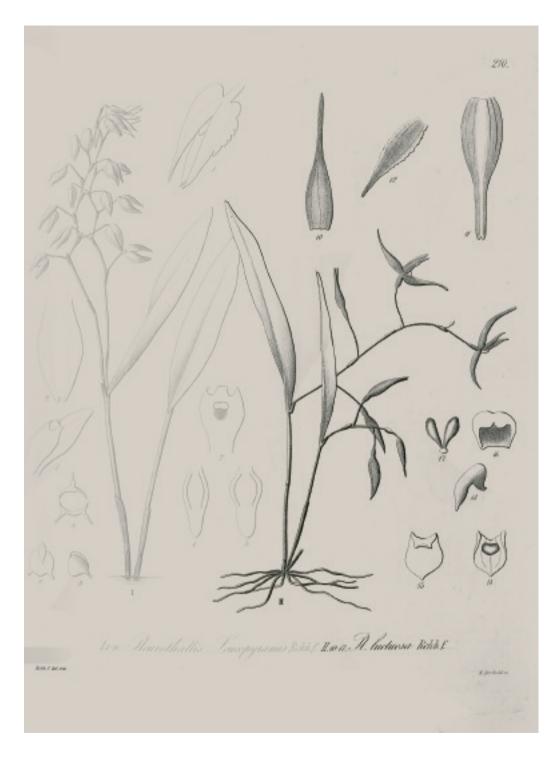


Fig. 1: Drawing of *Pleurothallis luctuosa*, from Xenia Orchidacea, 1878.

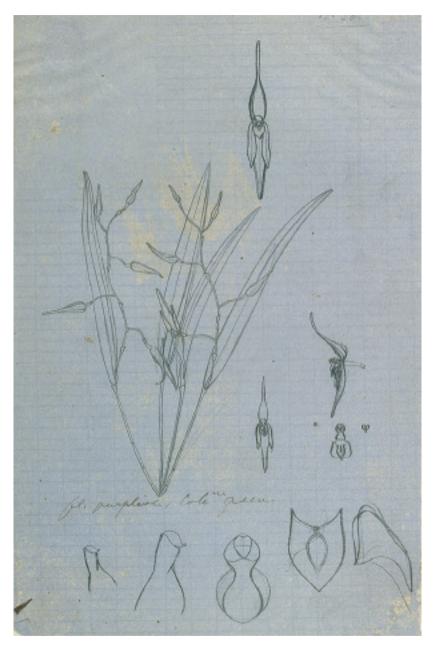


Fig. 2: Drawing of Pleurothallis luctuosa by A. R. Endrés [W-Rchb. Orch. 33417].

The illustrations sent from Costa Rica [W-Rchb. Orch. 33417!, 36294!] (Fig. 2–3) are a model of the typical "method" by Endrés, who was used to prepare a preliminary sketch, improving it in terms of composition and amount of details in subsequent versions of the same plate. While in other cases Reichenbach completely relied on Endrés' drawings to illustrate Costa Rican orchids to be published in Xenia, the plate of *P. luctuosa* (Fig. 1)

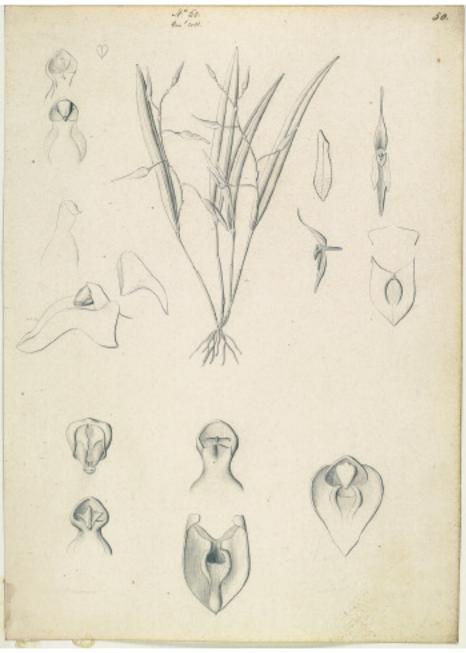


Fig. 3: Drawing of Pleurothallis luctuosa by A. R. Endrés [W-Rchb. Orch. 36294].

was ostensibly prepared from Reichenbach's own sketches, based on the living plant sent by Endrés and flowered in Hamburg.

In 1923, in his contributions to the orchidology of Central America, Schlechter – who had examined Endrés' records in Vienna – mentioned two additional collections of P.

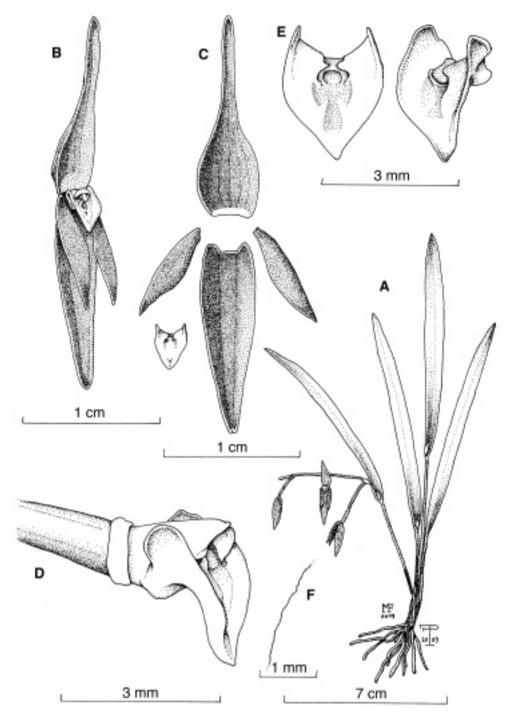


Fig. 4: *Pleurothallis luctuosa* RCHB.f. (from Pupulin 5311). A: Habit; B: Flower; C: Dissected perianth; D: Column and lip, lateral view; E: Lip, spread and in natural position; F: margin of petal. Drawn by D. Bogarín, M. Fernández and F. Pupulin.

luctuosa by the brothers Alfred and Kurt Brade from La Palma (SCHLECHTER 1923), one of the main passes through the Central Volcanic range connecting the central valley to the Caribbean in Costa Rica. Unfortunately, the collections examined by Schlechter were eventually lost in Berlin in 1943. By 1937, when Prof. Ames prepared an updated checklist of Costa Rican Orchidaceae for STANDLEY's "Flora of Costa Rica", P. luctuosa was still known only from a limited number of specimens. AMES (1937) quoted a Costa Rican collection by C.H. Lankester from the region of Acosta (AMES 1178), and two specimens found by M.A. Brenes around San Ramón, along the Caribbean slopes of the Tilarán mountain range. We were unable to locate the last two collections in AMES' herbarium, but Gustavo A. Romero kindly provided us with a manuscript note by Brenes about a collection made by him in 1925 at "Collines en Piedades, prés S. Ramón, 1025 m" (No. 38/1249 Herb. Brenes, AMES). While Lankester's specimen was recorded having "flowers maroon, lip greenish", the flowers of Brenes 38/1249 were noted as greenish yellow, marked with pale red along the yeins. It was not until 1976, when Luer produced the first, modern botanical illustration of *P. luctuosa* for his series on miscellaneous Pleurothallidinae species (LUER 1976), based on an Ecuadorian specimen collected in the province of Pichincha (LUER et al. 528, SEL). In his treatment of the species, LUER quoted collections referable to P. luctuosa also from Nicaragua and Colombia (LUER 1976). Luer's interpretation was followed by floristic treatments in the Mesoamerican region (i.e., HAMER 1984, GARCÍA CASTRO et al. 1993, PUPULIN 2002, LUER 2003, CORREA et al. 2004, OSSENBACH et al. 2005) and from South America (i.e., DODSON & DODSON 1980), but it is now quite clear that the specimens quoted in these works are referable to both the true *P. luctuosa* and to its sister, an undescribed species. It is fortunate that at LBG we have plants of both the "morphs" to critically compare them.

Taxonomic treatment

Pleurothallis luctuosa RCHB.f., Linnea 41: 48 (1877). – Fig. 4.

- = Humboldtia luctuosa (RCHB.f.) KUNTZE, Revis. Gen. Pl. 2: 667 (1891).
- Acronia luctuosa (RCHB.f.) LUER, Monogr. Syst. Bot. Missouri Bot. Gard. 103: 58 (2005).

Type: Costa Rica, Alajuela, San Ramón, 1867, A.R. Endrés s.n. [holotype: W-Rchb. Orch. 53791!].

<u>Herb</u> epiphytic, caespitose, erect, small, up to 18 cm tall. <u>Roots</u> slender, flexuous, to 1 mm in diameter. <u>Ramicauls</u> slender, erect, terete, 2.2–9.0 cm long, enclosed by 1-3 tubular, adpressed, papery, brown bracts, 0.4–3.1 cm long. <u>Leaves</u> erect, fleshy, coriaceous, subsemiterete, linear-lingulate, acute, coarsely 3-dentate, 4.2–12.8 x 0.4–0.7 cm, the cuneate-rounded base narrowing into a petiole up to 0.15 cm long. <u>Inflorescence</u> a lax, distichous, 3–6 simultaneously flowered raceme, 3.8–4.1 cm long including the 2.4 cm long peduncle produced at the base of the leaf from a small, conduplicate, linear, acute spathe. <u>Floral bracts</u> ovate, acute, conduplicate, membranaceous, 10 x 4 mm. <u>Pedicels</u> 9 mm long, persistent. <u>Ovary</u> cylindric, 4 mm long. <u>Flowers</u> with the sepals and the petals purple, the lip green suffused with purple, the column green, the anther greenish white. <u>Dorsal sepal</u> erect, ovate, acuminate, concave, 15 x 4 mm, 5-veined.

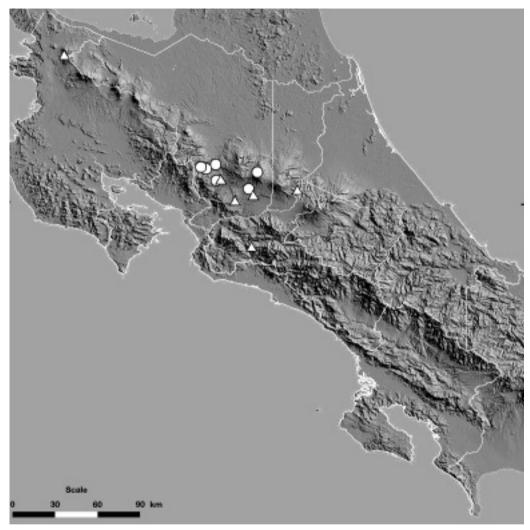
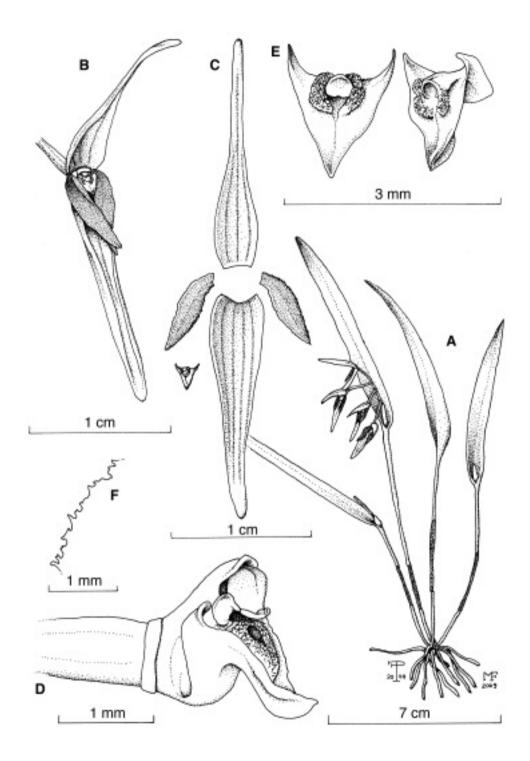


Fig. 5. Distribution map of Pleurothallis luctuosa (triangles) and P. neglecta (circles) in Costa Rica.

<u>Lateral sepals</u> connate into an ovate, acuminate, entire or sub-bidentulate, concave synsepal, 14 x 4 m, 3-veined. <u>Petals</u> ovate, acute, falcate, resting on the margins of the synsepal, the margins obsoletely serrato-denticulate, 8 x 2 mm. <u>Lip</u> triangular-hastate, sigmoid, acute or sub-apiculate, 3.5×1.5 mm, hinged to the column foot, the basal lobes erect; disc 2-carinate, the keels subobsolete, incurved, flanking the reniform glenion. <u>Column</u> short, cylindric-subclavate, 1 mm long, the clinandrium entire, the stigma apical, reniform, bilobed. <u>Anther cap</u> incumbent, ovate, emarginate. <u>Pollinia</u> 2, pyriform, on an ovate, retuse viscidium.

Fig. 6: *Pleurothallis neglecta* PUPULIN, BOGARÍN & MEL. FERNÁNDEZ (from Pupulin 7019). A: Habit; B: Flower; C: Dissected perianth; D: Column and lip, lateral view; E: Lip, spread and in natural position; F: margin of petal. Drawn by D. Bogarín, M. Fernández and F. Pupulin from the holotype.



Derivation of name: From the Latin *luctuosus*, sorrowful, in reference to the death of A. R. Endrés, who collected the type specimen.

Specimens examined: <u>Costa Rica</u>, [Alajuela:] San Ramón, A.R. Endrés s.n. [W-Rchb. Orch. 53791]; A.R. Endrés 50 [W-Rchb. Orch. 44222; W-Rchb. Orch. 2805; W-Rchb. Orch. 142268; AMES 118528; W-Rchb. Orch. 36294, drawing; W-Rchb. Orch. 36294, drawing; W-Rchb. Orch. 33417, drawing and manuscript description]; – San Ramón, Berlín, near the turning of the unpaved road to San Mateo, Cerro Pelón, Pacific watershed of the Cordillera de Tilarán, lower montane rain forest, 10° 00' 52" N 84° 23' 55" W, 1200 m, scrub vegetation with scattered trees on exposed, windy crests, F. Pupulin 5311 / 5304 & E. Salas-Pupulin [JBL]; – San Ramón, Angeles, road from San Ramón to La Fortuna, Ángeles Norte, 10° 08' 29.3" N 84° 28' 51.2" W, 1200 m, on crest of continental divide, premontane wet forest, remnant woods on the right of the road, F. Pupulin 6322B & E. Salas-Pupulin [JBL]; – [San José:] La Palma, 1400 m, A. Brade & K. Brade 1104 / 1216; Sabanillas de Acosta, 06.1928, C. H. Lankester 1178 [AMES]; – [Guanacaste:] Parque Nacional Guanacaste, Estación Biológica Volcán Cacao, Estación Pitilla, 1100 m, 24.10.1990, C. Chávez 396 [CR, MO]; <u>Costa Rica</u>, without specific locality, JBL 11663 [JBL].

Distribution: To assess the real distribution range of *P. luctuosa* is made quite difficult by the persistent confusion with its sister species. HAMER (1984) recorded *P. luctuosa* from Nicaragua and illustrated it on the basis of Heller 8013 [SEL], which corresponds to the species treated hereafter as *P. neglecta*. Even though HAMER (1984) reported the species as variable, it is still known in Nicaragua from a single collection only (HAMER 2001), and we therefore exclude this country from the distribution of *P. luctuosa*. We have not seen actual material of this species from the region of Chiriquí in Panama (D'ARCY 1987, CORREA et al. 2004), but on the basis of its morphologic features, the Ecuadorian specimen illustrated by LUER (1976) (LUER et al. 528 [SEL]) may perhaps correspond to a different and still undescribed species. The clone "Sweet Bay", which received a Certificate of Cultural Merit by the American Orchid Society in November 2008, under the name of *P. luctuosa* (KERSEY 2008) is surely misidentified; however, we have no information about the geographic origin of this highly different taxon. On the basis of the available data, *P. luctuosa* must likely be considered endemic to Costa Rica (Fig. 5) and perhaps to western Panama.

Distribution and habitat: Only known from the Tilarán range in northwestern Costa Rica and, possibly, also occuring in western Panama. Plants have been recorded growing epiphytic in premontane wet forest in secondary and primary vegetation.

Phenology: plants flower from May to September.

Pleurothallis neglecta Pupulin, BOGARÍN & MEL. FERNÁNDEZ, sp.n. (Fig. 6).

Type: Costa Rica, Alajuela: San Ramón, La Paz, continental divide, 10°08'09.9"N 84°30'48.5"W, 1130 m, premontane wet forest, 19 February 2008, F. Pupulin 7019, R.L. Dressler & A. Karremans [holotype: USJ; isotypes: JBL, CR, W].

Diagnosis: A Pleurothallide luctuosa RCHB.F. foliis latioribus distincte conduplicatis, sepalo postico latiore 3-nervato, petalis falcatis marginibus erosis et labello triangulare multo minore duabus carinis altis dense papillosis in disco ornato recedit.

<u>Herb</u> epiphytic, caespitose, erect, small, up to 16 cm tall. <u>Roots</u> slender, flexuous, to 1 mm in diameter. <u>Ramicauls</u> slender, erect, terete, 4.2–8.0 cm long, enclosed by 1-3 tubular, adpressed, papery, brown bracts, 0.2-2.7 cm long. <u>Leaves</u> erect, fleshy,



Fig. 7: Comparison of the flowers of (A) *Pleurothallis luctuosa* and of (B) *P. neglecta*. Vouchers: A – Pupulin 5305; B – Pupulin 7019. Scale bar = 1 cm.

coriaceous, narrowly elliptic-ovate, conduplicate, acute, retuse, $5.3-8.7 \times 0.9-1.3 \text{ cm}$, the rounded base narrowing into a petiole up to 0.15 cm long. Inflorescence a lax, distichous, simultaneously 3-flowered raceme, 4.6-5.0 cm long including the 1.4 cm long peduncle produced at the base of the leaf from a small, conduplicate, linear, acute spathe. Floral bracts ovate, acute, conduplicate, papyraceous, $19 \times 4 \text{ mm}$. Pedicels 1 mm long, persistent. Ovary cylindric, 1 mm long. Flowers with the sepals greenish yellow with purple veins, the petals brown-purple, the lip light green. Dorsal sepal erect, ovate, acuminate, concave, $19 \times 3 \text{ mm}$, 3-veined. Lateral sepals connate into an ovate, falcate, acute, erose, $7 \times 1 \text{ mm}$. Lip triangular, sigmoid, the lateral lobes erect-incurved, $2.5 \times 1.5 \text{ mm}$; disc with 2 high, rounded, incurved, densely papillous keels flanking a well developed, obreniform glenion. Column short, cylindric, 1.2 mm long, the clinandrium entire, the stigma subapical, bilobed. Anther cap incumbent, ovate. Pollinia 2, pyriform, on a rounded viscidium.

Derivation of name: From the Latin *neglectus*, neglected, disregarded, alluding to the fact that botanists did not pay proper attention to this species.

Paratypes: <u>Costa Rica</u>, <u>Alajuela</u>, [San Carlos] about 7 km east of Ciudad Quesada, Quebrada Marín, 10°22' N 84°24' W, 500 m, in shade forested stream edge and cleared slopes below the Methodist Rural Center, epiphyte on horizontal branch 10 cm diameter, 17-18.05.1968, W.C. **Burger 4958** & R. G. Stolze [CR]; – <u>Alajuela</u>: San Ramón, Ángeles, Reserva Biológica Alberto Manuel Brenes, 10°13'06" N 84°36'11" W, 800-900 m, 2 km después de la Estación, por el camino de acceso principal, bosque muy húmedo tropical transición a premontano, epífitas en bosque secundario a orillas del camino, 26.05.2006, **D. Bogarín 2859** & Botánica Forestal Avanzada-UCR [JBL]; – <u>Alajuela</u>: San Ramón, Ángeles, Reserva Biológica Alberto Manuel Brenes, 10°13' N 84°35' W, 950 m, sendero Pájaro Sombrilla, hacia el noroeste de la estación, **M. Blanco 2148** [USJ]; – <u>Alajuela</u>: San Ramón, camino a la Reserva Biológica Alberto Manuel Brenes, 600 m, 23.01.2001, **M. Blanco 1817** [USJ]; – <u>Alajuela</u>: San Ramón, La Paz, continental divide, 10°08'09.9" N 84°30'48.5" W, 1130 m, premontane wet forest, 19.02.2008, **F. Pupulin 7014**, R. L. Dressler and A. Karremans [JBL]; – <u>Alajuela</u>: San Ramón, Piedades, 1025 m, 05.06.1925, **A. M. Brenes 38/1249** [AMES]; – without locality data, **JBL 05153** [JBL]; – without locality data, **M. Blanco 1690** [USJ]. <u>Nicaragua</u>, Rivas, 11°27'00"N 85°31'00"W, 1300 m, **Heller 8013** [SEL, drawing seen].

Distribution and habitat: known from Costa Rica and Nicaragua. Plants have been recorded epiphytic in secondary and primary forest in premontane wet forest and tropical wet forest, premontane belt transition in Tilarán range, northwestern Costa Rica (Fig. 5). In Nicaragua it is known from the Maderas volcano at Ometepe Island, Rivas.

Discussion. *Pleurothallis neglecta* can be distinguished from *P. luctuosa* by the distinct conduplicate leaves (vs. subsemiterete), the flowers with the sepals greenish yellow with purple veins, the petals brown-purple, the lip light green to yellowish (vs. sepals and the petals purple, the lip green suffused with purple), triangular, smaller (2.5 vs. 3.5 mm long), the petals falcate, erose (vs. obsoletely serrato-denticulate) and the callus formed by two conspicuous, densely papillose keels (vs. low, glabrous) (Fig. 7). Also, it resembles the Colombian *Pleurothallis amphygia* LUER & ESCOBAR but differs in the distichous, simultaneously 3-flowered raceme (vs. single flowered), the acuminate sepals (vs. narrowly, long acuminate) and the color of the flowers, which are purple in *P. amphygia*.

Acronia was described by Carl PRESL in 1827, based on the Peruvian Acronia phalangifera. In 1861, REICHENBACH reduced Acronia to the synonymy of Pleurothallis.

Within Pleurothallis subgen, Pleurothallis sect, Pleurothallis [typyfied by Epidendrum ruscifolium JACQ. ≡ Pleurothallis ruscifolia (JACQ.) R.BR.] LUER (1986) created subsection Acroniae with A. phalangifera as the type, including here Pleurothallis luctuosa. In 1998, he divided subsection Acroniae into two series. Series Acroniae for those species with racemose inflorescences (including *P. luctuosa*) and series *Amphygiae* for those with single-flowered inflorescences (LUER 1998). The sections and subsections of *Pleurothallis* subgen. *Pleurothallis* were not supported as monophyletic groups by the molecular phylogenetic analysis of the Pleurothallidinae published by PRIDGEON et al. (2001). In 2001, species of Pleurothallis subgen. Pleurothallis, including members of subsections Acroniae and Macrophyllae-Fasciculatae, were segregated by SZLACHETKO and co-workers (SZLACHETKO & MARGONSKA 2001, SZLACHETKO & KULAK 2006a, 2006b) in the new genus Zosterophyllanthos SZLACH & MARG. More recently, LUER (2005) proposed the resurrection of Acronia, merging P. subsection Acroniae (with series Acroniae and Amphygiae) and P. subsection Macrophyllae-Fasciculatae, now elevated to the sectional rank, and reducing Zosterophyllanthos to the synonymy of Acronia. However, recent data based on nuclear ITS and preliminary plastid sequences information (WILSON et al. in press), support the results of PRIDGEON et al. (2001) and provide no support for the creation of segregate genera from within *Pleurothallis sensu* stricto (i.e. the creation of the genera Acronia and Zosterophyllanthos among others). According to the analysis of WILSON et al. (in press), the genus Acronia in particular. created to include subsection Macrophyllae-Fasciculatae and the subgenus Acroniae, is not a viable concept. For this reason we favor here the description of the new species as a member of the genus Pleurothallis.

Phenology: plants flower from May to July. A few specimens have been recorded in flower from July to September.

Acknowledgments

We thank Gustavo A. Romero, Keeper of the Oakes Ames Orchid Herbarium, Harvard University, for kindly providing information and comments on the Costa Rican collections preserved there. Acknowledgments are extended to Ernst Vitek and Heimo Rainer at W for scanning and making available for this study the specimens and drawings by A.R. Endrés kept in Reichenbach's herbarium. This paper is part of the project "The life and work of A.R. Endrés, orchidologist in Costa Rica", sponsored by the Vice-Presidency of Research, University of Costa Rica. The scientific services of the Costa Rican Ministery of Environment, Energy and Telecommunications (MINAET) and its National System of Conservation Areas (SINAC) kindly issued the collecting permits under which wild specimens treated in this paper were collected.

References

- AMES O., 1937: Orchidaceae. In: STANDLEY P.C. (ed.): Flora of Costa Rica. Field Mus. Nat. Hist. Bot. Ser. 28:197–306.
- ANONYMOUS, 1875: Obituary: M. Endrés. Gard. Chron., n.s., 3: 605.
- CORREA A., GALDAMES C. & DE STAPF M.S., 2004: Catálogo de las Plantas Vasculares de Panamá. 1. Panama: Smithsonian Tropical Research Institute, 599 pp.
- D'ARCY W.G., 1987: Flora of Panama. Checklist and Index. Monogr. Syst. Bot. Missouri Bot. Gard. 17(1): i–xxx, 1–328; 18(2): i–ix, 1–672.
- DODSON C.H. & DODSON P.M., 1980: Orchids of Ecuador. Icon. Pl. Trop. 3: 201-300.

- GARCÍA CASTRO J.B., MORA DE RETANA D.E. & RIVAS ROSSI M.E., 1993: Lista de orquídeas comunes a Costa Rica y Panamá. Brenesia 39–40: 93–107.
- HAMER F., 1984: Orchids of Nicaragua, part 5. Icon. Pl. Trop. fasc. 12. Marie Selby Botanical Gardens, plate 1115. Sarasota, Florida.
- HAMER F., 2001: Orchidaceae. In: STEVENS W.D., ULLOA ULLOA C., POOL A. & MONTIEL O.M. (eds.): Flora de Nicaragua. Monogr. Syst. Bot. Missouri Bot. Gard. 85 (2): 1809–1814.
- KERSEY M. (ed.), 2008: Atlanta Judging Center Awards November 2008. Atlanta Orch. Soc. Bull. 49 (12): 10.
- LUER C.A., 1976: Miscellaneous species of *Pleurothallis*. Selbyana 3 (1-2): 38-201.
- LUER C.A., 1986: Icones Pleurothallidinarum III. Systematics of Pleurothallidinae (Orchidaceae). Monogr. Syst. Bot. Missouri Bot. Gard. 20: 1–109.
- LUER C.A., 1998: Icones Pleurothallidinarum XVII. Systematics of subgen. *Pleurothallis* sect. *Abortivae*, sect. *Truncatae*, sect. *Pleurothallis*, subsect. *Acroniae*, subsect. *Pleurothallis*, subgen. *Dracontia*, subgen. *Unciferia*. Addenda to *Dracula*, *Lepanthes*, *Masdevallia*, *Porroglossum* and *Scaphosepalum* (Orchidaceae). – Monogr. Syst. Bot. Missouri Bot. Gard. 72: 1–121.
- LUER C.A., 2003: *Pleurothallis*. In: HAMMEL B.E., GRAYUM M.H., HERRERA C. & ZAMORA N. (eds.): Manual de plantas de Costa Rica, vol. III. – Missouri Botanical Garden Press: 386–452.
- LUER C.A., 2005: Icones Pleurothallidinarum XXVII. Dryadella and Acronia sect. Macrophyllaceae-Fasciculatae. – Monogr. Syst. Bot. Missouri Bot. Gard. 103: 1–311.
- OSSENBACH C., PUPULIN F. & DRESSLER R.L., 2005: Orquídeas del istmo centroamericano, catálogo y estado de conservación. Orchids of the Central American isthmus, checklist and conservation status Editorial 25 de mayo. 243 pp. San José.
- OSSENBACH C., PUPULIN F. & JENNY R., 2010: Orchid itineraries of Augustus R. Endrés in Central America: a biographic and geographic sketch. Lankesteriana 10 (1): 19–47.
- PRIDGEON A.M., SOLANO R. & CHASE M.W., 2001: Phylogenetic relationships in Pleurothallidinae (Orchidaceae). Combined evidence from nuclear and plastid DNA sequences. – Amer. J. Bot. 88 (12): 2286–2308.
- PUPULIN F., 2002: Catálogo revisado y actualizado de las Orchidaceae de Costa Rica. Lankesteriana 4: 1–88.
- REICHENBACH H.G., 1875: Masdevallia chimaera. Gard. Chron., n.s., 4: 258.
- REICHENBACH H.G., 1877: Pleurothallis (Brachystachyae) luctuosa. Linnaea 41: 48.
- REICHENBACH H.G., 1878: Pleurothallis luctuosa. Xenia Orch. 3: 15-16, pl. 210.
- SCHLECHTER R., 1923: Beiträge zur Orchideenkunde von Zentralamerika. II. Additamenta ad Orchideologiam Costaricensem. Repert. Sp. Nov. Regni Veg. Beih. 19.
- SZLACHETKO D.L. & MARGONSKA B.H., 2001: Genera et species Orchidalium. Polish Bot. J. 46: 113–121.
- SZLACHETKO D.L. & KULAK M., 2006a: New combinations in the genus Zosterophyllanthos SZLACH & MARG. (Orchidaceae, Pleurothallidinae). Richardiana 6: 131–135.
- SZLACHETKO D.L. & KULAK M., 2006b: New combinations in the genus Zosterophyllanthos SZLACH & MARG. (Orchidaceae, Pleurothallidinae). Richardiana 6: 183–195.
- WILSON M., BELLE C., DANG A., HANNAN P., KENYON C., LOW H., STAYTON T. & WOOLLEY M. (in press): A phylogenetic analysis of the genus *Pleurothallis*, with emphasis on *Pleurothallis* subsection *Macrophyllae-Fasciculatae*, using nuclear ITS and chloroplast DNA sequencing. — Proc. 3rd Scientific Conference on Andean Orchids. Quito, Pontificia Universidad Católica del Ecuador, 2008.