

A revised concept of *Rhipidoglossum* (Angraecinae, Orchidaceae)

JOÃO N. M. FARMINHÃO^{1,2*}, PIERRE MEERTS^{1,2}, PASCAL DESCOURVIÈRES³,
VINCENT DROISSART^{1,4,5,6}, MURIELLE SIMO-DROISSART⁶, TARIQ
STÉVART^{1,5,7}

¹*Herbarium et Bibliothèque de Botanique africaine, C.P. 265, Université Libre de Bruxelles, Campus de la Plaine, Boulevard du Triomphe 1050, Brussels, Belgium; E-mail: jnunesde@ulb.ac.be*

²*Plant Ecology and Biogeochemistry, C.P. 244, Université Libre de Bruxelles, Campus de la Plaine, Boulevard du Triomphe, 1050, Brussels, Belgium*

³*UMR 7207 CNRS-MNHN-UPMC, Centre de Recherche sur la Paléobiodiversité et les Paléoenvironnements, 57 rue Cuvier, CP 48, FR 75005, Paris, France*

⁴*AMAP Lab, IRD, CIRAD, CNRS, INRA, Université de Montpellier, Montpellier, France*

⁵*Missouri Botanical Garden, Africa and Madagascar Department, P.O. Box 299, St. Louis, Missouri 63166-0299, USA*

⁶*Plant Systematics and Ecology Laboratory, Higher Teachers' Training College, University of Yaoundé I, P.O. Box 047, Yaoundé, Cameroon*

⁷*Botanic Garden Meise, Domein van Bouchout, Nieuwelaan 38, B-1860 Meise, Belgium*

Abstract

Following the production of a near comprehensive generic phylogenetic analysis of African angraecoid orchids, paraphyly of the genus *Rhipidoglossum* relative to *Cribbia*, *Margelliantha* and *Rhaesteria* was in need of being resolved by integrating morphological observations into this newly available molecular framework. Accordingly, we critically revised the diagnostic traits of each genus by examining about 700 herbarium specimens ascribable to 50 species of *Rhipidoglossum* and three satellite genera. *Cribbia*, *Margelliantha* and *Rhaesteria* are here lumped with *Rhipidoglossum*, along with *Angraecopsis pusilla* and *Diaphananthe millarii*. The presence of pollinaria with two separate disk-shaped viscidia, a trilobed, non-papillate rostellum with midlobe more prominent than lateral lobes and an undivided lip are diagnostic of this more inclusive concept of *Rhipidoglossum*. In line with this new taxonomic arrangement, 11 new combinations in *Rhipidoglossum* are proposed.

Abstract (French)

Suite à des analyses phylogénétiques presque exhaustives pour les genres d'orchidées angraecoïdes d'Afrique, la paraphylie du genre *Rhipidoglossum* par rapport à *Cribbia*, *Margelliantha* et *Rhaesteria* avait besoin d'être révisée en intégrant des observations morphologiques dans ce nouveau contexte moléculaire. En conséquence, nous avons procédé à une révision critique des caractères diagnostiques de chaque genre en examinant environ 700 spécimens d'herbiers appartenant à 50 espèces de *Rhipidoglossum* et à trois genres satellites. *Cribbia*, *Margelliantha* et *Rhaesteria* sont à regrouper avec *Rhipidoglossum*, ainsi qu'*Angraecopsis pusilla* et *Diaphananthe millarii*. La présence de pollinies avec deux viscidies discoïdales séparées, un rostellum trilobé

non papilleux, avec son lobe médian plus proéminent que les lobes latéraux, et un labelle entier, sont les caractères diagnostics de ce concept plus inclusif du genre *Rhipidoglossum*. Conformément à ce nouvel arrangement taxonomique, 11 nouvelles combinaisons de *Rhipidoglossum* sont proposées.

Key words

African orchids, angraecoids, *Angraecopsis*, *Cribbia*, *Diaphananthe*, *Margelliantha*, *Mystacidium*, orchid taxonomy, *Rhaesteria*, *Sphyrarhynchus*, stigmatic callus, Vandaeae

Introduction

Rhipidoglossum is part of the mostly Afro-Malagasy subtribe Angraecinae, which has undergone a spectacular radiation event in the past five million years (Givnish *et al.* 2015). Generic boundaries in Angraecinae are considered by Chase *et al.* (2015) as one of the major remaining unresolved issues in Epidendroideae taxonomy and have thus been the focus of a large project concerning the taxonomy of this large group (Simondroissart *et al.* in press) of about 760 species (Pridgeon *et al.* 2014).

Rhipidoglossum Schlechter (1918: 81) was first revised by Summerhayes (1937), who designated *Rhipidoglossum xanthopollinium* (Reichenbach 1885: 382) Schlechter (1918: 81) as type species. As presently circumscribed (Cribb 2014a), *Rhipidoglossum* also includes taxa formerly placed in the defunct genera *Sarcorhynchus* Schlechter (1918: 104) and *Crossangis* Schlechter (1918: 141), comprising 38 accepted species confined to tropical and southern Africa (Govaerts *et al.* 2017). Based on an overall morphological similarity, Summerhayes (1960) subsumed *Rhipidoglossum*

under *Diaphananthe* Schlechter (1915: 53) as a section of the later, and this treatment was subsequently adopted by several authors working on the flora of Tropical Africa (e.g. Hall 1974, Rasmussen 1974, Cribb 1989, Geerinck 1992, la Croix & Cribb 1998). However, an enlarged concept of *Diaphananthe* including *Rhipidoglossum* was shown to be polyphyletic by the molecular studies in Carlswald *et al.* (2006) and Freudenstein & Chase (2015) and a recently produced broad phylogenetic analysis of Angraecinae (Simo-Droissart *et al.* in press), in which *Rhipidoglossum* is retrieved as sister to *Mystacidium* Lindley (1837: 205), *Angraecopsis* Kränzlin (1900: 171) and *Sphyrarhynchus* Mansfeld (1935: 706). This finding has given credit to the taxonomic treatment of Garay (1972), who was the first to reinstate *Rhipidoglossum*, drawing attention to the distinctive morphology of the pollinaria with two separate viscidia versus a single viscidium found in *Diaphananthe*. Molecular phylogenetics has also shown that *Rhaesteria* Summerhayes (1966: 191), *Cribbia* Senghas (1985: 19), part of *Margelliantha* Cribb (1979: 329) and *Angraecopsis pusilla* Summerhayes (1951: 258) are nested in *Rhipidoglossum* (Simo-Droissart *et al.* in press). Also, *Margelliantha caffra* (Bolus 1893: t. 8) Cribb & Stewart (1985: 413) and *Diaphananthe millarii* (Bolus 1905: 147) Linder (1989: 318), were found to be sister to *Rhipidoglossum* plus the satellite genera, *Cribbia*, *Margelliantha* and *Rhaesteria* (Simo-Droissart *et al.* in press). Accordingly, Simo-Droissart *et al.* (in press) suggested that all these taxa should be lumped into a broad concept of *Rhipidoglossum*. Here we critically review the morphological traits that support the taxonomic rearrangements proposed by Simo-Droissart *et al.* (in press). A short account of the nomenclatural history is provided for each genus or group of species to be moved into *Rhipidoglossum*, and the necessary nomenclatural changes, consisting of 11 new combinations in *Rhipidoglossum*, are also presented.

Materials and methods

About 700 specimens of 48 species of *Rhipidoglossum*, *Rhaesteria*, *Cribbia*, *Margelliantha*, *Angraecopsis pusilla* and *Diaphananthe millarii*, were examined using standard herbarium practices (de Vogel 1987), including material housed in BM, BR, BRLU, COI, K, LISC, LISU, NU, P, and UPS (acronyms following Thiers 2017, continuously updated). Additionally, the type specimens of *Diaphananthe millarii* and *Margelliantha caffra* were not available in these herbaria and were examined through the Global Plants facility (JSTOR 2000-2017). Photographs of living plants, retrieved from *Orchidaceae of Central Africa* (Droissart *et al.* 2017) and from the *World orchid iconography* (WOI 2015-2017) of the Swiss Orchid Foundation at the Herbarium Jany Renz and the Botanical Institute of the University of Basel, were also examined. The distribution of character states indicated as diagnostic for each genus in protologues, and other relevant literature, were critically reviewed considering a comprehensive phylogenetic analysis of the African angraecoids presented in Simo-Droissart *et al.* (in press). Accordingly, generic boundaries were reassessed adopting a strictly phylogenetic view of Linnaean taxonomy (*e.g.* Bateman 2009, Chase *et al.* 2015).

Taxonomic treatment

New generic boundaries and diagnostic traits of *Rhipidoglossum*

Rhipidoglossum forms a well-supported clade if *Rhaesteria*, *Cribbia*, part of *Margelliantha* (*i.e.* excluding *M. caffra*), and *Angraecopsis pusilla* are subsumed under it. This group of taxa can be recognised morphologically by the shared presence of

pollinaria with two separate disk-shaped viscidia, a trilobed non-papillate rostellum with midlobe more prominent than lateral lobes and an entire lip. Overall, the presence of two separate viscidia in African angraecoids is relatively infrequent and can only be found in *Dolabrifolia* (Pfitzer 1889: 216) Szlachetko & Romowicz (2007: 54) apart from the *Sphyrarhynchus-Angraecopsis-Mystacidium-Rhipidoglossum* clade (Simo-Droissart *et al.* in press). Two separate viscidia can also be found in *Angraecum claussensi* De Wildeman (1916: 184) and *A. firthii* Summerhayes (1958: 267), but in this case the two viscidia initially adhere to each other and come away together when removed from the column (Summerhayes 1958).

Margelliantha caffra and *Diaphananthe millarii* form a clade sister to this more inclusive concept of *Rhipidoglossum*, and since they also share the same general floral morphology (*e.g.* non-papillate rostellum with a prominent midlobe), they too are here included in *Rhipidoglossum*. In turn, *Mystacidium*, *Angraecopsis* and *Sphyrarhynchus* together are sister to this inclusive concept of *Rhipidoglossum*, and the four genera share the same trilobed rostellar structure. This observation led Rice (2005) to move *Cribbia*, *Margelliantha* and part of *Rhipidoglossum* into *Angraecopsis*, creating the new subgenera *Cardiochilos* Rice (2005: 19) and *Angraecopidoglossum* Rice (2005: 21) within the last to encompass these species. Contrary to what is stated by Cribb (2014a: 433), Rice (2006) did not formally move *Rhipidoglossum* into *Mystacidium*, despite his claim that no clear differences could be found among *Rhipidoglossum*, *Angraecopsis* and *Mystacidium*. However, *Angraecopsis* and *Mystacidium* present a distinctive trilobed lip and a rostellum in which lateral lobes are longer or subequal in length to the midlobe, which sets them apart from *Rhipidoglossum*. Additionally, in the case of *Mystacidium*, the lateral lobes of the rostellum are covered in conspicuous papillae absent in any other closely related taxa. In *Angraecopsis* sect. *Coenadenium*

Summerhayes (1951: 259), in *Mystacidium pulchellum* (Kränzlin 1900: 374) Schlechter (1918: 126) and in *Sphyrarhynchus*, the two viscidia are connate. A taxonomic revision of *Mystacidium*, *Angraecopsis* and *Sphyrarhynchus* (the ‘SAM clade’) is presented by Martos *et al.* (in press), shedding further light on the taxonomy of the SAM alliance and *Rhipidoglossum*. Martos *et al.* (2017) have notably found *Mystacidium* to be polyphyletic, with *Mystacidium tanganyikense* Summerhayes (1945: 113) from Tanzania and the Zambezian region located in *Rhipidoglossum* and satellite genera. Despite the presence of conspicuous papillae on the rostellum arms that sets the species apart (Martos *et al.* 2017), the prominent midlobe of the rostellum of *M. tanganyikense* together with its overall floral morphology also suggest that it is best treated in *Rhipidoglossum*. Finally, future revisionary work should focus on exploring the phylogenetic affinities of poorly known species of *Rhipidoglossum* (e.g. *Rhipidoglossum stellatum* (Cribb 1989: 538) Szlachetko & Olszewski 2001: 850, *Rhipidoglossum oxycentron* (Cribb 1977: 180) Senghas 1986: 1111) and the SAM clade (i.e. *Mystacidium nguruense* Cribb 1989: 596 and *M. pulchellum*) endemic to East Africa. Considering their overall floral morphology, *M. nguruense* may be best treated in *Rhipidoglossum*, whereas *M. pulchellum* with its single viscidium and zig-zag inflorescence axis (Schuiteman 1981) is probably best placed in *Sphyrarhynchus*. The inclusion of these species in a comprehensive molecular phylogenetic framework will be key to further clarify relationships of *Rhipidoglossum* and putatively morphologically similar taxa.

***Margelliantha caffra* and *Diaphananthe millarii*:**—These two species (Fig. 1F) form a well-supported clade (Simo-Droissart *et al.* in press) characterised by short stems, white

tepals contrasting with a green column, slender floral pedicels, an elongate cylindrical lip spur and a peg-like median rostellar lobe. Both species were formerly placed in *Mystacidium* (Bolus 1905) and are endemic to eastern South Africa (Govaerts *et al.* 2017). Rostellar structure and overall floral morphology of the two species are similar to those of *Rhipidoglossum curvatum* (Rolfe 1897: 174) Garay (1972: 195) (Figure 1B), and the white conspicuously pedicellate flowers with a contrasting green anther cap are reminiscent of those of *Margelliantha* and *Cribbia thomensis* la Croix & Cribb in Cribb & la Croix (1997: 745). The latter led Cribb & Stewart (1985) to move *Mystacidium caffrum* (Bolus) Bolus (1905: 145) to *Margelliantha*. Afterwards Linder (1989), recognising the clear similarity of *Mystacidium millarii* (1905: 147) and *Margelliantha caffra*, moved both into *Diaphananthe*, drawing attention to their rostellar structure and that of *Rhipidoglossum montanum* (Piers 1969: 248) Senghas (Senghas 1986: 1111) (see also Cribb & Stewart 1985), then regarded as part of *Diaphananthe*. Carlswald *et al.* (2006) were the first to retrieve *D. millarii* as sister to *Rhipidoglossum* and *Cribbia*, a relationship confirmed by Simo-Droissart *et al.* (in press) who found this species together with *M. caffra* as sister of *Rhipidoglossum*. We preliminarily considered creating a new genus that would be sister to *Rhipidoglossum* to accommodate these two species, but their overall floral resemblance to *Rhipidoglossum* led us to move both into a morphologically diverse (Figure 1) and geographically widespread *Rhipidoglossum*. In this way, we follow the general prescription of avoiding the recognition of small genera with little grouping information (Bateman 2009). *Mystacidium tanganyikense* was found to be nested in the same clade grouping *D. millarii* and *M. caffra* by Martos *et al.* (in press), who pointed out the presence of a penicillate callus in the mouth of the spur as a feature common to the three species. In habit, with its short stem and pendent wiry inflorescences, *M. tanganyikense* presents some similarities to *Rhipidoglossum*

melianthum (Cribb 1979: 335) from Tanzania. In turn, regarding its floral morphology, *M. tanganyikense* is morphologically similar to *R. stellatum* and *Rhipidoglossum tanneri* (Cribb in Cribb & Stewart 1985: 411) Senghas (1986: 1111), also from Tanzania, with which it shares a similar midlobe of the rostellum with a conspicuous bifid apex. Whether these morphological traits of *M. tanganyikense* and these *Rhipidoglossum* species are due to common descent are a result of convergent evolution associated to a common pollinator guild is something to be ascertained in future phylogenetic studies of *Rhipidoglossum*. Without a more comprehensive molecular sampling of *Rhipidoglossum* and SAM species, notably from East Africa, we prefer not to transfer *M. tanganyikense* to *Rhipidoglossum* at this time.

***Rhaesteria*:**—*Rhaesteria eggelingii* Summerhayes (1966: 191; Fig. 1E), the single species of *Rhaesteria*, was found to be deeply embedded in *Rhipidoglossum* (Simondroissart *et al.* in press). This Albertine Rift endemic is only known from the montane forests of Uganda and Rwanda (Fischer *et al.* 2010, Govaerts *et al.* 2017). Specimens attributed to this taxon were misidentified by Geerinck (1988, 1990) as *Angraecum humile* Summerhayes (1958: 269) and *A. petterssonianum* Geerinck (1990: 181; Delepierre & Lebel 2001). The morphological uniqueness of the genus supposedly rests on the presence of a hammer-shaped median rostellar lobe and connation of tepals along their basal third (Summerhayes 1966). Comparative morphological analysis revealed, however, that an identical hammer-shaped rostellum can also be found in some species of *Rhipidoglossum*, notably *R. melianthum* (Cribb 1979: 335) Senghas (1986: 1110), *R. ochyrae* Szlachetko & Olszewski (2001: 868), *R. stellatum* and *R. tanneri*, and the basal tepal connation, although not as evidently, is also observed in *R. adoxum* (Rasmussen 1974: 229) Senghas (1986: 1110). Rice (2005) pointed out the similarity of *Rhaesteria*

to some species of *Rhipidoglossum*, notably to *R. melianthum* and *R. stellatum*, for which he created the section *Malleiform* Rice (2005: 20) within *Angraecopsis*. Molecular evidence (Simo-Droissart *et al.* in press) indicates, however, a close relationship of *Rhaesteria* to *R. rutilum* (Reichenbach 1885: 382) Schlechter (1918: 81), but a more comprehensive sampling of *Rhipidoglossum* is needed to clarify infrageneric taxonomy. In any case, all results strongly support inclusion of *Rhaesteria* in *Rhipidoglossum*.

***Margelliantha*:**—The genus as circumscribed by Cribb (2014b) was revealed to be polyphyletic by Simo-Droissart *et al.* (in press) with *M. lebellii* Fischer & Killmann in Killmann & Fischer (2007: 745) being nested in *Diaphananthe*, and *M. caffra* sister to *D. millarii*, as previously discussed. Therefore, here we will discuss only the four species of *Margelliantha s.s.* originally enumerated by Cribb (1979) in his description of the genus: *Margelliantha leedalii* Cribb (1979: 333; Fig. 1G), the type species, *Margelliantha globularis* Cribb (1979: 331), *Margelliantha clavata* Cribb (1979: 331) and *Margelliantha burtii* Summerhayes (1937: 82) Cribb (1979: 331). These four species form a morphologically cohesive group. *Margelliantha burtii* (Fig. 1H) is nested within *Rhipidoglossum* as sister to *Cribbia* plus *Angraecopsis pusilla* (Simo-Droissart *et al.* in press). *Margelliantha burtii* was originally described by Summerhayes (1934) in *Diaphananthe* but later transferred to *Rhipidoglossum* (Summerhayes 1937). This species differs from the other three *Margelliantha* in its larger size and occurrence in the Albertine Rift (Govaerts *et al.* 2017). Cribb (1979) based the description of *Margelliantha* on the shared campanulate pearly white flowers, ecallose lip, thin-textured rostellum and prominent rim on the lower margin of the stigma. However, none of these character states is mutually exclusive relative to *Rhipidoglossum*, and Geerinck

(1992) was the first to question whether *Margelliantha* should instead be included in *Rhipidoglossum* (then *Diaphananthe* sect. *Rhipidoglossum*). A lip callus can actually be found in *M. clavata* (Fig. 1I), challenging the original description and delimitation of *Margelliantha*. A prominent lower rim on the stigma, which we suggest being termed a stigmatic callus, also occurs in *Cribbia* (being particularly conspicuous in *C. pendula* la Croix & Cribb in Cribb & la Croix (1997: 747) and in some species of *Rhipidoglossum* such as *R. candidum* (Cribb 1979: 335) Senghas (1986: 1110) and *R. tenuicalcar* (Summerhayes 1945: 109) Garay (1972: 196). Although the median rostellar lobe of *Margelliantha* (and *Cribbia*) has been described as thin-textured and digitiform and thus different from the peg-like one reported for *Rhipidoglossum*, intermediate states can be observed among *Rhipidoglossum* species, with *R. kamerunense* (Schlechter 1906: 161) Garay (1972: 195), and *R. mildbraedii* (Kränzlin 1909: 342) Garay (1972: 195), illustrating such morphological variation. *Rhipidoglossum mildbraedii*, a little known-species endemic to the volcano belt of the eastern Democratic Republic of the Congo (Govaerts *et al.* 2017), is particularly close to *Margelliantha* in its overall morphology. Finally, the striking similarity in floral morphology among *Margelliantha*, *C. thomensis* and *M. caffra*/*D. millari* is possibly due to convergent evolution associated with a shared group of pollinators. We therefore propose to lump *Margelliantha* with *Rhipidoglossum*.

***Cribbia*:**—All four species of *Cribbia* (Fig. 1J–M) were found to be nested in *Rhipidoglossum* with *Angraecopsis pusilla* as their sister (Simo-Droissart *et al.* in press). Senghas (1985) described *Cribbia* as including only *C. brachyceras* (syn. *Rangaeris biglandulosa* Summerhayes 1936: 228). It was a segregate of *Rangaeris* Summerhayes (1936: 227), and Senghas alluded to its divergent pollinarium structure

comprising two viscidia. Later, Senghas (1986) suggested a close relationship between *Cribbia* and *Rhipidoglossum* based on distinctiveness of their two separate viscidia, an opinion confirmed by Carlswald *et al.* (2006) in their molecular analysis. Cribb (1996) and Cribb & la Croix (1997) described three more species in the genus from the Atlantic side of central Africa, including two endemics from São Tomé (Stévant & Oliveira 2000). The column of *Cribbia* is similar to that of *Margelliantha*, and the same comparative considerations relative to *Rhipidoglossum* also apply here. The most distinctive traits of *Cribbia* are their narrowly ovate and not orbicular to flabellate sepals, petals and lip that also occur in most species of *Rhipidoglossum*. However, *Rhipidoglossum microphyllum* Summerhayes (1945: 93) and *R. montanum* also have narrowly ovate tepals, and the overall floral appearance of the former is reminiscent of that of *Cribbia*. Molecular data are pending to clarify whether this species is closely related to *Cribbia*. The molecular results of Simo-Droissart *et al.* (in press) identify a clade comprising *A. pusilla*, *Cribbia*, *Margelliantha*, *Rhipidoglossum arbonnieri* (Geerinck in Arbonnier & Geerinck 1993: 256) Fischer, Killman, Lebel & Delepierre (2011: 445) and *R. kamerunense*. These taxa share the same habit with short stems and possess conspicuously pedicellate flowers disposed along a distichous inflorescence and a dorso-ventrally flattened median rostellar lobe. This set of character states is divergent from most species of *Rhipidoglossum*, which develop long stems and have short pedicels. However, additional molecular sampling is needed to resolve the infrageneric taxonomy of our recircumscribed concept of *Rhipidoglossum*. Meanwhile, considering all evidence, *Cribbia* is to be subsumed in *Rhipidoglossum*.

***Angraecopsis pusilla*:**—This species (Fig. 1N) was identified as sister to *Cribbia* by Simo-Droissart *et al.* (in press), and consequently it is also embedded in

Rhipidoglossum. This dwarf epiphytic species endemic to the Albertine Rift (Fischer *et al.* 2010) was described by Summerhayes (1951), who erected the new section *Cardiochilos* based on its entire lip to accommodate this “aberrant species” of *Angraecopsis*. Its ovate lip, two separate viscidia and rostellar structure corroborate its relationships as highlighted by Simo-Droissart *et al.* (in press), and, thus, we propose to move this species to *Rhipidoglossum*. Two other species of *Angraecopsis* were included in section *Cardiochilos*, *Angraecopsis lovettii* Cribb (1989: 601) and *Angraecopsis malawiensis* Cribb in la Croix *et al.* (1983: 26), by Cribb & la Croix (1998), but to clarify their position relative to *A. pusilla* a detailed morphological examination and molecular analysis is needed for *Rhipidoglossum* and species in the SAM clade.

Rhipidoglossum Schlechter (1918: 80). Type species (designated by Summerhayes 1937: 80) *Rhipidoglossum xanthopollinium* (Rchb.f.) Schlechter (1918: 81).

Margelliantha Cribb (1979: 329). Type species *Margelliantha leedalii* Cribb (1979: 333)

Cribbia Senghas (1985: 19). Type species *Cribbia brachyceras* (Summerh.) Senghas (1985: 19)

Rhaesteria Summerhayes (1966: 191). Type species *Rhaesteria eggelingii* Summerhayes (1966: 191)

Rhipidoglossum brachyceras (Summerh.) Farminhão & Stévant, *comb. nov.* Basionym: *Aerangis brachyceras* Summerhayes (1934: 213). Type:—DEMOCRATIC REPUBLIC OF THE CONGO. Virunga Mts.: E. of Mt. Namlagira, Kanamharargi Lavas, January 1931, *Burt* 3123 (holotype K!, K000306405).

Homotypic synonyms:

Rangaeris brachyceras (Summerh.) Summerhayes (1936: 228)

Cribbia brachyceras (Summerh.) Senghas (1985: 19)

Azadehdelia brachyceras (Summerh.) Braem *nom. superfl.* (1988: 34)

Angraecopsis brachyceras (Summerh.) Rice (2005: 19).

Heterotypic synonym:

Rangaeris biglandulosa Summerh. (1936: 228). Type:—GUINEA. Fouta Djallon: Dalaba Plateau, Diaguissa, 1000–1300 m, October 1907, *Chevalier 18782* (holotype P!, MNHN-P-P00388173; isotype P!, MNHN-P-P00388172).

Rhipidoglossum caffrum (Bolus) Farminhão & Stévant, *comb. nov.* Basionym:

Angraecum caffrum Bolus (1893: t. 8). Type:—SOUTH AFRICA. Pondoland:

Emagusheni inter Fort William and Umtamvuna, 3500 ft, January 1886, *Tyson 2841* (lectotype BOL image!, BOL149998; isolectotype K).

Homotypic synonyms:

Mystacidium caffrum (Bolus) Bolus (1905: 145).

Margelliantha caffra (Bolus) Cribb & Stewart (1985: 413).

Diaphananthe caffra (Bolus) Linder (1989: 318).

Angraecopsis caffra (Bolus) Rice (2005: 19), *nom inval.*.

Rhipidoglossum clavatum (P.J.Cribb) Farminhão & Stévant *comb. nov.* Basionym:

Margelliantha clavata Cribb (1979: 331). Type:—TANZANIA. Lushoto District: W Usambara Mts, Magamba Forest Reserve, fl. in cult., 6 March 1943, *Eggeling in Moreau 400* (holotype K!, K000284750; isotype EA).

Homotypic synonyms:

Angraecopsis clavata (P.J.Cribb) Rice (2005: 21)

Rhipidoglossum confusum (P.J.Cribb) Farminhão & Stévant, *comb. nov.* Basionym:

Cribbia confusa Cribb (1996: 359). TYPE:—CAMEROON. Mt Cameroon, Mapanja to Mann's Spring, 6 October 1992, *Thomas 9365* (holotype K!, K000107356; isotype YA).

Homotypic synonyms:

Angraecopsis confusa (P.J.Cribb) Rice (2005: 19).

Rhipidoglossum eggelingii (Summerh.) Farminhão & Stévant, *comb. nov.* Basionym:

Rhaesteria eggelingii Summerhayes (1966: 191). Type:—UGANDA. Kigezi: Impenetrable Forest, on small savanna tree in grassland on outskirts, November 1948, *Eggeling 5849* (holotype K!, K000306602).

Heterotypic synonym:

Angraecum petterssonianum Geerinck (1990: 181). Type:—RWANDA. Nyungwe: 2300 m, 1975, *Troupin 15744* (holotype BR!, BR0000008814753).

Rhipidoglossum globulare (P.J.Cribb) Farminhão & Stévant, *comb. nov.* Basionym:

Margelliantha globularis Cribb (1979: 331). Type:—TANZANIA. Morogoro District: Uluguru Mts, 1250 m, 25 September 1932, *Wallace 172* (holotype K!, K000354425).

Homotypic synonym:

Angraecopsis globularis (P.J.Cribb) Rice (2005: 21).

Rhipidoglossum leedalii (P.J.Cribb) Farminhão & Stévant, *comb. nov.* Basionym:

Margelliantha leedalii P.J.Cribb (1979: 333). Type:—TANZANIA. Morogoro District: Uluguru Mts, Bondwa, track up to E ridge of peak, 23 January 1976, *Cribb & Grey-Wilson 10380* (holotype K!, K000284733).

Homotypic synonym:

Angraecopsis leedalii (P.J.Cribb) Rice (2005: 21).

Rhipidoglossum millarii (Bolus) Farminhão & Stévant, *comb. nov.* Basionym:

Mystacidium millarii Bolus (1905: 147). Type:—SOUTH AFRICA. Natal: near Durban, 8 January 1902, *Millar in Medley-Wood 8437* (holotype BOL image!, BOL149999).

Homotypic synonyms:

Diaphananthe millarii (Bolus) Linder (1989: 318).

Angraecopsis millarii (Bolus) Rice (2005: 19).

Rhipidoglossum pendulum (la Croix & P.J.Cribb) Farminhão & Stévant, *comb. nov.*

Basionym: *Cribbia pendula* la Croix & Cribb in Cribb & la Croix (1997: 747). Type:—SÃO TOMÉ AND PRÍNCIPE. Pico São Tomé: 28 February 1995, *Brune in la Croix ST38A* (holotype K!, K000220048).

Homotypic synonym:

Angraecopsis pendula (la Croix & P.J.Cribb) Rice (2005: 20).

Rhipidoglossum pusillum (Summerh.) Farminhão & Stévant, *comb. nov.* Basionym:

Angraecopsis pusilla Summerhayes (1951: 258). Type:—DEMOCRATIC REPUBLIC OF THE CONGO. Parc National Albert: Nyamlagira–Tsambene, 1700 m, 16 January 1945, *Germain 3432* (holotype BR!, BR0000008809872; isotype K!, 10664.000).

Rhipidoglossum thomense (la Croix & P.J.Cribb) Farminhão & Stévant, *comb. nov.*

Basionym: *Cribbia thomensis* la Croix & Cribb in Cribb & la Croix (1997: 745).

Type:—SÃO TOMÉ AND PRÍNCIPE. Pico São Tomé: *Brune in I. la Croix ST38*
(holotype K!, K000306404).

Homotypic synonym:

Angraecopsis summerhayesii Rice (2005: 20), published as a *nomen novum*.

.

Acknowledgements

We thank the curators and staff of BM, BR, BRLU, COI, K, LISC, LISU, NU, P and UPS for making their collections available and kindly allowing us to use the facilities of their institutions. Lab work and herbarium visits were supported by the U.S. National Science Foundation (1051547, T. Stévant as PI, G. M. Plunkett as Co-PI.). Additionally, within the framework of the first author's MSc and ongoing PhD work, funding was obtained from a TROPIMUNDO Erasmus Mundus Category B scholarship and by a grant of the Fund for Research Training in Industry and Agriculture (FNRS-FRIA). We are grateful to the American Orchid Society for support of the three last authors' work in Central Africa. We thank Benny Bytebier, Eberhard Fischer, Phillip J. Cribb and Thomas Couvreur for making available their photos of *Rhipidoglossum*. Finally, we thank editor Mark W. Chase and two anonymous reviewers for their comments and corrections, which helped to improve this manuscript substantially.

References

Arbonnier, M. & Geerinck, D. (1993) Contribution à l'étude des Orchidaceae du Burundi (première partie). *Belgian Journal of Botany* 126: 253–261.

- Bateman, R.M. (2009) Evolutionary classification of European orchids: the crucial importance of maximising explicit evidence and minimising authoritarian speculation. *Journal Europäischer Orchideen* 41: 243–318.
- Bolus, H. (1893) *Icones orchidearum Austro-Africanarum extra-tropicarum*. Wesley, London, 50 pl.
- Bolus, H. (1905) Contributions to the African flora. *Transactions of the South African Philosophical Society* 16: 135–152.
- Carlswald, B.S., Whitten, W.M., Williams, N.H. & Bytebier, B. (2006) Molecular phylogenetics of Vandaeae (Orchidaceae) and the evolution of leaflessness. *American Journal of Botany* 93: 770–786. <https://doi.org/10.3732/ajb.93.5.770>
- Chase, M.W., Cameron, K.M., Freudenstein, J.V., Pridgeon, A.M., Salazar G., van den Berg, C. & Schuiteman, A. (2015) An updated classification of Orchidaceae. *Botanical Journal of the Linnean Society* 177: 151–174. <https://doi.org/10.1111/boj.12234>
- Cribb, P.J. (1977) New orchids from south Central Africa. *Kew Bulletin* 32: 137–187.
- Cribb, P.J. (1979) New or little known orchids from East Africa. *Kew Bulletin* 34: 321–340.
- Cribb P.J. & Stewart J. (1985) Additions to the orchid flora of tropical Africa. *Kew Bulletin* 40: 399–419.
- Cribb P.J. (1989) Orchidaceae (part 3). In: Polhill R.M. (Ed.), *Flora of tropical East Africa*. Rotterdam, Balkema, pp. 413–652.
- Cribb, P.J. (1996) New species and records of Orchidaceae from West Africa. *Kew Bulletin* 51: 353–363.
- Cribb, P.J. & la Croix, I.F. (1997) A synopsis of the genus *Cribbia* Senghas (Orchidaceae), with two new species from São Tomé. *Kew Bulletin* 52: 743–748.

- Cribb P.J. (2014a) (2014) *Rhipidoglossum*. In: Pridgeon, A.M., Cribb, P.J., Chase, M.W. & Rasmussen F.N. (Eds.) *Genera orchidacearum 6, Epidendroideae (3)*. Oxford University Press, Oxford, pp. 431–433.
- Cribb P.J. (2014b) (2014) *Margelliantha*. In: Pridgeon, A.M., Cribb, P.J., Chase, M.W. & Rasmussen F.N. (Eds.) *Genera orchidacearum 6, Epidendroideae (3)*. Oxford University Press, Oxford, pp. 405–407.
- Delepierre, G. & Lebel J.-P. (2001) Supplément à l'étude des Orchidaceae du Rwanda et des environs (III). *Taxonomania* 2: 1–9.
- de Vogel, E.F. (1987) Manual of herbarium taxonomy: theory and practice. UNESCO Regional Office for Science and Technology for Southeast Asia, Jakarta, 164 pp.
- De Wildeman, É. (1916) Additions à la Flore du Congo. Bulletin du Jardin botanique de l'État à Bruxelles 5: 117–268.
- Droissart, V., Simo, M., Sonké, B., Geerinck, D. & Stévant, T. (2017) *Orchidaceae of Central Africa*. Available from: <http://www.orchid-africa.net/> (accessed 13 October 2017).
- Fischer, E., Killmann, D., Delepierre, G. & Lebel, J.P. (2010) *The orchids of Rwanda. An illustrated field guide* (Koblenz Geographical Colloquia, Series Biogeographical Monographs 2). Universität Koblenz-Landau, Koblenz, 439 pp.
- Fischer, E., Killmann, D., Lebel, J.-P. & Delepierre, G. (2011) *Diaphananthe liae*, eine neue Art aus dem Nyungwe Nationalpark, Ruanda—*Diaphananthe liae*, a new species from Nyungwe National Park, Rwanda. *Die Orchidee* 62: 440–446.
- Freudenstein, J.V. & Chase, M.W. (2015) Phylogenetic relationships in Epidendroideae (Orchidaceae), one of the great flowering plant radiations: progressive specialization and diversification. *Annals of Botany* 115: 665–681.
<https://doi.org/10.1093/aob/mcu253>

- Garay, L.A. (1972) On the systematics of the monopodial orchids I. *Botanical Museum Leaflets, Harvard University* 23: 149–212.
- Geerinck, D. (1988) Orchidaceae. In: Troupin, G. (Ed.), *Flore du Rwanda–Spermatophytes* 4. Musée Royal de l’Afrique Centrale, Tervuren, pp. 505–629.
- Geerinck, D. (1990). Notes taxonomiques sur des Orchidacées d’Afrique centrale X. *Bulletin du Jardin botanique national de Belgique/Bulletin van de Nationale Plantentuin van België* 60: 181–190.
- Geerinck, D. (1992) Orchidaceae (seconde partie). In: Bamps, P. (Ed.), *Flore d’Afrique Centrale (Zaire–Rwanda–Burundi) spermatophytes*. Jardin Botanique National de Belgique, Leuven, pp. 297–780.
- Givnish, T.J., Spalink, D., Ames, M., Lyon, S.P., Hunter, S.J., Zuluaga, A., Iles, W.J.D., Clements, M.A., Arroyo, M.T.K., Leebens-Mack, J., Endara, L., Kriebel, R., Neubig, K.M., Whitten, W.M., Williams, N.H. & Cameron, K.M. (2015) Orchid phylogenomics and multiple drivers of their extraordinary diversification. *Proceedings of the Royal Society of London: Biological Sciences* 282: 20151553.
- <https://doi.org/10.1098/rspb.2015.1553>
- Govaerts, R., Bernet, P., Kratochvil, K., Gerlach, G., Carr, G., Alrich, P., Pridgeon, A.M., Pfahl, J., Campacci, M.A., Holland Baptista, D., Tigges, H., Shaw, J., Cribb, P.J., George, A., Kreuz, K. & Wood, J. (2017). *World checklist of Orchidaceae*, Royal Botanic Gardens, Kew. Available from: <http://apps.kew.org/wcsp/> (accessed 10 July 2017).
- Hall, J.B. (1974) African orchids: XXXIV. *Kew Bulletin* 29: 427–429.
- JSTOR (2000–2016) *Global plants*. Available from: <http://plants.jstor.org> (accessed 10 July 2017).

- Killmann, D. & Fischer, E. (2007) *Margelliantha lebelii*, eine neue *Margelliantha*-Art aus dem Nyungwe Nationalpark, Ruanda – *Margelliantha lebelii*, a new species of *Margelliantha* from Nyungwe National Park, Rwanda. *Die Orchidee* 58: 83–90.
- Kränzlin, F. (1900) Orchidaceae africanae. In: Engler, A. (Ed.), Beiträge zur Flora von Afrika XIX. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 28: 162–179.
- Kränzlin, F. (1900) Orchidaceae. In: Engler, A. (Ed.), Beiträge zur Flora von Afrika XX. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 28: 367–374.
- Kränzlin, F. (1909) Orchidaceae. In: Engler, A. (Ed.), Beiträge zur Flora von Afrika XXXV. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 43: 330–343.
- la Croix, I.F., la Croix, E.A.S., la Croix, T.M., Hutson, J.A. & Johnston-Stewart, N.G.B. (1983) *Malawi orchids, volume I, epiphytic orchids*. Montfort, Blantyre, 150 pp.
- la Croix, I.F. & Cribb, P.J. (1998) Orchidaceae (part 2). In: Pope, G.V. (Ed.), *Flora Zambesiaca* 11(2). Royal Botanic Gardens, Kew, pp. 321–569.
- Linder, H. P. (1989) Notes on southern African angraecoid orchids. *Kew Bulletin* 44: 317–319.
- Lindley, J. (1837) Notes upon some genera and species of Orchidaceae in the collection formed by Mr. Drédge, at the Cape of Good Hope. *Companion to the Botanical Magazine* 2: 200–210.
- Mansfeld, R. (1935) Orchidaceae III. In: Mildbraed, J. (Ed.), Neue und seltene Arten aus Ostafrika (Tanganyika-Territ. Mandat) leg. H. J. Schlieben, X. *Notizblatt des Botanischen Gartens und Museums zu Berlin-Dahlem* 12: 703–706.
- Martos, F., Le Péchon, T., Johnson, S. D., & Bytebier, B. (2017) A reassessment of *Angraecopsis*, *Mystacidium* and *Sphyrarhynchus* (Orchidaceae: Vandeeae) based on

- molecular and morphological evidence. *Botanical Journal of the Linnean Society* 186: 1–17.
- Piers, F. (1969) Ober die Orchideen Ostafrikas—*Angraecum montanum*—eine neue Angraecum-Art aus Ostafrika. *Die Orchidee* 20: 248.
- Pfitzer, E.H.H. (1889) Orchidaceae. In: Engler A. & Prantl K. (Eds.). Die natürlichen Pflanzenfamilien 3: 52–220. Engelmann, Leipzig.
- Pridgeon, A.M., Cribb, P.J., Chase, M.W. & Rasmussen F.N. (2014) *Genera orchidacearum* 6, *Epidendroideae* (3). Oxford University Press, Oxford, 544 pp.
- Rasmussen, F.N. (1974) *Diaphananthe adoxa* sp. nov. (Orchidaceae) from southern Ethiopia and the inclusion of *Sarcorhynchus* in *Diaphananthe*. *Norwegian Journal of Botany* 21: 227–232.
- Reichenbach, H.G. (1885) Comoren-Orchideen Herrn Léon Humblot's. *Flora* 68: 377–382.
- Rice, R. (2005). A preliminary checklist & survey of the subtribe Aerangidinae (Orchidaceae). Oasis The Journal Publishing Department, Dora Creek, 51 pp.
- Rice, R. (2006) Notes on the subtribe Aerangidinae (Orchidaceae). *Oasis* 3: 13–16.
- Schlechter, R. (1906) Orchidaceae africanae IV. In: Engler, A. (Ed.), Beiträge zur Flora von Afrika XXIX. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 38: 142–165.
- Schlechter, R. (1915) Orchidaceae Stolzianae, ein Beiträge zur Orchideenkunde des Nyassa-Landes. In: Engler, A. (Ed.), Beiträge zur Flora von Afrika XVII. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 53: 477–605.
- Schlechter, R. (1918) Versuch einer natürlichen Neuordnung der afrikanischen angraekoiden Orchidaceen. *Beihefte zum Botanischen Centralblatt* 36: 62–181.
- Schuiteman, A. (1981) *Mystacidium pulchellum* (Krzl.) Schltr. syn. *Listrostachys pulchella* Krzl. *Orchideen* 43: 214–217.

- Senghas, K. H. (1985) *Cribbia* und *Microterangis*, zwei neue Orchideengattungen. *Die Orchidee* 36: 19–22.
- Senghas, K.H. (1986) 15. Tribus: Vandaeae. *In*: Brieger, F.G., Maatsch, R. & K.H. Senghas (Eds.), *Rudolf Schlechter Die Orchideen, Beschreibung, Kultur und Zuchtung, ed. 3*. Parey, Berlin, pp. 973–1130.
- Simo-Droissart, M., Plunkett, G. M., Droissart, V., Edwards, M. B., Farminhão, J. N. M., Ječmenica, V., D'hajjère, T., Lowry II, P. P., Sonké, B., Micheneau, C., Carlsward, B. S., Azandi L., Verlynde, S., Hardy, O. J., Martos, F., Bytebier, B., Fischer, E. & Stévert, T. (in press) New phylogenetic insights toward developing a natural generic classification of African angraecoid orchids (Vandaeae, Orchidaceae). *Molecular Phylogenetics and Evolution*.
<https://doi.org/10.1016/j.ympev.2018.04.021>
- Summerhayes, V.S. (1934) African orchids: VI. *Bulletin of Miscellaneous Information (Royal Botanic Gardens, Kew)* 1934: 205–214.
- Summerhayes, V.S. (1936) African orchids: VIII. *Bulletin of Miscellaneous Information (Royal Botanic Gardens, Kew)* 1936: 221–233.
- Summerhayes, V.S. (1937) A review of the genus *Rhipidoglossum* Schltr. *Blumea*, supplement 1: 78–86.
- Summerhayes, V.S. (1945) African orchids XVI. *Botanical Museum Leaflets, Harvard University* 12: 89–116.
- Summerhayes, V.S. (1951) A revision of the genus *Angraecopsis*. *Botanical Museum Leaflets, Harvard University* 14: 240–261.
- Summerhayes, V.S. (1958) African orchids: XXVI. *Kew Bulletin* 13: 257–281.
- Summerhayes, V.S. (1960) African orchids: XXVII. *Kew Bulletin* 14: 126–157.
- Summerhayes, V.S. (1966) African orchids: XXX. *Kew Bulletin* 20: 165–199.
- Stévert, T. & Oliveira, F. (2000) Guide des orchidées de São Tomé et Príncipe: Guia dos Orchídeas de São Tomé e Príncipe. ECOFAC, São Tomé, 258 pp.

- Szlachetko, D.L. & Olszewski, T.S. (2001) Orchidacées 3. *In*: Achoundong G. & Morat P. (Eds.), *Flore du Cameroun 36*. Ministère de la Recherche Scientifique et Technique, Yaoundé, pp. 666–948.
- Szlachetko, D.L. & Romowicz, A. (2007) *Dolabrifolia*, un nouveau genre d'orchidées de l'alliance *Angraecum*. *Richardiana* 7: 53–54.
- Thiers, B. (2017) *Index herbariorum: a global directory of public herbaria and associated staff*. New York Botanical Garden's Virtual Herbarium, New York. Available from: <http://sweetgum.nybg.org/ih/> (accessed 10 July 2017).
- WOI (2015-2017) *World orchid iconography*. Swiss Orchid Foundation at the Herbarium Jany Renz, Botanical Institute, University of Basel, Basel. Available from: <https://orchid.unibas.ch/index.php/en/database-search/advanced-search> (accessed 24 August 2017).

Figure 1. An overview of floral diversity in *Rhipidoglossum*, with illustrative photos of some species of the genus, including those formerly placed in *Rhaesteria*, *Cribbia* and *Margelliantha*. A. *Rhipidoglossum xanthopollinium*. B. *Rhipidoglossum curvatum*. C. *Rhipidoglossum densiflorum*. D. *Rhipidoglossum rutilum*. E. *Rhipidoglossum eggelingii*. F. *Rhipidoglossum millarii*. G. *Rhipidoglossum leedalii*. H. *Rhipidoglossum burtii*. I. *Rhipidoglossum clavatum*. J. *Rhipidoglossum thomense*. K. *Rhipidoglossum brachyceras*. L. *Rhipidoglossum confusum*. M. *Rhipidoglossum pendulum*. N. *Rhipidoglossum pusillum*. Photographs A & K by Vincent Droissart; B by Thomas Couvreur; C, D, J, L & M by Tariq Stévant; E, H & N by Eberhard Fischer; F by Benny Bytebier; G by Phillip J. Cribb; I by E. Tanner via the *World orchid iconography*.