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Tropical African *Cantharellus* Adans.: Fr. (Hydnaceae, Cantharellales) with lilac-purplish tinges revisited

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Tropical African *Cantharellus* Adans.: Fr. (Hydnaceae, Cantharellales) with lilac-purplish tinges revisited

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ABSTRACT

The authors discuss several African *Cantharellus* Adans.: Fr. species with lilac-purplish tinges on the pileus or stipe surface collected in the Central African rain forest or West African gallery forests. The morphology of *C. longisporus* Heinem. is discussed on the basis of new Central African collections and found profoundly different from two previously described subspecies from Madagascar which are here recombined as *C. littoralis* (Buyck & Randrianjohany) Buyck, comb. et stat. nov., and *C. isaloensis* (Buyck & Eyssartier) Buyck, comb. et stat. nov. *Cantharellus xanthocyaneus* Ndolo Ebika & Buyck, sp. nov., a new look-alike of *C. cyanoxanthus* R.Heim ex Heinem. with considerably smaller basidiospores is described, as well as a new chanterelle species from Togo, viz. *C. violaceoflavescens* De Kesel, Guelly, L.A.Parra & Buyck, sp. nov., that in the field is reminiscent of *C. littoralis* (Buyck & Randrianjohany) Buyck, comb. et stat. nov. A multigene phylogeny places both new species *Cantharellus xanthocyaneus* Ndolo Ebika & Buyck, sp. nov., and *Cantharellus violaceoflavescens* De Kesel, Guelly, L.A.Parra & Buyck, sp. nov., in the subgenera *Parvocantharellus* Eyssart. & Buyck and *Pseudocantharellus* Eyssart. & Buyck respectively, and *Cantharellus littoralis* (Buyck & Randrianjohany) Buyck, comb. et stat. nov., in the subgenus *Cinnabarini* Buyck & V.Hofst.

KEY WORDS

Berlinia,
Gilbertiodendron deweyrei,
Hydnaceae,
Madagascar,
multigene phylogeny,
Republic of the Congo,
Togo,
new combination,
new status,
new species.

RÉSUMÉ

Cantharellus Adans.: Fr. d'Afrique tropicale (Hydnaceae, Cantharellales) avec des teintes lilas-violacé revisités. Les auteurs discutent plusieurs espèces de *Cantharellus* Adans.: Fr. Africains avec des teintes lilas-violacé sur la surface du chapeau ou du pied récoltés dans la forêt pluviale d'Afrique Centrale ou dans les forêts galeries d'Afrique de l'Ouest. La morphologie de *C. longisporus* Heinem. est discutée sur la base de nouvelles collections d'Afrique Centrale et des profondes différences ont été trouvées entre deux sous-espèces précédemment décrites à Madagascar qui sont ici recombinaées comme *C. littoralis* (Buyck & Randrianjohany) Buyck, comb. et stat. nov., et *C. isaloensis* (Buyck & Eyssartier) Buyck, comb. et stat. nov. *Cantharellus xanthocyaneus* Ndolo Ebika & Buyck, sp. nov., une nouvelle espèce ressemblant à *C. cyanoxanthus* R.Heim ex Heinem. avec des basidiospores considérablement petites est décrite, aussi bien qu'une nouvelle espèce de chanterelle du Togo, viz. *C. violaceoflavescens* De Kesel, Guelly, L.A.Parra & Buyck, sp. nov., qui fait penser à *C. littoralis* (Buyck & Randrianjohany) Buyck, comb. et stat. nov., sur le terrain. Une phylogénie multigène place les deux nouvelles espèces *Cantharellus xanthocyaneus* Ndolo Ebika & Buyck, sp. nov., et *Cantharellus violaceoflavescens* De Kesel, Guelly, L.A.Parra & Buyck, sp. nov., dans les sous-genres *Parvocantharellus* Eyssart. & Buyck et *Pseudocantharellus* Eyssart. & Buyck respectivement, et *Cantharellus littoralis* (Buyck & Randrianjohany) Buyck, comb. et stat. nov., dans le sous-genre *Cinnabarini* Buyck & V.Hofst.

MOTS CLÉS

Berlinia,
Gilbertiodendron
dewevrei,
Hydnaceae,
Madagascar,
phylogénie multigène,
République du Congo,
Togo,
combinaison nouvelle,
nouveau statut,
espèces nouvelles.

INTRODUCTION

Tropical African *Cantharellus* Adans.: Fr. are well-documented compared to those from other tropical regions, and this is mainly through the contributions of P. Heinemann (1958, 1959, 1966). Since then, however, the taxonomy of African chanterelles has been neglected, except for a few purely morphological studies based on collections made in Burundi (Buyck 1994), Zambia (Eyssartier & Buyck 1998), Tanzania (Buyck *et al.* 2000), Madagascar (Eyssartier & Buyck 1999), Zimbabwe (Eyssartier *et al.* 2002) and Benin (De Kesel *et al.* 2011, 2016). All of these more recent studies were based on specimens gathered in woodland areas, while new *Cantharellus* collections from the Central African rain forest area remained unavailable for study until merely a few years ago.

The genus *Cantharellus* is infamous for its highly variable and deceptive field habit (Olariaga *et al.* 2015; Buyck *et al.* 2016c, 2018) as well as for its limited microscopic variation (Buyck *et al.* 2014), thereby making molecular data an essential part of any modern taxonomic revision. The strongly degraded DNA of the nearly one century-old type specimens of the many chanterelles described by Heinemann made them unfit for sequencing (De Kesel *et al.* 2016) and the lack of sequence data for these species nourished the confusion and uncertainty with regard to species recognition and infrageneric relationships among Old World *Cantharellus* (Buyck *et al.* 2014).

During the past few years, however, new and well-documented *Cantharellus* collections from the *Gilbertiodendron dewevrei* (De Wild.) J.Léonard (Fabaceae subfam. Detarioideae) rain forest have become available for morphological and molecular study. This resulted not only in the description of five new chanterelles from this particular habitat [*C. minutissimus* Buyck & V.Hofst. in Buyck *et al.* (2016a), *C. hydnooides* Buyck & V.Hofst. in Buyck *et al.* (2017), *C. griseoisabellinus* Buyck, Henkel & V.Hofst. in Buyck *et al.* (2018), *C. tomentosoides*

Buyck & V.Hofst. in Buyck *et al.* (2019), *C. subfloridulus* Buyck & V.Hofst. in Das *et al.* (2018)], but allowed also for the morphological and molecular epitypification of nine of the 16 rain forest chanterelles described by Heinemann (1958): *C. miniatescens* (Buyck *et al.* 2016b), *C. rufopunctatus* (De Kesel *et al.* 2016), *C. alboroseus* (Buyck *et al.* 2016b), *C. densifolius* and *C. luteopunctatus* (Buyck *et al.* 2019), *C. rhodophyllus*, with *C. incarnatus* being considered a synonym (Buyck & Hofstetter 2018), *C. isabellinus* (Buyck *et al.* 2018) and *C. goossensiae* in Hyde *et al.* (2019).

In the present paper, the authors report on some larger chanterelles with purplish-violaceous tints collected in the *Gilbertiodendron dewevrei* (De Wild.) J.Léonard monodominant forest in the Republic of the Congo and in the Democratic Republic of the Congo (both in Central Africa), as well as from gallery forests in Togo (West Africa). African *Cantharellus* with such colors are usually referred to as belonging to the *C. cyanoxanthus* R.Heim ex Heinem. species complex. This species complex was already the subject of an earlier morphological study (Buyck *et al.* 2012) that clearly demonstrated the need for sequence data to solve the long-standing taxonomic confusion among the main three constituent species and their possible relatives. So far, only one of these, *C. goossensiae* (Beeli) Heinem., has been redescribed and epitypified on the basis of newly sequenced specimens (in Hyde *et al.* 2019). The present contribution reports on new collections of *C. longisporus* Heinem., thus allowing for a correct appreciation of its morphology. *Cantharellus cyanoxanthus*, as interpreted and described by Heinemann, has still not been recollected. Nevertheless, these new observations allow for the introduction of four new species: two of these had previously been introduced as new subspecies of *C. longisporus* (Buyck *et al.* 2012), but are clearly too different to be considered as conspecific, while two more new species are here introduced on the basis of morphology and multi-locus sequence data.

TABLE 1. — Voucher table for newly sequenced specimens.

Extr. Nr	Voucher	Herbarium barcode	nucLSU	mitSSU	<i>rpb2</i>	<i>tef1</i>	Origin	Typification
<i>Cantharellus goossensiae</i> (Beeli) Heinem.								
1647	BB 16.063	PC0125002	MK422953	MT006319	MT002273	MK422932	Central African Republic	
1648	BB 16.064	PC0125008	MK422949	MT006320	MT002274	MK422928	Central African Republic	
<i>Cantharellus littoralis</i> (Buyck & Randrianjohany) Buyck, comb. et stat. nov.								
1007	ER 107	PC0085175	MT006311	MT006323	MT002275	MT002279	Madagascar	
1008	ER 2	PC0085174	MT006312	MT006324	MT002276	MT002280	Madagascar	Holotype
<i>Cantharellus violaceoflavescens</i> De Kesel, Guelly, L.A.Parra & Buyck, sp. nov.								
1757	ADK 4790	BR5020167050163	MT006307	MT006317	–	–	Togo	Holotype
1758	ADK 4791	BR5020167046128	MT006308	MT006318	–	–	Togo	Paratype
<i>Cantharellus xanthocyaneus</i> Ndolo Ebika & Buyck, sp. nov.								
1751	NEST 2333	PC0125127, Duplicate HICPC004	MT006309	MT006321	–	MT002277	Republic of the Congo	Paratype
1752	NEST 2353	PC0125128, Duplicate HICPC005	MT006310	MT006322	–	MT002278	Republic of the Congo	Holotype

METHODS

FIELD COLLECTING – SITE DESCRIPTION

Specimens were collected in the Departments of Sangha and Likouala in the northern Republic of the Congo. In the Sangha Department, samples were collected as part of the research activities on Biodiversity of the Goulougo Triangle Apes Project (GTAP). The research site of GTAP is located in the southern part of the Nouabalé-Ndoki National Park (2°12.69'N, 16°31.12'E; alt. 370 m). In the Likouala Department, the specimens were collected as part of the second author's PhD research within established permanent plots. The plot where specimens used for this paper were collected is located in Ipendja Forest Management Unit (2°33.84'N, 17°10.12'E; alt. 360 m). In both Departments, the samples were collected in monodominant forest of the ectomycorrhizal (ECM) canopy tree *Gilbertiodendron dewevrei*. Samples taken in the Democratic Republic of the Congo come from the Tshopo province. The vegetation is characterized by a tropical evergreen rain forest and some groves of semi-deciduous forests on hills and plateaus. The fungi were collected within COBIMFO plots (see acknowledgements) situated in the Man-and-Biosphere reserve of Yangambi (0°48.45'N, 24°30.01'E; alt. 440 m) and mainly dominated by *Gilbertiodendron dewevrei*, ECM *Brachystegia laurentii* (De Wild.) Louis, *Scorodophloeus zenkeri* Harms, *Prioria balsamifera* (Vermoesen) Breteler, and ECM *Julbernardia seretii* (De Wild.) Troupin. Specimens found in Togo come from the Plateau province (around Béna village, (07°32.36'N, 0°54.58'E; alt. 740 m) and were collected in semi-deciduous forest galleries and savannah woodlands on deep soils, situated between 650–850 m altitude and dominated by ECM *Berlinia grandiflora* (Vahl) Hutch. & Dalziel and/or ECM *Uapaca guineensis* Müll.Arg.

MORPHOLOGICAL DESCRIPTION

The color notations indicated in the descriptions are from Kornerup & Wanscher (1978). Macroscopic features are based on field notes and photographs. All microscopic observations

and measurements were made in ammoniacal Congo red, after a short aqueous KOH pretreatment to improve tissue dissociation. Original drawings for all elements of the hymenium or pileipellis were made at × 2400. Basidiospore measurements are based on 20 spores (n) per specimen and usually from spores dropped on surface of pileus or stipe to ensure their maturity. Measurement values in bold represent average values; these are flanked on either side with values minus/plus standard deviation and finally minimum/maximum values between brackets. Q represents length/width ratio of the spores and is presented in the same format as spore dimensions. Herbarium abbreviations follow Thiers (Continuously Updated).

TAXON SAMPLING, DNA EXTRACTION, AMPLIFICATION AND SEQUENCING

Genomic DNA was extracted from six *Cantharellus* collections: two collections of *C. littoralis* (Buyck & Randrianjohany) Buyck, comb. et stat. nov., two collections of *C. violaceoflavescens* De Kesel, Guelly, L.A.Parra & Buyck, sp. nov., and two collections of *C. xanthocyaneus* Ndolo Ebika & Buyck, sp. nov. (Table 1) following Hofstetter *et al.* (2002); DNA extraction of two collections of *C. longisporus* was unsuccessful. Amplification and sequencing were performed as in Buyck *et al.* (2014): eight sequences for rDNA mitochondrial small subunit (mitSSU), six sequences for rDNA nuclear large subunit (nucLSU), four sequences for RNA polymerase II second largest subunit (*rpb2*) and four sequences for transcription elongation factor 1-alpha (*tef1*) were obtained. These newly produced sequences were introduced in the *Cantharellus* 4-locus dataset used in Buyck *et al.* (2016d), which used *Craterellus tubaeformis* as an outgroup species.

PHYLOGENETIC ANALYSES

After introduction of the newly produced data in single locus alignments using MacClade 4.05 (Maddison & Maddison 2002) and the removal of ambiguously aligned regions (short highly variable regions in rDNA loci, a long intron [800–1200 bp]

in mitSSU sequences for *C. floridulus* Heinem., *C. humidicolus* Buyck & V.Hofst., *C. ambohitantelyensis* Buyck & V.Hofst., *C. albidolutescens* Buyck, Eyssart. & V.Hofst. and *C. amethysteus* (Quél.) Sacc., and spliceosomal introns in *rpb2* and *tefl*, the data were combined. The final 4-locus/103 taxa alignment used for phylogenetic analyses included 3339 characters (mitSSU: 522 characters; nuLSU: 1219 characters; *rpb2*: 969 characters; *tefl*: 629 characters).

Combinability tests were effected running analyses including 500 bootstrap replicates in PhyML v.3.0 (Guindon & Gascuel 2003) for each of the four loci. Each bootstrap replicate started from a distance-based tree with the proportion of invariable sites, the gamma shape parameter, and the number of substitutions categories estimated during the search. Conflict was assumed significant if two different relationships for the same set of taxa were inferred with significant support (bootstrap values $\geq 70\%$ (Mason-Gamer & Kellogg 1996)) by two different loci.

Three independent searches for the most likely tree were conducted in PhyML, with the same settings as for single locus analyses. Branch robustness was inferred based on 1000 BS replicates. Bootstrap values (BS) were considered significant when $\geq 70\%$ (Alfaro *et al.* 2003).

RESULTS

PHYLOGENY

Comparing single locus analyses, no significant conflict was detected and the 4-locus data were combined. The resulting most likely tree (Fig. 1) suggests that the here newly described species, even if sharing several morphological features, nest in different subgenera of the genus *Cantharellus*. Our 4 locus/103 taxa phylogeny places *C. xanthocyaneus* Ndolo Ebika & Buyck, sp. nov. (BS = 99%) monophyletic (BS = 91%) and sister to *C. subcyanoxanthus* (BS = 92%) in sect. *Cyanomaculati* Buyck & V.Hofst., while *C. violaceoflavescens* De Kesel, Guelly, L.A.Parra & Buyck, sp. nov. (BS = 97%) is suggested to be closely related to *C. miniatescens* (BS = 100%), a species belonging in subg. *Pseudocantharellus* Eyssart. & Buyck, however without significant support. Our phylogeny therefore lacks support to place *C. violaceoflavescens* De Kesel, Guelly, L.A.Parra & Buyck, sp. nov., firmly in any particular subgenus, possibly due to missing sequence data for this species.

Medium-sized to large, more or less fleshy chanterelles with dark violaceous tints are typical for subg. *Cantharellus* sect. *Amethystini* Buyck & V.Hofst. (see Buyck *et al.* 2018) which is typified by the Asian *C. subamethysteus* Eyssart. & D.Stubbe, for sect. *Cyanomaculati* (the *C. subcyanoxanthus* lineage, which was provisionally attached to subg. *Parvocantharellus*, see Buyck *et al.* 2014) and was recently documented for subg. *Pseudocantharellus* (*C. goossensiae*, see Hyde *et al.* 2019). A few much more fragile and, particularly, much smaller chanterelles in subg. *Cinnabarini* Buyck & V.Hofst. also possess some violaceous tints, e.g. the African *C. conspicuus* Eyssart., Buyck & Verbeke and *C. fistulosus* Tibuhwa & Buyck, or the Asian *C. diminutivus* Corner. All these species groups are indicated by blue bars in Figure 1.

The present multilocus phylogeny (Fig. 1) places the Malagasy *C. littoralis* (Buyck & Randrianjohany) Buyck, comb. et stat. nov. (BS = 100%) – from a morphological point of view rather unexpectedly – in subg. *Cinnabarini* (BS = 96%), where it is strongly supported to be monophyletic (100% MLBS) and sister to *C. afrociarius* Buyck & V.Hofst. (BS = 100%). The latter is a fleshy, yellow chanterelle from the African miombo woodlands with a well-developed, veined hymenophore resembling a robust or stout version of *C. cibarius*. Within subg. *Cinnabarini*, *C. littoralis* (Buyck & Randrianjohany) Buyck, comb. et stat. nov., has the violaceous tinges in common with a few much smaller chanterelles, but these are actually even more distantly related to *C. littoralis* (Buyck & Randrianjohany) Buyck, comb. et stat. nov., than is the morphologically very different *C. afrociarius*.

TAXONOMY

Family HYDNACEAE Chevall.
Genus *Cantharellus* Adans.:Fr.

Cantharellus longisporus Heinem.
(Figs 2; 3)

Cantharellus longisporus Heinem., *Bulletin du Jardin botanique de l'État, Bruxelles* 28 (4): 409 (1958).

TYPE MATERIAL. — **Holotype**. Central Africa, Democratic Republic of Congo (ex Belgium Congo and Zaïre), district forestier central, Binga, gregarious and on the ground in a *Gilbertiodendron dewevrei* forest, IV.1928, *M. Goossens-Fontana* 692 (BR).

MATERIAL EXAMINED. — **Republic of the Congo**, Sangha department: Nouabalé-Ndoki National Park, Goulougo, 40 km E-SE from Bomassa, 2°12.82'N, 16°31.93'E; 12.I.2012, herb. *S. T. Ndolo Ebika* 737 (NEST[NEST737], HICPC[HICPC294]), *S. T. Ndolo Ebika* 744 (NEST744, HICPC295).

Democratic Republic of the Congo, oriental province, Tshopo district, Yangambi, Man-and-Biosphere Reserve, rain forest dominated by *Gilbertiodendron dewevrei*; 00°47.85'N, 24°29.87'E; alt. 450 m; 26.X.2012; P. Ballings leg.; herb. *De Kesel* 5210 (ADK[ADK 5210], BR[BR 5020212167440V]); near Binga, in groups on the soil in *Gilbertiodendron dewevrei* forest, IV.1928, *M. Goossens-Fontana* 692 (holo-, BR).

ICONOGRAPHY. — Heinemann (1958: fig. 44; 1959: pl. XVII, fig. 4).

ORIGINAL DIAGNOSIS. — “*Pileus carnosus, centro depressus, lobatus, tomentosus, glabrescens, lilacino-armeniacus. Stipes solidus, lilacino-roseus, deorsum luteus, pallescens. Lamellae latiusculae, distantes, armeniaca, aciem versus aurantiaca, pallescentes, furcatae, leviter intervenulatae. Caro alba, in pileo dilute armeniaca, basi stipite luteola; sapor pungens. Sporae subcylindricae vel leviter arcuatae, 8-10,5 × 3,8-4,8 μm.*”

ORIGINAL DESCRIPTION (FREELY TRANSLATED FROM FRENCH). — “*Pileus* 6-12 cm diam., thick and fleshy, convex with incurved margin, then plane with more or less depressed center; margin lobed, crenulate; surface dull, tomentose, becoming glabrous, pinkish lilac with paler margin, then slightly to distinctly more orange, in the center tinged with pink, vinaceous to brownish.

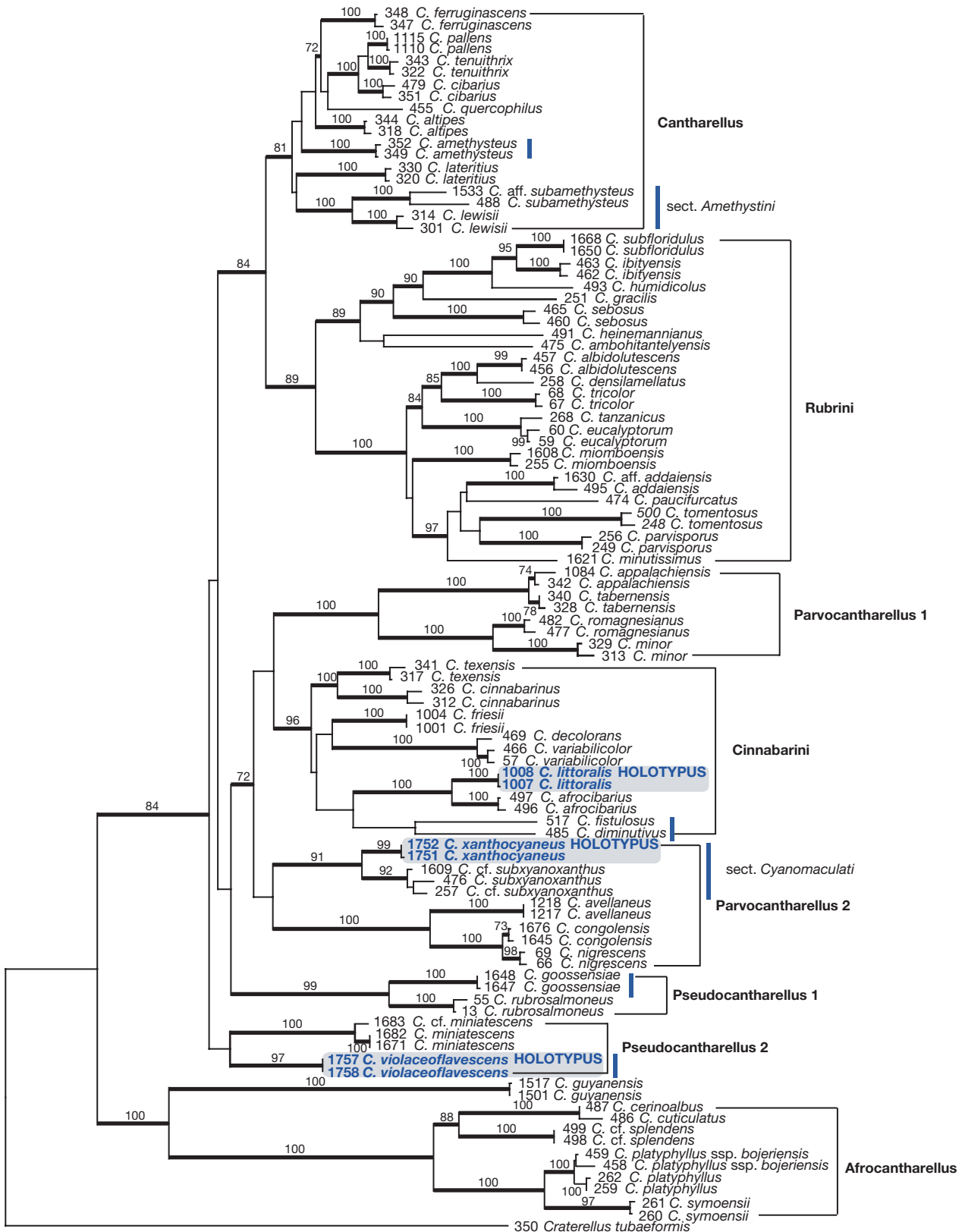


FIG. 1. — Most likely phylogram obtained by analyses of the 4-locus/103 taxa dataset ($-ln = 23519.35654$). Branches significantly supported are **bold** with BS values indicated along the branches. New taxa are in **bold blue**. Names of clades refer to subgenera recognized in Buyck *et al.* (2014). — (note the orthographic correction for subgenera *Rubrini* and *Cinnabarini*). **Blue bars** indicate the distribution of taxa with violaceous tinges in the phylogeny. Scale bar: 0.01 substitution per site.



FIG. 2. — *Cantharellus longisporus* Heinem.: **A**, young specimens ([HICPC294] with inserted original watercolor of holotype from Heinemann 1959); **B, D**, details of the pileus [HICPC295]; **C**, cylindrical or widening upwards stipe with hymenophore; **E**, detail of context. Photos: S. T. Ndolo Ebika & P. Ballings.

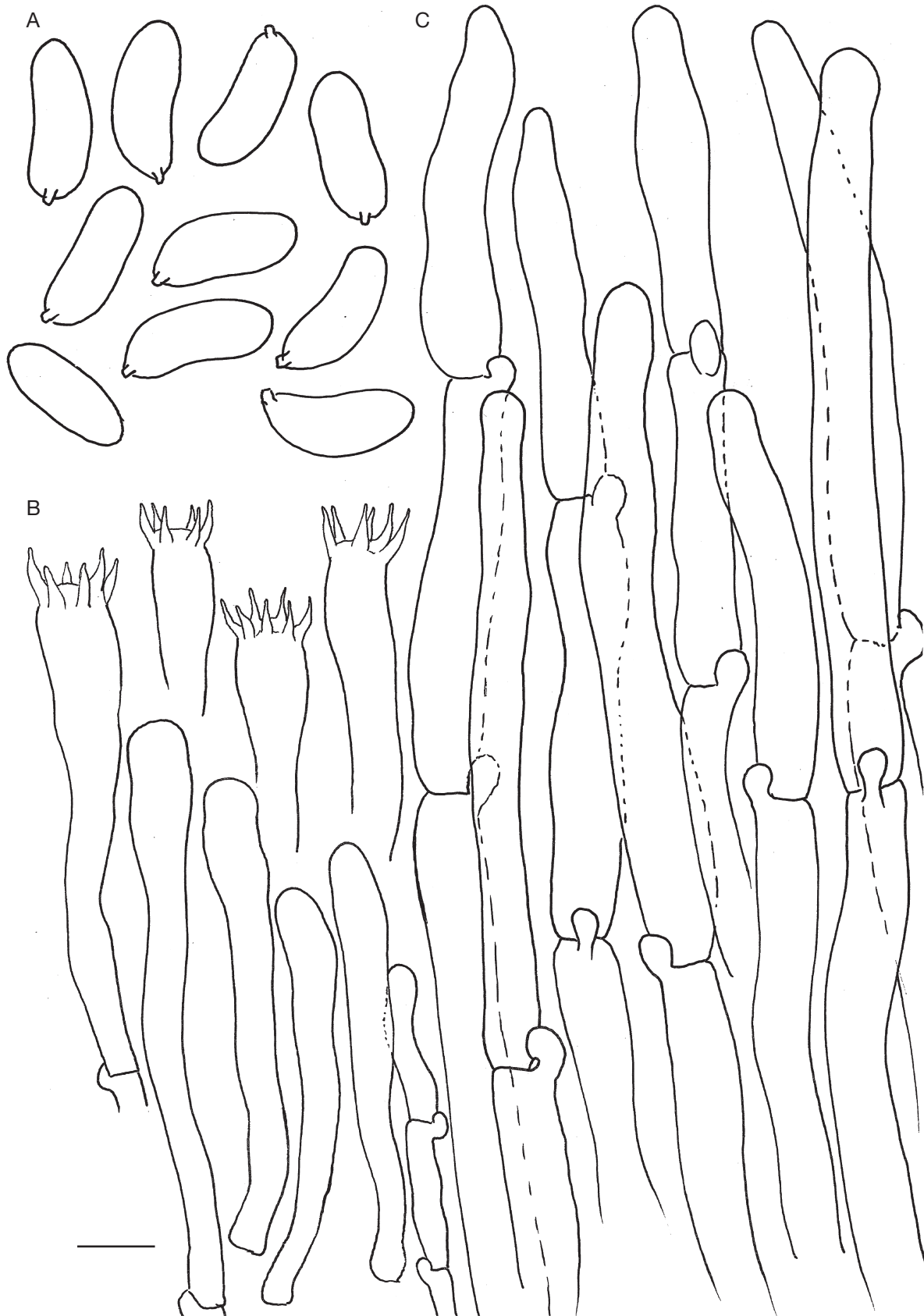


FIG. 3. — *Cantharellus longisporus* Heinem. (HICPC294): **A**, spores; **B**, basidia and basidiola; **C**, hyphal endings of the pileipellis. Scale bar: 10 μ m, but only 5 μ m for spores. Drawings: B. Buyck.

Stipe 50-90 × 9-25 mm, cylindrical or more irregular, solid inside, light reddish lilac, yellowish toward the base, becoming paler with age, sometimes coalescent at the base, basal mycelium apparent. *Hymenophore* with gill folds up to 5(7) mm high, rather spaced, at first pinkish orange to bright orange near the cap margin, then light pinkish with orange shades, rather thin, unequal and forked, with some subtle transversal veins. *Context* firm, white, tinged with yellow near the stipe base, and with pinkish or orange in the pileus. *Taste* acrid. *Smell* weakly of *C. cibarius* when boiling a small piece of the exsiccatum.

Spore print white to pale. *Exsiccatum* brownish grey to ochraceous brown, stipe concolorous or slightly more yellow, hymenophore reddish brown, context ochraceous to ferruginous. *Spores* 8-10.5 × 3.8-4.8 µm, narrowly ellipsoid to subcylindrical or weakly curved, presenting often a slight depression at the adaxial side, thin-walled, with a small apiculus. *Basidia* measuring for ex. 65 × 7.5 µm, four-spored. *Pileipellis* composed of slender, cylindrical hyphae, measuring 4-11 µm diam., thin-walled and slightly yellowish. *Clamp connections* present.”

HABITAT. — Dense rain forests of Central Africa, under ECM *Gilbertiodendron deuvevei*, either in monospecific stands or mixed with ECM *Julbernardia seretii* and *Paramacrolobium coeruleum* (Taub.) J.Léonard.

DESCRIPTION

Basidiomata

Large, very firm and fleshy, frequently with few individuals fused together in the lower stipe (Fig. 2A-D), up to 100 mm high and between 85-130 mm wide when fully expanded.

Pileus

Plano-concave to slightly depressed (Fig. 2A), in age often becoming funnel-shaped; the margin first inrolled (Fig. 2A), becoming strongly lobed, wavy and straight at maturity (Fig. 2B, D); pileus surface azonate, when young entirely dark greyish violet to purple brown (10-11F2-4) from appressed, minute, dark squamules on the orange-yellow background of the surface underneath (Fig. 2A), remaining so with age in the pileus center, squamules towards the margin gradually more spaced, losing their dark color at the margin fading to yellowish orange or orange-yellow (4A4-6) (Fig. 2B, D).

Hymenophore

Deeply decurrent (Fig. 2C), 3-5(-7) mm high, when young composed of spaced, well-differentiated gill folds (4-6 long ones per cm at pileus margin) separated by smooth interstitial spaces and intermixed with up to four lengths of short lamellulae near the pileus margin, not forked, except near the very pileus margin; the interstitial spaces becoming with age gradually more veined over their entire surface with the veins descending on the sides of the gill folds, pale yellowish (4A2-3), brighter and more orange (4A4-6) near the pileus margin, hardly changing when bruised.

Stipe

45-90 mm high, thick and fleshy, up to 20 mm diam., cylindrical or widening upwards, sometimes splitting upwards, thereby forming more than one cap (Fig. 2C), white to yellowish (4A2) toward the base, marked with

violet brown (10-11E2-5) in the upper part from minute squamules.

Context

Fibrous, whitish, clearly yellow in the base of the stipe and just beneath the pileipellis, unchanging when cut or injured (Fig. 2E).

Taste

Distinctly peppery.

Odour

Weak, not striking.

Spore print

Off-white on gill folds, pale yellowish in deposit (4A2).

Spores (Fig. 3A)

Narrowly ellipsoid to elongate, 7.7-9.1-10.5(-10.7) × 3.4-3.9-4.5(-4.5) µm {N=25}, Q = 1.96-2.33-2.7(-2.75), hyaline, thin-walled, smooth.

Basidia (Fig. 3B)

51-64-72 × 8.5-10-11.5 µm {N=7}, 4-6-spored.

Subhymenium

Subfilamentous, composed of rather narrow, more or less cylindrical cells.

Pileipellis (Fig. 3C)

Composed of thin-walled, elongated elements, sometimes slightly wider near the septa, 6.5-10 µm diam.; the terminal cell up to 95 µm long, predominantly subcylindrical, but frequently slightly constricted or somewhat narrowing at the tip.

Clamp connections

Conspicuous on hyphae of all tissues.

NOTES

Cantharellus longisporus has been variously misinterpreted in the past (e.g. Morris 1987; Ryvarden *et al.* 1994) most likely due to the remarkably long basidiospores – the apparently most prominent feature, reflected in its name – which are also found in a few other African *Cantharellus* species, all of which share thin-walled hyphal extremities at the pileus surface, although mostly lacking clamp connections.

Field notes for the new collections of *C. longisporus* confirm the distinctly acrid taste mentioned in the original description. This suggests that taste should consistently be recorded when collecting *Cantharellus* in the field as it is a potentially interesting character to distinguish between different *Cantharellus* from this habitat. Another character from the original description is the presence of weak anastomosing veins in between the yellow-orange gill folds in the more mature stages. These veins are principally running down as vertical “ribs” on the lower gill sides.

However, we did not observe the appearance of pinkish-lilac colors that Heinemann mentioned for the older stages of the hymenophore.

The extremely variable pileus coloration, which was described (and illustrated) as a mixture of pink, lilac, orange, brown and vinaceous (Heinemann 1958, 1959), made it indeed difficult to decide whether or not specimens with at least one of the aforementioned colors and similar microscopy, belonged to the same species or not. As a consequence, Buyck *et al.* (2012) published two new and microscopically similar subspecies for *C. longisporus* from different habitats in Madagascar. One of these new subspecies, *C. longisporus* subsp. *littoralis* Buyck & Randrianjohany, is associated with coastal *Uapaca* species on the sandy soils of Madagascar's east coast, while the other one, *C. longisporus* subsp. *isaloensis* Buyck & Eyssart., was collected in *Uapaca bojeri* Baill. – Sarcolaenaceae woodland on the lateritic soils of the Central Plateau.

We were unable to obtain sequences from these more recent Central African specimens of *C. longisporus*, as well as for its Malagasy subsp. *isaloensis*, but we did obtain most genes for subsp. *littoralis* thanks to more recent collections. The latter subspecies actually corresponds to what Heim (1936) originally described as *C. cyanoxanthus* nom. inval., a name later validated – but differently interpreted – for a Central African chanterelle by Heinemann (1958). Even in the absence of good sequence data for the Central African *C. longisporus*, the distinctive morphology of this species revealed here makes it completely different from both Malagasy subspecies. Consequently, these Malagasy subspecies are recombined below as new species as they undoubtedly represent independent, Malagasy *Cantharellus* lineages.

Cantharellus littoralis (Buyck & Randrianjohany)
Buyck, comb. et stat. nov.

Cantharellus longisporus subsp. *littoralis* Buyck & Randrianjohany, *Cryptogamie, Mycologie* 33 (2): 173 (2012) (basonym).

Cantharellus cyanoxanthus Heim, *Traité de Pathologie exotique vétérinaire et comparée* 3: 301 (1936), nom. inval.

MYCOBANK. — MB 835033.

Cantharellus isaloensis (Buyck & Eyssartier)
Buyck, comb. et stat. nov.

Cantharellus longisporus subsp. *isaloensis* Buyck & Eyssartier, *Cryptogamie, Mycologie* 33 (2): 175 (2012) (basonym).

MYCOBANK. — MB 835034.

Cantharellus xanthocyaneus Ndolo Ebika & Buyck, sp. nov.
(Figs 4; 5)

MYCOBANK. — MB 835035.

TYPE MATERIAL. — **Holotype.** Republic of the Congo, Likouala Department; 3.38 km South from Makao village, Plot 1 in *Gilbertiodendron dewevrei* forest (PG1); 2°33.84'N, 17°10.12'E; alt. 360 m; 17.XI.2016, S. T. Ndolo Ebika 2353 (holo-, PC[PC0125128]; iso-, HICPC[HICPC005]).

DIAGNOSIS. — Differs from *C. cyanoxanthus* essentially in the distinctly smaller, particularly narrower basidiospores, measuring (5.7-)6-7.0-8.1(-8.8) × 3.2-3.7-4.3 μm, Q = (1.46-)1.56-1.91-2.26(-2.39).

ETYMOLOGY. — Composed of two Greek color terms, xanthos (yellow) and cyanos (dark blue), referring to the dominant colors of the fruiting body.

HABITAT. — On the ground in *Gilbertiodendron dewevrei* forest, on terra firma.

ADDITIONAL EXAMINED AND SEQUENCED MATERIAL. — **Republic Of The Congo**, Likouala Department; 3.38 km South from Makao village, Plot 1 in *Gilbertiodendron dewevrei* forest (PG1); 2°33.84'N, 17°10.12'E; alt. 360 m; 14.XI.2016; S. T. Ndolo Ebika 2333 (para-, PC[PC0125127]; iso-, HICPC[HICPC004]).

DESCRIPTION

Basidiomata (Fig. 4)

Solitary or in pairs, medium-sized and up to 75 mm high.

Pileus (Fig. 4A)

Thin-fleshed, 50-63 mm wide, plano-concave to slightly funnel-shaped, mottled with dark purplish-violaceous tinges on a yellowish background, smooth.

Hymenophore (Fig. 4C)

Composed of well-differentiated, forking gill folds, pale ochraceous with distinct pinkish tinges, strongly interveined towards the cap margin, up to 7 mm high.

Stipe (Fig. 4B, D)

55-57 × 12-17 mm, cylindrical to fluted and bumpy (when fluted), flushed with purple-violaceous to pinkish tones, particularly in its middle portion, distinctly yellowish at the base which is swollen and hollowing, becoming whitish near the junction with the gill folds.

Context

Off-white, rather thin towards the pileus margin.

Smell

Insignificant.

Taste

Unknown.

Spore print

Not obtained.

Spores (Fig. 5A)

Ellipsoid to elongated, somewhat concave at the adaxial side and more or less kidney-shaped, (5.7-)6-7.0-8.1(-8.8) ×



FIG. 4. — *Cantharellus xanthocyaneus* Ndolo Ebika & Buyck, sp. nov. (holotype; PC0125128): **A**, pileus; **B, D**, cylindrical to fluted and bumpy stipe with hymenophore; **C**, detail of hymenophore. Freshly collected fruiting bodies. Photos: S. T. Ndolo Ebika.

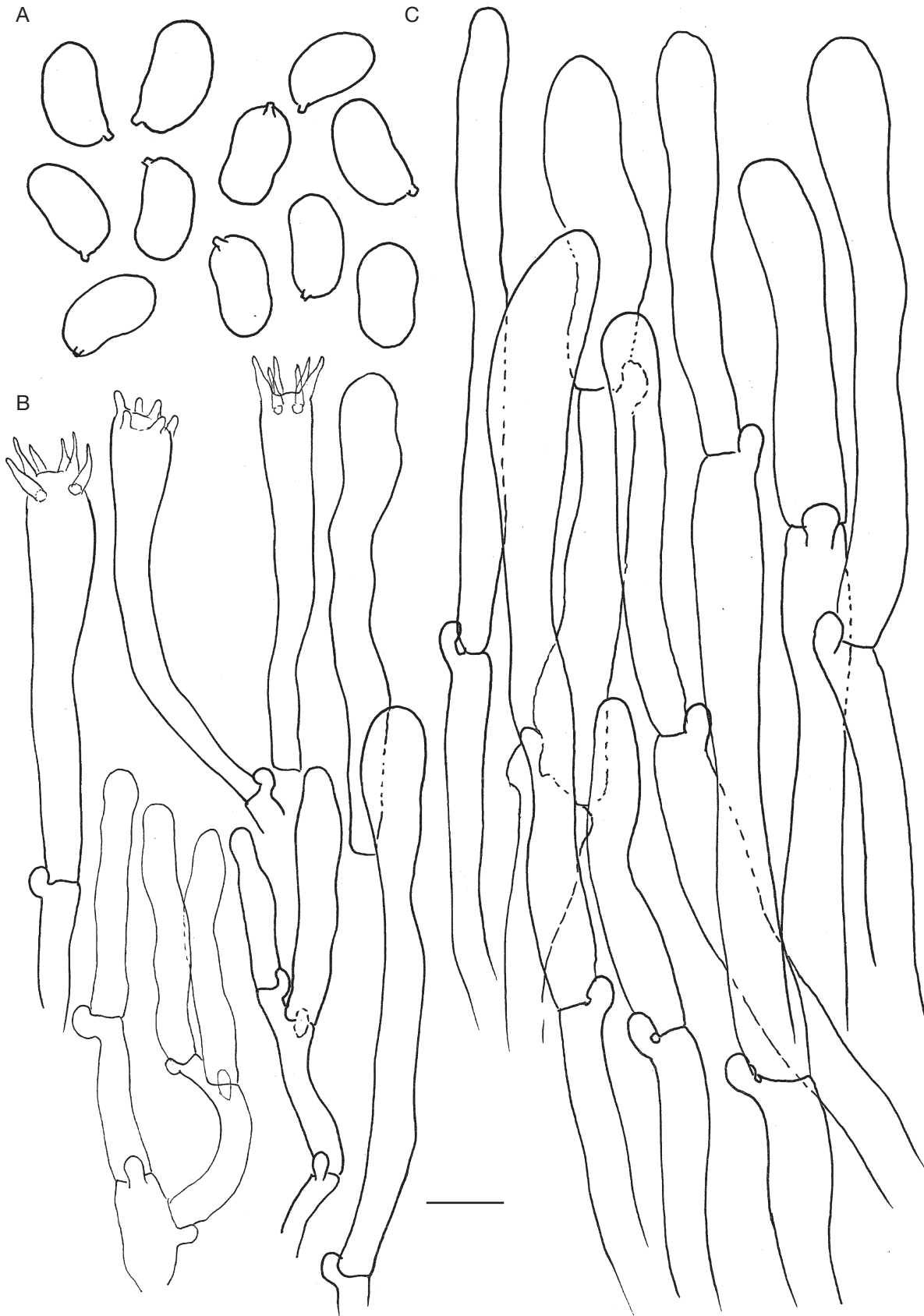


FIG. 5. — *Cantharellus xanthocyaneus* Ndolo Ebika & Buyck, sp. nov. (holotype; ; PC0125128): **A**, spores; **B**, basidia and basidiola; **C**, hyphal endings of the pileipellis. Scale bar: 10 μm , but only 5 μm for spores. Drawings: B. Buyck.

3.2-3.7-4.3 µm {N=58}, Q = (1.46-)1.56-1.91-2.26(-2.39), smooth, with a small apiculus.

Basidia (Fig. 5B)

46-70 × 5.6-8-10 µm {N=9}, predominantly six-spored.

Cystidia

Absent.

Subhymenium

Subfilamentous, composed of narrow, cylindrical cells that are sometimes slightly larger than the basis of the basidia.

Pileipellis (Fig. 5C)

Composed of thin-walled, elongated elements, mostly widening towards the septa or towards the tip, quite a few of the terminal and subterminal cells filled with a distinctly dark lilac-brown pigment. Incrusting pigment present on some particularly narrower, subterminal cells and narrow hyphae in the pileipellis. Terminal cells subcylindrical to faintly clavate, mostly 40-100 µm long and (5)8-15(22) µm diam., with thin to slightly thickened (refracting) cell walls.

Clamp connections

Very distinct on hyphae of all tissues.

NOTES

In the field, *Cantharellus xanthocyaneus* Ndolo Ebika & Buyck, sp. nov., is very similar to *C. cyanoxanthus* sensu Heinemann because of its color. However, it cannot be the same species because of the distinctly larger basidiospores of *C. cyanoxanthus* (see below), albeit with a similar length-width ratio. We have measured the holotype of *C. xanthocyaneus* Ndolo Ebika & Buyck, sp. nov., twice independently (to exclude subjective approaches) with near identical results [S. T. Ndolo Ebika: (5.7-)6-7.0-8.1(-8.8) × (3.2-)3.2-3.7-4.2(-4.3) µm, Q = (1.46-)1.56-1.91-2.26(-2.39) versus Buyck: (6.0)6.4-6.81-7.2(7.7) × (3.3)3.4-3.67-3.9(4.1) µm, Q = (1.6)1.7-1.86-2.0(2.2)]. Also the paratype shows an identical spore size [(5.8)6.3-6.73-7.1(7.3) × (2.9)3.3-3.55-3.8(4.0) µm, Q = (1.6)1.7-1.9-2.0(2.2)].

Heinemann's (1958) values for spore length of the Central African *C. cyanoxanthus* seem a bit too low compared to more recent measurements made by Eyssartier (2001) and A. De Kesel (this study) on the holotype (Goossens-Fontana 2082): P. Heinemann (1958: 7.5-9.3 × 4.4-5.4 µm), G. Eyssartier (2001: (7)8-8.83-10 × 4-4.87-5.5 (6) µm, Q = 1.45-1.82-2.0) and A. De Kesel: (7.6-)8.2-9.4-10.5 (-10.6) × (4.4-)4.3-5.5-5.6(-5.9) µm, Q = (1.59-)1.61-1.89-2.17(-2.27), but all these are very different from the Malagasy *C. littoralis* (Buyck & Randrianjohany) Buyck, comb. et stat. nov. (synonym of *C. cyanoxanthus* sensu Heim) which has spores that are very similar to those of *C. longisporus* (Buyck *et al.* 2012: (8.1)8.5-9.01-9.5(9.8) × (3.5)3.8-4.07-4.4(4.8) µm, Q = (1.9)2.0-2.21-2.4(2.5)). Some recent collections made near the type locality all confirm the narrower spores of this Malagasy species for a similar length

compared to Central African *C. cyanoxanthus*, resulting in higher Q values [H. 110: 9.08 × 4.15 µm, Q = 2.20; EJ 107: 9.07 × 4.13 µm, Q = 2.21; EJ 108: 8.81 × 4.06 µm, Q = 2.18; EJ 122: 9.06 × 4.08 µm, Q = 2.14].

Cantharellus violaceoflavescens De Kesel, Guelly,

L.A.Parra & Buyck, sp. nov.

(Figs 6; 7)

MYCOBANK. — MB 835036.

DIAGNOSIS. — Medium-sized species with violet-tinged and minutely squamulose pileus and stipe, with pure white hymenophore composed of well-developed, forking gill folds, entirely and strongly yellowing with age. Spores ellipsoid, (6.2)6.9-7.38-7.8(8.3) × (4.1)4.3-4.58-4.9(5.2) µm, Q = (1.3)1.5-1.61-1.7(1.8). Clamp connections abundant in all tissues. In gallery forests with *Berlinia grandiflora*.

TYPE MATERIAL. — **Holotype.** Togo, Plateau province, Ola, galerie Okpa-Fou, on the ground in a semi-deciduous gallery forest dominated by *Berlinia grandiflora* and *Uapaca guineensis*; 07°33.44'N, 0°52.35'E; alt. 700 m; 12.V.2010; A. De Kesel leg.; *De Kesel 4790* (holo-, BR[BR5020167050163]).

ETYMOLOGY. — *Violaceoflavescens*, a combination of the latin words *violaceo* (meaning color violet) and *flavescens* (meaning becoming yellow).

ADDITIONAL STUDIED AND SEQUENCED MATERIAL. — **Togo**, Plateau province, Ola, galerie Okpa-Fou, on the ground in a semi-deciduous gallery forest dominated by *Berlinia grandiflora* and *Uapaca guineensis*; 07°33.44'N, 0°52.35'E; alt. 700 m; 12.V.2010, A. De Kesel leg.; *De Kesel 4791* (para-, ADK[ADK4791], BR[BR 5020167046128]). *Ibid.*, gallery Gonobé, on the ground in semi-deciduous gallery forest dominated by *Berlinia grandiflora* and *Uapaca guineensis*; 07°32.73'N, 0°55.06'E; alt. 680 m; 17.V.2010; A. De Kesel leg.; *De Kesel 4829* (ADK[ADK4829], BR[BR5020167049150]). *Ibid.*, gallery Néoubengnoua, on the ground in semi-deciduous gallery forest dominated by *Uapaca guineensis*; 07°51.55'N, 0°47.68'E; alt. 670 m; 28.VI.2011; A. De Kesel leg.; *De Kesel 4963* (ADK[ADK4963], BR[BR5020184227653]). *Ibid.*, Béna-Ola, gallery Néhou-Begnoi, gallery forest dominated by *Berlinia grandiflora* and *Uapaca beude-lotii*; 07°33.51'N, 0°52.33'E; alt. 690 m; 7.VII.2007; A. De Kesel leg.; *De Kesel 4187* (ADK[ADK4187], BR[BR5020163641020]). *Ibid.*, gallery forest dominated by *Berlinia grandiflora*; 07°33.24'N, 0°53.517'E; alt. 650 m; 10.VII.2007, A. De Kesel leg.; *De Kesel 4273* (ADK[ADK4273], BR[BR5020158469684]). *Ibid.*, on the ground in gallery forest dominated by *Berlinia grandiflora* and *Uapaca guineensis*; 07°31.73'N, 0°54.96'E; alt. 780 m; 15.V.2010; A. De Kesel leg.; *De Kesel 4815* (ADK[ADK4815], BR[BR5020167047132]). *Ibid.*, Imoussa, gallery Iklouou, on the ground in semi-deciduous gallery forest dominated by *Berlinia grandiflora*; 07°33.36'N, 0°56.54'E; alt. 740 m; 13.V.2010; A. De Kesel; *De Kesel 4802* (ADK[ADK4802], BR[BR5020167051177]).

HABITAT. — Gallery forests with *Berlinia grandiflora*, sometimes mixed with *Uapaca guineensis*.

DESCRIPTION

Basidiomata

Solitary or in groups of two to four (Fig. 6A, B, E).

Pileus

40-60 mm diam., thin-fleshed, broadly depressed to infundibuliform when mature; margin incurved, sharp, straight or slightly upturned, striate and undulating at maturity;

surface finely tomentose-fibrillose in the center, disrupting into very minute squamules towards the margin, at first very dark greyish violet (14-16DEF6-8, 17F5) and remaining so in the center (Fig. 6A, B), outside the center quickly a paler violet to greyish violet (17DEF5-7), at maturity often maintaining a narrow, whitish marginal edge, developing irregular, whitish patches outside the pileus center and quickly staining light yellow (1A2, 3A1-3), also when bruised, with age entirely becoming yellow (4A2-3) from the margin inwards.

Hymenophore

Deeply decurrent and well-delimited from the sterile stipe surface, composed of arcuate gill folds, moderately spaced (3-6 per cm near pileus margin), often forked near the margin (Fig. 6E), gill sides developing thick vertical ribs or veins, occasional transversal connections and anastomoses usually rare and remaining rather low, never becoming reticulate-alveolar in aspect, of a contrasting pure white at first (Fig. 6E), sometimes with local purplish-violet tinges near the cap margin, rapidly bruising yellowish, with age becoming entirely off-white to pale yellow (3A2-3) (Fig. 6C-D).

Stipe

Slender, 40-60 × 4-6(7) mm, rarely straight, subcylindrical or tapering downward, smooth or sparsely beset with minute dark violet squamules, white near the base, whitish to greyish violet (17AB2) elsewhere, bruising yellow particularly near the very base, with time becoming entirely pale yellow to greyish yellow (4AB2-3), solid or becoming fistulose within.

Context

Thin, whitish, unchanged when cut, with age yellowing just beneath pileus and stipe surface.

Taste

Peppery, moderately strong after 15 seconds.

Odour

Weak, insignificant.

Spore print

Not obtained.

Spores (Fig. 7A)

Ellipsoid, (6.2)6.9-7.38-7.8(8.3) × (4.1)4.3-4.58-4.9(5.2) μm, Q = (1.3)1.5-1.61-1.7(1.8), smooth, hyaline.

Basidia (Fig. 7B)

Very long and slender, (65-)80-110 × 7-9 μm, (5-)6-spored.

Cystidia

Absent.

Subhymenium

Filamentous, composed of long and slender, cylindrical cells.

Pileipellis (Fig. 7C)

Composed of thin-walled elements, terminal elements subcylindrical to clavate, 8-12 μm diam., frequently with a slightly thickened and refringent wall.

Clamp connections

Rather small, but on hyphae of all tissues.

NOTES

Cantharellus violaceoflavescens De Kesel, Guelly, L.A.Parra & Buyck, sp. nov., is still only known from a few sites around the type locality. The description is based on the holotype, but spore measurements on a few other collections result in very similar values as for the holotype. This confirms that this species differs from other known chanterelles with more or less similar coloration in the size and form of its spores:

ADK4790 (6.2)6.9-7.38-7.8(8.3) × (4.1)4.3-4.58-4.9(5.2) μm, Q = (1.3)1.5-1.61-1.7(1.8);

ADK4802 (6.4)6.7-7.18-7.6(8.5) × (3.7)4.1-4.29-4.5(4.8) μm, Q = (1.5)1.6-1.68-1.8(1.9);

ADK4815 (6.2)6.7-7.04-7.4(7.9) × 3.9)4.2-4.54-4.8(5.0) μm, Q = (1.4)1.5-1.56-1.7(1.8).

Cantharellus violaceoflavescens De Kesel, Guelly, L.A.Parra & Buyck, sp. nov., is unmistakable in the field because of the contrast between the pure white hymenophore with low interstitial anastomosing veins and the dark violaceous, squamulose surfaces of stipe and pileus of young specimens, followed by a spectacular yellowing with age. The only more or less similar species so far is the here newly combined Malagasy *C. littoralis* (Buyck & Randrianjohany) Buyck, comb. et stat. nov., which differs in its much more fleshy basidiomata, the better developed gill folds without interstitial venation, and the weaker yellowing with age. *Cantharellus conspicuus*, described from miombo woodland in Zimbabwe, is much smaller, shows a strongly squamulose surface of pileus and stipe, as well as stronger interstitial venation between gill folds.

Acknowledgements

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FIG. 6. — *Cantharellus violaceoflavescens*: **A, E**, fresh, young fruiting bodies (holotype; BR5020167050163); **B**, paratype (A. De Kesel 4971); **C-D**, strongly yellowing of all tissues illustrated in older fruiting bodies [**C**, A. De Kesel 4829; **D**, A. De Kesel 4963]. Photos: A. De Kesel, L. Parra Sánchez.



FIG. 7. — *Cantharellus violaceoflavescens* (holotype; BR5020167050163): **A**, spores; **B**, basidia and basidiola; **C**, hyphal endings of the pileipellis. Scale bar: 10 μm , but only 5 μm for spores. Drawings: B. Buyck.

and delivering fine logistic support in Togo, as well as Petra Ballings and Luis A. Parra for photographing some collections of *C. longisporus* and *C. violaceoflavescens* De Kesel, Guelly, L.A. Parra & Buyck, sp. nov. respectively. The authors thank the reviewers Terry Henkel and Vladimír Antonín for their valuable comments.

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