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AN ELEGY TO *RANGAERIS*, INCLUDING A DESCRIPTION OF TWO NEW GENERA IN THE *CYRTORCHIS–TRIDACTYLE* CLADE (ORCHIDACEAE, ANGRAECINAE)[1]

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ABSTRACT

The phylogenetic position of *Rangaeris* (Schltr.) Summerh. has been one of the most problematic issues of angraecoid orchid taxonomy. A recently published phylogenetic tree with nearly comprehensive taxon sampling of African angraecoid orchids suggested that this genus was polyphyletic, as its species appear nested within different subclades of the *Cyrtorchis–Tridactyle* clade. However, the lack of DNA data for the generic type, *R. muscicola* (Rchb. f.) Summerh., and for the little-known species *R. longicaudata* (Rolfe) Summerh. and *R. trilobata* Summerh., has precluded an integrative reappraisal of the delimitation of this genus. Here we present the results of a new phylogenetic analysis of one nuclear (ITS) and five plastid markers (*matK*, *rps16*, *trnC-petN* intergenic spacer, *trnL-trnF* intergenic spacer, *ycf1*) for all six species of *Rangaeris*, including those recently transferred to *Podangis* Schltr. and *Ypsilopus* Summerh., together with a representative sampling of 14 other species of the genera *Cyrtorchis* Schltr., *Listrostachys* Rchb. f., *Plectrelminthus* Raf., *Summerhayesia* P. J. Cribb, *Tridactyle* Schltr., and *Ypsilopus*. Based on molecular and morphological evidence, *R. muscicola* is transferred to *Podangis*, where *Rangaeris* is reduced to the rank of section. In addition, *R. longicaudata* and *R. trilobata* are each moved to new monotypic genera, *Planetangis* Stévart & Farminhão and *Aziza* Farminhão & D'haijère, respectively. An identification key for all genera of the *Cyrtorchis–Tridactyle* clade is presented, together with one for the three species of recircumscribed *Podangis*. Finally, taxonomic accounts of the new genera are presented, including amended descriptions, illustrations, distribution maps, and preliminary conservation status assessments of their species.

Key words: Africa, Angola, *Aziza*, Democratic Republic of the Congo, Epidendroideae, IUCN Red List, lectotypification, new combinations, *Planetangis*, *Podangis*, Vandeae, Welwitsch.

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(Footnotes continue on next page.)

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Over the past two decades, a significant effort has been made to clarify relationships in the large Orchidaceae, including phylogenetic studies based on molecular data (Chase et al., 2015; Freudenstein & Chase, 2015). Within the largest subfamily, Epidendroideae, and more specifically within the tribe Vandeae, several recent studies have focused on the systematics of subtribe Angraecinae in Madagascar and the Mascarene Islands (see Carlsward et al., 2006; Micheneau et al., 2008; Andriananjamanantsoa et al., 2016), in the Neotropics (Carlsward et al., 2003; Pessoa et al., 2018), and in tropical Africa (Simo-Droissart et al., 2018a). Based on the results of Simo-Droissart et al. (2018a), five papers were recently published that together have reassessed the taxonomy of most African angraecoid genera (Descourvières et al., 2018; Farminhão et al., 2018; Simo-Droissart et al., 2018b, 2018c; D'haijère et al., 2019), although some groups remain to be treated. Among these, the genus *Rangaeris* (Schltr.) Summerh. continues to be one of the key unresolved issues in this large angraecoid radiation (Carlsward, 2014; Cribb, 2014a; Simo-Droissart et al., 2018a). *Rangaeris* was first coined by Schlechter (1918: 121) for a section of *Aerangis* Rchb. f. (of which it is an anagram) to accommodate nine "species" characterized by two separate stipes and one or two viscidia. Summerhayes (1936a, 1936b), adhering to Schlechter's (1918) morphological definition, raised *Rangaeris* to the rank of genus and recognized seven species, including *R. trilobata* Summerh as a novelty. However, Summerhayes clearly had doubts about its delimitation, stating: "*Rangaeris* is a rather heterogeneous assemblage composed of several groups of closely allied species. Whether it will be possible to maintain it when further discoveries, which are inevitable, are made and further investigations have been carried out, is open to question" (Summerhayes, 1936b: 227–228).

Indeed, several recent molecular studies have now shown that *Rangaeris* is polyphyletic and that species historically assigned to the genus are nested in *Angraecum* Bory, *Diaphananthe* Schltr., *Rhipidoglossum* Schltr., and mostly in a clade including *Cyrtorchis* Schltr., *Listrostachys* Rchb. f., *Podangis* Schltr., *Plectrelminthus* Raf., *Tridactyle* Schltr., and *Ypsilopus* Summerh. (Carlsward et al., 2006; Simo-Droissart et al., 2018a; D'haijère et al., 2019). Based on both molecular and morphological evidence, the process of dismantling *Rangaeris* has recently started, with one species being moved to *Podangis* (Cribb & Carlsward, 2012) and two species to *Ypsilopus* (D'haijère et al., 2019). This taxonomic exodus from *Rangaeris* to closely allied genera highlights the need for an exhaustive reassessment of the phylogenetic position of *R. muscicola*, the generic type, and the two other currently recognized species that remain in the genus (i.e., *R. longicaudata* (Rolfe) Summerh. and *R. trilobata* Summerh.) in the broader context of a reappraisal of generic delimitations in the *Cyrtorchis–Tridactyle* clade. *Rangaeris longicaudata* is a little-known species from tropical West and Central Africa whose morphology and ecology were first described in some detail by Pérez-Vera (2003). *Rangaeris trilobata*, another poorly known species confined to Central Africa (Droissart et al., 2009), exhibits a distinctive scandent habit, which led Rice (2006) to transfer it to *Solenangis* Schltr., together with *Dinklageella* Mansf. (see Rice, 2006), a taxonomic decision that was, however, not accepted by Cribb (2014a) based on several morphological traits. Thus, the positions of *R. longicaudata* and *R. trilobata* remained unclear, mainly because of a lack of adequate material for molecular phylogenetic analysis. Indeed, of all former members of *Rangaeris*, only *R. longicaudata* and *R. trilobata* had never been included or discussed in any phylogenetic analysis, which precluded understanding the position of *Rangaeris* within angraecoids, and in turn made it impossible to adequately recircumscribe the genus. However, recent fieldwork in Gabon and São Tomé and Príncipe, as well as sampling of the orchid collection from Jardi-Gab in Libreville, Gabon, has provided the opportunity to obtain DNA sequence data for these two taxonomically puzzling species.

Here we have produced new sequences from six markers (ITS, *matK*, *rps16*, *trnC-petN* intergenic spacer, *trnL-trnF*

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intergenic spacer, *ycf1*), expanding the dataset of Simo-Droissart et al. (2018a), who used three markers to examine phylogenetic relationships across all major lineages of African angraecoids, with the notable exception of two key *Rangaeris* species (viz. *R. muscicola* and *R. trilobata*). Given the new availability of samples from these species, we have investigated the phylogenetic relationships within *Rangaeris*, which could not be unraveled by Simo-Droissart (2018a). We have followed an approach combining maximum likelihood and Bayesian analyses that has proved useful for exploring relationships among angraecoids in other recent studies (Martos et al., 2017; D'haijère et al., 2019). The goal of this study is to assess the monophyly of *Rangaeris* by clarifying the phylogenetic position of *R. longicaudata* and *R. trilobata* relative to the generic type, *R. muscicola*, and of the genus relative to the other genera in the larger clade that includes *Cyrtorchis* and *Tridactyle*, using both molecular phylogenetic analyses and complementary morphological observations. We also provide an identification key to the genera included in the *Cyrtorchis–Tridactyle* clade, along with a key to species belonging to a redefined genus *Podangis* and amended detailed descriptions, distribution maps, and conservation status of *R. longicaudata* and *R. trilobata*.

Materials and Methods

Taxon sampling for molecular analyses

Thirty-nine samples representing 25 species in the following 12 genera were sampled: *Aerangis*, *Cyrtorchis*, *Listrostachys*, *Mystacidium* Lindl., *Nephrangis* (Schltr.) Summerh., *Podangis*, *Plectrelminthus*, *Rangaeris*, *Solenangis*, *Summerhayesia* P. J. Cribb, *Tridactyle*, and *Ypsilopus* (Appendix 1). Specimens of *Eggelingia* Summerh., currently regarded as synonymous with *Tridactyle* (see Rice, 2005; Simo-Droissart et al., 2018a), were also included. All currently recognized species of *Rangaeris* were sampled. To explore the position of *Rangaeris* in the clade containing *Cyrtorchis* and *Tridactyle*, we also included representatives from all the genera of this clade. The outgroup comprised four accessions from *Aerangis*, *Mystacidium*, *Nephrangis*, and *Solenangis*, which were selected based on the topologies obtained by Carlsward et al. (2006) and Simo-Droissart et al. (2018a). Leaf tissue samples were obtained from São Tomé and Príncipe, Cameroon, and Gabon. Plants from Cameroon and Gabon were grown in shade houses monitored by our teams in Yaoundé (for those collected in Cameroon), Libreville (Sibang and Jardi-Gab collection), and Tchimbélé (see Stévart et al., 2020). Plants cultivated in the shade houses yielded high-quality flowering specimens that ensure accuracy in species identification of the leaf material used for DNA extraction.

The 63 newly obtained sequences were combined with 71 previously published sequences (Carlsward et al., 2006; Simo-Droissart et al., 2018a; D'haijère et al., 2019) retrieved from GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>). Voucher specimens and respective metadata are provided in Appendix 1.

DNA extraction, amplification, and sequencing

Genomic DNA was extracted from silica gel–dried leaf material and herbarium specimens using a modified version of the Doyle and Doyle (1987) protocol (using 1 g of fresh leaf tissue or 0.2–0.3 g of dried material) or the NucleoSpin plant kit protocol from Macherey-Nagel (Düren, Germany), according to the manufacturer's instructions. The following primers were used for PCR amplification and sequencing of the six DNA regions: (1) primers ITS-A and ITS-C for ITS (Blattner, 1999); (2) primers trnL (UAA) 3′ exon and trnF (GAA) gene for the *trnL–F* intergenic spacer (Taberlet et al., 1991); (3) primers 19F (Molvray et al., 2000), 1326R (Cuénoud et al., 2002), 390F (Cuénoud et al., 2002), and trnK-2R (Johnson & Soltis, 1994) for *matK*; (4) primers rps16-1F and rps16-2R for the *rps16* intron (Oxelman et al., 1997); (5) primers trnC and petN-1R for the *trnC-petN* intergenic spacer (Lee & Wen, 2004); and (6) primers 3720F, IntR, IntF, and 5500R (Neubig et al., 2009) for *ycf1*. One of three thermocyclers (Biometra TProfessional thermocycler, PTC-100 or PTC-200, Bio-Rad Laboratories, Inc., Hercules, California, U.S.A.) was used for PCR amplification. The reaction mixtures for all markers included 0.125 μL (5 U/μL) of Taq polymerase (Qiagen, Valencia, California, U.S.A.), 0.25 μL of each primer (10 μM), 1–2 μL of template genomic DNA extract (of unquantified concentration), 2.5 μL PCR buffer, 1 μL $MgCl_2$ (25 mM), 0.5 μL dNTPs (10 μM), and ultrapure H_2O to a final volume to 25 μL. The amplification program included an initial denaturation at 94°C (3 min.), 30 cycles of denaturation at 94°C (30 sec.), annealing at 50°C (*ycf1*) or 52°C (all others) (30 sec.), elongation at 72°C (1 min. 30 sec. for *matK* and *ycf1*, 1 min. for all others), and a final elongation step at 72°C for 10 min.

The ExoSAP (Qiagen) enzyme mixture was used to purify the amplified products, and the BigDye Terminator v. 3.1 Cycle Sequencing Kit (Applied Biosystems, Inc., ABI, Lennik, the Netherlands) was used in cycle-sequencing reactions of both complementary strands, using one of two primers used in PCR amplifications. The reaction mixture contained 1.5 μL of sequencing buffer, 1 μL of BigDye terminator, 0.2 μL of 10 μM primer, 1–3 μL of unquantified amplified product, and 4.3–6.3 μL of H_2O, for a total reaction volume of 10 μL. More detailed information on cycle sequencing conditions is provided in Simo-Droissart et al. (2018a).

Phylogenetic analyses

Automatic base calling was inspected manually by examining electropherograms in Geneious version 9.0.5

(Drummond et al., 2012). Sequences were aligned in MUSCLE (Edgar, 2004) as implemented in Geneious, and then manually adjusted using the same software. Phylogenetic analyses were conducted on three datasets: ITS alone, the concatenated plastid loci of the five plastid markers (*matK*, *rps16*, *trnC-petN* intergenic spacer, *trnL-trnF* intergenic spacer, *ycf1*), and a combined dataset of all nuclear and plastid sequences. We analyzed the data using two approaches, maximum likelihood (ML) and Bayesian inference (BI), to estimate phylogenetic relationships among the different genera. To select the best evolutionary model for each marker, we used PartitionFinder (2.1.1) (Lanfear et al., 2016), and a gamma distribution was used to model site heterogeneity. The ML analyses were run with RAxML-HPC2 on XSEDE (8.2.12) (Stamatakis, 2014) through the CIPRES Science Gateway (Miller et al., 2010). The support was analyzed using a bootstrap procedure that allowed RAxML to halt the bootstrapping automatically when the required criteria are met, instead of specifying the number of bootstraps for the analysis. Bootstrap support (BS) values that we considered were poor ($<$ 50%), weak (50%–70%), moderate ($>$ 70%–85%), or strong ($>$ 85%), following Kress et al. (2002). The model available in CIPRES that was closest to those recommended by PartitionFinder was GTR + Γ for all markers in the three matrices. The specific criteria are configured using subsequent entry fields. BI analyses were run using MrBayes (3.2.6 x86) (Huelsenbeck & Ronquist, 2001; Ronquist et al., 2012) via the CIPRES Science Gateway. Posterior probabilities (PP) were considered poor ($<$ 0.90), weak (0.90 to $<$ 0.95), moderate (0.95 to $<$ 0.98), and strong ($\geq$ 0.98), following Erixon et al. (2003). The models available in MrBayes that were closest to those suggested by PartitionFinder were GTR + Γ for all markers in all matrices. Two separate Markov chain Monte Carlo (MCMC) runs were set up with a random tree and eight chains in parallel (Huelsenbeck & Ronquist, 2001). We performed two runs in parallel of four MCMC for 20×10^6 (30×10^6 for the combined matrix) generations, with trees sampled every 1000 generations (Huelsenbeck & Ronquist, 2001). Convergence between both runs was checked against the stationary distribution by examining whether the potential scale-reduction factors were close to 1 in the pstat file, the standard deviation of split frequencies fell below 0.01 in the log file, and assessing the p file using the program Tracer 1.7.1 (Rambaut et al., 2018). A burn-in of 25% of the sampled trees was applied to obtain the 50% majority-rule consensus trees and the clade posterior probabilities.

MORPHOLOGICAL STUDY

Morphological data were obtained through detailed examination of ca. 800 dried and alcohol-preserved specimens deposited in BM, BR, BRLU, COI, K, LBV, LISC, LISU, MO, P, W, WAG, and YA (herbarium acronyms follow Thiers, continuously updated) of (1) the genera of the *Cyrtorchis–Tridactyle* clade (i.e., *Cyrtorchis*, *Listrostachys*, *Plectrelminthus*, *Podangis*, *Rangaeris*, *Summerhayesia*, *Tridactyle*, and *Ypsilopus*); (2) *Nephrangis* (sister to *Cyrtorchis–Tridactyle* in the trees of Simo-Droissart et al., 2018a); (3) *Solenangis* and *Dinklageella* (which vegetatively bear a great resemblance to *R. trilobata*); and (4) *Aerangis* and *Mystacidium* (both included in the outgroup in the molecular phylogenetic analyses). Additional scans of specimens housed in FHI and LD were consulted through the Global Plants database (JSTOR, 2000–2018). All type specimens of *Rangaeris* and *Podangis* were seen, as were all collections of *R. longicaudata* and *R. trilobata* housed in European herbaria. Details of color, phenology, habit, and habitat were derived from photographs, field notes, observations of living material, and herbarium labels. Some photos of *P. dactyloceras* Schltr. and *R. muscicola* from Cameroon, the Democratic Republic of the Congo, and Tanzania were retrieved from the World Orchid Iconography (2015–2018) of the Swiss Orchid Foundation at the Herbarium Jany Renz and the Botanical Institute of the University of Basel; from Senckenberg's *West African Plants* (Brunken et al., 2008); and from *Orchidaceae of Central Africa* (Droissart et al., 2018). Flowers of spirit specimens, and of dried specimens after being boiled in water and rehydrated in Copenhagen mix, were observed using a Stemi SV11 stereo microscope (Carl Zeiss AG, Oberkochen, Germany). Measurements of plants were made with an uncertainty of 0.5 mm using a scale ruler or graph paper. Plant descriptions were prepared following the terminology of the Systematics Association Committee for Descriptive Biological Terminology (1962a, 1962b) and Beentje (2016). Distributions for each species were derived from the material examined and compared with chorological data available from the World Checklist of Selected Plant Families (Govaerts et al., 2019). Preliminary assessments of risk of extinction were made using the IUCN Red List categories and criteria (IUCN, 2012, 2019). We imported the georeferenced specimen data into R software (R Core Team, 2019) and used the ConR package (Dauby et al., 2017; <https://CRAN.R-project.org/package=ConR>) to calculate area of occupancy (AOO) and extent of occurrence (EOO). The cell size for AOO was set at 2×2 km as recommended by IUCN (2019). The number of "locations," as defined by IUCN (2019), was calculated considering the type of threats, such that a single "location" may encompass more than one adjacent subpopulation.

RESULTS

MOLECULAR PHYLOGENETICS

We generated a total of 63 new sequences: 13 for ITS, five for *matK*, four for *trnL-trnF* intergenic spacer, 12 for

trnC-petN intergenic spacer, 14 for *rps16*, and 15 for *ycf1*. All sequences were deposited in GenBank (Appendix 1). We combined them with 71 additional sequences available from GenBank (mostly produced by our team for previous studies), and from these we generated three datasets: a nuclear dataset based on ITS, a plastid dataset based on the combination of the five plastid markers (*matK*, *rps16*, *trnC-petN* intergenic spacer, *trnL-trnF* intergenic spacer, *ycf1*), and a combined nuclear and plastid dataset. The ITS dataset comprises 36 sequences (representing 24 taxa) with an aligned length of 385 characters; the plastid dataset includes 36 sequences (26 taxa) with 6174 characters (*matK*: 1860, *rps16*: 1010, *trnC-petN* intergenic spacer: 938, *trnL-F* intergenic spacer: 557, and *ycf1*: 1809 characters), and the combined dataset contains 39 sequences (26 taxa) of 6559 characters. Trees inferred from the plastid and combined datasets were better resolved than the tree inferred from the ITS dataset alone.

Phylogenetic reconstructions produced with ML and BI methods resulted in congruent topologies and differed only in poorly supported nodes. Besides the four outgroups (*Aerangis*, *Mystacidium*, *Nephrangis*, and *Solenangis*), all trees resulting from both approaches resulted in the same three clades (Figs. 1–3): clade A, containing *Cyrtorchis*, *Podangis*, *Rangaeris longicaudata*, and *R. muscicola*, with a support value of 83% (BS) and 0.98 (PP) in the combined analyses (Fig. 1), 62% (BS) and 0.5 (PP) in the ITS analyses (Fig. 2), and 57% (BS) and 0.74 (PP) in the plastid analyses (Fig. 3); clade B, containing *R. trilobata* with a support value of 100% (BS) and 1.0 (PP) in all analyses; and clade C, containing *Tridactyle* with a support value of 100% (BS) and 1.0 (PP) in the combined analyses (Fig. 1), 38% (BS) and 0.5 (PP) in the ITS analyses (Fig. 2), and 97% (BS) and 1.0 (PP) in the plastid analyses (Fig. 3).

Three other clades were retrieved from the plastid and combined analyses, but not from the ITS analyses: clade D, containing *Summerhayesia* with a support value of 100% (BS) and 1 (PP) in both combined and plastid analyses (Figs. 1, 3); clade E, containing *Ypsilopus* with a support value of 69% (BS) and 0.99 (PP) in the combined analysis (Fig. 1) and of 74% (BS) and 0.99 (PP) in the plastid analyses (Fig. 3); and clade F, containing *Plectrelminthus* and *Listrostachys* with a support value of 79% (BS) and 0.89 (PP) in the combined analyses (Fig. 1) and of 81% (BS) and 0.94 (PP) in the plastid analyses (Fig. 3).

Within clade A, two groups are strongly supported in all analyses: subclade a1 containing *Podangis*, with a support value of 100% (BS) and 1.0 (PP) in both combined and plastid analyses (Figs. 1, 3) and of 90% (BS) and 1.0 (PP) in the ITS analyses (Fig. 2); and subclade a3 containing *Cyrtorchis*, with a support value of 100% (BS) and 1.0 (PP) in both combined and ITS analyses (Figs. 1, 2) and 85% (BS) and 0.90 (PP) in the plastid analyses (Fig. 3). A third subclade, a2, containing *Rangaeris longicaudata*, is strongly supported with a value of 100% (BS) and 1.0 (PP) in both the combined and the ITS analyses (Figs. 1, 2), but poorly supported with a value of 79% (BS) and 0.65 (PP) in the plastid analyses. Finally, subclade a2 is sister to subclade a3 (*Cyrtorchis*) in both the combined and plastid analyses (Figs. 1, 3), well supported with a value of 0.99 (PP) in the BI tree based on the combined data (Fig. 1) but poorly supported with a value of 0.84 (PP) in the BI trees based on plastid data (Fig. 3). For the maximum likelihood analyses, clade a2 is poorly supported with a value of 59% (BS) in the ML trees based on plastid data (Fig. 3) and moderately supported with a value of 80% (BS) in the ML analysis of the combined dataset (Fig. 1).

The position of *Rangaeris muscicola* within clade A is left unresolved in the trees resulting from the analyses of all three datasets and both methods.

MORPHOLOGICAL SURVEY

Of all genera in the outgroup (viz., *Aerangis*, *Nephrangis*, *Solenangis*, and *Mystacidium*), *Mystacidium* presents the most divergent structure of the column, characterized by the well-developed rostellar midlobe and two separate stipes and viscidia. *Aerangis* is notably recognizable by the deeply concave stigmatic cavity with winged margins and a pollinarium with a single stipe and a thick viscidium. *Nephrangis* is unique in the arrangement of the perianth, with the lateral sepals adnate to the lip. *Solenangis* is distinctive because of its scandent habit and the inflorescences perpendicular to the stem.

No diagnostic synapomorphies were identified for the *Cyrtorchis–Tridactyle* clade (Fig. 1, clades A–F) when compared with genera in the outgroup.

Species in clade A (Fig. 1), namely *Rangaeris muscicola*, *R. longicaudata*, *Podangis*, and *Cyrtorchis*, share an undivided epichile and a suite of character states that could be inferred as ancestral in the *Cyrtorchis–Tridactyle* clade (viz., pollinaria with two free stipes connected to a single saddle-shaped viscidium, lateral rostellar lobes longer than the midlobe and not adnate to it).

Despite the fact that *Rangaeris muscicola* and the two species of *Podangis* form part of a polytomy rather than a clade in the trees resulting from our phylogenetic analyses (Fig. 1, clade A), these three species share an identical gynostemium morphology (e.g., a saddle-shaped viscidium and two slender stipes) and growth habit. *Rangaeris muscicola*, as well as *P. dactyloceras* and *P. rhipsalisocia* (Rchb. f.) P. J. Cribb & Carlsward, can be distinguished from closely related taxa in clade A (viz., *R. longicaudata* and *Cyrtorchis*) based on the

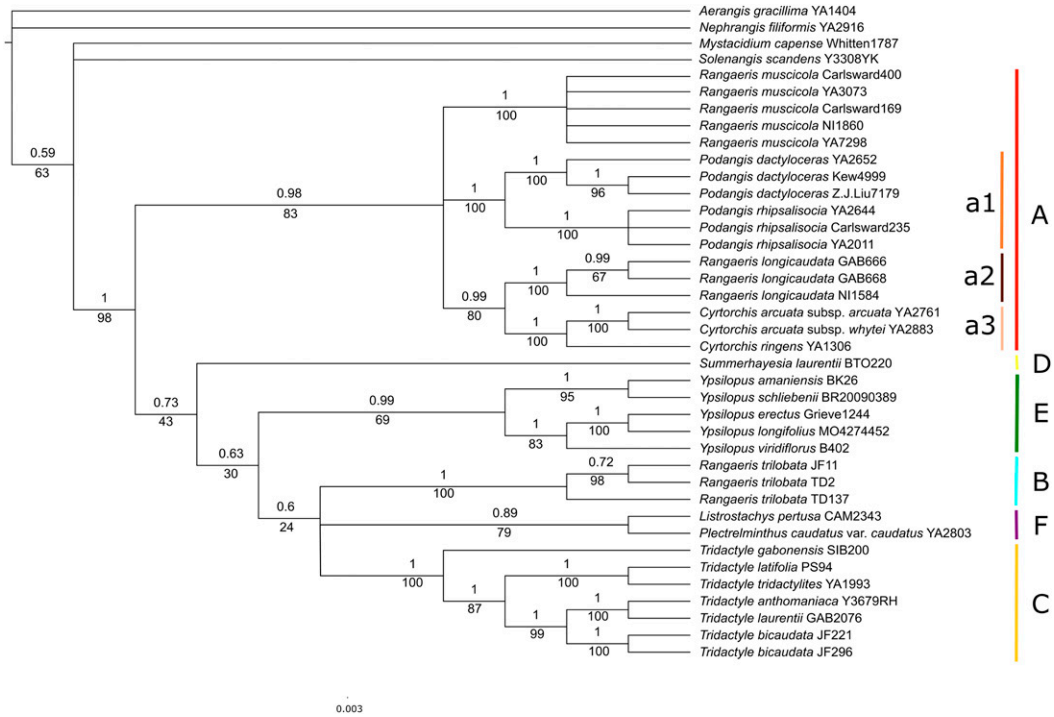

Figure 1. Phylogenetic tree of *Rangaeris* (Schtr.) Summerh. and allied genera, resulting from Bayesian and maximum likelihood analyses of the combined dataset, based on the combination of six markers (ITS, *matK*, *rps16*, *trnC-petN* intergenic spacer, *trnL-F* intergenic spacer, *ycf1*) from 39 specimens representing 26 taxa using MrBayes (under the GTR + Γ substitution model, with posterior probabilities shown above branches), and using RAxML (with the GTR + Γ substitution model, with bootstrap percentages shown below the branches). Clade labels refer to clades discussed in the text.

presence of a lip that is dissimilar in shape to the other tepals, stipes that do not broaden markedly toward the apex, and parallel lateral rostellar lobes. All these morphological observations separate *Podangis* and *R. muscicola* from the remaining taxa in clade A and suggest that *R. muscicola*, and therefore the genus *Rangaeris*, may better be included in *Podangis*.

The single species in clade a2 (*Rangaeris longicaudata*) is sister to clade a3 (*Cyrtorchis*), which is corroborated by the shared presence of an "isotepaloid" perianth (i.e., the lip is identical in shape to the remaining tepals), stipes markedly broadened toward the apex, and connivent lateral rostellar lobes. However, *R. longicaudata* differs in several floral traits from species in clade a3 (*Cyrtorchis*), notably in its rounded ovary and the saddle-shaped viscidium that is about twice as long as wide. Other distinctive characters of *R. longicaudata* include the broad, beveled apex of the lateral rostellar lobes and the bilobed callus present on the lower rim of the stigma.

Species in clade a3 (*Cyrtorchis*) are particularly homogeneous morphologically and share distinctive floral characteristics such as the ribbed triquetrous ovary together with the forward-pointing base of the petals and sepals, the anterior expansion of the viscidium, and the very short column that touches the lip spur mouth along its lower margin.

Within clade A, the gain in grouping information associated with the inclusion of *Rangaeris longicaudata* in *Cyrtorchis* appears to be outweighed by the loss of morphological diagnosability of both taxa that would result from lumping these genera. Therefore, we argue that the recognition of *R. longicaudata* as a new monospecific genus, distinct from *Cyrtorchis*, best reflects the evolutionary distinctiveness of these two "isotepaloid" lineages.

Clade B contains only *Rangaeris trilobata*, which is both morphologically and ecologically distinctive, presenting grasping crozier-shaped root apices convergent to those of the unrelated *Solenangis* and *Dinklageella*, thus being the only scandent (i.e., climbing) species in the *Cyrtorchis–Tridactyle* alliance (Fig. 1, clades A–F). The truncate anterior margin of the viscidium and its deeply trilobed lip are reminiscent of genera such as *Plectrelminthus* and *Tridactyle*, setting *R. trilobata* apart from any other species formerly placed in *Rangaeris*. However, it differs from these two genera and from *Listrostachys* by the absence of auricles at the lip base; and from *Tridactyle*, *Plectrelminthus*, *Listrostachys*, and *Summerhayesia* in its

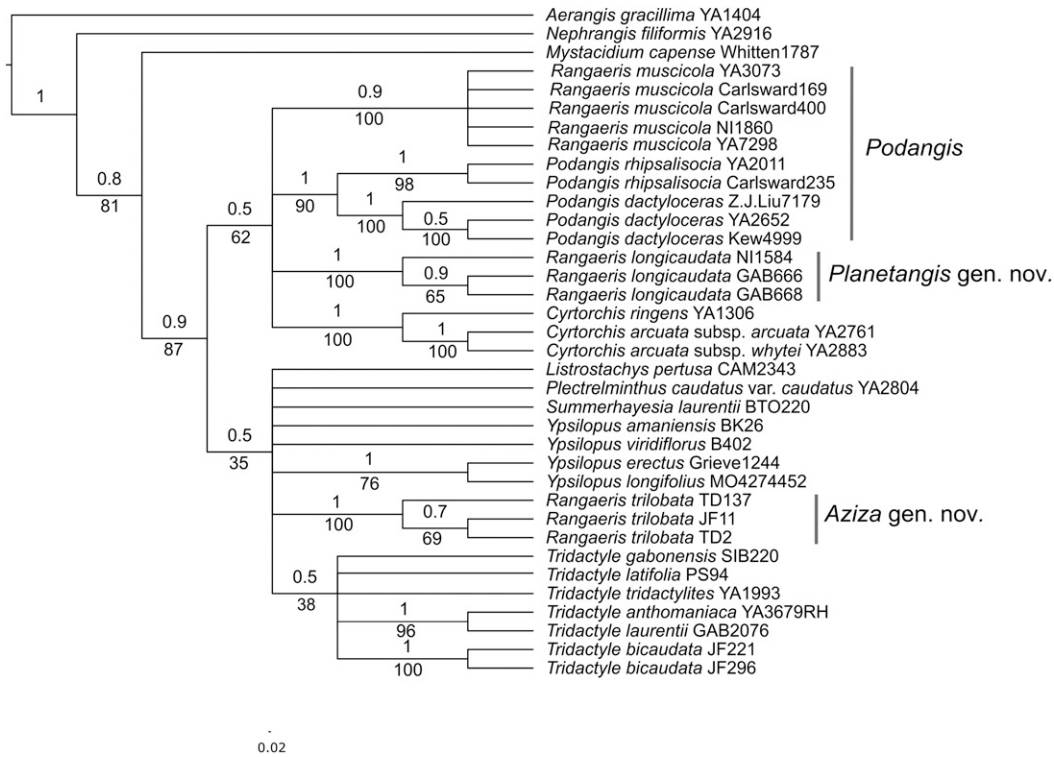

Figure 2. Phylogenetic tree of *Rangaeris* (Schtr.) Summerh. and allied genera, resulting from Bayesian and maximum likelihood analyses of the nuclear dataset ITS from 36 specimens representing 24 taxa using MrBayes (under the GTR + Γ substitution model, with posterior probabilities shown above branches), and using RAxML (under the GTR + Γ substitution model, with bootstrap percentages shown below the branches).

rostellar lobes, which are free, not fused to the midlobe along their inner margins. *Rangaeris trilobata* is morphologically similar to *Ypsilopus* in having concave stigmata with spreading margins but differs from this genus in having two separate stipes. Hence, based on the great morphological distinctiveness of *R. trilobata*, we suggest that it is better treated as a new monotypic genus.

Species in clade D (*Summerhayesia*) are characterized by their non-resupinate flowers and geniculate rostellum.

Our findings related to the diagnostic morphological characters of clade C (*Tridactyle*), clade E (*Ypsilopus*, including *Y. amaniensis* (Kraenzl.) D'haijère & Stévart and *Y. schliebenii* (Mansf.) D'haijère & Stévart, both formerly placed in *Rangaeris*) and clade F (*Plectrelminthus* and *Listrostachys*) are identical to those from D'haijère et al. (2019), who extensively analyzed and discussed the systematics of these genera.

Taxonomic Treatment

Key to Genera in *Cyrtorchis–Tridactyle* Alliance, *Nephrangis*, and *Solenangis*

1a. Scandent plants; roots developing clasping crozier-shaped apices.
  2a. Leaves coriaceous or thin-textured, apex obtuse, subequally bilobed; inflorescences suberect, perpendicular to the stem, with peduncle shorter than rachis; column shorter than sepals and petals; anther cap apex acute; pollinaria with a single stipe; fruits ellipsoid, ca. 3× as long as wide . . . . . *Solenangis* Schltr.
  2b. Leaves thin-textured, apex acute, unequally bifid; inflorescences pendent with peduncle as long as or longer than rachis; column prominent, projecting well above sepals and petals; anther cap apex truncate; pollinaria with two separate stipes; fruits narrowly ellipsoid, ca. 6× as long as wide . . . . . *Aziza* Farminhão & D'haijère
1b. Erect, suberect or pendent plants; root apices not clasping.
  3a. Stigma with concave margins; rostellar lobes free, not fused along their length.
    4a. Leaves acicular; inflorescences subsessile . . . . . *Nephrangis* (Schltr.) Summerh.
    4b. Leaves not acicular; inflorescences markedly pedunculate.

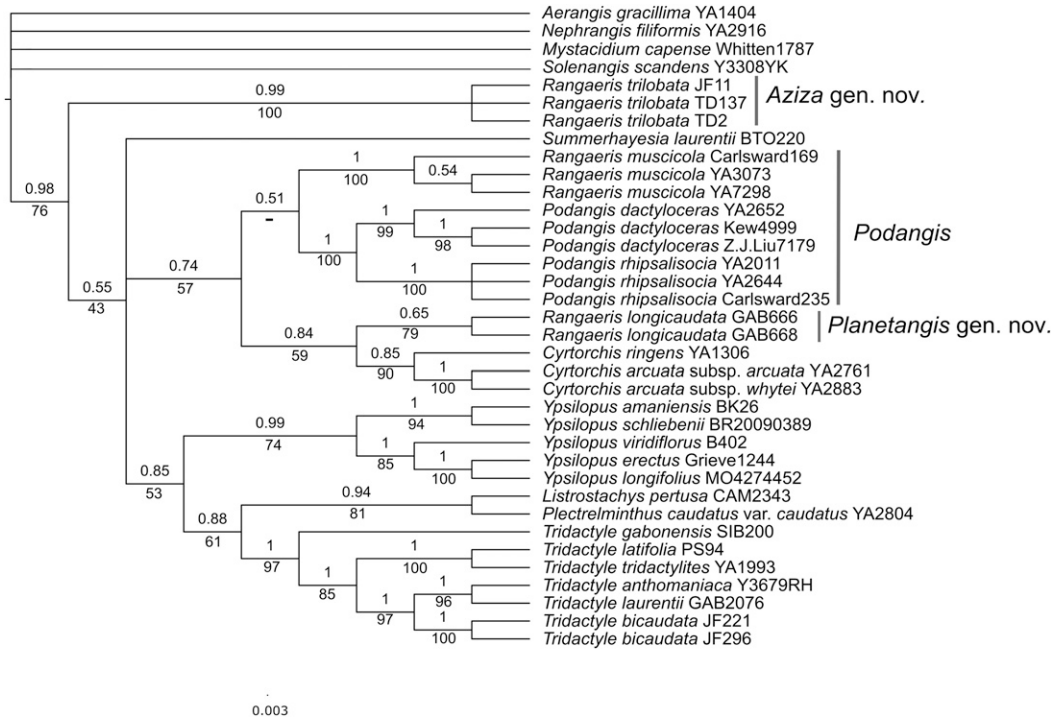

Figure 3. Phylogenetic tree of *Rangaeris* (Schtr.) Summerh. and allied genera, resulting from Bayesian and maximum likelihood analyses of the plastid dataset, based on the concatenation of five markers (*matK*, *rps16*, *trnC-petN* intergenic spacer, *trnL-F* intergenic spacer, *ycf1*) from 36 specimens representing 26 taxa using MrBayes (under the GTR + Γ substitution model, with posterior probabilities shown above branches), and using RAxML (under the GTR + Γ substitution model, with bootstrap percentages shown below branches).

5a. Pollinaria with a single Y-shaped stipe . . . . . *Ypsilopus* Summerh.
5b. Pollinaria with two stipes, separate along their full length.
6a. Lip dissimilar to remaining tepals; stipes linear to clavate, slightly broadening toward the apex; rostellar lateral lobes parallel to each other . . . . . *Podangis* Schltr.
6b. Lip similar to remaining tepals; stipes obtriangular to obtrullate, markedly broadening toward the apex; rostellar lateral lobes connivent.
7a. Petals reflexed; column elongate, ca. 2× as long as wide, exposed; insertion point of the stipes halfway along the length of the viscidium; anterior margin of the viscidium deeply bilobed; ovary and fruits with rounded cross section . . . . . *Planetangis* Stévart & Farminhão
7b. Petals bent forward; column very short, ca. as long as wide, concealed by the petals; insertion point of the stipes at the rear third of the length of the viscidium; anterior margin of the viscidium bifid; ovary and often the fruits triquetrous . . . . . *Cyrtorchis* Schltr.
3b. Stigma relatively flat with laterally spreading to reflexed rounded wings; rostellar lobes fused along inner margins.
8a. Flowers hyper-resupinate; lip entire, concave, with no auricles at base; a single stipe; rostellum geniculate . . . . . *Summerhayesia* P. J. Cribb
8b. Flowers resupinate to hyper-resupinate; lip obscurely to markedly tridentate, with auricles at base; 1 or 2 stipes; rostellum not geniculate.
9a. Column foot prominent; pollinaria with 2 stipes broadening toward the apex and a horseshoe-shaped viscidium . . . . . *Listrostachys* Rchb. f.
9b. Column foot absent or obscure; pollinaria with a single stipe and a viscidium circular to elliptic, rarely horseshoe-shaped.
10a. Leaves imbricate, without ligules; flowers hyper-resupinate; lip with prominent acute auricles at base, spur helically twisted, 15–25 cm long, with a raised acute tooth in mouth . . . *Plectrelminthus* Raf.
10b. Leaves imbricate to well spaced, with or without ligules; flowers resupinate to hyper-resupinate; lip with acute to rounded auricles at base, spur not helically twisted, shorter than 15 cm, without a raised tooth in mouth . . . . . *Tridactyle* Schltr.

PODANGIS REDEFINED

Podangis Schltr., Beih. Bot. Centralbl. 36(2): 82. 1918. TYPE: *Podangis dactyloceras* (Rchb. f.) Schltr., Beih. Bot. Centralbl. 36(2): 82. 1918.

Neowolffia O. Gruss, Orchid. Atlas: 239. 2007. TYPE: *Neowolffia rhipsalisocia* (Rchb. f.) O. Gruss, Orchid. Atlas: 239. 2007. Basionym: *Angraecum rhipsalisocium* Rchb. f., Flora 48: 189. 1865.

Rangaeris (Schltr.) Summerh., Bull. Misc. Inform. Kew 1936: 227. 1936. TYPE: *Rangaeris muscicola* (Rchb. f.) Summerh. in J. Hutchinson & J. M. Dalziel, Fl. W. Trop. Afr. 2: 450. 1936. Basionym: *Aeranthes muscicola* Rchb. f., Flora 48: 190. 1865.

Notes. The genus *Rangaeris* (with its type, *R. muscicola*) is here subsumed under *Podangis* based on morphological evidence, but *R. longicaudata* and *R. trilobata* are each moved to newly described monotypic genera (see below).

Podangis was monotypic for the greater part of its taxonomic history, until the recent transfer of *P. rhipsalisocia* from *Rangaeris*. The two species formed a strongly supported clade and also shared the same psygmoid habit and an identical column morphology (Cribb & Carlsward, 2012; Cribb, 2014b). Both species also have iridiform leaves, campanulate (i.e., not fully open) flowers, obovoid pollinia, proportionally broad lateral rostellar arms, and a chromosome count of $2n = 46$ (Arends & van der Laan, 1986), which distinguish them from *R. muscicola*, which has conduplicate leaves, stellate flowers, subglobose pollinia, very slender rostellar arms, and a chromosome count of approximately $2n = 100$ (Jones, 1967). These differences can be accommodated in the sectional treatment proposed herein, which also eliminates the need to recognize another monotypic genus, which would provide little additional grouping information for an otherwise morphologically cohesive species group. Floral autapomorphies in the three species of *Podangis* are probably strongly associated with three divergent pollination syndromes, with *R. muscicola* likely being sphingophilous, considering its white, jasmine-scented flowers and slender lip spur longer than 4 cm (see Martins & Johnson, 2007). Similarly to Carlsward et al. (2006), we were unable to fully resolve the phylogenetic position of *R. muscicola* relative to *Podangis* when considering only molecular data. Future phylogenetic studies with a more comprehensive molecular dataset would be helpful in providing stronger support for a clade uniting the three species of *Podangis*, in agreement with our taxonomic decision to include *R. muscicola* within *Podangis*. Our redelimitation of *Podangis* and accompanying phylogenetic hypothesis are intended to provoke further systematic research. Phylogenomic analysis may one day reveal whether our treatment withstands the test of evidence and whether candidate synapomorphies (viz., the saddle-shaped viscidium and two slender stipes) will need to be reinterpreted as symplesiomorphic.

KEY TO *PODANGIS*

1a. Leaves conduplicate; flowers stellate, petals and sepals convex, bent backward; lip spur 4–12 cm; ovary and pedicel lepidote; lateral rostellar lobes ca. 4× as long as wide; pollinia subglobose . . . *P. muscicola* (Rchb. f.) Farminhão & D'haijère

1b. Leaves iridiform; flowers campanulate (i.e., not fully open), petals and sepals concave, bent forward; lip spur < 2 cm; ovary and pedicel glabrous or glandular; lateral rostellar lobes ca. 2× as long as wide; pollinia obovoid.

2a. Inflorescence a secund raceme, flowers alternate; floral bracts obtuse, brownish orange; lip spur hook-shaped; anther cap whitish to cream, truncate at apex; floral pedicel and ovary green, densely glandular, covered in whitish articulate trichomes . . . . . *P. rhipsalisocia* (Rchb. f.) P. J. Cribb & Carlsward

2b. Inflorescence a condensed corymbiform raceme, flowers spirally arranged; floral bracts acute, whitish to light brown; lip spur conical, constricted in middle and inflated into two umbonate lobules at apex; anther cap green turning yellow in late anthesis, acute at apex; floral pedicel white and ovary green with whitish ribs, glabrous . . . . . *P. dactyloceras* (Rchb. f.) Schltr.

Podangis sect. **Podangis.**

Podangis dactyloceras (Rchb. f.) Schltr., Beih. Bot. Centralbl. 36(2): 82. 1918. Basionym: *Listrostachys dactyloceras* Rchb. f., Flora 48: 190. 1865. *Angorchis dactyloceras* (Rchb. f.) Kuntze, Revis. Gen. Pl. 2: 651. 1891. *Angraecum dactyloceras* (Rchb. f.) Schltr., Westafr. Kautschuk-Exped: 283. 1900. TYPE: Angola. Malanje: prope cataractum magnum fl. Cuanza et in insula Calemba [Cataratas do Condo and Ilha Calemba], 18 Mar. 1857, *F. M. J. Welwitsch 677* (holotype, W image! [W-0011349], isotypes BM! [BM-000534987], COI!, K! [K-000306626], LISU! [LISU-221680]). Figure 4G–I.

Listrostachys forcipata Kraenzl., Bot. Jahrb. Syst. 19: 254. 1894. *Angraecum forcipatum* (Kraenzl.) Engl. in H. G. A. Engler & O. Drude, Veg. Erde 9(II): 420. 1908. TYPE: Cameroon. Southwest: Urwald westlich Buea, *P. R. Preuss s.n.* (holotype, B†).

Listrostachys saxicola Kraenzl., Bot. Jahrb. Syst. 48: 399. 1912. TYPE: Cameroon. Adamaoua: beim Passe Tschâpe, *C. L. Ledermann 2783* (holotype, B†).

Notes. We have located additional isotypes of *Listrostachys dactyloceras* at COI and LISU, which had not been cited in previous floristic treatments. As a historical note, it is almost certain that Reichenbach derived

the species epithet "*dactyloceras*" from the generic name of "*Dactyloceras flabellata* Welw." ined. This unpublished name for a new genus and species is found handwritten by Welwitsch himself on the duplicates housed at BM and LISU, on which the earlier alternative spelling "*Dactylorchis flabellata* Welw." ined. can also be read.

Podangis rhipsalisocia (Rchb. f.) P. J. Cribb & Carlsward, Phytotaxa 71: 46. 2012. Basionym: *Angraecum rhipsalisocium* Rchb. f., Flora 48: 189. 1865. *Angorchis rhipsalisocia* (Rchb. f.) Kuntze, Revis. Gen. Pl. 2: 651. 1891. *Listrostachys rhipsalisocia* (Rchb. f.) Rolfe in D. Oliver & auct. suc. (eds.), Fl. Trop. Afr. 7: 158. 1897. *Aerangis rhipsalisocia* (Rchb. f.) Schltr., Beih. Bot. Centralbl. 36(2): 123. 1918. *Rangaeris rhipsalisocia* (Rchb. f.) Summerh. in J. Hutchinson & J. M. Dalziel, Fl. W. Trop. Afr. 2: 449. 1936. *Neowolffia rhipsalisocia* (Rchb. f.) O. Gruss, Orchid. Atlas: 239. 2007. TYPE: Angola. Cuanza Norte: Golungo Alto, Sobati [Sobado] de Quibombo, Mar. 1856, *F. M. J. Welwitsch 662* (holotype, W image! [W-0011597]; isotypes BM! [BM-000540219], K! [K-000306339], LISU! [LISU-221675]). Figure 4D–F.

Listrostachys trachypus Kraenzl., Bot. Jahrb. Syst. 19: 253. 1894. *Rangaeris trachypus* (Kraenzl.) Guillaumin in Guillaumin & Rose, Bull. Mus. Natl. Hist. Nat., sér. 2, 31: 118. 1959. TYPE: Cameroon. Yaundé-Station, *G. A. Zenker 420* (holotype, B†).

Angraecum cordatiglandulum De Wild., Bull. Jard. Bot. État Bruxelles 5: 184. 1916. *Listrostachys cordatiglandula* De Wild., Bull. Jard. Bot. État Bruxelles 5: 184. 1916, nom. illeg. *Aerangis cordatiglandula* (De Wild.) Schltr., Beih. Bot. Centralbl. 36(2): 121. 1918. TYPE: Democratic Republic of the Congo. Haut-Uele: Environs de Nala, *F. Seret 754* (holotype, BR! [BR-000000881480]).

Notes. The duplicates of the type gatherings of *Angraecum rhipsalisocium* and *Listrostachys dactyloceras* housed at W are here confirmed as holotypes, following Cribb (1989), Szlachetko and Olszewski (2001), and Figueiredo and Smith (2008). This is based on the analysis of the correspondence between Welwitsch and H. G. Reichenbach and the presence of original notes and drawings associated with the material kept at W, which indicate that these duplicates were the only ones used by the author of the names (sensu Art. 9.1.b, Turland et al., 2018). We have also located an additional isotype of *A. rhipsalisocium* at LISU, which had not been cited in previous floristic treatments.

Podangis sect. **Rangaeris** (Schltr.) Farminhão & D'haijère, comb. nov. Basionym: *Aerangis* sect. *Rangaeris* Schltr., Beih. Bot. Centralbl. 36(2): 121. 1918. *Rangaeris* (Schltr.) Summerh., Bull. Misc. Inform. Kew: 227. 1936.

Podangis muscicola (Rchb. f.) Farminhão & D'haijère, comb. nov. Basionym: *Aeranthes muscicola* Rchb. f., Flora 48: 190. 1865. *Epidorkis muscicola* (Rchb. f.) Kuntze, Revis. Gen. Pl. 2: 660. 1891. *Mystacidium muscicola* (Rchb. f.) T. Durand & Schinz, Consp. Fl. Afric. 5: 54. 1894. *Listrostachys muscicola* (Rchb. f.) Rolfe in D. Oliver & auct. suc. (eds.), Fl. Trop. Afr. 7: 158. 1897. *Aerangis muscicola* (Rchb. f.) Schltr., Bot. Jahrb. Syst. 53: 599. 1915. *Rangaeris muscicola* (Rchb. f.) Summerh. in J. Hutchinson & J. M. Dalziel, Fl. W. Trop. Afr. 2: 450. 1936. TYPE: Angola. Malanje: Pungo Andongo, Tunda Quilombo, Apr. 1857, *F. M. J. Welwitsch 699* (holotype, W image! [W-0011604]; isotypes, BM! [BM-000540213], COI!, K! [K-000306341], LISU! [LISU-221674]). Figure 4A–C.

Angraecum englerianum Kraenzl., Bot. Jahrb. Syst. 7: 333. 1886. *Listrostachys engleriana* (Kraenzl.) Kraenzl., Bot. Jahrb. Syst. 19: 254. 1894. *Aerangis engleriana* (Kraenzl.) Schltr., Bot. Jahrb. Syst. 53: 599. 1915. TYPE: Cameroon. Littoral: Mungo [Moungo], Sep. 1874, *R. W. Buchholz s.n.* (holotype, B†; drawing, K!).

Mystacidium batesii Rolfe in D. Oliver & auct. suc. (eds.), Fl. Trop. Afr. 7: 172. 1897. *Angraecum batesii* (Rolfe) Schltr., Westafr. Kautschuk-Exped.: 283. 1900, nom. illeg. *Aerangis batesii* (Rolfe) Schltr., Bot. Jahrb. Syst. 53: 599. 1915. *Aerangis mixta* Schltr., Beih. Bot. Centralbl. 36(2): 122. 1918. TYPE: Cameroon. Sud: Efulen, 20 Sep. 1895, *G. L. Bates 382* (lectotype, here designated, K! [K-000306340]; isolectotype, BM! [BM-000540209]).

Aerangis falcifolia Schltr., Bot. Jahrb. Syst. 53: 598. 1915. TYPE: Tanzania. Mbeya: Station Kyimbila, Mulinda Wald, Mar. 1913, *A. F. Stolz 1960* (lectotype, here designated, K! [K-000306346]; isolectotype, LD scan! [LD-1220164]).

Angraecum solheidii De Wild., Bull. Jard. Bot. État Bruxelles 5: 191. 1916. *Listrostachys solheidii* De Wild., Bull. Jard. Bot. État Bruxelles 5: 191. 1916. *Aerangis solheidii* (De Wild.) Schltr., Beih. Bot. Centralbl. 36(2): 123 (1918). TYPE: Democratic Republic of the Congo. Tshopo: env. de Yambuya, s.d., *A. F. Solheid 127* (lectotype, here designated, BR! [BR-0000008814814]; isolectotype, BR! [BR-0000008814821]).

Listrostachys floribunda Rolfe, Bull. Misc. Inform. Kew 1918: 236. 1918. *Aerangis floribunda* (Rolfe) Summerh., Bull. Misc. Inform. Kew 1932: 509. 1932. TYPE: Uganda. Umpala, *s. coll.*, *s.n.* (holotype, K! [K-000306345]).

Notes. *Podangis muscicola* presents two different leaf habits. Numerous specimens from East and Southeast Africa, as well as specimens from Central Africa growing as lithophytes (e.g., *V. Droissart 1319* [BRLU!]), present arcuate, strongly conduplicate leaves, more reminiscent in habit to species in section *Podangis* (see Fig. 4A), whereas most other specimens from West and Central Africa present straight and not strongly conduplicate leaves (see Fig. 4C). These differences are possibly due to either ecotypical variation or phenotypic plasticity related to sunlight exposure. Specimens of *P. muscicola* in herbaria generally tend to blacken after being dried, whereas those of *P. dactyloceras* and

Figure 4. Overview of *Podangis* Schltr. A–C. *Podangis muscicola* (Rchb. f.) Farminhão & D'haijère. —A. Habit of a plant with arcuate and strongly conduplicate leaves from Mazumbai (Tanzania). —B. Flower, side view, recorded in Lualaba, Kakanda (Democratic Republic of the Congo). —C. Habit of a fruiting plant with straight conduplicate leaves, cultivated at the Nimba shade house (Guinea). D–F. *Podangis rhipsalisocia* (Rchb. f.) P. J. Cribb & Carlsward. —D. Habit of a plant grown at the University of Yaoundé I shade house (Cameroon). —E. Inflorescence, taken at the Nimba shade house (Guinea). —F. Immature fruits, recorded at Nimba shade house (Guinea). G–I. *Podangis dactyloceras* (Rchb. f.) Schltr. —G. Habit, recorded in Mpati Hill (Cameroon). —H. Inflorescence, taken at the University of Yaoundé I shade house (Cameroon). —I. Flowers, face view (Tanzania). A by C. Gray-Wilson via the World Orchid Iconography; B by Warren McCleland via Senckenberg's *West African Plants*; C and E by E. Bidault; D by Murielle Simo-Droissart; G by Marco Schmidt via Senckenberg's *West African Plants*; H by G. Kamdem; and I by W. Bachmann via the World Orchid Iconography.

P. rhipsalisocia tend to stay green. The duplicate of the type gathering of *Aeranthes muscicola* housed at W is here confirmed as the holotype, following Cribb (1989: 572), Szlachetko and Olszewski (2001: 676), and Figueiredo and Smith (2008: 193). In relation to the Angolan collections of Friedrich Welwitsch, Albuquerque et al. (2009) suggest that names published based on specimens sent to specialists before Welwitsch's death are to be typified by material in the herbarium of the author of the name. The duplicate at W is the only one with associated original notes and drawings of Heinrich Gustav Reichenbach and with a direct reference to the protologue handwritten by Reichenbach himself. Furthermore, based on the analysis of the correspondence between Welwitsch and Reichenbach in the year of the publication of the name (Natural History Museum's Library and Archives, 2019), it is likely that the specimen found at W was the only one used by Reichenbach (sensu Art. 9.1.b, Turland et al., 2018). We have also located additional isotypes at COI and LISU, which had not been cited in previous floristic treatments. Concerning the typifications of *Mystacidium batesii* and *Angraecum solheidii* De Wild., both heterotypic synonyms of *P. muscicola*, we chose as lectotypes the syntypes gathered by the eponymous collectors. Finally, an additional duplicate of the type series of *Aerangis falcifolia* Schltr. was almost certainly housed at B and destroyed during the bombing of the Berlin Herbarium.

New Genera

Aziza Farminhão & D'haijère, gen. nov. TYPE: *Rangaeris trilobata* Summerh., Bull. Misc. Inform. Kew 1936: 229. 1936.

Diagnosis. *Aziza* Farminhão & D'haijère is vegetatively most similar to *Solenangis* Schltr. and *Dinklageella* Mansf., with which it shares a scandent habit with elongate internodes and clasping crozier-shaped root apices, but differs in inflorescence structure (pendent with peduncle as long as or longer than rachis vs. suberect with peduncle shorter than rachis in *Solenangis*), column structure (prominent column projecting well above the sepals and petals and an anther cap with a truncate apex vs. small column, shorter than sepals and an anther cap with an acute apex in *Solenangis*), in the pollinarium (two stipes vs. a single stipes in *Solenangis*), and fruit morphology (narrowly ellipsoid capsules, 6 to 7 times as long as wide vs. ellipsoid to narrowly ellipsoid capsules 1.5 to 3.5 times as long as wide in *Solenangis*). From any other species of the *Cyrtorchis–Tridactyle* alliance, including those formerly placed in *Rangaeris* (Schltr.) Summerh., it differs in its scandent habit and climbing roots with crozier-shaped apices. From *Podangis* Schltr. (including *Rangaeris muscicola* (Rchb. f.) Summerh.) it also differs in its pendent inflorescences (vs. erect to suberect), deeply trilobed (vs. entire or subentire) lip, the structure of the column (apterous in *Aziza* vs. with prominent spreading wings adnate to lip base in *Podangis*), and the shape of the viscidium (truncate anterior margin vs. notched anterior margin in *Podangis*).

Etymology. The name of this monospecific genus commemorates the homonymous miniature forest-dwelling figures of Dahomey mythology. According to some descriptions, *Aziza* are fairylike creatures with a single long hair that covers them entirely and makes them invisible, controlling the hunt and all that pertains to the forest (Blier, 1996). The gender is feminine.

Aziza trilobata (Summerh.) Farminhão & D'haijère, comb. nov. Basionym: *Rangaeris trilobata* Summerh., Bull. Misc. Inform. Kew 1936: 229. 1936. *Solenangis trilobata* (Summerh.) R. Rice, Oasis 3: 14. 2006. TYPE. Nigeria. Akwa Ibom: Eket Distr., 1912–1913, *P. A. Talbot & D. A. Talbot 3299* (holotype, BM! [BM000540223]; isotype, K! [K000306411]). Figures 5, 6A–C.

Scandent, epiphytic herb, monopodial. Roots numerous, produced all along the stem, branching, slender, tortuous, 0.5–2 mm diam., grayish to brownish; apex crozier-shaped clinging to other roots and surrounding vegetation. Stem pendent or climbing, leafy, covered by leaf sheaths, with elongate internodes, up to 60 × 0.2–0.35 cm. Leaves numerous, alternate and distichous, articulated to sheathing base, spaced 3–5 cm apart; lamina 4–10.8 × 0.7–1.7 cm, elliptic to narrowly elliptic, thin-textured, flat, margin entire, bifid or unequally and acutely bilobed at apex with no notch, light to dark green. Inflorescence a secund raceme, axillary, pendent, lax, 2- to 9-flowered, 3–23.1 cm, axis dark green to brownish; peduncle up to 13.2 cm, covered by up to 5 dark brown ochreate sterile bracts, 3.5 mm; rachis terete, flexuose, sparsely lepidote, floral node 9–17 mm; floral bracts inconspicuous, 3.5 mm, ochreate, barely sheathing floral pedicels, dark brown. Flowers whitish, turning salmon to dull brownish orange in late anthesis, stellate, resupinate; sepals and base of petals pinkish orange; dorsal surface of sepals and spur clothed with brown scales; lip white with greenish spur, petals cream, all tepals convex and markedly reflexed; column white; anther cap cream, pollinia light yellow. Dorsal sepal 7.5–9.5 × 3–4 mm, ovate, sharply constricted in apical third, obtuse, entire. Lateral sepals 8.5–10 × 2.5–3.5 mm, narrowly ovate, sometimes slightly falcate, obtuse, entire. Petals 7.5–10 × 1.5–2.5 mm, narrowly triangular, acute, entire but sometimes obscurely trilobed at base. Lip 8.5–10 × 4.5–8 mm, trilobed, ecallose; median lobe 7–8 × 1.5–3 mm, narrowly triangular, obtuse, entire; lateral lobes 1.5–3 × 1.5–3 mm, subreniform, anterior margin crenate to asymmetrically dentate, posterior margin entire; lip spur 5–6.1 cm, filiform, tapering toward apex, pendent, helically twisted. Column 4.5–6 × 2 mm, exposed; stigma 1.5 × 2 mm, subcircular, concave, lower rim prominent, forming an acute downward-

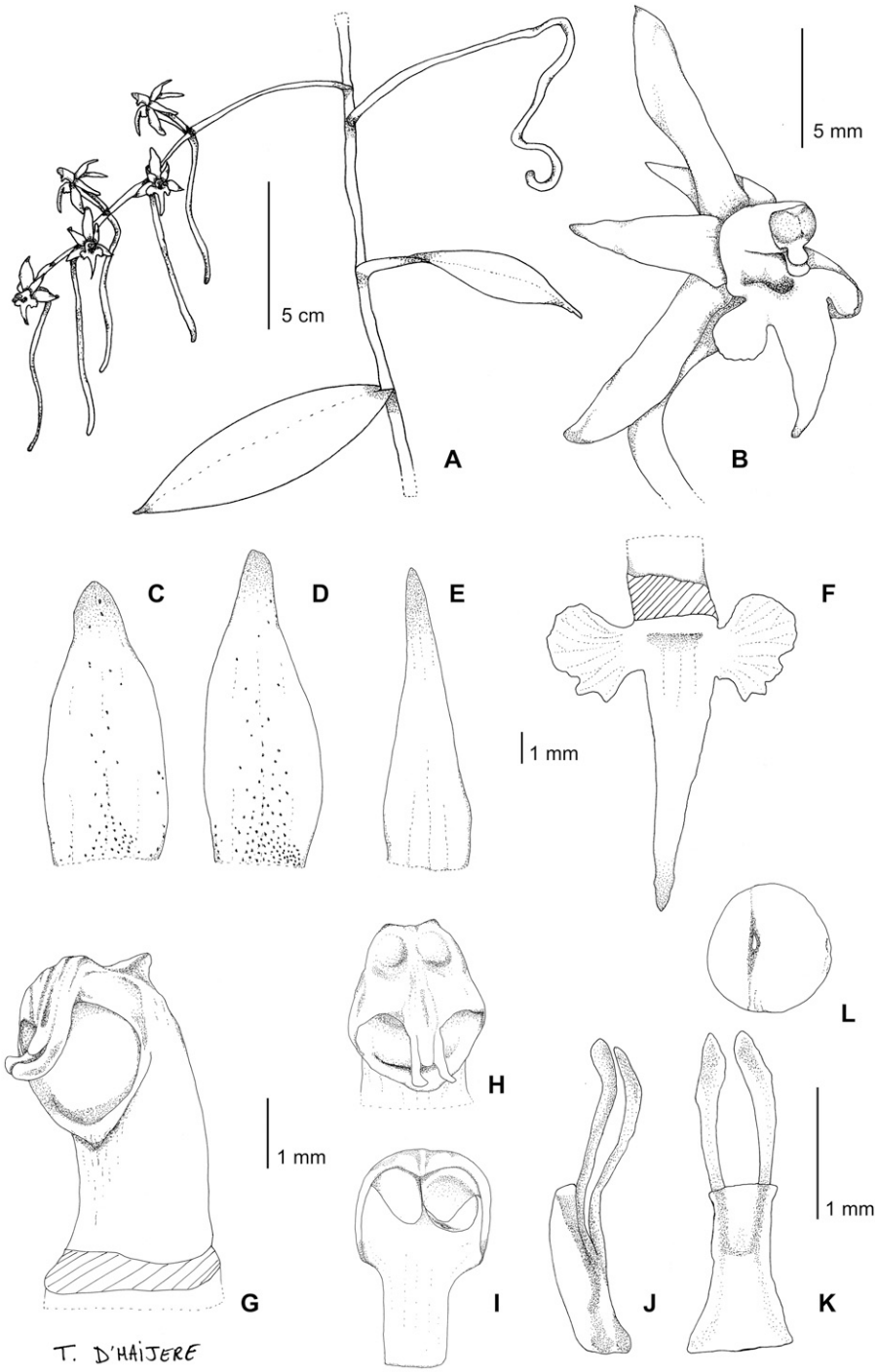

Figure 5. *Aziza trilobata* (Summerh.) Farminhão & D'haijère. —A. Habit. —B. Flower. —C. Dorsal sepal. —D. Lateral sepal. —E. Petal. —F. Lip. —G. Column, lateral view. —H. Column, face view. —I. Anther cap, ventral view. —J. Pollinaria, dorsal view. —K. Pollinaria, ventral view. —L. Pollinium. A from *Stévart, Leal & Nguema 2467* (BRLU); B adapted from a photo of a plant in cultivation in Tchimbélé (Gabon); C–F, J, K from *Stévart 662* (BRLU); G from *Primo & Stévart 71* (BRLU); H from *Farminhão 11* (BRLU); I and L from *Stévart, Ngok & Mendu 1121* (BRLU). Drawn by Tania D'haijère.

Figure 6. Overview of *Aziza* Farminhão & D'haijère and *Solenangis* Schltr. A–C. *Aziza trilobata* (Summerh.) Farminhão & D'haijère. —A. Habit, plant growing over a small stream in the forest (*D'haijère et al. 137*). —B. Flowers (*Dewynter s.n.*). —C. Fruits (*D'haijère et al. 2*). D, E. *Solenangis clavata* (Rolfe) Schltr. —D. Old fruits of a plant growing in Lagoa Amélia crater bog (São Tomé). —E. Inflorescence (São Tomé). A, C, D by João N. M. Farminhão; B by Maël Dewynter/Fondation Biotope pour la biodiversité; and E by Tariq Stévart.

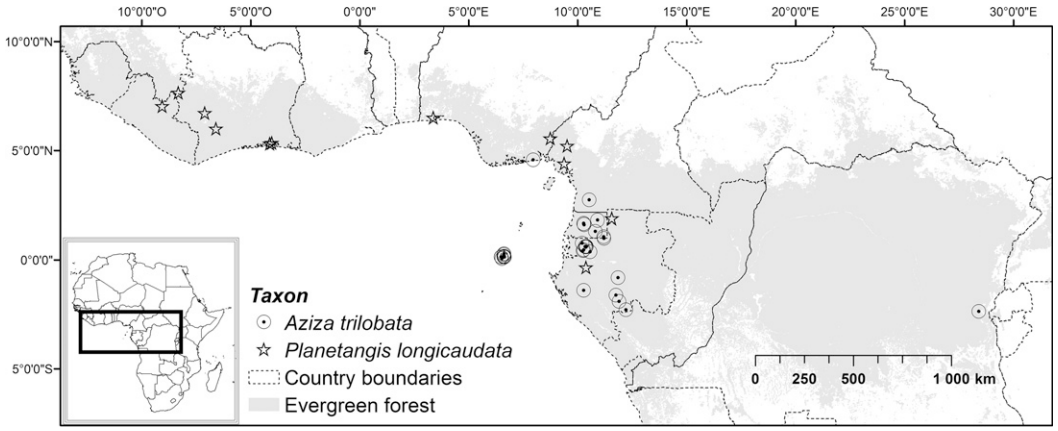

Figure 7. Geographical distribution of *Aziza trilobata* (Summerh.) Farminhão & D'haijère and *Planetangis longicaudata* (Rolfe) Stévart & Farminhão in tropical Africa.

projecting callus; anther cap 2.5 × 1.5 mm, 1 mm tall, cucullate, with a truncate beaklike expansion covering the rostellum; pollinia 2, globose, porate, dark brown when preserved in spirit; stipes 2, 1.5 mm, linear, slightly clavate, insertion point halfway along length of viscidium, turning yellowish brown when preserved in spirit; a single viscidium, 1 mm, saddle-shaped with a truncate anterior margin, whitish, hyaline, turning green when preserved in spirit; rostellum trifid, midlobe oblong, rounded, lateral lobes ca. 1.5× as long as midlobe, pendulous and upcurved, parallel to each other, linear, apices rounded. Ovary and pedicel 9–13 mm, slender, light brown densely covered in dark brown scales. Fruit a narrowly ellipsoid capsule, triquetrous, up to 4.3–4.7 × 0.25–0.5 cm, brown, often with a marcescent lip spur.

Phenology. *Aziza trilobata* typically flowers from July to January, but some old collections record flowering in April (e.g., *G. M. P. C. Le Testu 5405*) and May (*C. F. A. Onochie & M. G. Latilo 32937*). Fruits have been recorded from October to May.

Habitat and ecology. This species is a low or canopy shade scandent epiphyte in lowland and submontane evergreen rainforest (Stévart & Oliveira, 2000). It is often found in inundated and riparian forest, namely near waterfalls, where it is most commonly observed climbing on low vegetation. It also occurs in the herbaceous, shrubby, and forest-fringe communities of the inselberg-rainforest ecotone (Droissart et al., 2009).

Distribution. *Aziza trilobata* is found in Lower Guinea (western Nigeria, Cameroon, Rio Muni, and Gabon), Gulf of Guinea Islands (São Tomé and possibly Príncipe; Stévart & Oliveira, 2000), and the Congolian Region (Democratic Republic of the Congo) in Central tropical Africa, at elevations of 10–1550 m. Figure 7.

Conservation status. The species is given an IUCN Red List status of Least Concern [LC]. The EOO of *Aziza trilobata* is estimated to be 869,144 km², far exceeding the 20,000 km² upper limit for Vulnerable status under the criterion B1. Its AOO is estimated to be 120 km², which falls within the limits for Endangered status under the criterion B2. The species is known from 30 subpopulations in Nigeria, Rio Muni, Gabon, São Tomé, and the Democratic Republic of the Congo. *Aziza trilobata* is an epiphyte in lowland and submontane evergreen rainforest, between 10 and 1100 m elevation. Several collections of *A. trilobata* come from four protected areas: two in Rio Muni (Monte Alén National Park and Piedra Bere Natural Monument), one in Gabon (Monts de Cristal National Park), and one in São Tomé (Obô Natural Park). These sites are not under threat and appear well managed. The other collections of the species are documented from unprotected sites, some of which are currently subjected to great human pressure, especially from shifting agriculture, selective logging, and timber harvesting for small-scale subsistence. A total of 30 subpopulations of the species are identified, representing 19 different locations (sensu IUCN, 2019), much more than 10 locations, which is the upper limit for Vulnerable status under the subcriterion *a* of criterion B2. Notwithstanding these human activities, with varying levels of impact, the number of subpopulations of *A. trilobata*, as well as its EOO and AOO, likely will not decrease substantially in the near future. Since the conditions for applying subcriteria *a* and *c* under criterion B2 are not met, IUCN criteria therefore indicate that the species cannot be regarded as Endangered even though its AOO falls below the threshold of 500 km² for criterion B2. *Aziza trilobata* is thus assigned a preliminary status of LC.

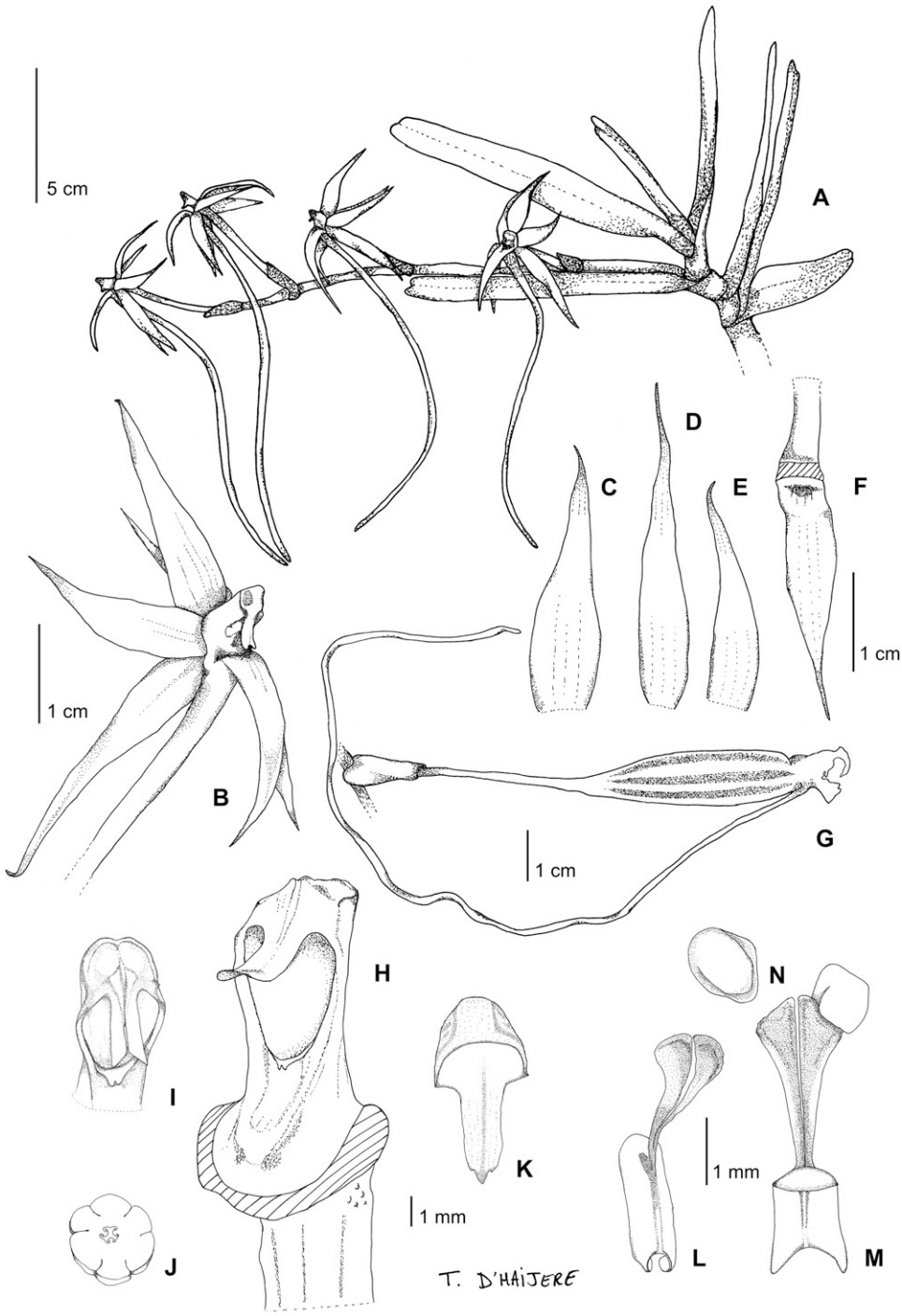

Figure 8. *Planetangis longicaudata* (Rolfe) Stévart & Farminhão. —A. Habit. —B. Flower. —C. Dorsal sepal. —D. Lateral sepal. —E. Petal. —F. Lip. —G. Developing fruit with marcescent lip spur. —H. Column. —I. Column, face view. —J. Ovary, transversal cut. —K. Anther cap, ventral view. —L. Pollinaria, dorsal view. —M. Pollinaria, ventral view with one pollinium in situ. —N. Pollinium. A adapted from a photograph of Pérez-Vera (2003). B from a photograph of a plant in cultivation in Libreville (*BTO 440*). C–F from *GAB 583*. G from *Simo & Zapfack SIP 124* (BRLU). H–N from *GAB 668*. Drawn by Tania D'haijère.

Figure 9. Overview of *Planetangis* Stévart & Farminhão and *Cyrtorchis* Schltr. A, B. *Planetangis longicaudata* (Rolfe) Stévart & Farminhão. —A. Flowers, face view, cultivated at Jardi-Gab shade house (Gabon). —B. Habit, cultivated at Jardi-Gab shade house (Gabon). —C. *Cyrtorchis letouzeyi* Szlach. & Olszewski, habit, Dja Faunal Reserve (Cameroon). —D. *Cyrtorchis ringens* (Rchb. f.) Summerh., flowers, face view, grown at the University of Yaoundé I shade house (Cameroon). —E. *Cyrtorchis chailluana* (Hook. f.) Schltr., fruit, face view, grown at the University of Yaoundé I shade house (Cameroon). A and B by Tariq Stévart; C by V. Droissart; D by G. Kamdem; and E by Laura Azandi.

Notes. The phylogenetic position of *Aziza trilobata* is not fully resolved, but it appears to be an isolated lineage in the *Cyrtorchis–Tridactyle* clade. A more comprehensive molecular dataset, with more samples and markers, is needed to disentangle further the relationships between genera in the *Cyrtorchis–Tridactyle* clade, but the evidence already seems sufficient to conclude that *A. trilobata* is evolutionarily isolated and warrants recognition as a distinct genus.

The lack of records of *Aziza trilobata* between southwestern Nigeria and southern Cameroon–Rio Muni–Gabon is probably due in part to a collecting gap in Bioko and Cameroon, namely around Mount Cameroon, where species distribution modeling predicts its occurrence with a high probability (Deblauwe et al., 2016). The recent discovery of *A. trilobata* in Mulolo Forest (Shabunda Territory), in eastern Democratic Republic of the Congo, has significantly expanded its extent of occurrence. Further fieldwork in the Congo Basin would likely reduce the current distributional gap between Atlantic Central Africa and South Kivu.

The crenation/dentation of the anterior margin of the lateral lobes of the lip of *Aziza trilobata* presents a great degree of asymmetry, with one lobe often presenting larger teeth than the other. This can be interpreted as a case of fluctuating asymmetry, which is a relatively little-studied phenomenon in plants (Rudall et al., 2002).

Additional specimens examined. NIGERIA. **Akwa Ibom:** Eket, Big town, on path from village to Western boundary of Stubbs Creek F.R., 13 May 1953, *Onochie & Latilo 32937* (FHI, K). CAMEROON. **Sud:** Akom II (rte. Kribi–Ebolowa, campement à 3h de marche au S du village, sommet à 3h de marche au N du campement, N2°44′20.04″ E10°31′55.92″, 1075 m, 4 June 2006, *Droissart 132* (BRLU). EQUATORIAL GUINEA (RIO MUNI). **Centro Sur:** Mirador, dalle rocheuse de Monte Alén, 3 km à l'O de la station Ecofac (Parc Nat. de Monte Alén), N1°40′ E10°17′, 1200 m, 1 July 1999, *T. Stévart 589* (BRLU); ibid. loc., 1100 m, 5 Feb. 2001, *T. Stévart 755* (BRLU); Parc National de Monte Alén, dalle rocheuse d'Engong, 5 km à l'ouest du Village d'Engong, N1°37′ E10°18′, 1100 m, 11 May 2002, *Parmentier & Esono 2794* (BRLU). **Wele-Nzas:** Mungum (inselberg de), à 45 minutes de marche du village de Kukumancoc, N1°19′ E10°49′, 735 m, 24 May 2002, *Stévart, Ndong Bokung & Ndong Maye 1537* (BRLU); inselberg de Akoak Ebanga, à 1h de marche du village de Ngong Mocomo, à 10 km de Nsork, N1°04′ E11°12′, 570 m, 31 May 2002, *Parmentier & Esono 3521* (BRLU). **S. loc:** inselberg, 25 June 1999, *Parmentier & Nguema 1128* (BRLU). GABON. **Woleu-Ntem:** Inselberg de Ntan (Bikougou), à 1 h 30 de marche du village de La Hollande (à 2 km de Sam), 790 m, 22 Jan. 2000, *Parmentier & Nguema 790* (BRLU). **Estuaire:** Mont Séni (Ekoko), 2 Oct. 2002, *Stévart 1781* (BRLU); ca. 10 km along the rd. Tchimbele–Kinguele, N0°37′ E10°21′, 620 m, 27 Jan. 1986, *van der Laan 1332* (WAG); ibid. loc., 22 Nov. 1993, *Arends 1011* (WAG); Tchimbélé (carrière de) près du bras mort du lac, N0°37′8.93″ E10°24′4.21″, 570 m, 7 Sep. 2002, *Stévart 1808* (BRLU); Tchimbélé hydroelectric compound, around houses, N0°37′13″ E10°24′26″, 543 m, 21 Nov. 2002, *Strijk 450* (WAG); Tchimbélé, forêt aux environs du barrage, N0°36′8.78″ E10°24′1.68″, 25 Sep. 2001, 460 m, *Stévart et al. 1098* (BRLU); ibid. loc., 23 Sep. 2002, *Stévart 1747* (BRLU); Tchimbélé, ancien lit de la rivière qui descend du barrage, N0°36′8.41″ E10°23′9.95″, 440 m, 8 Sep. 2001, *Stévart et al. 1121* (BRLU); Monts de Cristal, cascade sur la rive Est de la Mbé, juste au-dessus de Kinguélé, N0°27′48″ E10°16′52″, 140 m, 25 Oct. 2017, *D'haijère et al. 2* (BRLU, LBV); Lower Mbé Valley, SW from Kinguelé & NE from Mfoul Mengoma, at the foot of Mt. Mbilan, N0°25′37″ E10°15′13″, 121 m, 26 Oct. 2017, *Farminhão et al. 11* (BRLU); Monts de Cristal, Upper Komo Valley, SEEF concession area, ca. 4.5 km SE from Violaineville, N0°22′37″ E10°34′33″, 485 m, 4 Nov. 2017, *Farminhão et al. 52* (BRLU). **Ngounié:** Massif du Chaillu, Bouvala area, Mont Songo, 1°38′58.3″S 11°45′47.6″E, 790 m, 5 Oct. 2007, *Stévart, Leal & Nguema 2467* (BRLU); dans la haute Ngounyé, chute de la Mboumi à Mbigou, 30 Apr. 1927, *Le Testu 5405* (BM); ibid. loc., 2 Apr. 1927, *Le Testu s.n.* (K); Balamboula (près de), 2°17′3.52″S 12°13′11.26″E, 620 m, *Dewynter s.n.* (BRLU [photo]). SÃO TOMÉ AND PRÍNCIPE. **São Tomé:** Morro Chamiço, N 0°17′0″ E 6°37′30″, 1100 m, 1 Sep. 1999, *Stévart 662* (BRLU); ibid. loc., 12 Aug. 2002, *Primo & Stévart 71* (BRLU); Bombaim, entre la Roça et Formoso Pequeno, N0°14′46.86″ E6°37′0.90″, 504 m, 2 Dec. 2017, *D'haijère et al. 137* (BRLU); Pico Maria Fernandes, N0°10′ E06°38′, 150 m, 26 Aug. 1997, *Stévart & Oliveira 91* (BRLU); ibid. loc., 11 Oct. 1997, *Stévart 261* (BRLU); ibid. loc., N0°10′15″ E 6°38′30″, 150 m, 1 Sep. 1999, *Stévart 677* (BRLU); Rio Ió Grande, s.d., N0°9′45″ E6°36′45″, 200 m, *Stévart 703* (BRLU); ibid. loc., 20 Aug. 2002, *Primo & Stévart 80* (BRLU); margem do Rio Yo Grande, 1999, *Oliveira 137/1999* (BRLU); Vale Carmo, bordo do caminho, N0°9′ E 6°37′, 259 m, 14 Sep. 2007, *Oliveira 1087* (BRLU); Angolares, Lagoa, Angra de São João, Jan. 1886, *Quintas 1028* (BM, COI); Rio Xufexufe, N0°08′ E6°30′, 230 m, 1 Oct. 1997, *Stévart 203* (BRLU). DEMOCRATIC REPUBLIC OF THE CONGO. **Sud-Kivu:** Shabunda, Itanga/Mulolo, N0°10′15″ E 6°38′30″, 1532 m, 13 Dec. 2018, *L. Dumbo 16* (LWI).

Planetangis Stévart & Farminhão, gen. nov. TYPE: *Rangaeris longicaudata* (Rolfe) Summerh. Basionym: *Mystacidium longicaudatum* Rolfe in D. Oliver & auct. suc. (eds.), Fl. Trop. Afr. 7: 170. 1897.

Diagnosis. Planetangis Stévart & Farminhão is most similar to *Cyrtorchis* Schltr., with which it shares white, stellate flowers; a lip similar in shape to the remaining tepals; two stipes clearly broadening toward the apex; and connivent lateral rostellar lobes, but differs in the markedly deflexed petals exposing the column (vs. column covered by petals); the elongate column, about twice as long as wide (vs. column very short, about as long as wide); the deeply concave stigma, obovate, in which the lower margin bears a small bilobed callus and does not touch the entrance of the lip spur (vs. stigma slightly concave, oblong, the lower margin touching the entrance of the lip spur); the saddle-shaped viscidium, triangular when flattened, with a deeply bilobed anterior margin, where the insertion point of the stipes is at half of its length (vs. viscidium either linear and hyaline or triangular comprising an indurate saddle-shaped proximal part and a hyaline distal part, in both cases with bifid anterior margin and the insertion point of the stipes at the rear third of its length); the rostellum, which is exposed and presents broad lateral lobes, not tapering, and beveled at the apex (vs. rostellum sunken into mouth of the spur, with tapering lateral lobes acute at the apex); and the rounded cross-section of the ovary and fruits (vs. triquetrous ovary and often fruit). It differs

from *Podangis* Schltr. based on the previously mentioned traits shared with *Cyrtorchis* (vs. lip dissimilar in shape to remaining tepals, two stipes only slightly broadening toward the apex, and parallel lateral rostellar lobes). It also superficially resembles *Aerangis* Rchb. f., but differs in having erect to suberect inflorescences (vs. pendent) and pollinaria with two stipes (vs. a single stipe).

Etymology. The name of this monospecific genus derives from the ancient Greek stem *planēt-*, which literally translates to "wanderer" and *ángos*, "vessel." This refers to the puzzling taxonomic position of this satellite taxon in the *Cyrtorchis–Podangis* clade, and the ending *-angis* alludes to other angraecoid generic names such as *Aerangis* and *Podangis* with which it shares the same overall floral habit. The name's gender is feminine.

Planetangis longicaudata (Rolfe) Stévart & Farminhão, comb. nov. Basionym: *Mystacidium longicaudatum* Rolfe in D. Oliver & auct. suc. (eds.), Fl. Trop. Afr. 7: 170. 1897. *Rangaeris longicaudata* (Rolfe) Summerh. in J. Hutchinson & J. M. Dalziel, Fl. W. Trop. Afr. 2: 449. 1936. TYPE: Nigeria. Lagos: Lagos, 26 Mar. 1896, *H. Millen 188* (holotype, K! [K-000306412]). Figures 8, 9A, B.

Erect to suberect epiphytic herb, monopodial, often forming large clumps. Roots stout, branching, emerging all along stem, 3.5–4 mm in diam., grayish. Stem pendent to suberect, leafy, covered by leaf sheaths, with elongate leaf nodes, up to 18.1 cm long, 5–6 mm diam. Leaves numerous, alternate and distichous, articulated to a sheathing base, spaced 1–2 cm; lamina 6–12 × 1–1.8 cm, narrowly oblong, fleshy and very coriaceous, revolute, margin entire, emarginate to unequally bilobed at apex with rounded lobes, light green to dark green above and grass-green beneath. Inflorescence a secund raceme, axillary, suberect to erect, lax, 3- to 8-flowered, 8–20 cm; axis light green; peduncle up to 6 cm, covered by 2 to 3 dark brown ochreate sterile bracts, 10–12 mm; rachis terete, flexuose, glabrous, floral node 25–35 mm; floral bracts prominent, 10–16 mm, broadly triangular, markedly sheathing floral pedicels, obtuse, dark brown. Flowers ivory white turning yellowish in late anthesis, stellate, resupinate; all tepals white, glabrous, convex, markedly reflexed, narrowly ovate, caudate, and with entire margin; lip spur white to greenish becoming orange toward tip; column white, anther cap orange turning dark brown when senescent. Dorsal sepal 20–32 × 5.5–8 mm. Lateral sepals 28–36 × 4.5–6 mm. Petals 21–27 × 4.5–6 mm. Lip 24–30 × 4–5 mm, subsimilar to other tepals, ecallose; lip spur 15–20.3 cm, filiform with a narrowly conical mouth and tapering toward apex, pendent, not twisted. Column 6–8 × 3–4 mm, exposed; stigma 4.5 × 3 mm, obovate, deeply concave, lower rim prominent forming a small bilobed downward-projecting callus; anther cap 6 × 3 mm, 2 mm tall, cucullate, with a tridentate beaklike expansion covering the rostellum; pollinia 2, subglobose, cleft, dull brownish yellow when preserved in spirit; stipes 2, 3.5 mm, obtriangular, much broadened at apex, insertion point halfway along length of viscidium, dull brownish yellow when preserved in spirit; a single viscidium, 3 mm, saddle-shaped, triangular when flattened, with a deeply bilobed anterior margin, whitish, hyaline; rostellum trifid, midlobe triangular, acute, inconspicuous, lateral lobes prominent, ca. 2× as long as midlobe, pendulous, connivent, linear, with broadly beveled apices. Ovary and pedicel with a rounded cross section, 4.6–7.1 cm, green, glabrous. Fruit an ellipsoid capsule, constricted toward base, ribbed, 3.8 × 0.9 cm, often with marcescent lip spur.

Phenology. *Planetangis longicaudata* typically flowers from October to January, but a single flowering specimen (*H. Millen 188*, the type, from 1896) was recorded at the end of March. Flowers are reported to last from two to three weeks (Pérez-Vera, 2003). The single known record of a fruit (*P. Simo & L. Zapfack SIP 124*) dates from December.

Distribution. *Planetangis longicaudata* is found in Upper (Liberia, Guinea, Ivory Coast) and Lower Guinea (Nigeria, Cameroon, and Gabon) in West and Central tropical Africa, at 10–650 m. Figure 7.

Habitat and ecology. This species is a large and medium-sized branch, heliophilous epiphyte in lowland evergreen and semi-deciduous rainforest, where it is found growing on tall trees (Adam, 1981; Pérez-Vera 2003). In Ivory Coast, *Entandrophragma utile* (Dawe & Sprague) Sprague is reported as a typical phorophyte (Pérez-Vera, 2003).

IUCN Red List category. *Planetangis longicaudata* is given an IUCN Red List status of Near Threatened [NT]. The EOO of this species is estimated to be 821,624 km^2, which far exceeds the 20,000 km^2 upper limit for Vulnerable status under criterion B1. Its area of occupancy is estimated to be 48 km^2, which falls within the limits for Endangered status under criterion B2. The species is known from 12 subpopulations in the six countries mentioned above. *Planetangis longicaudata* grows on tall trees in lowland evergreen and semi-deciduous rainforest between 10 and 650 m elevation. The species has been collected inside the Cross River National Park, a protected area that has unfortunately been considerably affected by human activities, including logging, slash and burn farming, and poaching (Adetola & Adetoro, 2014). In Haut-Sassandra, severe encroachment of cocoa into forested areas (see Barima et al., 2016), not far from one of the collecting locations of *P. longicaudata*, has probably taken a toll on the demographics of this subpopulation. In some

unprotected areas where the species occurs, its habitat is also threatened because of human activities such as shifting agriculture and selective logging. These pressures are gradually leading to the degradation of the quality of its habitat. The main threat to the species is certainly small-scale agriculture, and the 12 subpopulations represent 11 different locations (sensu IUCN, 2019), more than the upper limit for Vulnerable status under subcriterion "a" of criterion B2. Because the conditions for applying at least two subcriteria under criterion B1 or B2 are not met, the species cannot be regarded as threatened even though its AOO falls below the threshold for criterion B2. However, considering the ongoing loss of its habitat within and outside protected areas, the species could become threatened in the near future, a situation that justifies a preliminary risk of extinction assessment of Near Threatended (NT).

Notes. Duplicates of some gatherings from Ivory Coast have been deposited at ABI (*Pérez-Vera 533*), GDA (*Pérez-Vera 146*), and UCJ (*Pérez-Vera 146*) (see Pérez-Vera, 2003), but we were unable to examine these specimens.

Additional specimens examined. LIBERIA. **Nimba:** Ganta, Teayi, à 60 km au Sud du Nimba, 426 m, 11 Nov. 1975, *Adam 30203* (P). GUINEA. **Nzérékoré:** Lola, 07°40′02″N 008°19′26″W, 498 m, 16 Jan. 2013, *Nimba shade house series 1368* (WAG); ibid. loc., *Nimba shade house series 1438* (BRLU); ibid. loc., 3 July 2013, *Nimba shade house series 1439* (MO). IVORY COAST. **Montagnes:** Guézon, route de Guessabo à Duékoué, 1 Nov. 1973, *Pérez-Vera 533* (P). **Bas-Sassandra:** Forêt d'Ouréyo, July 1971, cult. in Daloa, Nov. 1972 (fl.), *Pérez-Vera 146* (K). **Abidjan:** Abidjan, 28 Nov. 1975, *de Koning 6213* (WAG); Adiopodoumé, 17 km W of Abidjan, Garden of Centre Néerlandais, N5°19′59″ W4°7′59″, 26 Nov. 1978, *Dekker 330* (WAG). NIGERIA. **Cross River:** C.R.N. Reserve [Cross River Nature Reserve], Nov. 1959, 21 Dec. 1961 (fl.), *Cooper 79* (K). **S. loc.:** cult. in Ibadan, 16 Nov. 1950, FHI 42078 (K, K000615019). CAMEROON. **Southwest:** Kupe-Manengouba, Mongo-Mdor, N5°13′46″, E9°31′16″, 590 m, 7 Dec. 2002, *P. Simo & Zapfack SIP 124* (BRLU, YA); Meme Division, 10 km W of Banga, near Mukete Plantation, N4°25′ E9°23′, 50 m, 30 Oct. 1985, *Thomas 4907* (FHI, K, MO, P, WAG, YA). GABON. **Woleu-Ntem:** région près du Cameroun, Odingoto, 200–300 m, 1 Oct. 1997, *Biteau & Stévart 31* (BRLU); ibid. loc.?, fl., 1 Nov. 2016, *Gabon shade house series 507* (BRLU). **Moyen-Ogooué**: Région de Bifoun, fl., 1 Nov. 2016, *Gabon shade house series 666*, *668*, *815*, *883*, and *897* (BRLU).

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Appendix 1. List of the 39 specimens utilized in the molecular analyses including outgroups. Sampled species are listed alphabetically. The herbarium where the voucher specimen is currently housed is cited in parentheses. GenBank accession numbers are included for each of the six genic regions used in the current study (ITS, *trnL-trnF* intergenic spacer, *matK*, *rps16*, *trnC-petN* intergenic spacer, and *ycf1*). The asterisk (*) indicates those sequences produced during this study. The en dash (–) denotes that no data are available for that region.

Aerangis gracillima (Kraenzl.) J. C. Arends & J. Stewart, *Yaoundé shade house series 1404* (BRLU), MH237060, MH237436, MK685530, *, *, *; *Aziza trilobata* (Summerh.) Farminhão & D'haijère, Gabon, *D'haijère et al. 2* (BRLU), *, –, *, –, –, *; *Aziza trilobata* (Summerh.) Farminhão & D'haijère, Gabon, *Farminhão et al. 11* (BRLU), *, –, *, –, –, *; *Aziza trilobata* (Summerh.) Farminhão & D'haijère, São Tomé and Príncipe, *D'haijère et al. 137* (BRLU), *, –, *, –, –, –; *Cyrtorchis arcuata* (Lindl.) Schltr. subsp. *arcuata*, Cameroon, *Yaoundé shade house series 2761* (BRLU), *, –, –, *, *, *; *Cyrtorchis arcuata* (Lindl.) Schltr. subsp. *whytei* Summerh., Cameroon, *Yaoundé shade house series 2883* (BRLU), *, –, –, *, *, *; *Cyrtorchis ringens* (Rchb. f.) Summerh., Cameroon, *Yaoundé shade house series 1306* (BRLU), MH237053, MH237428, MK685421, *, *, *; *Listrostachys pertusa* (Lindl.) Rchb. f., Cameroon, *unvouchered*, MH237083, MH237463, MK685556, *, *, *; *Mystacidium capense* (L. f.) Schltr., ex hort. Countryside Orchids, *Whitten 1787* (FLAS), DQ091571, DQ091485, DQ091360, *, *, *; *Nephrangis filiformis* (Kraenzl.) Summerh., Cameroon, *Yaoundé shade house series 2916* (BRLU), MH237085, MH237466, MK685558, *, *, *; *Planetangis longicaudata* (Rolfe) Stévart & Farminhão, Gabon, *Gabon shade house series 666* (BRLU), *, –, *, –, –, –; *Planetangis longicaudata* (Rolfe) Stévart & Farminhão, Gabon, *Gabon shade house series 668* (BRLU), MH237161, MH237546, –, –, *, *; *Planetangis longicaudata* (Rolfe) Stévart & Farminhão, Guinea, *Nimba shade house series 1584* (BRLU), *, –, –, –, –, –; *Plectrelminthus caudatus* (Lindl.) Summerh., Cameroon, *Yaoundé shade house series 2803* (BRLU), MH237090, MH237470, MK685563, MK721992, –, MK722023; *Podangis dactyloceras* (Rchb. f.) Schltr., Cameroon, *Yaoundé shade house series 2652* (BRLU), MH237089, MH237469, MH748944, *, *, *; *Podangis dactyloceras* (Rchb. f.) Schltr., cult. K, *Kew 4999* (K), DQ091628, DQ091510, DQ091385, *, *, *; *Podangis dactyloceras* (Rchb. f.) Schltr., unknown provenance, *Z. J. Liu 7179* (NOCC), KJ021018, KJ021010, KJ021022, –, –, –; *Podangis rhipsalisocia* (Rchb. f.) P. J. Cribb & Carlsward, Cameroon, *Yaoundé shade house series 2011* (BRLU), MH237092, MH237473, MK685566, *, *, *; *Podangis rhipsalisocia* (Rchb. f.) P. J. Cribb & Carlsward, Cameroon, *Yaoundé shade house series 2644* (BRLU), –, MH237472, MK685565, *, *, *; *Rangaeris muscicola* (Rchb. f.) Summerh., cult. SEL, *Carlsward 169* (SEL), DQ091630, DQ091513, DQ091387, *, *, EU490774; *Rangaeris muscicola* (Rchb. f.) Summerh., Countryside Orchids, *Carlsward 400* (FLAS), DQ091631, –, –, –, –, –; *Rangaeris muscicola* (Rchb. f.) Summerh., Guinea, *Nimba shade house series 1860* (BRLU), *, –, –, –, –, –; *Rangaeris muscicola* (Rchb. f.) Summerh., Cameroon, *Yaoundé shade house series 3073* (BRLU), *, –, –, –, –, *; *Rangaeris muscicola* (Rchb. f.) Summerh., Cameroon, *Yaoundé shade house series 7298* (BRLU), *, –, –, –, –, *; *Solenangis scandens* (Schltr.) Schltr, Cameroon, *cult. Yaoundé shadehouse Y 3308 YK*, –, MK722044, MK722038, MK722019, MK721987, MK697510; *Summerhayesia laurentii*

(De Wild.) P. J. Cribb, Gabon, in cult. Jardi-Gab *BTO 220*, *, *, –, *, –, *; *Tridactyle anthomaniaca* (Rchb. f.) Summerh., Cameroon, *cult. Yaoundé shade house Y3679 RH* (BRLU), MH236990, MH237359, MK685461, MK721977, MK697519, MK722009; *Tridactyle bicaudata* (Lindl.) Schltr., Rwanda, *Farminhão & Dumbo 221* (BRLU), *, *, *, *, *, –; *Tridactyle bicaudata* (Lindl.) Schltr., Rwanda, *Farminhão & Dumbo 296* (BRLU), *, *, *, *, *, –; *Tridactyle gabonensis* (P. J. Cribb & Laan) R. Rice, Gabon, *cult. Ombrière de Sibang 200* (BRLU), MH237166, MH237551, MK685633, *, *, *; *Tridactyle latifolia* Summerh., Príncipe, *Primo & Stévart 94* (BRLU), MH237024, MH237398, MK685491, MK721988, MK697509, MK722020; *Tridactyle laurentii* (De Wild.) Schltr., Gabon, *unvouchered*, MH236982, MH237351, MK685453, MK721996, MK697523, MK722027; *Tridactyle tridactylites* (Rolfe) Schltr., Cameroon, *Yaoundé shade house series 1993* (BRLU), MH236989, MH237358, MK685460, MK721975, MK697516, MK722007; *Ypsilopus amaniensis* (Kraenzl.) D'haijère & Stévart, Kenya, *Bytebier & Kirika 26* (EA), DQ091634, DQ091512, DQ091386, MK721981, MK697524, MK722013; *Ypsilopus erectus* (P. J. Cribb) P. J. Cribb & J. Stewart, Kenya, *Grieve 1244* (EA), MK714122, MK722042, MK722036, MK721991, MK697515, MK722022; *Ypsilopus longifolius* (Kraenzl.) Summerh., cult. NYBG, MO4274452 (NY), MH237190, MH237578, –, MK722000, MK697532, MK722032; *Ypsilopus schliebenii* (Mansf.) D'haijère & Stévart, *cult. BR 20090389-40*, MH236965, MH237334, MK685438, –, –, –; *Ypsilopus viridiflorus* P. J. Cribb & J. Stewart, Tanzania, *Bytebier 402* (EA), DQ091633, –, DQ091395, MK721971, –, MK722003.

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