

PHYLOGENETIC REASSESSMENT OF *ACIANTHERA* (ORCHIDACEAE: PLEUROTHALLIDINAE)

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Abstract. The phylogenetic relationships within the *Acianthera* affinity are re-evaluated using Bayesian analyses of nrITS and chloroplast *matK* sequence data. Emphasis is made on species from the Antilles, Central America and the Andean South America as those have been less represented in previous studies. *Acianthera* is retrieved largely monophyletic, but is redefined to include the genera *Aberrantia*, *Antilla*, *Apoda-prorepentia*, *Arthrosia*, *Brenesia*, *Cryptophoranthus*, *Didactylus*, *Dondodia*, *Kraenzlinella*, *Ogygia*, *Pleurobotryum*, *Proctoria*, *Sarracenella* and *Unguella*. Four well-supported subgenera are proposed for *Acianthera* and characterized both geographically and morphologically. The species belonging to the three newly proposed subgenera are listed.

Keywords: *Antilla*, *Brenesia*, *Kraenzlinella*, molecular phylogeny, synonyms, systematics

The genus *Acianthera* Scheidw. (Orchidaceae: Pleurothallidinae) was historically considered a synonym of *Pleurothallis* R.Br. (Luer, 1986; Pupulin et al., 2007). On the basis of the molecular studies of the Pleurothallidinae by Pridgeon et al. (2001), it was re-instated by Pridgeon and Chase (2001) and Pridgeon (2005), and broadened to include the generic concepts of *Cryptophoranthus* Barb. Rodr., *Brenesia* Schltr., and *Sarracenella* Luer. Additional species were subsequently transferred to the genus by several authors, most notably Luer (2004).

Chiron and van den Berg (2012) revised the systematics of *Acianthera* on the basis of a broader molecular study of nrITS by Chiron et al. (2012). The latter especially included Brazilian material, where *Acianthera* is richest in species numbers. The authors expanded the concept of the genus, including into its synonymy the genera *Arthrosia* Luer and *Pleurobotryum* Barb.Rodr. A sectional and subsectional classification for the genus was proposed by the authors. However, due to the relatively reduced representation, the phylogenetic placement of the Central American, Antillean and Andean clades of *Acianthera* was not completely resolved.

The relationships of several additional genera with *Acianthera* were subsequently noted. Bogarín et al. (2008) gave formal recognition to the synonymy of *Aberrantia* Luer, as suggested by Luer (2004). Stenzel (2004; 2007) and Karremans (2016) added *Antilla* (Luer)

Luer, following a suggestion by the same Luer (2000). *Apoda-prorepentia* (Luer) Luer, as suggested by Solano-Gómez (2011), and shown by Stenzel (2004) was reconsidered by Karremans and Rincón-González (2015), while *Ogygia* Luer was synonymized by Solano-Gómez (2003; 2015). Close relationships with *Acianthera* of *Didactylus* Luer and *Unguella* Luer were suggested by Luer (2004), while *Dondodia* Luer and *Proctoria* Luer were suggested to be *Acianthera* relatives by Luer (2006), Stenzel (2007) and Karremans (2016). Additionally, the single sequence of *Kraenzlinella* Kuntze analyzed by Pridgeon et al. (2001) was retrieved in a clade together with the genera *Brachionidium* Lindl. and *Myoxanthus* Poepp. & Endl. and therefore *Kraenzlinella* was accepted by Pridgeon and Chase (2001) and Pridgeon (2005). Nevertheless, Karremans (2016) pointed out that additional unpublished DNA data placed genus *Kraenzlinella* in the *Acianthera* affinity, as had already been suggested by Luer (1994) based on morphological similarity.

In an attempt to re-evaluate and clarify the phylogenetic relationships within the *Acianthera* affinity as defined by Karremans (2016), we have reconstructed a DNA-based phylogeny inferred from a combined nrITS and *matK* matrix from a broad set of species. It covers about one third of the ±300 species and most of the generic names proposed within the group. A subgeneric classification of *Acianthera* is proposed.

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MATERIALS AND METHODS

Plant material in Costa Rica was collected under the scientific permits granted by the Costa Rican Ministry of Environment (MINAE) to researchers at JBL. Individual plants were photographed, illustrated and preserved as spirit specimens (only including flowers and young leaf tissue) in formaldehyde: acetic acid: ethanol (FAA: 53% ethanol, 37% water, 5% formaldehyde and 5% glycerol) for future reference, deposited at JBL-spirit and L-spirit. The DNA extracts were preserved at the Naturalis Biodiversity Center.

The data matrix is composed of 143 terminals (Table 1), including 126 nrITS and 52 *matK* accessions, of which 66 were produced for this study. The remaining sequences were obtained from GenBank (from Pridgeon et al., 2001; Borba et al., 2002; Stenzel, 2004; Lahaye et al., 2008; Chiron et al., 2012; Karremans, 2014; Karremans and Rincón-González, 2015; and Rodrigues et al., 2015). The DNA sequences of *Acianthera fornograndensis* L.Kollmann & A.P.Fontana and *Acianthera maculiglossa* Chiron & N.Sanson were obtained from the plants that served as type material (Chiron et al., 2012). The specimens of *Acianthera cabiriae* Pupulin, G.A.Rojas & J.D.Zuñiga come from the type locality.

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 the chloroplast gene *matK* was amplified and sequenced using the Kew *matK* primers 2.1aF and 5R. 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 and Maddison, 2007), where they were checked for base calling errors, each locus was aligned separately using MAFFT version 7.1 (Kato and Standley, 2013). The ends of each data set were trimmed to eliminate possible erroneous data, and gaps were regarded as missing data. *Arpophyllum giganteum* Hartw. ex Lindl. was used as the 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 + *matK* dataset using BEAST v1.8.0. (Drummond et al., 2012). Parameters were set to preset, except for substitution model GTR with 10 categories for ITS and 8 categories for *matK*, clock models uncorrelated lognormal and exponential respectively, tree prior Yule process, and number of generations 30,000,000. The resulting trees were combined using TreeAnnotator v1.8.0., where the first 20% of the 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.

TABLE 1. List of the accessions used in the phylogenetic analysis. The vouchers, NCBI GenBank accession number, and source are given.

TAXON	VOUCHER COLLECTOR AND NUMBER	ITS	<i>matK</i>	SOURCE
<i>Acianthera aberrans</i> (Luer) Pupulin & Bogarín	<i>Pupulin 7839A</i> ; JBL-spirit	KY084267	KY218740	This Study
<i>Acianthera aberrans</i> (Luer) Pupulin & Bogarín	<i>Pupulin 7839B</i> ; JBL-spirit	KY084268	KY218741	This Study
<i>Acianthera aberrans</i> (Luer) Pupulin & Bogarín	<i>Pupulin 7839C</i> ; JBL-spirit	–	KY218742	This Study
<i>Acianthera adamantinensis</i> (Brade) F.Barros	None	AF366936	–	Borba et al. 2002
<i>Acianthera aphthosa</i> (Lindl.) Pridgeon & M.W.Chase	<i>van den Berg 1998</i>	JQ306355	–	Chiron et al. 2012
<i>Acianthera asaroides</i> (Kraenzl.) Pridgeon & M.W.Chase	<i>Chiron 11227</i>	JQ306431	–	Chiron et al. 2012
<i>Acianthera atropurpurea</i> (Barb.Rodr.) Chiron & Van den Berg	<i>Zampin 25</i>	KT599874	–	Rodrigues et al. 2015
<i>Acianthera auriculata</i> (Lindl.) Pridgeon & M.W.Chase	<i>Chase 1456</i>	AF262856	–	Pridgeon et al. 2001
<i>Acianthera barbacenensis</i> (Barb.Rodr.) Pridgeon & M.W.Chase	<i>van den Berg 2004</i>	JQ306423	–	Chiron et al. 2012
<i>Acianthera binotii</i> (Regel) Pridgeon & M.W.Chase	<i>van den Berg 2044</i>	JQ306361	–	Chiron et al. 2012
<i>Acianthera binotii</i> (Regel) Pridgeon & M.W.Chase	<i>van den Berg 2083</i>	JQ306430	–	Chiron et al. 2012
<i>Acianthera bragae</i> (Ruschi) F.Barros	<i>van den Berg 1990</i>	JQ306362	–	Chiron et al. 2012
<i>Acianthera breedlovei</i> Soto Arenas, Solano & Salazar	<i>Karremans 3962</i> ; JBL-spirit	KY084269	KY218743	This Study
<i>Acianthera brunnescens</i> (Schltr.) Karremans	<i>Karremans 2746</i> ; JBL-spirit	KR816549	KR816558	Karremans and Rincón-González 2015
<i>Acianthera brunnescens</i> (Schltr.) Karremans	<i>Karremans 2460A</i> ; JBL-spirit	–	KY218744	This Study

TABLE 1 CONT. List of the accessions used in the phylogenetic analysis.

TAXON	VOUCHER COLLECTOR AND NUMBER	ITS	matK	SOURCE
<i>Acianthera brunnescens</i> (Schltr.) Karremans	Karremans 2460B; JBL-spirit	–	KY218745	This Study
<i>Acianthera brunnescens</i> (Schltr.) Karremans	Karremans 4511; JBL-digital	–	KY218746	This Study
<i>Acianthera brunnescens</i> (Schltr.) Karremans	Karremans 4912; JBL-spirit	–	KY218747	This Study
<i>Acianthera brunnescens</i> (Schltr.) Karremans	Karremans 5204; JBL-spirit	–	KY218748	This Study
<i>Acianthera butcheri</i> (L.O.Williams) Pridgeon & M.W.Chase	Pupulin 8127; no voucher	KY084270	KY218749	This Study
<i>Acianthera cabiriae</i> Pupulin, G.A.Rojas & J.D.Zuñiga	Karremans 5439; JBL-digital	KY084271	KY218750	This Study
<i>Acianthera cabiriae</i> Pupulin, G.A.Rojas & J.D.Zuñiga	Karremans 5440; JBL-spirit	KY084272	KY218751	This Study
<i>Acianthera capanemae</i> (Barb.Rodr.) Pridgeon & M.W.Chase	Chiron 09573	JQ306367	–	Chiron et al. 2012
<i>Acianthera capillaris</i> (Lindl.) Pridgeon & M.W.Chase	van den Berg 2081	JQ306424	–	Chiron et al. 2012
<i>Acianthera capillaris</i> (Lindl.) Pridgeon & M.W.Chase	van den Berg 2153	JQ306425	–	Chiron et al. 2012
<i>Acianthera circumplexa</i> (Lindl.) Pridgeon & M.W. Chase	Karremans 3119; JBL-spirit	–	KY218752	This Study
<i>Acianthera cogniauxiana</i> (Schltr.) Pridgeon & M.W. Chase	Karremans 5879; no voucher	KR816545	KR816554	Karremans and Rincón-González 2015
<i>Acianthera cogniauxiana</i> (Schltr.) Pridgeon & M.W. Chase	Karremans 6012; JBL-spirit	–	KY218753	This Study
<i>Acianthera compressiflora</i> (Barb.Rodr.) Chiron & Van den Berg	van den Berg 2111	JQ306436	–	Chiron et al. 2012
<i>Acianthera costaricensis</i> (Schltr.) Pupulin & Karremans	Karremans 5727; no voucher	KR816547	KR816556	Karremans and Rincón-González 2015
<i>Acianthera costaricensis</i> (Schltr.) Pupulin & Karremans	Pupulin 6241; no voucher	–	EU214424	Lahaye et al. 2008
<i>Acianthera crassilabia</i> (Ames & C.Schweinf.) Luer	Karremans 5870; no voucher	KY084273	KY218754	This Study
<i>Acianthera crepiniana</i> (Cogn.) Chiron & Van den Berg	Rodrigues 502	KT599875	–	Rodrigues et al. 2015
<i>Acianthera crinita</i> (Barb.Rodr.) Pridgeon & M.W.Chase	Chiron 11223	JQ306434	–	Chiron et al. 2012
<i>Acianthera crinita</i> (Barb.Rodr.) Pridgeon & M.W.Chase	Chiron 11225	JQ306435	–	Chiron et al. 2012
<i>Acianthera cryptantha</i> (Barb.Rodr.) Pridgeon & M.W.Chase	Chiron 11039	JQ306433	–	Chiron et al. 2012
<i>Acianthera decipiens</i> (Ames & C. Schweinf.) Pridgeon & M.W. Chase	Karremans 4229; no voucher	KR816546	KR816555	Karremans and Rincón-González 2015
<i>Acianthera decipiens</i> (Ames & C. Schweinf.) Pridgeon & M.W. Chase	Karremans 4032; JBL-spirit	KY084274	KY218755	This Study
<i>Acianthera fabiobarrosii</i> (Borba & Semir) F.Barros & F.Pinheiro	van den Berg 2080	JQ306426	–	Chiron et al. 2012
<i>Acianthera fenestrata</i> (Barb.Rodr.) Pridgeon & M.W. Chase	Chase 6798	AF262857	AF265468	Pridgeon et al. 2001
<i>Acianthera foetens</i> (Lindl.) Chiron & Van den Berg	van den Berg 2107	JQ306432	–	Chiron et al. 2012
<i>Acianthera fornograndensis</i> L.Kollmann & A.P.Fontana	Kollmann 7266	JQ306448	–	Chiron et al. 2012
<i>Acianthera fornograndensis</i> L.Kollmann & A.P.Fontana	van den Berg 2133	JQ306353	–	Chiron et al. 2012
<i>Acianthera freyi</i> (Luer) F.Barros & V.T.Rodrigues	van den Berg 2141	JQ306494	–	Chiron et al. 2012
<i>Acianthera geminicaulina</i> (Ames) Pridgeon & M.W. Chase	Karremans 5209A; JBL-spirit	KY084275	KY218756	This Study
<i>Acianthera geminicaulina</i> (Ames) Pridgeon & M.W. Chase	Karremans 5209B; JBL-spirit	KY084276	KY218757	This Study
<i>Acianthera geminicaulina</i> (Ames) Pridgeon & M.W. Chase	Karremans 3205; JBL-spirit	–	KY218758	This Study
<i>Acianthera glanduligera</i> (Lindl.) Luer	Chiron 09511	JQ306369	–	Chiron et al. 2012

TABLE 1 CONT. List of the accessions used in the phylogenetic analysis.

TAXON	VOUCHER COLLECTOR AND NUMBER	ITS	<i>matK</i>	SOURCE
<i>Acianthera gracilisepala</i> (Brade) Luer	van den Berg 2077	JQ306404	–	Chiron et al. 2012
<i>Acianthera hamata</i> Pupulin & G.A.Rojas	Bogarín 5114; JBL-spirit	KY084277	KY218759	This Study
<i>Acianthera hamosa</i> (Barb.Rodr.) Pridgeon & M.W.Chase	van den Berg 2055	JQ306374	–	Chiron et al. 2012
<i>Acianthera hamosa</i> (Barb.Rodr.) Pridgeon & M.W.Chase	Chiron 11079	JQ306447	–	Chiron et al. 2012
<i>Acianthera hatschbachii</i> (Schltr.) Chiron & Van den Berg	Karremans 4850; no voucher	KY084278	–	This Study
<i>Acianthera hatschbachii</i> (Schltr.) Chiron & Van den Berg	van den Berg 2149	JQ306406	–	Chiron et al. 2012
<i>Acianthera hatschbachii</i> (Schltr.) Chiron & Van den Berg	Rodrigues 503	KT599876	–	Rodrigues et al. 2015
<i>Acianthera heringeri</i> (Hoehne) F.Barros	van den Berg 2045	JQ306363	–	Chiron et al. 2012
<i>Acianthera hondurensis</i> (Ames) Pridgeon & M.W.Chase	Karremans 6062; JBL-spirit	KY084279	KY218760	This Study
<i>Acianthera hondurensis</i> (Ames) Pridgeon & M.W.Chase	Bogarín 9255; no voucher	KY084280	KY218761	This Study
<i>Acianthera hygrophila</i> (Barb.Rodr.) Pridgeon & M.W.Chase	Karremans 4829; L-spirit	KY084281	–	This Study
<i>Acianthera hystrix</i> (Kraenzl.) F.Barros	Rodrigues 507	KT599877	–	Rodrigues et al. 2015
<i>Acianthera johannensis</i> (Barb.Rodr.) Pridgeon & M.W.Chase	None	AF366939	–	Borba et al. 2002
<i>Acianthera johnsonii</i> (Ames) Pridgeon & M.W.Chase	Karremans 5720; JBL-spirit	KY084282	KY218762	This Study
<i>Acianthera jordanensis</i> (Brade) F.Barros	van den Berg 2134	JQ306378	–	Chiron et al. 2012
<i>Acianthera karlii</i> (Pabst) C.N.Gonç. & Waechter	van den Berg 2085	JQ306489	–	Chiron et al. 2012
<i>Acianthera klotzschiana</i> (Rchb.f.) Pridgeon & M.W.Chase	van den Berg 2099	JQ306445	–	Chiron et al. 2012
<i>Acianthera lanceana</i> (Lodd. ex Lindl.) Pridgeon & M.W. Chase	Karremans 5451A; JBL-spirit	KY084283	KY218763	This Study
<i>Acianthera lanceana</i> (Lodd. ex Lindl.) Pridgeon & M.W. Chase	Karremans 5451B; JBL-spirit	–	KY218764	This Study
<i>Acianthera lanceana</i> (Lodd. ex Lindl.) Pridgeon & M.W. Chase	Karremans 5452; JBL-spirit	KY084284	KY218765	This Study
<i>Acianthera lepidota</i> (L.O.Williams) Pridgeon & M.W.Chase	Karremans 5796; L-spirit	KY084285	KY218766	This Study
<i>Acianthera leptotifolia</i> (Barb.Rodr.) Pridgeon & M.W.Chase	Chase 5622	AF262854	–	Pridgeon et al. 2001
<i>Acianthera limae</i> (Porto & Brade) Pridgeon & M.W.Chase	APF1152	JQ306450	–	Chiron et al. 2012
<i>Acianthera luteola</i> (Lindl.) Pridgeon & M.W.Chase	Chiron 10007	JQ306364	–	Chiron et al. 2012
<i>Acianthera macropoda</i> (Barb.Rodr.) Pridgeon & M.W.Chase	van den Berg 2123	JQ306449	–	Chiron et al. 2012
<i>Acianthera maculiglossa</i> Chiron & N.Sanson	van den Berg 2090	JQ306455	–	Chiron et al. 2012
<i>Acianthera maculiglossa</i> Chiron & N.Sanson	Chiron 09291	JQ306453	–	Chiron et al. 2012
<i>Acianthera mantiquyrana</i> (Barb.Rodr.) V.T. Rodrigues & F. Barros	Rodrigues 520	KT599878	–	Rodrigues et al. 2015
<i>Acianthera melanochthoda</i> (Rchb.f.) Pridgeon & M.W. Chase	Chase 1419	AF262853	–	Pridgeon et al. 2001
<i>Acianthera micrantha</i> (Barb.Rodr.) Pridgeon & M.W.Chase	van den Berg 2017	JQ306373	–	Chiron et al. 2012
<i>Acianthera minima</i> (Cogn.) F.Barros	Chiron 05816	JQ306382	–	Chiron et al. 2012
<i>Acianthera montana</i> (Barb.Rodr.) F.Barros & L.R.S.Guim.	van den Berg 2114	JQ306437	–	Chiron et al. 2012
<i>Acianthera murex</i> (Rchb.f.) Luer	Stenzel 483	KY081772	–	Stenzel 2004
<i>Acianthera nemorosa</i> (Barb.Rodr.) F.Barros	van den Berg 2119	JQ306466	–	Chiron et al. 2012
<i>Acianthera ochreatea</i> (Lindl.) Pridgeon & M.W.Chase	van den Berg 2015	JQ306354	–	Chiron et al. 2012
<i>Acianthera ochreatea</i> (Lindl.) Pridgeon & M.W.Chase	van den Berg 2118	JQ306427	–	Chiron et al. 2012

TABLE 1 CONT. List of the accessions used in the phylogenetic analysis.

TAXON	VOUCHER COLLECTOR AND NUMBER	ITS	<i>matK</i>	SOURCE
<i>Acianthera ochreatea</i> (Lindl.) Pridgeon & M.W.Chase	<i>C293 AY</i>	AF262858	AY008458	Pridgeon et al. 2001
<i>Acianthera octophrys</i> (Rchb.f.) Pridgeon & M.W.Chase	<i>Rodrigues 521</i>	KT599879	–	Rodrigues et al. 2015
<i>Acianthera odontotepala</i> (Rchb.f.) Luer	<i>Stenzel 784</i>	KY081773	–	Stenzel 2004
<i>Acianthera panduripetala</i> (Barb.Rodr.) Pridgeon & M.W.Chase	<i>van den Berg 2132</i>	JQ306371	–	Chiron et al. 2012
<i>Acianthera pantasmi</i> (Rchb.f.) Pridgeon & M.W. Chase	<i>Karremans 4950; JBL-spirit</i>	–	KY218767	This Study
<i>Acianthera pantasmi</i> (Rchb.f.) Pridgeon & M.W. Chase	<i>Karremans 4952; JBL-spirit</i>	–	KY218768	This Study
<i>Acianthera papillosa</i> (Lindl.) Pridgeon & M.W.Chase	<i>Chiron 11038</i>	JQ306501	–	Chiron et al. 2012
<i>Acianthera pavimentata</i> (Rchb.f.) Pridgeon & M.W.Chase	<i>Chiron 09784</i>	JQ306443	–	Chiron et al. 2012
<i>Acianthera pavimentata</i> (Rchb.f.) Pridgeon & M.W.Chase	<i>van den Berg 2112</i>	JQ306444	–	Chiron et al. 2012
<i>Acianthera pectinata</i> (Lindl.) Pridgeon & M.W.Chase	<i>Chase 1296</i>	AF262849	–	Pridgeon et al. 2001
<i>Acianthera per-dusenii</i> (Hoehne) F.Barros & L.R.S.Guim.	<i>van den Berg 2082</i>	JQ306454	–	Chiron et al. 2012
<i>Acianthera platystachys</i> (Regel) Chiron & Van den Berg	<i>Chiron 09472</i>	JQ306428	–	Chiron et al. 2012
<i>Acianthera pubescens</i> (Lindl.) Pridgeon & M.W.Chase	<i>Chiron 04848</i>	JQ306365	–	Chiron et al. 2012
<i>Acianthera pubescens</i> (Lindl.) Pridgeon & M.W.Chase	<i>van den Berg 2131</i>	JQ306366	–	Chiron et al. 2012
<i>Acianthera hystrix</i> (Kraenzl.) F.Barros	<i>APs.n.; no voucher</i>	KC425836	–	This Study
<i>Acianthera ramosa</i> (Barb.Rodr.) F.Barros	<i>van den Berg 2120</i>	JQ306438	–	Chiron et al. 2012
<i>Acianthera recurva</i> (Lindl.) Pridgeon & M.W.Chase	<i>van den Berg 2145</i>	JQ306375	–	Chiron et al. 2012
<i>Acianthera rodriguesii</i> (Cogn.) Pridgeon & M.W.Chase	<i>Chiron 11044</i>	JQ306446	–	Chiron et al. 2012
<i>Acianthera rubroviridis</i> (Lindl.) Pridgeon & M.W.Chase	<i>Stenzel 893</i>	KY081774	–	Stenzel 2004
<i>Acianthera saundersiana</i> (Rchb.f.) Pridgeon & M.W.Chase	<i>van den Berg 2109</i>	JQ306452	–	Chiron et al. 2012
<i>Acianthera saurocephala</i> (Lodd.) Pridgeon & M.W. Chase	<i>van den Berg 1985</i>	JQ306356	–	Chiron et al. 2012
<i>Acianthera serpentula</i> (Barb.Rodr.) F.Barros	<i>Chiron 09029</i>	JQ306370	–	Chiron et al. 2012
<i>Acianthera serpentula</i> (Barb.Rodr.) F.Barros	<i>van den Berg 2135</i>	JQ306411	–	Chiron et al. 2012
<i>Acianthera sicaria</i> (Lindl.) Pridgeon & M.W.Chase Rincón-González 2015	<i>Pupulin 7190; JBL-spirit</i>	KR816550	KR816559	Karremans and
<i>Acianthera sicaria</i> (Lindl.) Pridgeon & M.W.Chase	<i>Karremans 121; JBL-spirit</i>	KY084286	KY218769	This Study
<i>Acianthera sicaria</i> (Lindl.) Pridgeon & M.W.Chase	<i>Bogarín 7727; JBL-spirit</i>	–	KY218770	This Study
<i>Acianthera sicaria</i> (Lindl.) Pridgeon & M.W.Chase	<i>Karremans 4939; JBL-spirit</i>	–	KY218771	This Study
<i>Acianthera sicaria</i> (Lindl.) Pridgeon & M.W.Chase	<i>Chase 5609</i>	AF262848	–	Pridgeon et al. 2001
<i>Acianthera sp.</i>	<i>Karremans 5432; JBL-spirit</i>	KY084287	KY218772	This Study
<i>Acianthera sonderiana</i> (Rchb.f.) Pridgeon & M.W.Chase	<i>van den Berg 2098</i>	JQ306377	–	Chiron et al. 2012
<i>Acianthera sonderiana</i> (Rchb.f.) Pridgeon & M.W.Chase	<i>van den Berg 2144</i>	JQ306496	–	Chiron et al. 2012
<i>Acianthera spilantha</i> (Barb.Rodr.) Luer	<i>van den Berg 2037</i>	JQ306359	–	Chiron et al. 2012
<i>Acianthera spilantha</i> (Barb.Rodr.) Luer	<i>van den Berg 2046</i>	JQ306360	–	Chiron et al. 2012
<i>Acianthera teres</i> (Lindl.) Borba	None	AF366935	–	Borba et al. 2002
<i>Acianthera teres</i> (Lindl.) Borba	None	AF366937	–	Borba et al. 2002
<i>Acianthera teres</i> (Lindl.) Borba	<i>Karremans 4849; no voucher</i>	KY084288	–	This Study

TABLE 1 CONT. List of the accessions used in the phylogenetic analysis.

TAXON	VOUCHER COLLECTOR AND NUMBER	ITS	matK	SOURCE
<i>Acianthera testifolia</i> (Sw.) Solano	Karremans 4914; JBL-spirit	KR816551	KR816560	Karremans and Rincón-González 2015
<i>Acianthera testifolia</i> (Sw.) Solano	Stenzel 656	KR816552	–	Stenzel 2004
<i>Acianthera translucida</i> (Barb.Rodr.) Luer	van den Berg 2092	JQ306368	–	Chiron et al. 2012
<i>Acianthera tricarinata</i> (Poepp. & Endl.) Pridgeon & M.W.Chase	Chiron 07792	JQ306495	–	Chiron et al. 2012
<i>Acianthera tricarinata</i> (Poepp. & Endl.) Pridgeon & M.W.Chase	Karremans 5954; L-spirit	KY084289	KY218773	This Study
<i>Acianthera wilsonii</i> (Lindl.) Pridgeon & M.W.Chase	Stenzel 621	KY081776	–	Stenzel 2004
<i>Anathallis lewisiae</i> (Ames) Solano & Soto Arenas	Bogarín 1056; JBL-spirit	KC425733	KC425858	Karremans 2014
<i>Anathallis obovata</i> (Lindl.) Pridgeon & M.W.Chase	Karremans 4796; L-spirit	KF747797	–	Karremans 2014
<i>Anathallis pabstii</i> (Garay) Pridgeon & M.W. Chase	Karremans 4821; L-spirit	KC425737	KC425859	Karremans 2014
<i>Anathallis sertularioides</i> (Sw.) Pridgeon & M.W.Chase	Solano 807	AF262871	–	Pridgeon et al. 2001
<i>Antilla erosa</i> (Urb.) Luer	Karremans 6469; L-spirit	–	KY218774	This Study
<i>Antilla erosa</i> (Urb.) Luer	Karremans 7315; L-spirit	KY084290	KY218775	This Study
<i>Antilla parvula</i> (Ames & C. Schweinf.) Luer	Karremans 7316; no voucher	–	KY218776	This Study
<i>Antilla prostrata</i> (Lindl.) Luer	Stenzel 856	KY081777	–	Stenzel 2004
<i>Antilla trichophora</i> (Lindl.) Luer	Stenzel 606	KY081778	–	Stenzel 2004
<i>Antilla trichophora</i> (Lindl.) Luer	Stenzel 630	KY081779	–	Stenzel 2004
<i>Arpophyllum giganteum</i> Hartw. ex Lindl.	None	AF266742	AF265485	Pridgeon et al. 2001
<i>Dilomilis montana</i> (Sw.) Summerh.	Chase 206	AF262915	AF263765	Pridgeon et al. 2001
<i>Kraenzlinella anfracta</i> (Luer) Luer	Karremans 5499; no voucher	KY084291	KY218777	This Study
<i>Kraenzlinella anfracta</i> (Luer) Luer	Karremans 5790; L-spirit	KY084292	–	This Study
<i>Kraenzlinella echinocarpa</i> (C. Schweinf.) Luer	AP213; no voucher	KF747840	–	This Study
<i>Kraenzlinella erinacea</i> (Rchb.f.) Solano	Karremans 5984; L-spirit	KY084293	KY218778	This Study
<i>Kraenzlinella erinacea</i> (Rchb.f.) Solano	Solano 900	AF262923	–	Pridgeon et al. 2001

RESULTS

The resulting “target” tree of the Bayesian analysis of the combined nrITS and *matK* matrices have been used to establish the clades (Fig. 1). Support measures are given as P.P. (Posterior Probabilities). The *Acianthera* affinity forms a well-supported clade (P.P.=1) that is here divided into four subclades.

Clade *Brenesia* (P.P.=1) is recovered as sister to a clade that includes the clades *Kraenzlinella* and *Antilla* with low support (P.P.=0.66). It includes the accessions of *Acianthera costaricensis* (type species of *Brenesia*), and *A. johnsonii*.

Clade *Kraenzlinella* (P.P.=1) is sister to the *Antilla* clade (P.P.=1) and includes the accessions of *Kraenzlinella echinocarpa* and *K. erinacea*.

Clade *Antilla* (P.P.=1) includes the accessions of *Acianthera murex*, and *Antilla erosa*, *A. parvula*, *A. prostrata*, and *A. trichophora* (type species of *Antilla*).

Clade *Acianthera* (P.P.=1) contains all the remaining species of *Acianthera*, including *Acianthera aberrans* (type species of *Aberrantia*), *A. atropurpurea* (type species of *Pleurobotryum*), *A. auriculata* (type species of *Arthrosia*), *A. bragae* (type species of *Sarracenella*), *A. butcheri* (type species of *Didactylus*), *A. fenestrata* (type species of *Cryptophoranthus*), *A. lepidota* (type species of *Unguella*), *A. recurva* (type species of *Acianthera*), and *A. testifolia* (type species of *Apoda-proreparentia*).

DISCUSSION

Our nrITS+*matK* combined analysis of a broad set of *Acianthera* species complements and expands the analyses of Pridgeon et al. (2001) and Chiron et al. (2012). The placement in *Acianthera* of the genera *Arthrosia*, *Brenesia*, *Cryptophoranthus*, *Pleurobotryum* and *Sarracenella*, as previously proposed (Pridgeon and Chase, 2001; Pridgeon, 2005; Chiron and van den Berg, 2012), is confirmed. In addition, the analysis of the type species of *Aberrantia*, *Antilla*, *Apoda-proreperntia*, *Didactylus* and *Unguella*, and of two representative species of *Kraenzlinella*, shows that these genera are also imbedded within a broad circumscription of *Acianthera*. No DNA data of the monotypic *Dondodia*, *Ogygia*, and *Proctoria* were available for this study, but the three genera are included within *Acianthera* on the basis of their morphological similarity.

Aberrantia was proposed by Luer (2005) to accommodate a single species previously placed by the author in *Pleurothallis* subgen. *Aberrantia* Luer (2004). It was not included in *Acianthera* because of a “floral structure that is incompatible,” namely the bicallose, truncate petals ending into a short apiculum and long claw of the lip. However, other morphological features, especially the leaf with margins decurrent on the ramicaul, the short inflorescence, borne above the base of the leaf and the glabrous, gapping flowers, are common to several other *Acianthera* species (Bogarín et al., 2008). The accessions of *A. aberrans* were here retrieved embedded within *Acianthera* in a clade containing mainly species found from Costa Rica to Ecuador.

Antilla was proposed by Luer (2004) to accommodate a dozen species with pendulous plants and leaves with dentate margins, endemic to the Greater Antilles, which he noted were related to *Acianthera* (Luer, 2000). The species of *Antilla* have mostly been considered as members of *Pleurothallis* (Luer, 1986, 2000; Pridgeon, 2005). Here species of *Antilla* are found in a highly supported clade. We give subgeneric status to this clade to distinguish it from the members of *Kraenzlinella* to which it is closely related, but that have quite different morphologies and distribution.

Apoda-proreperntia was proposed by Luer (2004) to segregate about ten species, with highest diversity in the Ecuadorian and Colombian Andes, previously assigned to *Pleurothallis* subgen. *Apoda-proreperntia* Luer (1986). Luer (2007) characterized the group by the repent, often pendent habit, with broad, short-stemmed, overlapping leaves, single-flowered (sometimes successive) inflorescences, fleshy sepals often pubescent externally, never spreading, commonly connate, single-veined and spatulate petals and an apically denticulate to fringed lip with a pair of lateral lobes. Stenzel (2004) and Karremans and Rincón-González (2015) found *A. testifolia*, type species of *Apoda-proreperntia*, embedded within *Acianthera*, as suggested by Solano-Gómez et al. (2011). Here the accessions of two species assigned to this genus are found in a highly supported clade including several other species with mainly pendent habits and mostly found from Costa Rica down to Ecuador.

Arthrosia was proposed by Luer (2006) to accommodate 14 species previously assigned to *Pleurothallis* subgen. *Arthrosia* Luer (Luer, 1986). The species assigned to this

genus form a monophyletic group in the analyses, however, it is well embedded within *Acianthera*. Sectional status was given to this particular clade as *Acianthera* sect. *Arthrosiae* (Luer) Chiron & van den Berg. The species belonging to this clade are mostly found in Bolivia and Brazil.

Brenesia was proposed to recognize the distinctness of a species with Pleurothallidinae-like flowers but with the inflorescence arising from a basal node of the stem rather than the apex of the ramicaul. Luer (2004) transferred the species of *Echinosepala* Pridgeon & M.W. Chase, some of which also have rhizomatous inflorescences, to *Brenesia* in the believe that they were related to each other. However, such a relationship has been disproven by DNA data (Pridgeon et al., 2001; Pupulin and Karremans, in prep.). The clade that includes the type species of *Brenesia* is found sister (with low support) to a clade that includes *Antilla* and *Kraenzlinella*, altogether highly supported as sisters to the rest of *Acianthera*. Four species of Central American distribution are recognized in this clade, which is here given subgeneric status.

Cryptophoranthus was proposed to recognize a group of species distinguished by the connation of the dorsal sepal with the synsepal at the base and apex, forming a pair of lateral “windows.” It is now known that flowers with diversely connate sepals occur in several different affinities within Pleurothallidinae (Karremans, 2016), and the species once included in *Cryptophoranthus* belong to several unrelated genera (Luer, 1986). The type species, however, was found embedded within *Acianthera*. Six Brazilian endemic species characterized, aside from the lateral “windows,” by the short ramicauls and 1–2 flowered inflorescences were given section status by Chiron and van den Berg (2012).

Didactylus was proposed by Luer (2005) to accommodate four species previously placed by the author in *Pleurothallis* subgen. *Didactylus* Luer (2004). They were not included within *Acianthera* in essence because of the presence of “two narrow, curved, lateral lobes on the rostellum.” The species of *Didactylus* are otherwise indistinguishable from other *Acianthera*. The accession of *A. butcheri*, type species of *Didactylus*, is found in a clade including several other species with pendent habits, distributed mostly ranging from Costa Rica to Ecuador.

Dondodia Luer was proposed to segregate *Acianthera cymbiformis* (Dod) Pridgeon & M.W.Chase, an unusual species known only from Hispaniola. It had been previously placed in *Pleurothallis* sect. *Cryptophoranthae* Luer (1986) on account of the connation of the dorsal sepal with the lateral synsepal. The species of that section would later be found embedded within *Acianthera* (Pridgeon et al., 2001) and transferred to the genus (Pridgeon and Chase, 2001), transferring this species too. Karremans (2016) suggested that *A. cymbiformis* is related to the also Antillean species placed in the genera *Antilla* and *Proctoria*, rather than to the Brazilian members of *Acianthera* sect. *Cryptophoranthae*. No DNA data of the species were available for this study but the thickly coriaceous leaf with erose margins, infundibuliform floral bract, the sepals externally papillose,

the dorsal sepal connate apically to the lateral sepals, lanceolate petals, thick, verrucose lip, with a rounded margin and a basal claw, and the clavate column with a denticulate apex are reminiscent of several other Antillean *Acianthera* species.

Kraenzlinella was proposed more than a century ago but received little recognition as a distinct genus (Luer, 1986; Luer, 1994) until it was re-circumscribed by Pridgeon and Chase (2001). The single sequence of *Kraenzlinella* analyzed by Pridgeon et al. (2001) was retrieved in a clade together with the genera *Brachionidium* and *Myoxanthus* rather than *Acianthera*. That same sequence is here found embedded with high support within *Acianthera*, alongside other sequences of *Kraenzlinella*. It is likely that the relatively long branches of the accessions of both *Kraenzlinella* and *Brachionidium* had initially misplaced the two genera in Pridgeon et al. (2001), as neither is related to *Myoxanthus* (Karremans, 2016). Here *Kraenzlinella* is given subgeneric status to distinguish its nine species with stout erect habits distributed from Mexico through Central America southwards into Bolivia, from the members of *Antilla* to which they are closely related.

Ogygia was proposed by Luer (2006) to accommodate a single species endemic to the Revillagigedo Archipelago in Mexico, and of which the only available specimens, at the time of proposal, were sterile. Solano-Gómez (2003) transferred the species to *Acianthera* after studying fertile material of *A. unguicallosa* from the type locality. Even though no DNA data was available for this study the author's illustration shows a species that is indeed morphologically similar to other *Acianthera* species from Mexico.

Pleurobotryum was proposed by Barbosa Rodrigues (1877) to accommodate a species distinguished among the Pleurothallidinae by the conspicuously long articulate, motile lip and the unusual cylindrical leaves. *Pleurobotryum* was later redefined and expanded by Hoehne (1936) adding a handful of species to it, but the genus has been mostly considered a synonym of *Pleurothallis* (Luer, 1986; Pridgeon, 2005). Chiron et al., (2012) found it to be embedded within *Acianthera*, creating *Acianthera* sect. *Pleurobotryae* Chiron & van den Berg (2012), and assigning seven Brazilian endemic species to it. Rodrigues et al. (2015) revised the section and reduced it to only four species.

Proctoria was proposed by Luer (2004) for the only species of Pleurothallidinae found in the Cayman Islands,

and which the author believed it to be a "long isolated" relative of *Acianthera*. No DNA data were available for this study, but the shortly creeping rhizome, thick, sessile leaves, with irregular margins, the long, lax inflorescence, and the three-lobed lip, with a pair of calli near the middle, auricles at the base and apically obtuse are indeed reminiscent of species of *Acianthera* subgen. *Antilla*. The distribution of this species, Cayman Islands and Cuba (Luer, 2006; Stenzel, 2007), is compatible with this hypothesis.

Sarracenella was proposed for two Brazilian endemics characterized by the creeping rhizome with thick leaves, and a short raceme with a pair of fleshy, tubular flowers. Not long after, Luer (1986) would place *Sarracenella* under the synonymy of *Pleurothallis* recognizing that besides the unusual sepaline tube, the two species could be otherwise placed among the latter. Pridgeon et al. (2001) found the two species of *Sarracenella* well embedded within *Acianthera*. *Acianthera* sect. *Sarracenella* (Luer) Chiron & van den Berg (2012) was created to accommodate these two species.

Unguella was proposed by Luer (2005) to accommodate two species previously placed by the author in *Pleurothallis* subgen. *Unguella* Luer (2004). They were not included within *Acianthera* because of the presence of "a narrow claw of a three-lobed lip that articulates with a narrow extension of the column-foot." The species of *Unguella* are otherwise indistinguishable from other *Acianthera*. The accession of *A. lepidota*, type species of *Unguella*, is found in a clade together with the type of *Didactylus*, and other species with pendent habits from Costa Rica, Panama, Colombia and Ecuador.

Acceptance of the splinter generic concepts within *Acianthera* subgen. *Acianthera* would require their complete recircumscription and/or the establishment of additional segregate generic concepts, which we believe to be unnecessary. *Antilla*, *Brenesia* and *Kraenzlinella* are given subgeneric status in recognition of their unique morphologies and distribution, supported by genetic distance, as has been previously done with *Specklinia* Lindl. (Karremans et al., 2016). Their overall similarity to other species of *Acianthera* prevents us from recognizing them as distinct genera. The 14 validly published generic concepts that are here placed within the *Acianthera* affinity are regarded as synonyms of the latter. As such, the genus, just shy of 300 species, is manageable in size, well-defined and morphologically diagnosable (Fig. 2, 3).

TAXONOMIC TREATMENT

***Acianthera* Scheidw., Allg. Gartenzeitung 10: 292. 1842.**

TYPE: *Acianthera punctata* Scheidw., Allg. Gartenzeitung 10: 292. 1842.

Synonyms: *Centranthera* Scheidw., Allg. Gartenzeitung 10: 293. 1842, *nom. illeg.*

Pleurobotryum Barb.Rodr., Gen. Spec. Orchid. 1: 20. 1877.

Cryptophoranthus Barb.Rodr., Gen. Spec. Orchid. 2: 79. 1881.

Otopetalum F.Lehm. & Kraenzl., Bot. Jahrb. Syst. 26: 457. 1899, *nom. illeg.*

Kraenzlinella Kuntze in T.E.von Post, Lex. Gen. Phan.: 310. 1903.

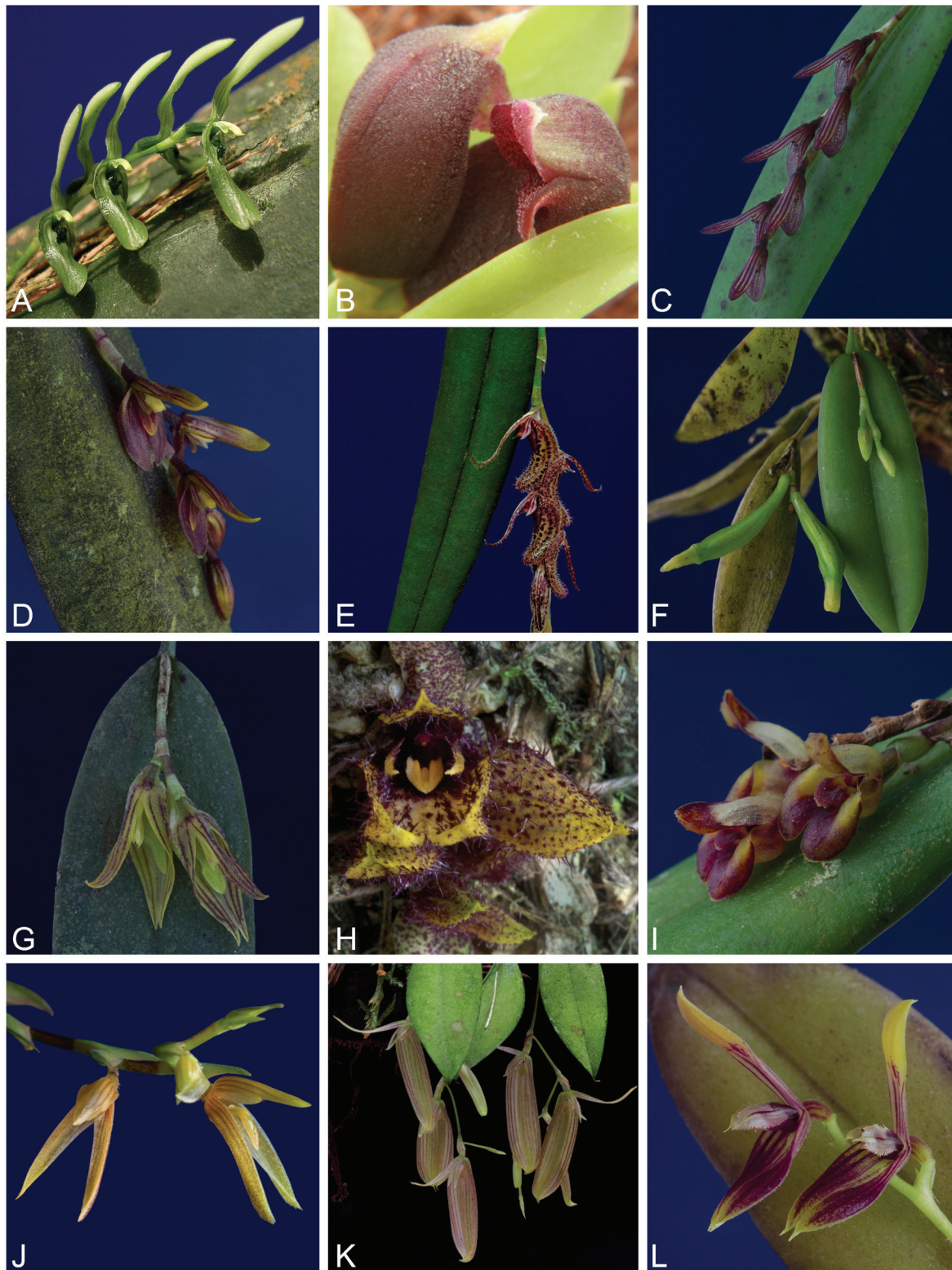
Brenesia Schltr., Repert. Spec. Nov. Regni Veg., Beih. 19: 199. 1923.

Geocalpa Brieger, Die Orchidee 440. 1975, *nom. inval.*

Sarracenella Luer, Selbyana 5: 388. 1981.

Aberrantia (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 253. 2004, *nom. inval.*

Antilla (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 255. 2004.



A - *Acianthera aberrans* (FP4857)

B - *Acianthera bragae*

C - *Acianthera breedlovei* (AK3962)

D - *Acianthera brunnescens* (AK5204)

E - *Acianthera butcheri* (FP2503)

F - *Acianthera cabiriae* (AK5439)

G - *Acianthera cachensis* (MF333)

H - *Acianthera costaricensis* (AK4981)

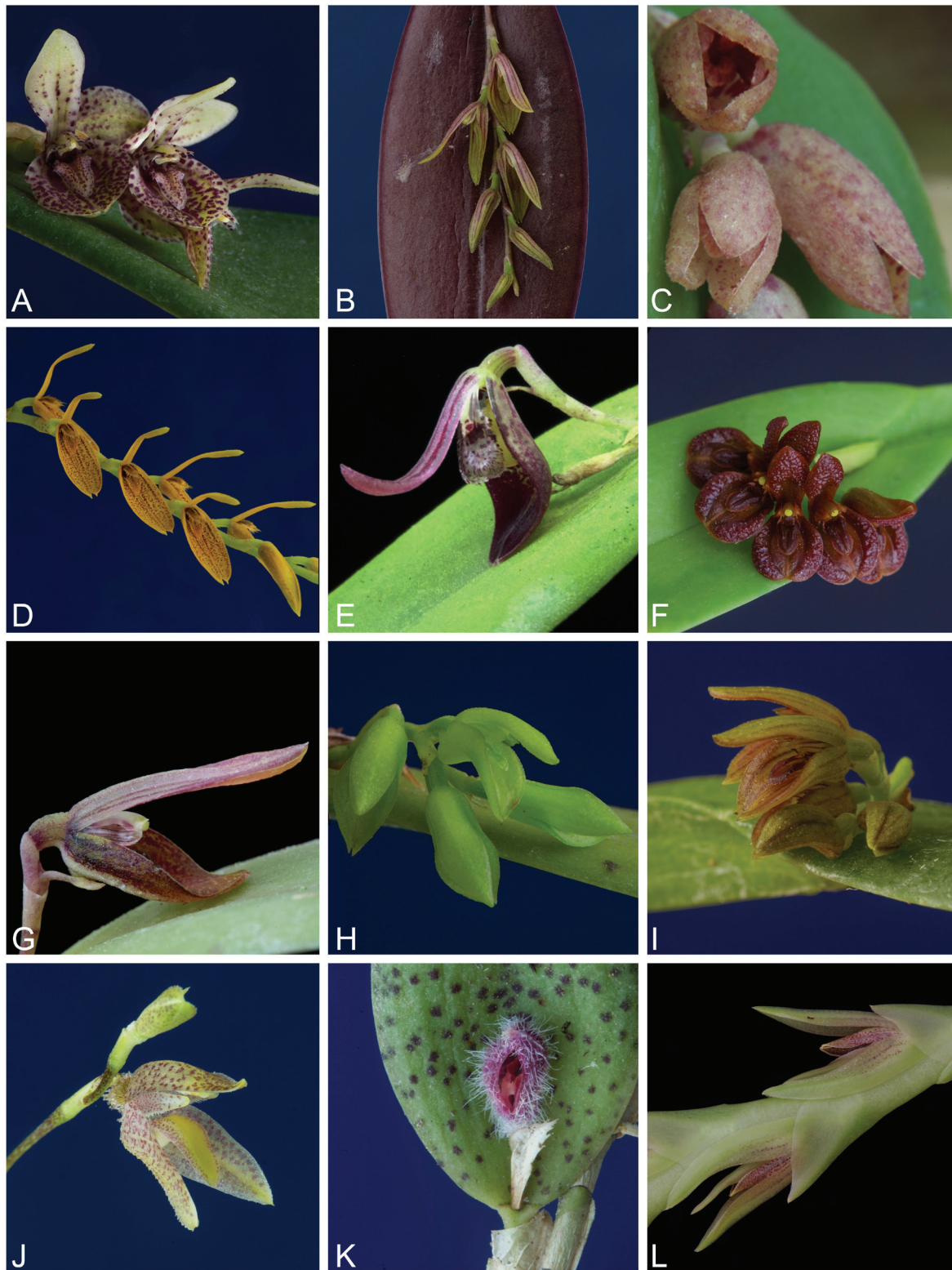
I - *Acianthera decipiens* (AK4032)

J - *Acianthera erinacea*

K - *Acianthera erosa* (AK7315)

L - *Acianthera geminicaulina* (AK5209)

FIGURE 2. Species of *Acianthera*, including the type species of the genera *Aberrantia* (A), *Brenesia* (H), *Didactylus* (E) and *Sarracenella* (B), and representative species of *Acianthera* subgen. *Antilla* (K) and *Acianthera* subgen. *Kraenzlinella* (J). Photographs by F. Pupulin (A, E, F, J), M. Díaz (D, I, L), W. Driessen (B, K), A.P. Karremans (C, H) and D. Bogarín (G). Vouchers for A, C, D, E, I and L at JBL (spirit).



A - *Acianthera hamata* (DB5114)

B - *Acianthera hondurensis* (AK6062)

C - *Acianthera johnsonii*

D - *Acianthera lanceana* (AK5451)

E - *Acianthera panduripetala*

F - *Acianthera pantasmii* (AK4952)

G - *Acianthera saundersiana*

H - *Acianthera sicaria* (AK4939)

I - *Acianthera sicaria* (FP7190)

J - *Acianthera sigmoidea* (DB8360)

K - *Acianthera testifolia* (AK4914)

L - *Acianthera tricarinata*

FIGURE 3. Species of *Acianthera*, including the type species of genus *Apoda-prorepentia* (K), and representative species of *Acianthera* subgen. *Brenesia* (C) and *Acianthera* subgen. *Kraenzlinella* (J). Photographs by M. Díaz (A, D, F, H, I), W. Driessen (C, E, G, L), A.P. Karremans (B, K) and D. Bogarín (J). Vouchers for A, B, D, F, H, I and K at JBL (spirit).

Apoda-prorepentia (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 255. 2004.

Didactylus (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 257. 2004, *nom. inval.*

Proctoria Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 258. 2004.

Unguella (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 265. 2004, *nom. inval.*

Aberrantia Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 103: 310. 2005.

Didactylus Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 103: 310. 2005.

Unguella Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 103: 310. 2005.

Arthrosia Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 105: 248. 2006.

Dondodia Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 105: 85. 2006.

Ogygia Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 105: 252. 2006.

1. *Acianthera* subgen. *Acianthera*

Synonyms: *Acianthera* Scheidw., Allg. Gartenzeitung 10: 292. 1842. *Centranthera* Scheidw., Allg. Gartenzeitung 10: 293. 1842, *nom. illeg.* *Pleurothallis* sect. *Acianthera* (Scheidw.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 20: 12. 1986. *Pleurothallis* sect. *Brachystachyae* Lindl., Fol. Orchid. *Pleurothallis* 21. 1859. *Pleurothallis* sect. *Sarcodanthae* Barb.Rodr., Gen. Sp. Orchid. 2: 10. 1882. TYPE: *Acianthera recurva* (Lindl.) Pridgeon & M.W.Chase, Lindleyana 16: 246. 2001.

Pleurothallis sect. *Sicariae* Lindl., Fol. Orchid. *Pleurothallis* 12. 1859. *Acianthera* sect. *Sicariae* (Lindl.) Chiron & van den Berg, Richardiana 12(2): 69. 2012. *Pleurothallis* sect. *Sicariae* subsect. *Sicariae* (Lindl.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 20: 20. 1986. *Acianthera* sect. *Sicariae* subsect. *Sicariae*. TYPE: *Acianthera sicaria* (Lindl.) Pridgeon & M.W.Chase, Lindleyana 16: 246. 2001.

Pleurobotryum Barb.Rodr., Gen. Spec. Orchid. 1: 20. 1877. *Pleurothallis* subgen. *Pleurobotryum* (Barb. Rodr.) Luer., Monogr. Syst. Bot. Missouri Bot. Gard. 20: 53. *Acianthera* sect. *Pleurobotryum* (Barb.Rodr.) Chiron & van den Berg, Richardiana 12(2): 68. 2012 [as *Acianthera* sect. *Pleurobotryae* Chiron & van den Berg]. *Pleurothallis* sect. *Pleurobotryum* (Barb. Rodr.) Cogn., NEW 3(4): 587. 1896. 1986. TYPE: *Acianthera atropurpurea* (Barb.Rodr.) Chiron & Van den Berg, Richardiana 12(2): 72. 2012.

Cryptophoranthus Barb.Rodr., Gen. Spec. Orchid. 2: 79. 1881. *Pleurothallis* sect. *Cryptophoranthae* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 20: 16. 1986. *Acianthera* sect. *Cryptophoranthae* (Luer) Chiron & van den Berg, Richardiana 12(2): 68. 2012. TYPE: *Acianthera fenestrata* (Barb.Rodr.) Pridgeon & M.W.Chase, Lindleyana 16: 243. 2001.

Sarracenella Luer, Selbyana 5: 388. 1981. *Geocalpa* Brieger, Die Orchidee 440. 1975, *nom. inval.* *Pleurothallis* subgen. *Sarracenella* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 20: 73. *Acianthera* sect. *Sarracenella* (Luer) Chiron & van den Berg, Richardiana 12(2): 67. 2012 [as *Acianthera* sect. *Sarracenellae* Chiron & van den Berg]. TYPE: *Acianthera bragae* (Ruschi) F.Barros, Hoehnea 30: 183. 2003.

Pleurothallis sect. *Tomentosae* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 20: 22. 1986. *Acianthera* sect. *Tomentosae* (Luer) Chiron & van den Berg, Richardiana 12(2): 71. 2012. TYPE: *Acianthera herzogii* (Schltr.) Baumbach, Orchidee (Hamburg) 58: 100. 2007.

Pleurothallis sect. *Tricarinatae* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 20: 22. 1986. *Acianthera* sect. *Tricarinatae* (Luer) Chiron & van den Berg, Richardiana 12(2): 72. 2012. TYPE: *Acianthera tricarinata* (Poepp. & Endl.) Pridgeon & M.W.Chase, Lindleyana 16: 246. 2001.

Apoda-prorepentia (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 255. 2004. *Pleurothallis* subgen. *Apoda-prorepentia* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 20: 31. 1986. *Pleurothallis* sect. *Apodae-Prorepenes* Lindl., Fol. Orchid. *Pleurothallis* 42. 1859. TYPE: *Acianthera testifolia* (Sw.) Solano, Acta Bot. Mex. 97: 50. 2011.

Aberrantia Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 103: 310. 2005. *Aberrantia* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 253. 2004, *nom. inval.* *Pleurothallis* subgen. *Aberrantia* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 76. 2004, *nom. inval.* TYPE: *Acianthera aberrans* (Luer) Pupulin & Bogarín, Lankesteriana 8(2): 53. 2008.

Didactylus Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 103: 310. 2005. *Didactylus* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 257. 2004, *nom. inval.* *Pleurothallis* subgen. *Didactylus* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 77. 2004, *nom. inval.* TYPE: *Acianthera butcheri* (L.O.Williams) Pridgeon & M.W.Chase, Lindleyana 16: 242. 2001.

Unguella Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 103: 310. 2005. *Unguella* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 265. 2004, *nom. inval.* *Pleurothallis* subgen. *Unguella* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 77. 2004, *nom. inval.* TYPE: *Acianthera lepidota* (L.O.Williams) Pridgeon & M.W.Chase, Lindleyana 16: 244. 2001.

Arthrosia (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 105: 248. 2006. *Pleurothallis* subgen. *Arthrosia* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 20: 34. 1986. *Acianthera* sect. *Arthrosia* (Luer) Chiron & van den Berg, Richardiana 12(2): 67. 2012 [as *Acianthera* sect. *Arthrosiae* Chiron & van den Berg]. TYPE: *Acianthera auriculata* (Lindl.) Pridgeon & M.W.Chase, Lindleyana 16: 242. 2001.

Ogygia Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 105: 252. 2006. TYPE: *Acianthera unguicallosa* (Ames & C.Schweinf.) Solano, Icon. Orchid. 5-6: t. 512. 2002 (2003).

Pleurothallis sect. *Leptotifolia* Pabst, Orchid. Bras. 1: 156. 1975. TYPE: *Acianthera leptotifolia* (Barb. Rodr.) Pridgeon & M.W.Chase, Lindleyana 16: 244. 2001.

Acianthera sect. *Crinitae* Chiron & van den Berg, Richardiana 12(2): 68. 2012. TYPE: *Acianthera crinita* (Barb.Rodr.) Pridgeon & M.W.Chase, Lindleyana 16: 243. 2001.

Acianthera sect. *Sulcatae* Chiron & van den Berg, Richardiana 12(2): 71. 2012. TYPE: *Acianthera luteola* (Lindl.) Pridgeon & M.W.Chase, Lindleyana 16: 244. 2001.

Acianthera sect. *Sicariae* subsect. *Auritae* Chiron & van den Berg, Richardiana 12(2): 70. 2012. TYPE: *Acianthera glanduligera* (Lindl.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 253. 2004.

Pleurothallis sect. *Sicariae* subsect. *Pectinatae* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 20: 20. 1986.

Acianthera sect. *Sicariae* subsect. *Pectinatae* (Luer) Chiron & van den Berg, Richardiana 12(2): 71. 2012. TYPE: *Acianthera pectinata* (Lindl.) Pridgeon & M.W.Chase, Lindleyana 16: 245. 2001.

Out of the 299 species currently accepted in *Acianthera*, 268 belong to *Acianthera* subgen. *Acianthera*. It is premature at this time to present a full list of species belonging to this subgenus (as is done hereafter for the three remaining subgenera), and a thorough revision of *Acianthera* subgen. *Acianthera* is left for a future study. Most species have been revised in previous studies (Luer, 2004; Chiron and van den Berg, 2012; Rodrigues et al., 2015; Solano-Gómez, 2015), but there are still some obscure names that require attention. Species belonging to this subgenus are variable morphologically, but can be recognized in general terms by the stout habit, a more or less bilobed ramicaul with a depression along the middle, a sessile leaf, fleshy flowers, commonly pubescent to verrucose, lateral sepals fused into a concave synsepal, petals lanceolate, denticulate, the lip thick, oblong, bicalous, with lateral lobes below the middle, and a pair of auricles at the base. *Acianthera* species are distributed from Mexico to Argentina and Uruguay, through Central America and the Antilles, and the genus is notably species-rich in Brazil.

Formal sectional status has been assigned to several groups of species belonging to subgen. *Acianthera* (Lindley, 1859; Barbosa Rodrigues, 1882; Luer, 1986; Chiron and van den Berg, 2012), and a few subsections were also proposed (Chiron and van den Berg, 2012). Our genetic analyses do not include enough samples in some of the groups to test their consistence on a broader geographical scale, and our inclusions of the sectional groups into the synonymy of subgen. *Acianthera* is aimed at providing a general frame of the subgenus' taxonomy and of those names that actually refer to the same taxa.

2. *Acianthera* subgen. *Antilla* (Luer) Karremans, *comb. nov.*

Basionym: *Antilla* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 255. 2004. *Pleurothallis* subgen. *Antilla* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 79: 39. 2000. *Acianthera* sect. *Antilla* (Luer) A.Douchette, Phytotaxa 275(3): 270. 2016. TYPE: *Acianthera trichophora* (Lindl.) A.Douchette, Phytotaxa 275(3): 270.

Synonyms: *Proctoria* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 258. 2004. *Acianthera caymanensis* (C.D.Adams) Karremans.

Dondodia Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 105: 85. 2006. TYPE: *Acianthera cymbiformis* (Dod) Pridgeon & M.W.Chase, Lindleyana 16: 243. 2001.

Acianthera alainii (Dod) A.Douchette, Phytotaxa 275(3): 270. 2016.

Basionym: *Pleurothallis alainii* Dod, Moscosoa 3: 54. 1978.

Acianthera alpestris (Sw.) A.Douchette, Phytotaxa 275(3): 270. 2016.

Basionym: *Epidendrum alpestre* Sw., Prodr. Veg. Ind. Occ.: 125. 1788.

Acianthera appendiculata (Cogn.) A.Douchette, Phytotaxa 275(3): 270. 2016.

Basionym: *Pleurothallis appendiculata* Cogn., in I.Urban, Symb. Antill. 7: 174. 1912.

Acianthera bahorucesense (Luer) A.Douchette, Phytotaxa 275(3): 270. 2016.

Basionym: *Pleurothallis bahorucesis* Luer, Lindleyana 14: 108. 1999.

Acianthera caymanensis (C.D.Adams) Karremans, *comb. nov.*

Basionym: *Pleurothallis caymanensis* C.D.Adams, Orquideologia 6: 146. 1971.

Acianthera compressicaulis (Dod) Pridgeon & M.W. Chase, Lindleyana 16(4): 243. 2001.

Basionym: *Pleurothallis compressicaulis* Dod, Moscosoa 3: 113. 1981.

Acianthera cymbiformis (Dod) Pridgeon & M.W.Chase, Lindleyana 16: 243. 2001.

Basionym: *Pleurothallis cymbiformis* Dod, Moscosoa 3: 101. 1984. Replacement name for *Cryptophoranthus erosus* Garay.

Acianthera denticulata (Cogn.) Karremans, *comb. nov.*

Basionym: *Pleurothallis denticulata* Cogn. in I.Urban, Symb. Antill. 6: 425. 1909.

Synonym: *Pleurothallis parvula* Ames & C.Schweinf., Schedul. Orchid. 8: 30. 1925.

Acianthera erosa (Urb.) A.Douchette, *Phytotaxa* 275(3): 270. 2016.

Basionym: *Pleurothallis erosa* Urb., *Repert. Spec. Nov. Regni Veg.* 15: 104. 1917.

Acianthera laxa (Sw.) A.Douchette, *Phytotaxa* 275(3): 270. 2016.

Basionym: *Epidendrum laxum* Sw., *Prodr. Veg. Ind. Occ.*: 125. 1788.

Acianthera murex (Rchb.f.) Luer, *Monogr. Syst. Bot. Missouri Bot. Gard.* 115: 257. 2009.

Basionym: *Pleurothallis murex* Rchb.f., *Flora* 48: 276. 1865.

Synonym: *Pleurothallis papulifolia* Luer, *Lindleyana* 14(2): 116. 1999.

Acianthera oricola (H. Stenzel) Karremans, Chiron & Van den Berg, *Phytotaxa* 270(1): 60. 2016.

Basionym: *Pleurothallis oricola* H. Stenzel, *Willdenowia* 32(1): 101. 2002.

Acianthera pendens (Dod) A.Douchette, *Phytotaxa* 275(3): 270. 2016.

Basionym: *Pleurothallis pendens* Dod, *Moscoso* 1(2): 49. 1977.

Acianthera privigna (Luer) A.Douchette, *Phytotaxa* 275(3): 270. 2016.

Basionym: *Pleurothallis privigna* Luer, *Lindleyana* 14: 118. 1999.

Acianthera prostrata (Lindl.) A.Douchette, *Phytotaxa* 275(3): 270. 2016.

Basionym: *Pleurothallis prostrata* Lindl., *Ann. Mag. Nat. Hist.*, III, 1: 327. 1858.

Acianthera quisqueyana (Dod) A.Douchette, *Phytotaxa* 275(3): 270. 2016.

Basionym: *Pleurothallis quisqueyana* Dod, *Moscoso* 1: 51. 1977.

Acianthera stenzelii Luer, *Mem. New York Bot. Gard.* 109: 575. 2014.

Acianthera trichophora (Lindl.) A.Douchette, *Phytotaxa* 275(3): 271. 2016.

Basionym: *Pleurothallis trichophora* Lindl., *Ann. Mag. Nat. Hist.*, III, 1: 326. 1858.

Eighteen species belong to *Acianthera* subgen. *Antilla*. They can be recognized by the ramicaul shorter to about as long as the, elliptical and sessile, leaf. The leaves are notably coriaceous, sometimes verruculose on the adaxial surface and frequently with denticulate or erose margins. The inflorescence is a loose, frequently flexuous and pendulous, raceme emerging from the spathe at the base of the leaf. The ovary of most species is notoriously spiculate-verrucose. Dorsal sepal almost completely free, ovate, acute, lateral sepals connate, concave, bifid at the apex. The

petals are narrow, entire to microscopically serrate, acute. The lip in most species is conspicuously unguiculate, the blade is bicallous, with a pair of lateral lobes near the middle and minutely auriculate at the base, with the apex obtuse. The column is elongate, clavate, broadly winged close to the apex, conspicuously fimbriate-dentate at the apex. The species of *Antilla* are endemic to the Antilles, where they are restricted to the Cayman Islands, Cuba, Hispaniola, Jamaica and Puerto Rico (Luer 2014).

3. *Acianthera* subgen. *Brenesia* (Schltr.) Karremans, *comb. nov.*

Basionym: *Brenesia* Schltr., *Repert. Spec. Nov. Regni Veg.*, Beih. 19: 199. 1923. TYPE: *Acianthera costaricensis* (Schltr.) Pupulin & Karremans.

Acianthera costaricensis (Schltr.) Pupulin & Karremans, *comb. nov.*

Basionym: *Brenesia costaricensis* Schltr., *Repert. Spec. Nov. Regni Veg. Beih.* 19: 200. 1923.

This species has traditionally been considered a synonym of *A. johnsonii*, however, it is morphologically quite different. *Acianthera costaricensis* has larger plants that mostly produce basal inflorescences (vs. mostly apical), has yellow sepals that are conspicuously long hirsute (vs. reddish-cream and shortly puberulent), and has lanceolate petals (vs. oblong). Photographs of both are shown in the figures.

Acianthera herrerae (Luer) Solano & Soto Arenas, *Icon. Orchid.* 5-6: x. 2002 [2003].

Basionym: *Pleurothallis herrerae* Luer, *Lindleyana* 6: 100. 1991.

Acianthera johnsonii (Ames) Pridgeon & M.W. Chase, *Lindleyana* 16(4): 244. 2001.

Basionym: *Pleurothallis johnsonii* Ames, *Sched. Orch.* 2: 21. 1923.

Acianthera sotoana Solano, *Lankesteriana* 9(3): 447. 2010.

Species of *Acianthera* subgen. *Brenesia* can be recognized by the large fleshy plants, and especially by the multiflowered inflorescence that can be produced both on the apex and the lowermost nodes of the ramicaul. The flowers do not spread widely, are fleshy and hirsute-papillose externally. The four species of this subgenus are only found from Mexico to Panama (Bogarín et al., 2014; Solano-Gómez, 2015).

4. *Acianthera* subgen. *Kraenzlinella* (Kuntze) Karremans, *comb. nov.*

Basionym: *Kraenzlinella* Kuntze, *Lex. Gen. Phan.*: 310. 1903.

Synonyms:

Otopetalum F.Lehm. & Kraenzl., *Bot. Jahrb. Syst.* 26: 457. 1899, *nom. illeg.*

Pleurothallis subgen. *Kraenzlinella* (Kuntze) Luer, *Monogr. Syst. Bot. Missouri Bot. Gard.* 20: 44. 1986.

Acianthera sect. *Kraenzlinella* (Kuntze) A.Douchette, Phytotaxa 275(3): 271. 2016. TYPE: *Acianthera tunguraguae* (F.Lehm. & Kraenzl.) A.Douchette, Phytotaxa 275(3): 272.

Acianthera echinocarpa (C.Schweinf.) A.Douchette, Phytotaxa 275(3): 271. 2016.
Basionym: *Pleurothallis echinocarpa* C.Schweinf., Bot. Mus. Leaflet. 10: 179. 1942.

Acianthera erinacea (Rchb.f.) A.Douchette, Phytotaxa 275(3): 271. 2016.
Basionym: *Pleurothallis erinacea* Rchb.f., Bonplandia (Hannover) 3: 72. 1855.

Acianthera gigantea (Lindl.) A.Douchette, Phytotaxa 275(3): 271. 2016.
Basionym: *Pleurothallis gigantea* Lindl., Fol. Orchid. 9: 28. 1859.

Acianthera hintonii (L.O.Williams) A.Douchette, Phytotaxa 275(3): 271. 2016.
Basionym: *Pleurothallis hintonii* L.O.Williams, Amer. Orchid Soc. Bull. 9: 69. 1940.

Acianthera lappago (Luer) A.Douchette, Phytotaxa 275(3): 272. 2016.
Basionym: *Pleurothallis lappago* Luer, Phytologia 46: 368. 1980.

ADDITIONAL TRANSFERS TO *ACIANTHERA*

Acianthera albiflora (Barb.Rodr.) Karremans, *comb. nov.*
Basionym: *Pleurothallis albiflora* Barb.Rodr., Vellozia, ed. 2, 1: 116. 1891.

Pleurothallis albiflora has traditionally been placed under the synonym of *Acianthera hygrophila* (Barb.Rodr.) Pridgeon & M.W.Chase. From Barbosa Rodrigues' original drawings and descriptions it can be distinguished from the latter by the wider and longer leaves, the much shorter and congested inflorescences, the more compact flowers, the sub-trapezoid petals and the differently shaped lip, with a much larger difference between the width below the middle and below the apex, and a recurved apex. The flowers are said to be fully white, and not dirty-white with carmine markings.

Acianthera barthelemyi (Luer) Karremans, *comb. nov.*
Basionym: *Pleurothallis barthelemyi* Luer, Bull. Mus. Natl. Hist. Nat., B, Adansonia 16: 231. 1994(1995).

Acianthera beyrodtiana (Kraenzl.) Karremans, *comb. nov.*
Basionym: *Pleurothallis beyrodtiana* Kraenzl., Repert. Spec. Nov. Regni Veg. 6: 65. 1908.

The type specimen of this species clearly shows the plant morphology of a species of *Acianthera* as defined here.

Acianthera brunnescens (Schltr.) Karremans, *comb. nov.*
Basionym: *Pleurothallis brunnescens* Schltr., Repert. Spec. Nov. Regni Veg. Beih. 19: 183. 1923.

Acianthera nellyae (P.Ortiz) Karremans, *comb. nov.*
Basionym: *Pleurothallis nellyae* P.Ortiz, Orquideología 20: 325. 1997.

Acianthera phrynoglossa (Luer & Hirtz) A.Douchette, Phytotaxa 275(3): 272. 2016.
Basionym: *Pleurothallis phrynoglossa* Luer & Hirtz, Monogr. Syst. Bot. Missouri Bot. Gard. 65: 116. 1998.

Acianthera sigmoidea (Ames & C.Schweinf.) A.Douchette, Phytotaxa 275(3): 272. 2016.
Basionym: *Pleurothallis sigmoidea* Ames & C.Schweinf., Schedul. Orchid. 10: 36. 1930.

Acianthera tunguraguae (F.Lehm. & Kraenzl.) A.Douchette, Phytotaxa 275(3): 272. 2016.
Basionym: *Otopetalum tunguraguae* F.Lehm. & Kraenzl., Bot. Jahrb. Syst. 26: 457. 1899.

Nine species belong to *Acianthera* subgen. *Kraenzlinella*. They can be recognized by the short, stout ramicaul and a longer, fleshy, sessile leaf, a racemose inflorescence with successive flowers, and the ovaries variously ornamented. The flowers are fleshy and have more or less free, carinate sepals. The petals are more or less auriculate at the base, the unguiculate lip with a biauriculate claw. The column is slender, winged, the clinandrium hooded. They are distributed from Mexico through Central America into Bolivia (Luer, 1994).

Pleurothallis brunnescens originally described from San Ramón, Costa Rica has long been considered a synonym of *Acianthera lojiae* (Schltr.) Luer, based on a type from Loja, Ecuador. The two localities have little flora in common, and even though the floral details might be somewhat similar the two have quite dissimilar plant morphology. As it is hard to believe that they represent the same species, a combination for *P. brunnescens* in *Acianthera* is required.

Acianthera cachensis (Ames) Karremans, *comb. nov.*
Basionym: *Pleurothallis cachensis* Ames, Schedul. Orchid. 4: 17. 1923.

Luer placed this species in genus *Unguella* which is here considered a synonym of *Acianthera*.

Acianthera minuta (Rolfe) Karremans, *comb. nov.*
Basionym: *Cryptophoranthus minutus* Rolfe, Bull. Misc. Inform. Kew 1895: 5. 1985.

This species is most probably closely related to *Acianthera punctatiflora* and *A. minima*, it would have priority over any of the two.

Acianthera paradoxa (Luer & Dalström) Karremans, *comb. nov.*
Basionym: *Pleurothallis paradoxa* Luer & Dalström, Lindleyana 11: 177. 1996.

Luer (2005) placed this species in genus *Didactylus* which is here considered a synonym of *Acianthera*.

Acianthera purpurascens (Luer & Hirtz) Karremans, *comb. nov.*

Basionym: *Pleurothallis purpurascens* Luer & Hirtz, *Lindleyana* 11(3): 181. 1996.

Acianthera scabripes (Lindl.) Karremans, *comb. nov.*

Basionym: *Pleurothallis scabripes* Lindl., *Edwards's Bot. Reg.* 25(Misc.): 94. 1839.

We agree with Luer (1992) that this is not a *Myoxanthus* species on account of the few flowers born from a spathe,

with sepals much longer than petals and lateral sepals fused into a synsepal.

Acianthera thysana (Luer & J.Portilla) Karremans, *comb. nov.*

Basionym: *Pleurothallis thysana* Luer & J.Portilla, *Revista Soc. Boliv. Bot.* 3: 62. 2001.

Luer (2005) placed this species in genus *Didactylus* which is here considered a synonym of *Acianthera*.

ADDITIONAL PROPOSED TRANSFERS

Anathallis anfracta (Luer) Karremans, *comb. nov.*

Basionym: *Pleurothallis anfracta* Luer, *Monogr. Syst. Bot. Missouri Bot. Gard.* 52: 92. 1994.

This unusual species was placed in *Kraenzlinella* by

Luer (1994). The DNA evidence presented here shows that it actually belongs in genus *Anathallis* Barb.Rodr. It is most likely closely related to *Anathallis smaragdina* (Luer) Pridgeon & M.W.Chase.

LITERATURE CITED

- BARBOSA RODRIGUES, J. 1877. *Genera et Species Orchidearum Novarum*, I. Sebastianopolis, Brazil.
- . 1882. *Genera et species orchidearum novarum II*. Sebastianopolis, Brazil.
- BOGARÍN, D., A. P. KARREMANS, AND F. PUPULIN. 2008. New species and records of Orchidaceae from Costa Rica. *Lankesteriana* 8(2): 53–74.
- BOGARÍN, D., D., Z. SERRACÍN, Z. SAMUDIO, R. RINCÓN, AND F. PUPULIN. 2014. An updated checklist of the Orchidaceae of Panama. *Lankesteriana* 14 (1): 135–364.
- BORBA, E. L., G. J. SHEPPERD, C. VAN DEN BERG, AND J. SEMIR. 2002. Floral and Vegetative Morphometrics of Five *Pleurothallis* (Orchidaceae) Species: Correlation with Taxonomy, Phylogeny, Genetic Variability and Pollination Systems. *Annals of Botany* 90: 219–230.
- CHIRON, G. R., AND C. VAN DEN BERG. 2012. Révision taxinomique du genre *Acianthera* (Orchidaceae, Pleurothallidinae). *Richardiana* 12: 59–77.
- CHIRON, G. R., J. GUIARD, AND C. VAN DEN BERG. 2012. Phylogenetic relationships in Brazilian *Pleurothallis* sensu lato (Pleurothallidinae, Orchidaceae): evidence from nuclear ITS rDNA sequences. *Phytotaxa* 46: 34–58.
- DRUMMOND, A. J., M. A. SUCHARD, D. XIE, AND A. RAMBAUT. 2012. Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Mol. Biol. Evol.* 29: 1969–1973.
- HOEHNE, F. C. 1936. *Orchidaceas dos Herbários de Alexandre Curt Brade e do Museu Nacional*. *Boletim do Museu Nacional* 12: 1–37.
- KARREMANS, A. P. 2014. *Lankesteriana*, a new genus in the Pleurothallidinae (Orchidaceae). *Lankesteriana* 13(3): 319–332.
- . 2016. *Genera Pleurothallidarum*: an updated phylogenetic overview of Pleurothallidinae. *Lankesteriana* 16(2): 219–241.
- KARREMANS, A. P., AND M. RINCÓN-GONZÁLEZ. 2015. Nomenclatural notes in the Pleurothallidinae (Orchidaceae): Apodaproprepentia. *Phytotaxa* 238(2): 174–182.
- KARREMANS, A. P., F. J. ALBERTAZZI, F. T. BAKKER, D. BOGARÍN, M. C. M. EURLINGS, A. PRIDGEON, F. PUPULIN, AND B. GRAVENDEEL. 2016. Phylogenetic reassessment of *Specklinia* and its allied genera in the Pleurothallidinae (Orchidaceae). *Phytotaxa* 272(1): 1–36.
- KATO, K., AND D. M. STANDLEY. 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Mol. Biol. Evol.* 30: 772–780. <http://dx.doi.org/10.1093/molbev/mst010>.
- LAHAYE, R., M. VAN DER BANK, D. BOGARÍN, J. WARNER, F. PUPULIN, G. GIGOT, O. MAURIN, S. DUTHOIT, T.G. BARRACLOUGH, AND V. SAVOLAINEN. 2008. DNA barcoding the floras of biodiversity hotspots. *Proc. Natl. Acad. Sci. USA* 105: 2923–2928.
- LINDLEY, J. 1859. *Folia Orchidacea*. Matthews, London.
- LUER, C. A. 1986. Systematics of the genus *Pleurothallis* (Orchidaceae). *Monogr. Syst. Bot. Missouri Bot. Gard.* 20: 1–108.
- . 1992. *Icones Pleurothallidarum IX*. Systematic of *Myoxanthus*. Addenda Addenda to *Platystele*, *Pleurothallis*, subgenus *Scopula* and *Scaphosepalum* (Orchidaceae). *Monogr. Syst. Bot. Missouri Bot. Gard.* 44: 1–128.
- . 1994. *Icones Pleurothallidarum XI* Systematics of *Lepanthes* Subgenus *Brachycladium* and *Pleurothallis* Subgenus *Aenigma*, Subgenus *Elongatia*, Subgenus *Kraenzlinella* (Orchidaceae). *Monogr. Syst. Bot. Missouri Bot. Gard.* 52: 1–137.
- . 2000. *Icones Pleurothallidarum XX*. Systematics of *Jostia*, *Andinia*, *Barbosella*, *Barbrodia*, *Pleurothallis* subgen. *Antilla*, subgen. *Effusia*, subgen. *Restrepioidia*. Addenda to *Lepanthes*, *Masdevallia*, *Platystele*, *Pleurothallis*, *Restrepiopsis*, *Scaphosepalum*, and *Teagueia*. *Monogr. Syst. Bot. Missouri Bot. Gard.* 79: 1–140.
- . 2004. *Icones Pleurothallidarum XXVI*. Systematics of *Pleurothallis* subgenus *Acianthera* (Orchidaceae); A second century of new species of *Stelis*; *Epibator*, *Ophidion*, *Zootrophion*. *Monogr. Syst. Bot. Missouri Bot. Gard.* 95: 1–265.
- . 2005. *Icones Pleurothallidarum XXVII*. *Dryadella* and *Acronia* section *Macrophyllae-Fasciculatae*. *Monogr. Syst. Bot. Missouri Bot. Gard.* 103: 1–310.
- . 2006. *Icones Pleurothallidarum XXVIII*. Reconsideration of *Masdevallia*, and the Systematics of *Specklinia* and vegetatively similar genera (Orchidaceae). *Monogr. Syst. Bot. Missouri Bot. Gard.* 105: 1–274.
- . 2007. *Icones Pleurothallidarum XXIX*. A third century of *Stelis* of Ecuador; Systematics of *Apoda-proprepentia*; Systematics of Miscellaneous small genera; Addenda: new genera, species and combination (Orchidaceae). *Monogr. Syst. Bot. Missouri Bot. Gard.* 112: 1–130.
- . 2014. *Pleurothallis*. Pages 366–429 in J. D. Ackerman, ed., *Orchid Flora of the Greater Antilles*. The New York Botanical Garden Press, New York.
- MADDISON, W. P., AND D. R. MADDISON. 2007. Mesquite: a modular system for evolutionary analysis. *Mesquite v. 2.72*. <http://mesquiteproject.org>

- PRIDGEON, A. M. 2005. *Acianthera*. Pages 328–331 in A. M. PRIDGEON, P. J. CRIBB, M. W. CHASE AND F. N. RASMUSSEN, EDS. *Genera Orchidacearum*, 4. Epidendroideae (Part One). Oxford University Press, Oxford.
- AND M. W. CHASE. 2001. A phylogenetic reclassification of Pleurothallidinae (Orchidaceae). *Lindleyana* 16: 235–271.
- PRIDGEON, A. M., R. SOLANO-GÓMEZ, AND M. W. CHASE. 2001. Phylogenetic relationships in Pleurothallidinae (Orchidaceae): combined evidence from nuclear and plastid dNA sequences. *Am. J. Bot.* 88: 2286–2308. <http://dx.doi.org/10.2307/3558390>
- PUPULIN, F., G. ROJAS, AND J. D. ZÚÑIGA. 2007. Three new species of *Acianthera* (Orchidaceae: Pleurothallidinae) from Costa Rica. *Harv. Pap. Bot.* 12(1): 155–162.
- RAMBAUT, A. 2009. FigTree v1.3.1. <http://tree.bio.ed.ac.uk/software/>
- RODRIGUES, V. T., E. C. SMIDT, AND F. BARROS. 2015. Revisão taxonômica de *Acianthera* sect. *Pleurobotryae* (Orchidaceae, Pleurothallidinae). *Hoehnea* 42(4): 615–627.
- SOLANO-GÓMEZ, R. 2003. *Acianthera unguicallosa* (L.O. Williams) Solano. Plate 512 in E. HÁGSATER AND M. A. SOTO, EDS. *Orchids of Mexico*, parts 2 and 3. *Icones Orchidacearum* 5–6. Instituto Chinoín, A. C., Mexico D. F.
- . 2015. A taxonomic synopsis of the Mexican species of *Acianthera* (Orchidaceae: Pleurothallidinae) including a new species. *Phytotaxa* 218(1): 39–60.
- , G. A. SALAZAR, AND R. JIMÉNEZ. 2011. New combinations in Orchidaceae of Mexico. *Acta Bot. Mex.* 97: 49–56.
- STADEN, R., D. P. JUDGE, AND J. K. BONFIELD. 2003. Analyzing sequences using the Staden Package and EMBOSS. Pages 393–410 in S. A. KRAWETZ AND D. D. WOMBLE, EDS. *Introduction to Bioinformatics. A Theoretical and Practical Approach*. Human Press Inc., New Jersey.
- STENZEL, H. 2004. Systematics and evolution of the genus *Pleurothallis* R. Br. (Orchidaceae) in the Greater Antilles. Dissertation thesis. Mathematisch–Naturwissenschaftlichen Fakultät I der Humboldt–Universität zu Berlin.
- . 2007. Orchidaceae II. Pleurothallidinae 1. Pages 1–152 in W. GREUTER AND R. RANKIN RODRÍGUEZ, EDS. *Flora de la Republica de Cuba*. Fascicle 12(2). Gantner, Liechtenstein.
- SUN, Y., D. Z. SKINNER, G. H. LIANG, AND H. HULBERT. 1994. Phylogenetic analysis of *Sorghum* and related taxa using internal transcribed spacers of nuclear ribosomal DNA. *Theor. Appl. Genet.* 89: 26–32