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Two rare Phallales recorded from São Tomé

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Abstract – Two little known species of Phallales, *Mutinus zenkeri* and *Blumenavia angolensis*, were collected on the volcanic island of São Tomé in the Gulf of Guinea, Africa. Descriptions and *in situ* photographs are provided for both species. Inferences of their phylogenetic relationships within the Phallales are provided based on partial nucLSU rDNA sequence data.

Africa / Basidiomycota / gasteromycetes / Phallales / taxonomy

Résumé – Deux espèces de Phallales peu connues ont été récoltées sur l'île volcanique de São Tomé dans le golfe de Guinée, Afrique, *Blumenavia angolensis* et *Mutinus zenkeri*. Ces deux espèces sont redécrites et illustrées par des photographies *in situ*. Des inférences de leurs relations phylogénétiques au sein des Phallales, réalisées sur base de données partielles de séquences nucLSU rDNA, sont présentées.

Afrique / Basidiomycota / gastéromycètes / Phallales / taxinomie

INTRODUCTION

The tropical African gasteromycetes are fairly well known, mainly through the works of Dissing & Lange (1962, 1963, 1964), Dring (1964), Dring & Rayner (1967), Demoulin & Dring (1975), Dring & Rose (1977) and Calonge *et al.* (1997). Recently, Desjardin & Perry (2009) added *Phallus drewesii* Desjardin & B.A. Perry from Obô National Park, Saõ Tomé (Gulf of Guinea, Africa).

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During a short field trip at Obô National Park in April 2011, we (JD & CD) repeatedly observed *P. drewesii*, producing abundant basidiomata on fallen logs or stumps. Two other representatives of the Phallales were collected also locally: the small-sized *Mutinus zenkeri* (Henn.) E. Fisch. and the rare and poorly documented *Blumenavia angolensis* (Welw. & Curr.) Dring.

Both species are re-described, illustrated, and their phylogenetic affinities are presented.

MATERIALS AND METHODS

Fungal material

Specimens were collected at Obô National Park, São Tomé, approx. N 0°17′.315, E 6°36′.745, elev. 1200 m, during a field trip conducted by two of us (JD & CD) in April 2011. Macroscopic descriptions are based on field notes and *in situ* photographs. They only refer to the material collected in São Tomé. Colours codes (between square brackets) and names correspond with the Methuen Handbook of Colour (Kornerup & Wanscher, 1983).

The microscopic structures were observed in a 1% Congo-red solution in concentrated ammonia. Measurements were performed using an Olympus BX51 light microscope, with digital camera and AnalySIS® Five imaging software (Soft Imaging System GmbH). Mean values (in italics) ± 1.96 * standard deviations, and minimum-maximum values (between parentheses) are given for spores and derived parameter Q (length/width ratio). The numbers of spores measured (= N) are given in the brackets. The collections are deposited at the National Botanic Garden of Belgium's herbarium 'BR' (abbreviation following Holmgren *et al.*, 1990).

Sequencing

DNA extraction, amplification, and sequencing of the nuclear ribosomal 5′ end of the LSU are as described in Decock *et al.* (2007). The primers pair LROR and LR5 was used for PCR amplifications. Successful PCR resulted in a single band observed on an 0.8% agarose gel, corresponding to approximately 900 bp. Sequencing reactions were performed using CEQ DTCS Quick Start Kit (Beckman Coulter) according to the manufacturer's recommendations with primers LROR, LR3, LR3R, LR5 (http://biology.duke.edu/fungi/mycolab/primers.htm).

Phylogenetic analysis

Fifty-four sequences were included in the phylogenetic analysis. Materials and sequences used in this study are listed in Table 1. Nucleotide sequences were automatically aligned with Clustal X (version 2.0.11) (Thompson *et al.*, 1997). Potentially ambiguously aligned segments were detected using the Gblocks v0.91b program (Castresana, 2000; http://molevol.cmima.csic.es/castresana/Gblocks.html) with the settings "allow smaller final blocks", "allow gaps within blocks". The alignment was then manually adjusted as necessary with the text editor in PAUP* (version 4.0b10, Swofford 2003). *Ramaria testaceoflava*

Table 1. List of species, collections, and sequences used in the phylogenetic analyses

Species name	*Authorships*	*Culture / herbarium collection*	*Accession number nucLSU / ITS*
Anthurus archeri	(Berk.) E. Fisch.	REB2182	DQ218624
		GEL5392	AJ406479
Aseroe rubra	Dring	OSC122632	DQ218625
Blumenavia angolensis	(Welw. & Curr.) Dring	JD772	KC128653
Clathrus chrysomycelinus	Möller	PDD75096	DQ218626
Clathrus ruber	P. Micheli ex Pers.	T-9354	AF213127
Dictyophora duplicata	(Bosc) E. Fisch.	OSC38819	DQ218481
Dictyophora indusiata	(Vent.) Desv.	OSC36088	DQ218627
Dictyophora multicolor	Berk. & Broome	MEL1054289	DQ218628
Gelopellis macrospora	Zeller	BAFC30373	DQ218629
Gelopellis sp.		H4571	DQ218631
		H4397	DQ218630
		MEL2063389	DQ218632
Ileodictyon cibarium	Tul. ex M. Raoul	OSC122734	DQ218633
		OSC107652	AY574641
Ileodictyon gracile	Berk.	MEL2024221	DQ218634
		MEL2037639	DQ218635
Kjeldsenia aureispora	W. Colgan, Castellano & Bougher	OSC56970	DQ218637
Kobayasia nipponica	(Kobayasi) S. Imai & A. Kawam.	OSC122863	DQ218639
		OSC122862	DQ218638
Laternea triscapa	Turpin	OSC122864	DQ218640
Lysurus borealis	(Burt) Henn.	OSC39531	DQ218641
Lysurus mokusin	(L.) Fr.	MB02012	DQ218507
Mutinus zenkeri	Henn.	JD781	KC128654/ KC128650
		JD782	KC128655/ KC128651
		JD837	KC128656/ KC128652
Mutinus caninus	(Huds.) Fr.	ADK2659	KC128657
		ADK2665	KC128658
Mutinus elegans	(Mont.) E. Fisch.	OSC107657	AY574643
Phallobata alba	G. Cunn.	PDD76197	DQ218642
Phallus costatus	Vent.	MB02040	DQ218513
Phallus GM2009a		AH31862	FJ785522
Phallus hadriani	Vent.	AFTOL-ID 683	AY885165
		OSC107658	DQ218514
Phallus impudicus	L.	FO 46622	AY152404
Phallus ravenelii	Berk. & M.A. Curtis	CUW s.n.	DQ218515
Phlebogaster laurisylvicola	Fogel	CUP1289	DQ218643
Protubera borealis	S. Imai	OKM21898	DQ218516
Protubera canescens	G.W. Beaton & Malajczuk	MEL2063471	DQ218644
		MEL2105035	DQ218645
Protubera clathroidea	Dring	BPI	DQ218646
Protubera jamaicensis	(Murrill) Zeller	T28248	DQ218647
Protubera maracuja	Möller	LSU2-42	DQ218518
Protubera parvispora	Castellano & Beever	OSC59689	DQ218648
Protubera sabulonensis	Malloch	T12737	DQ218649
Protubera sp.		JM98/351	AF261555
Protubera sp.		SM10143	DQ218650
Pseudocolus fusiformis	(E. Fisch.) Lloyd	DSH 96-033	AF518641
		ASM4705	AF213128
Ramaria testaceoflava	(Bres.) Corner	KGN93	AY586708
Simblum sphaerocephalum	Schltdl.	MB02016	DQ218521
Trappea darkeri	(Zeller) Castellano	OSC65085	DQ218651
Trappea phillipsii	(Harkn.) Castellano	OSC56042	DQ218522
Trappea pinyonensis	States	AHF530	DQ218597

(AY586708), a species belonging to the Gomphales clade according to Hosaka *et al.* (2006), was designated as outgroup.

Phylogenetic analyses were performed using Bayesian inference (BI) as implemented in MrBayes v3.1.2 (Ronquist & Huelsenbeck, 2003), and Maximum likelihood (ML) searches were conducted with RAxML 7.0.4 (Stamatakis, 2006). The general time reversible model (GTR), using proportion of invariant sites and distribution of rates at variable sites modeled on a discrete gamma distribution with four rate classes, was estimated as the best-fit likelihood model of evolution for Bayesian inference and Maximum likelihood, using the AIC (Akaike Information Criterion) as implemented in Modeltest 3.7 (Posada & Crandall, 1998).

Bayesian analyses were implemented with two independent runs, each with four simultaneous independent chains for three million generations, starting from random trees, and keeping one tree every 1000th generation. All trees sampled after convergence (average standard deviation of split frequencies < 0.01, confirmed using Tracer v1.4 (Rambaut & Drummond, 2007) were used to reconstruct a 50% majority-rule consensus tree (BC) and to estimate posterior probabilities. The posterior probability (BPP) of each node was estimated based on the frequency at which the node was resolved among the sampled trees with the consensus option of 50% majority-rule (Simmons *et al.*, 2004). Clades with BPP above 0.95 were considered significantly supported by the data.

Maximum likelihood (ML) searches conducted with RAxML involved 1000 replicates under the GTRGAMMAI model, with all model parameters estimated by the program. The tree with the best likelihood value served as the starting tree for the Bayesian analyses. In addition 1000 rapid bootstrap (BS) replicates were run with the same GTRGAMMAI model. Clades with Maximum likelihood bootstrap values of 75% or greater were considered to be significantly supported.

RESULTS AND DISCUSSION

LSU analysis

Within the Phallales, the length of our aligned LSU fragments resulted in 693 positions. Using the Akaike information criterion of MrModeltest 2.3 (Posada & Crandall, 1998), the best-fit model to the nucLSU data was GTR+I+G with unequal base frequencies (A = 0.23507, C = 0.23648, G = 0. 31880, T = 0. 209642), a gamma distribution shape parameter of 0.488051, and a proportion of invariable sites of 0.42062. Thirteen characters judged too ambiguous to be aligned were excluded from the analysis. The two Bayesian runs converged to stable likelihood values (-ln 5323.521 – -ln 5325.616) after 1.000.000 generations and 4000 stationary trees from each analysis were used to compute a 50% majority rule consensus tree in PAUP* to calculate posterior probabilities. In the ML searches with RAxML the nucLSU alignment had 393 distinct patterns with a proportion of gaps and undetermined characters of 14.08%.

The BC tree and the optimal ML tree (tree score of -lnL = 4630.360037) were mostly identical. The Bayesian consensus tree is represented in Fig. 1.

The topologies of the trees regarding the recovery and the relative position of the different major Phallales generic entities considered were

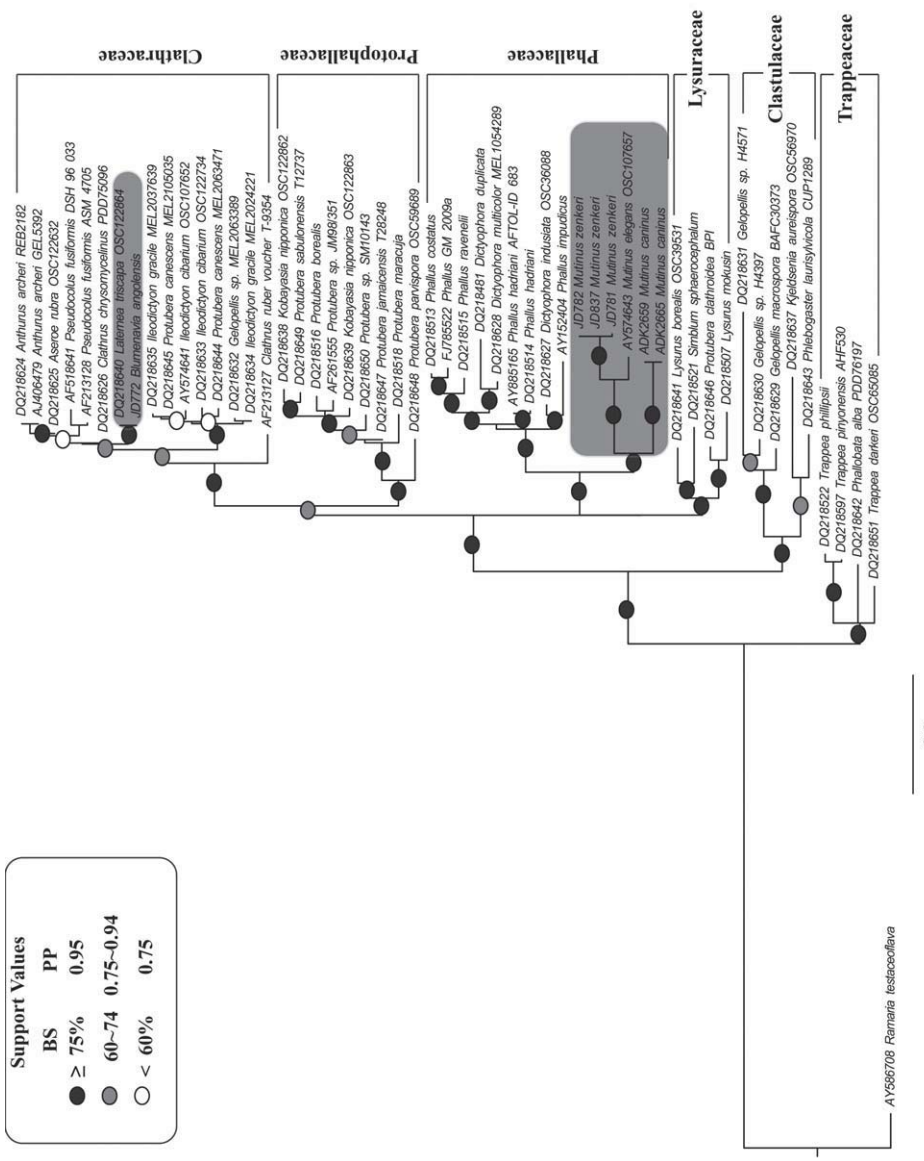

Fig. 1. The 50% majority-rule consensus tree from Bayesian inference of the LSU dataset.

consistent between all the phylogenetic inferences and in accordance with previously published phylogenies (see Hosaka *et al.*, 2006) at least for the clades with strong support.

Our phylogenetic inferences recovered the São Tomean collections of *Mutinus zenkeri* (JD781, JD782, JD837) as a well-supported, monophyletic clade within a lineage comprising *Mutinus elegans* (AY574643) and two specimens from Benin identified as *Mutinus caninus* (ADK 2659, ADK 2665). This "*Mutinus*"

clade is unequivocally placed within the Phallaceae where they appear to be, so far, in a sister position to the "*Phallus - Dictyophora*" clade.

Our collection of *Blumenavia angolensis* (JD772) clusters together with *Laternea triscapa* (DQ218640), within the Clathraceae clade. Sequences of the two specimens show only 3bps difference in the nucLSU fragment considered, (and furthermore in a ambiguous region of the alignment that were excluded from the analysis) and they will probably need further, more variable gene sequenced to be fully resolved at species level. The voucher specimen of DQ218640 was unavailable, impeding a deeper comparison based on more genes for the time being.

Nevertheless, a BLAST search of the ITS-5.8S region against NCBI database (http://blast.ncbi.nlm.nih.gov/) showed that the sequences were most similar respectively to *Mutinus caninus* voucher KM81429 (95% similar) and *Clathrus ruber* voucher KM143411 (96%). All sequences from the ITS-5.8s region of the specimen identified as *Mutinus zenkeri* (Henn.) have been deposed in the GenBank database for Barcoding purposes (Table 1). We weren't able to produce any ITS-5.8s sequences of the other specimens probably because of the age or the poor quality of the samples.

Although our phylogenetic analysis inferred from the nucLSU rDNA was largely enough to resolve the relative phylogenetic position of the two species it lacks resolution and does not fully resolve the evolutive relationship of the deeper internodes. In order to obtain a more robust phylogeny of the Phallales more gene sequences should be integrated.

TAXONOMY

Mutinus zenkeri (Henn.) E. Fisch., *Neue Denkschr. Schweiz. Naturf. Ges.* 36: 47 (1900) **Figs 2A, B**
= *Floccomutinus zenkeri* Henn., *Engl. Bot. Jahrb.* 22: 109 (1885).

Egg ochraceous white to orange white [5A2] below, cracked into fine light brown [6D4] scales above, ovoid, up to 8 × 5 mm, dehiscent into two lobes, with thick white mycelial strands at the base, up to 1 mm diameter; *receptacle* thin-walled, fusiform, resembling annular ridges, up to 30 × 3 mm; *fertile part* differentiated from sterile part by greater width (~ 1 mm), upper 1/3 of receptacle (~ 4 mm) and brownish orange [6C7] when young, then elongating up to 1/2 length of receptacle (up to 18 mm) and light orange to pale orange [5A5-A3], slightly curved; *sterile part* whitish, somewhat orange-tinted below the fertile part, straight or slightly curved, cylindrical, not chambered; *gleba* scanty, olive brown [4D4], smelling of fish, not fetid.

Basidiospores hyaline, ellipsoid, (3.2–)3.2–*4*–4.8(–5.2) × (1.3–)1.5–*1.8*–2.1(–2.1) µm, Q = (1.81–)1.85–*2.25*–2.65(–2.88) [N = 75].

Habitat: lignicolous in primary forest.

Known distribution: AFRICA: Cameroon, D.R. Congo, Gabon, Ghana, São Tomé.

Specimens examined: São Tomé, Obô National Park, N 0°17′.643 E 6°36′.351, 1300 m, on stump of dead tree, unidentified angiosperm, 13 Apr. 2011, *Degreef* 782; ibid., caminho del fugido, N 0°17′.475 E 6°36′.357, 1250 m, on rotten wood, 15 Apr. 2011, *Degreef* 837.

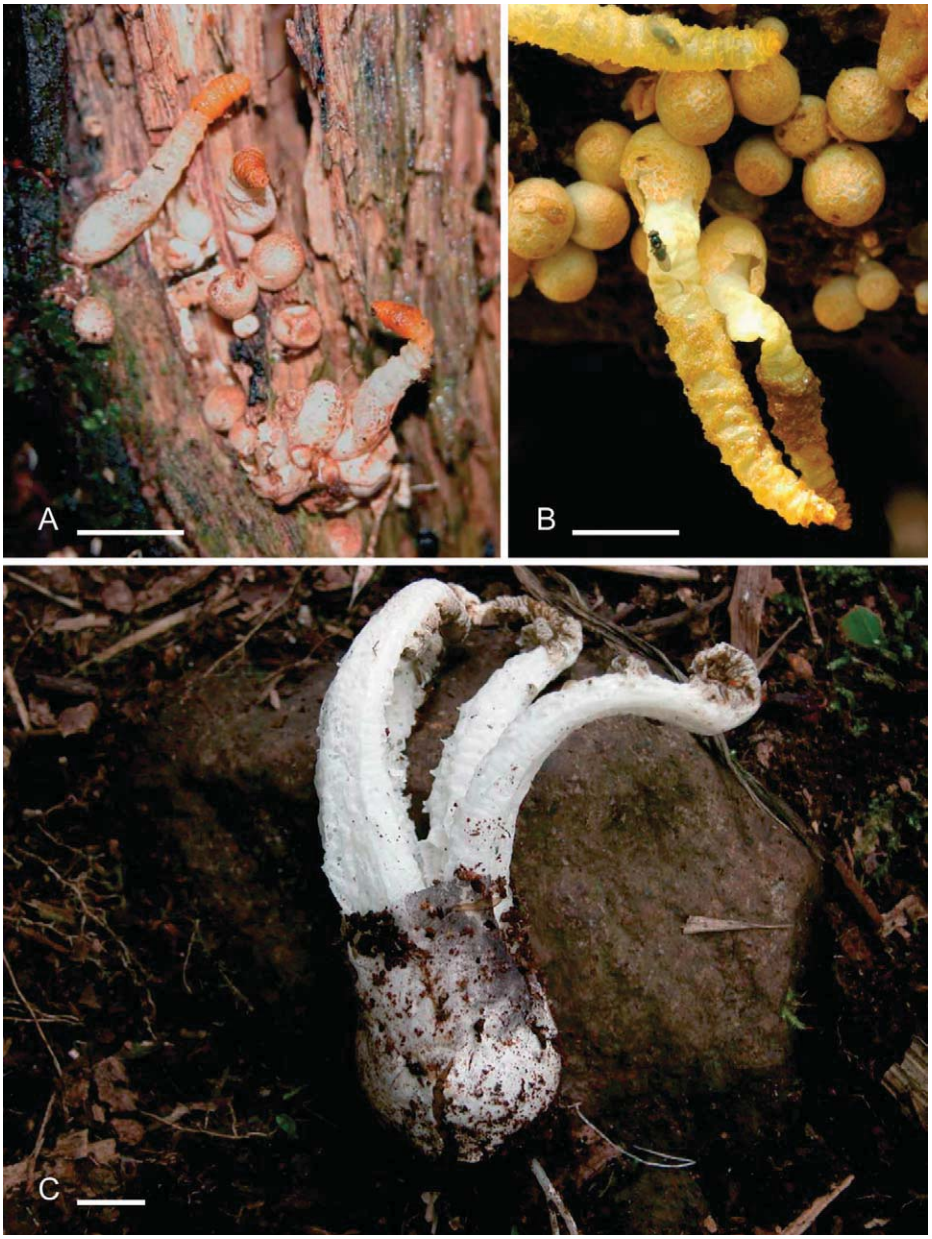

Fig. 2. **A.** *Mutinus zenkeri* from São Tomé (specimen: *Degreef* 782); **B.** *Mutinus zenkeri* from Gabon (specimen: C. Decock, GA-09-638); **C.** *Blumenavia angolensis* from São Tomé (specimen: *Degreef* 772). Scale bar = 10 mm.

Comments: Mutinus is a widespread genus of forest dwelling saprotrophs. It is distinguished from *Phallus* (inclusive of *Dictyophora*), the other genus in the family Phallaceae, by the absence of a cap. The gleba is thus directly borne by the top of the receptacle. A dozen species of *Mutinus* are usually accepted, but

the genus has not been monographed since Fischer (1900, 1933). In 1933, Fischer broke up the genus, but his simpler 1900 concept is usually preferred. *Mutinus zenkeri* is very rare and was only known through the type collection during the period 1895 to 1975. It is however such a peculiar fungus that it has been abundantly figured and discussed by Fischer (1900, 1933), Demoulin & Dring (1975) and Dring & Rose (1977). It is unique in the genus by the lack of an external wall to the locules of the receptacle. The gleba is thus borne by the tangential wall of the locules. This feature does not seem sufficient to place the species in a separate genus *Floccomutinus* as originally done by Hennings and accepted by Fischer in 1933, but justifies its isolation in *Mutinus* subg. *Floccomutinus* (Henn.) E. Fisch. In addition to this character, *Mutinus zenkeri* is remarkable through the combination of small size, absence of reddish colour, bilabiate dehiscence of the egg and lignicolous habitat.

Three species of *Mutinus* are reported in tropical Africa: *Mutinus argentinus* Speg., in Ghana (Dring & Rose, 1976), *M. bambusinus* (Zoll.) E. Fisch. known from the Democratic Republic of Congo (Demoulin & Dring, 1975), and *M. zenkeri* (Henn.) E. Fisch., reported from Cameroon (Hennings 1885), D.R. Congo (Demoulin & Dring, 1975), Gabon (Decock, pers. obs., Fig. 2B), and Ghana (Dring & Rose, 1976).

The specimens of *M. zenkeri* from São Tomé mainly differ from the continental African representatives in having the fertile part orange-coloured and covering the upper 1/3 to 1/2 of the receptacle (Fig. 2A). The fertile part is described as ochraceous and covering the upper 2/3 of the receptacle in specimens from D.R. Congo and Ghana. A collection from Gabon[1] (Fig. 2B) is somewhat intermediate combining the extended fertile part of the DR Congo's collection with the clear colour of the specimen from São Tomé.

The basidiospore dimensions of the material from D.R. Congo were erroneously mentioned by Demoulin & Dring (1975) as 3 × 1 µm; all cited specimens (*Rammeloo* Z347, Z352, Z367, Z397) were re-checked and show similar dimensions as recorded in our material from São Tomé. It is probable that the same dimensions reported by Dring & Rose (1977) are also erroneous.

Blumenavia angolensis (Welw. & Curr.) Dring, *Kew Bull.* 35(1): 53 (1980). **Fig. 2C**
= *Laternea angolensis* Welw. & Curr., *Trans. Linn. Soc. London* 26: 286 (1870)
= *Clathrus angolensis* (Welw. & Curr.) E. Fisch., *Jahr. Bot. Gart. Mus. Berlin* 4 : 70 (1886)
= *Colonnaria angolensis* (Welw. & Curr.) E. Fisch. in Engler & Prantl, *Nat. Pflanzenfam.* 2 Aufl. 7a: 85 (1933).
= *Blumenavia usambarensis* Henn., *Engler Bot. Jahrb.* 33: 37 (1902).

Egg whitish to brownish-grey [10C2-E2], subglobose, 3 cm diameter, gelatinous, with thick, white basal mycelial strands, up to 1.5 mm diameter; *receptacle* pure white, 8.5 × 3.5 cm, consisting of 4 unbranched spongy arms, each 1 cm diameter at the base, narrowing above, free below, united at the apex, sometimes breaking apart, quadrangular in transverse section; upper quarter of the inner part of each arm bearing 3 rows of dentate glebiferous wings, greyish-green [30C2]; *tubes* 6-8, irregular in shape and position,

1. GABON, Prov. Estuaire, Monts de Cristal National Park, Tchimbele area, approx. N 00°37′.50, E10°24′.1, elev. approx. 550 m, on a dead fallen trunk, unidentified angiosperm, 13 Apr. 2009, C. Decock & P. Yombiyeni GA-09-638 (HNG/IRET).

intercommunicating; *gleba* restricted to the upper quarter of the receptacle, greyish-green [30D7], gelatinous, smelling of vinegar, not foetid.

Basidiospores ellipsoid, (3.2–)3.3–*3.6*–4(–4) × (1.3–)1.4–*1.6*–1.8(–1.9) µm, Q = (1.88)1.89–*2.25*–2.61(–2.68) [N = 75].

Habitat: saprotrophic in secondary forest.

Known distribution: AFRICA: Angola, São Tomé, Tanzania. THE AMERICAS: Brazil, Trinidad, Chile?

Specimen examined: São Tomé, Obô National Park, track from Botanic Garden of Bom Sucesso to Lagoa Amelia, N 0°17′.315 E 6°36′.745, approx. 1200 m alt., on aerial litter in a *Ficus* tree, 12 Apr. 2011, *Degreef* 772.

Comments: Blumenavia is a small genus of Clathraceae with a *Laternea* morphology but a gleba supported by membranes that are lateral to the arms of the basidiomata. The genus is only known from Africa and South America. Descriptions of *B. rhacodes* Möller and *B. angolensis* (Welw. & Curr.) Dring are to be found in Dring (1980). *Blumenavia toribiotalpaensis* was recently described from Mexico by Vargas-Rodriguez & Vazquez-Garcia (2005), who give a table of the differences among the three species. *Blumenavia angolensis* is the palest coloured species, with smallest number of tubes by column and gleba limited to the most restricted part of the column (upper one third to one quarter). Both *B. rhacodes* and *B. angolensis* have large distributions in tropical to subtropical Africa and Americas, while *B. toribiotalpaensis* is only known from the state of Jalisco in Mexico. *Blumenavia angolensis* has recently been reported in the Houston area of Texas, where it is possibly introduced (Kuo, 2012).

Blumenavia angolensis was first described from Angola (Welwitsch & Currey, 1870[2]). It was later recorded from Tanzania, in the Usambara mountain range, under the name of *B. usambarensis* (Hennings 1902[3], Eichelbaum 1907[4] ("1906"). Eichelbaum (1907) reported much larger basidiospores (6 × 2 µm), which could indicate this is another taxon. These specimens are also the origins of the citation from South Africa by Dring (1980) through confusion of the South African Drakenberg's Mountains and Drachenberg near Amani in the East Usambara Mountains of Tanzania (Coetzee, 2010).

According to Dring (1980), *B. angolensis* is also present in South America, with records from Brazil (São Paulo, Inst. Botanica, Parque, 14 Oct. 1966, *Dring* s.n.) and Trinidad (Naranja, northern side range beside Tucuche trail, 600 m, 2 Oct. 1949, *Dennis* s.n.). Its occurrence in Chile (Valdivia) remains questionable (Dring, 1980).

Dring (1980) compared the spore dimensions measured by himself (from South American collections) and those recorded by Eichelbaum (1907, cf. above) and questioned the conspecificity of the South American and African materials. The spore dimensions of our material from São Tomé (3.3–*3.6*–4.0 × 1.4–*1.6*–1.8 µm) agree with the size range reported by Hennings (1902) for *B. usambarensis* (3–3.5 × 1.5 µm) and with the description of Dring (1980, 3–3.5 × 1.5 µm).

The colour of the egg seems to be variable in *B. angolensis*. The eggs of American material are described as dark-coloured (brown in Dennis' collection from Trinidad, almost black in Dring's from Brazil, with the outer surface cracking into large scales to reveal the whitish tissue beneath). The sketch by Welwitsch of the type of *B. angolensis* does not show a dark volva but that of

2. Pungo Andongo, pr. Catete, 10 Dec. 1856, *Welwitsch* 120, drawing only, holotype K(M)
3. Usambara, 19 Jan. 1900, *Scheffler* s.n., *Kummer* c.n. 60, *ut B. usambarensis* Henn.
4. Amani, 22 Oct. 1903, *Warnecke* s.n.: 89, *ut B. usambarensis* Henn.

B. usambarensis, described by Hennings, was evidently coloured: "*volva… extus pallida, subolivaceo maculata*". Our specimen from São Tomé shows a whitish to brownish-grey egg [10C2-E2].

Dennis (see Dring, 1980: 50), interestingly, commented on the limited distribution of *Blumenavia* emphasizing "a particularly close connection between the fungus floras of Africa and eastern South America without extension to other tropical areas". He argues that this is not necessarily evidence of continental drift or of former land bridges across the South Atlantic but may equally well be an incidental human introduction, consequence of centuries of active slave trading between Portuguese colonies in Angola, Guinea and Brazil'. The presence of *B. angolensis* on the volcanic island of São Tomé, never connected by a land bridge to the African mainland, and another former Portuguese ownership is then particularly noteworthy.

Further sequence data from *Blumenavia* may not only help clarify its relationship to *Laternea* but also shed light on the genetical relationship between the African and American populations.

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