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Cantharellus hygrophorus, a new species in subgenus *Afrocantharellus* from tropical southwestern China

Shi-Cheng SHAO[a,c], *Bart BUYCK*[b*], *Valérie HOFSTETTER*[e], *Xiao-Fei TIAN*[c], *Yan-Hong GENG*[d], *Fu-Qiang YU*[c] *& Pei-Gui LIU*[c]

[a]*Key Laboratory of Tropical Plant Resources and Sustainable Use,*
Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences,
email: shaoshicheng@xtbg.org.cn

[b]*Museum national d'histoire naturelle, Dept. of Systematics and Evolution,*
UMR 7205, 12 rue Buffon, 75005 Paris, France, email: buyck@mnhn.fr

[c]*Key Laboratory of Biodiversity and Biogeography, Kunming Institute of Botany,*
Chinese Academy of Sciences, Kunming, 650204, Yunnan, China

[d]*Environmental education department, Xishuangbanna Tropical Botanical Garden,*
Chinese Academy of Sciences, Menglun 666303, Yunnan, China

[e]*Department of plant protection, Agroscope Changins-Wadenswil Research Station*
ACW, Rte de Duiller, 1260, Nyon, Switzerland

Abstract – *Cantharellus hygrophorus* is described and illustrated from tropical Yunnan, China. It is characterized by its medium to large, fleshy fruitbodies, the deep orange-red color of pileus and part of the stipe, the yellow-orange hymenophore composed of well-developed gill folds, a pileipellis of suberect hyphal extremities and absence of clamps. These characters place it in *Cantharellus* subg. *Afrocantharellus* sect. *Cutirellus* as a look-alike of the tropical African *C. splendens*. Both morphological features as well as a phylogenetic analysis of nLSU sequences argue strongly against the recognition of *Afrocantharellus* as a separate genus, which is here considered a later synonym of *Cantharellus*.

Afrocantharellus / biodiversity / Cutirellus / chanterelles / LSU / phylogeny / taxonomy

INTRODUCTION

Ongoing studies on chanterelles in southwestern China are revealing a rich diversity of at least 23 different species (Shao-Sheng, unpubl.) including several new, interesting taxa (Tian *et al.*, 2012; Shao *et al.*, 2011; Shao *et al.*, 2012). We refer to the latter papers for a short history on the inventory of *Cantharellus* in China. In this paper, the authors describe a new species from the tropical rain forest of Xishuangbannan in Yunnan province that is characterized by the absence of clamp connections.

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[*] Correspondence author: buyck@mnhn.fr

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MATERIAL AND METHODS

Morphology. – Macroscopic descriptions are based on features of fresh materials and microscopic characters were examined under a Nikon E400 microscopic (10 × 100) using dried materials. Sections of basidia, basidiospores and pileipellis were recovered in 5% KOH solution before observation. Line drawings were made with the aid of a drawing tube (Y-IDT, Japan). At least 20 spores were measured from each sample; (m/n/p) indicates measurements based on m spores from n basidiomata in p collections. Spore dimensions are given following the form (a-)b-c(-d), with b-c containing at least 90% of all values and the extremes (a, d) enclosed in parentheses. Q indicates the basidiospore length/width ratio, with Q_m denoting the average Q of all spores ± sample standard deviation. The holotype and additional examined material have been deposited in the Herbarium of Cryptogams, Kunming Institute of Botany, Chinese Academy of Sciences (KUN-HKAS).

DNA extraction, amplification and sequencing. – Genomic DNA extraction followed the modified CTAB method proposed by Doyle and Doyle (1987) for *C. hygrophorus* and Hofstetter *et al.* (2002) for the other species. For *C. hygrophorus* primers ITS4R and LR5 were used to amplify nucLSU (Feibelman *et al.*, 1997) and the PCR product was purified using a quick purification kit (Sangon, China), while sequencing was accomplished by Sangon company (Shanghai, China) on an ABI 3730XL automatic sequencer by using the same primer pair as for PCR**.** Amplification and sequencing of the nucLSU for the other newly generated sequences were performed as described in Buyck *et al.* (2014).

Phylogenetic analyses. – Alignment of nucleotide sequences was performed by eye using the editor of MacClade 4.06 (Maddison and Maddison 2003, Sinauer Associates, Inc. Sunderland, Massachusetts). Maximum parsimony (MP) analyses were conducted in PAUP (Swofford, 2002). Search for the most parsimonious tree(s) used 500 replicates of random addition sequence (RAS), with MAXTREE = 1000, TBR branch swapping, MULPARS option on, and gaps treated as missing characters. Branch robustness was estimated based on 500 MP bootstrap pseudoreplicates, each of 10 RAS, and with the same settings as for the search for the most parsimonious tree(s). Branches that received MP bootstrap support (MPbs) ≥ 70% were considered as significantly supported (Mason-Gamer and Kellogg 1996). MP analyses were all implemented with characters of type "unordered", multistate taxa interpreted as uncertainty, one tree held at each step during stepwise addition, steepest descent option not in effect, and branches collapsed if minimum branch length were zero.

RESULTS

Phylogenetic analyses

Out of the 67 sequences of the nuclear large subunit of ribosomal DNA (nucLSU) used for phylogenetic analyses 49 were sampled from previous studies (Buyck *et al.*, 2014; Tibuwa *et al.*, 2012; Wilson *et al.*, 2012) and 19 newly produced for this study and deposited in GenBank (Table 1). Six sequences were sampled in outgroup genera *Clavulina*, *Hydnum* and *Craterellus* and 61 sequences were

Table 1. Voucher table listing sequenced taxa with full authorities and year of publication, voucher specimen, country of origin and Genbank numbers. Genbank numbers preceded by an asterisk are newly produced sequences for this study. Abbreviations are as follows: AV: Annemieke Verbeken, BB: Bart Buyck, DDT: Donata Tibuhwa,DS: Dirk Stubbe, EC: Emanuele Campo, ER: Emile Randrianjohany, GE: Guillaume Eyssartier, JJ: Jay Justice, JV: Jan Versterholt, TH: Terry Henkel, SSCS: Shi-Cheng Shao

Taxon	*Voucher Extraction nr/ coll. Nr.*	*Origin*	*nucLSU*
Genus *Afrocantharellus*			
Afroc. fistulosus (Tibuhwa & Buyck) Tibuhwa 2012	DDT 43	Tanzania	JQ976965
Afroc. fistulosus	DDT 31	Tanzania	JQ976959
Afroc. splendens (Buyck) Tibuhwa 2012	DDT 57	Tanzania	JQ976967
Afroc. splendens	DDT 17	Tanzania	JQ976956
Genus *Cantharellus*			
C. addaiensis Henn. 1898	494 / BB 96.010	Zambia	*KM484680
C. afrocibarius Buyck & V. Hofstetter 2012	496 / BB 96.235 **holotype**	Zambia	KF294668
C. albidolutescens Buyck & V. Hofstetter 2014	456 / BB 08.057	Madagascar	KF294645
C. altipes Buyck & V. Hofstetter 2011	344 / BB 07.162 **paratype**	USA	KF294636
C. ambohitantelyensis Buyck & V.Hofstetter 2014	475 / BB 08.336 **holotype**	Madagascar	KF294656
C. amethysteus (Quél.) Quél.1888	349 / BB 07.284	Slovakia	KF294639
C. appalachiensis R.H. Petersen 1971	342 / BB 07.123	USA	KF294635
C. cerinoalbus Eyssart. & Walleyn 2009	487 / AV 06.051 **isotype**	Malaysia	KF294663
C. cibarius Fr. :Fr. 1821	479 / GE 07.025	France	KF294658
C. cinnabarinus (Schwein.) Schwein. 1834	312 / BB 07.001 **neotype**	USA	KF294624
C. congolensis Beeli 1928	512 / BB 98.058	Tanzania	KF294673
C. congolensis aff.	69 / BB 06.197	Madagascar	KF294608
C. congolensis	247 / BB 98.039	Tanzania	KF294609
C. cuticulatus Corner 1966	486 / DS 06.283	Malaysia	KF294662
C. decolorans Eyssart. & Buyck 1999	469 / BB 08.278 **epitype**	Madagascar	KF294654
C. densifolius Heinem. 1958	258 / BB 98.013	Tanzania	KF294616
C. diminutivus Corner 1969	485 / DS 06.033	Malaysia	KF294661
C. ferruginascens P.D. Orton 1969	480 / GE sn	France	*KM484681
C. fistulosus Tibuhwa & Buyck 2008	517 / DDT 43 **isotype**	Tanzania	KF294674
C. flavus M.J. Foltz & T.J.Volk 2013	1077 / JJ NC-Canth3	USA	*KM484682
C. formosus Corner 1966	1212 / BB 13.163	USA	*KM484683
C. friesii Quél. 1872	1001 / EC09.15	Italy	*KM484684
C. gracilis Buyck & V. Hofstetter 2012	251 / BB 98.234 **holotype**	Tanzania	KF294612
C. guyanensis Montagne	TH9201	Guyana	JQ915132
C. humidicolus Buyck & V. Hofstetter 2012	250 / BB 98.036 **holotype**	Tanzania	KF294666
C. hygrophorus sp nov 2014	SSCS 2014 **holotype**	China	KJ004002
C. ibityensis	463 / BB 08.203 **paratype**	Madagascar	KF294651
C. ibityensis Buyck & V. Hofstetter 2014	462 / BB 08.196 **holotype**	Madagascar	KF294650
C. ilicis Olariaga & Salcedo 2008	1122 / BB 12.089	Italy	*KM484685
C. isabellinus var. parvisporus Eyssart. & Buyck 2000	249 / BB 98.037 **paratype**	Tanzania	KF294611
C. lateritius (Berk.) Singer 1949 cf	1076 / JJ NC-Canth2	USA	*KM484686
C. lewisii Buyck & V. Hofstetter 2011	301 / BB 02.197 **paratype**	USA	KF294623

Table 1. Voucher table listing sequenced taxa with full authorities and year of publication, voucher specimen, country of origin and Genbank numbers *(continued)*

Taxon	*Voucher Extraction nr/ coll. Nr.*	*Origin*	*nucLSU*
C. lilacinopruinatus Hermitte, Eyssart. & Poumarat 2005	1006 / EC09.91	Italy	**KM484687*
C. longisporus ssp. littoralis Buyck & Randrianjohany 2012	1007 / ER 107	Madagascar	**KM484688*
C. minor Peck 1872	313 / BB 07.002	USA	*KF294625*
C. paucifurcatus.Buyck & V. Hofstetter 2014	474 / BB 08.320 **holotype**	Madagascar	*KF294655*
C. platyphyllus Heinemann 1966	262 / BB 98.126 **epitype**	Tanzania	*KF294620*
C. platyphyllus subsp. bojeriensis Eyssart. & Buyck 1999	458 / BB 08.158	Madagascar	*KF294647*
C. pseudominimus Eyssart. & Buyck 1999	477 / JV 00.663	Portugal	*KF294657*
C. quercophilus Buyck, Lewis, Eyssart. & V. Hofstetter 2010	636/ BB 07.097 **holotype**	USA	*KF294644*
C. ruber Heinem. 1966	DDT 60	Tanzania	*JQ976969*
C. romagnesianus Eyssart. & Buyck 1999	1002 / EC09.17	Italy	**KM484689*
C. roseocanus (Redhead, Norvell & Danell) Redhead, Norvell & Moncalvo 2012	1209 / BB 13.151	USA	**KM484690*
C. sebosus Buyck & V. Hofstetter 2014	460 / BB 08.162 **paratype**	Madagascar	*KF294649*
C. spectaculus M.J. Foltz & T.J.Volk 2013	1085 / JJ MO-Canth4	USA	**KM484691*
C. splendens Buyck 1994	499 / BB 96.199	Zambia	*KF294671*
C. subamethysteus Eyssart. & Stubbe 2009	488 / DS 06.218 **isotype**	Malaysia	*KF294664*
C. subcyanoxanthus Buyck, Randrianjohany & Eyssart. 2012 aff	257 / BB 98.014	Tanzania	*KF294615*
C. subincarnatus subsp. rubrosalmoneus Buyck & V. Hofstetter 2014	13 / BB 06.080 **holotype**	Madagascar	*KF294601*
C. subpruinosus Eyssart. & Buyck 2001	484 / GE 07.080	France	*KF294660*
C. symoensii Heinem. 1966	261 / BB 98.113 **epitype**	Tanzania	*KF294619*
C. symoensii aff	464 / BB 08.210	Madagascar	**KM484692*
C. tabernensis Feibelman & Cibula 1996	328 / BB 07.056	USA	*KF294631*
C. tanzanicus Buyck & V. Hofstetter 2012	268 / BB 98.040 **holotype**	Tanzania	*KF294622*
C. tenuithrix Buyck & V. Hofstetter 2011	322 / BB 07.035 **paratype**	USA	*KF294629*
C. texensis Buyck & V. Hofstetter 2011	317 / BB 07.018 **holotype**	USA	*KF294626*
C. tomentosus Eyssart. & Buyck 2000	500 / BB 98.060 **holotype**	Tanzania	*KF294672*
C. sp.ined.	1041 / BB 11.041	Madagascar	**KM484693*
Genus *Clavulina*			
Cl. cf. cristata	1123 / BB 12.083	Italy	**KM484694*
Genus *Craterellus*			
Cr. sp.	1024 / BB 09.079	New Caledonia	**KM484695*
Cr. lutescens (Pers.) Fr. cf	1203 / BB 13.048	Canada	**KM484696*
Cr. tubaeformis(Fr.) Quél. cf	1208 / BB 13.125	USA	**KM484697*
Genus *Hydnum*			
H. rufescens Pers.	355 / BB 07.340	Slovakia	**KM484698*
H. repandum L.	356 / BB 07.341	Slovakia	*KF294643*

representative of the genus *Cantharellus sensu* Buyck *et al.* (2014). The full nucLSU sequences alignment was of 1485 characters. After exclusion of ambiguously aligned regions (604 charaters) the alignment used for phylogenetic analyses included 881 characters of which 688 were constant and 162 were parsimony-informative. One of the best MP trees (Length = 308, Consistency Index = 0.75, Rescaled Consistency Index = 0.6947) is depicted in Fig. 1. This tree suggests with maximal support (MPbs = 100%) that *C. hygrophorus* clusters within subgenus *Afrocantharellus* (clade 6 in Buyck *et al.*, 2014). This species nests in section *Cutirellus* Corner without significant support. Our phylogeny also resolved with high support the placement of *C. guyanensis* as basal to all other subgenera of *Cantharellus* (MPbs = 99%), including subgenus *Afrocantharellus* (MPbs = 100%), occupying an intermediate position between *Cantharellus* and the other Cantharellales sampled as outgroup. Finally, this tree shows that the collections DDT43 and DDT31, described as *Afrocantharellus fistulosus* by Tibuhwa *et al.* (2012) do not cluster with the type specimen for *C. fistulosus* sequenced by Buyck *et al.* (2014) and used for the description of the species. The latter is placed with high support (MPbs = 99%) in subgenus *Cantharellus*, whereas Tibuhwa's collections are placed with maximal support in subgenus *Afrocantharellus*.

Taxonomy

Cantharellus Adans.: Fr., *Systema Mycologicum* 1: 318 (1821)

= *Afrocantharellus* (Eyssart. & Buyck) Tibuhwa, *IMA Fungus* 3: 33. 2012, syn. nov.

Cantharellus hygrophorus S. C. Shao, Buyck & F. Q. Yu **sp. nov.** **Fig. 2**

Mycobank nr.: MB 807389

Etymology.: The specific epithet refers to its overall similarity to genus *Hygrophorus.*

Basidiomata extremely fleshy, medium-sized, 58-120 mm in height. **Pileus** quite large, 45-130 mm in diam., with surface smooth, bright red, firstly strongly convex with inrolled margin, later becoming more or less plane with age; margin regular or folded, smooth, thin. **Context** solid, fleshy, at mid-radius already much thinner, 2-4 mm thick, unchanging, with strong mushroom flavor. **Hymenophore** decurrent to one third of stipe, of relatively few, well-developed gill-folds, up to 8 mm in height, forking and anastomosing only near the cap margin, light yellow. **Stipe** solid, subcylindrical, 58-120 × 11-18 mm, concolorous or slightly paler than the cap. **Spore print** not obtained.

Basidiospores large and ellipsoid to narrowly ellipsoid, (9.5-)10-12.0(-12.5) × (6.0-)6.5-8.0(-8.5) µm, Q = 1.30-1.75, Q_m = 1.50 ± 0.1, smooth, colorless and hyaline, thin-walled, mostly with one droplet. **Basidia** long and slender, mostly (73.0-)76-137 × 7.0-11.5 µm, narrowly clavulate to subcylindrical, with 2-6 sterigmata. **Cystidia** absent. **Hymenophoral trama**, composed of filamentous hyphae 4.0-13.5 µm diam., colorless, thin-walled; **Pileipellis** a loose tissue of intermixed, ascending, subcylindrical hyphal extremities with many free endings, measuring 3.5-17.5(-23.5) µm diam., without observable pigment, thin-walled, with terminal cells measuring mostly ca. 10.0-69.0 × 4.5-8.0 µm. **Clamp connections** absent.

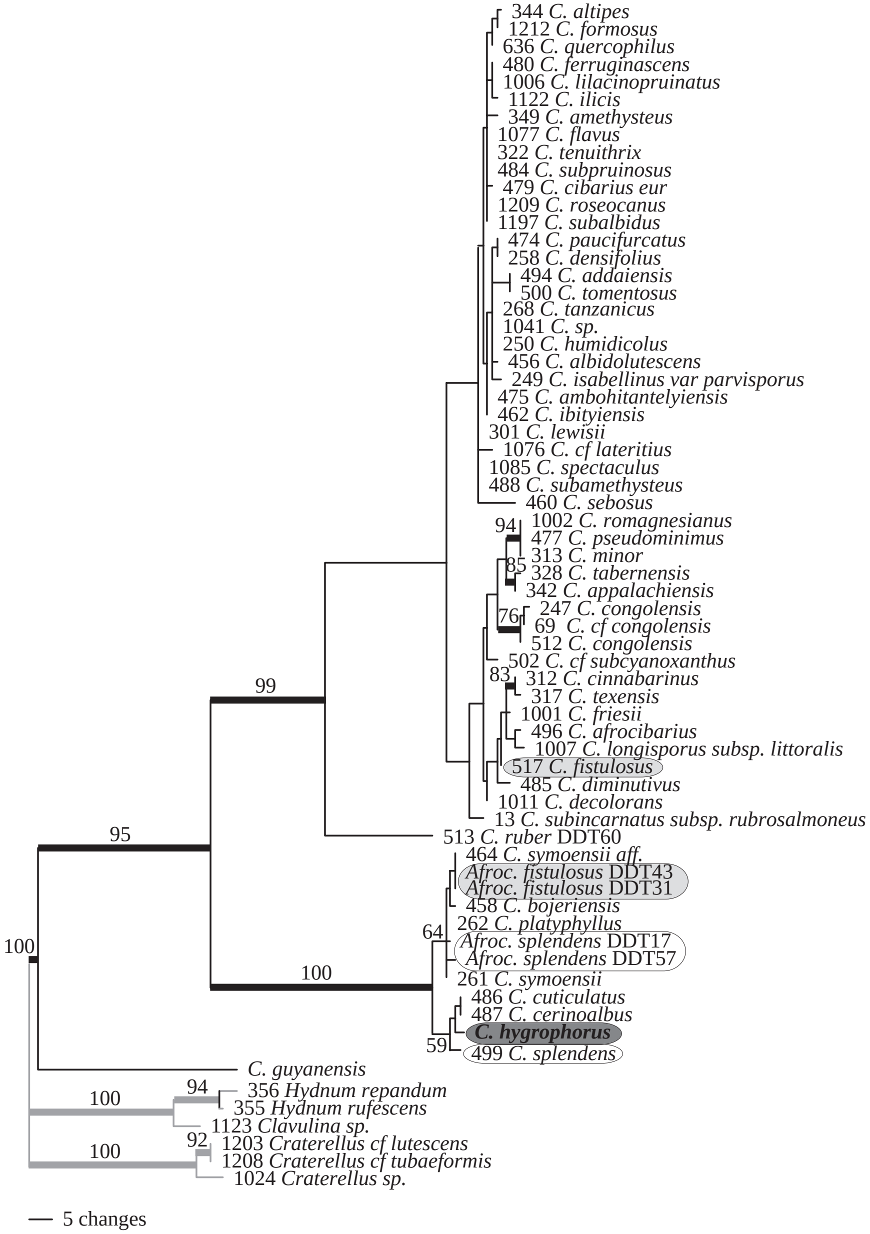

Fig. 1. MP best tree inferred from the analysis of nucLSU sequences for 67 species. Branches with high support ≥ 50% are in bold and values are reported along the branches. The name of the new species is highlighted in light green, whereas discussed collections for both *Afroc./C. fistulosus* and *Afroc./C. splendens* are highlighted in gray and transparent boxes respectively. Tree branches delimiting genus *Cantharellus* are in black, those for outgroups in gray. *C. hygrophorus* clusters within subgenus *Afrocantharellus* (clade 6 in Buyck *et al.*, 2014) with MPbs = 100%. *C. guyanensis* is highly supported (99% value) as basal to all other subgenera of *Cantharellus*, including subgenus *Afrocantharellus* (MPbs = 100%).

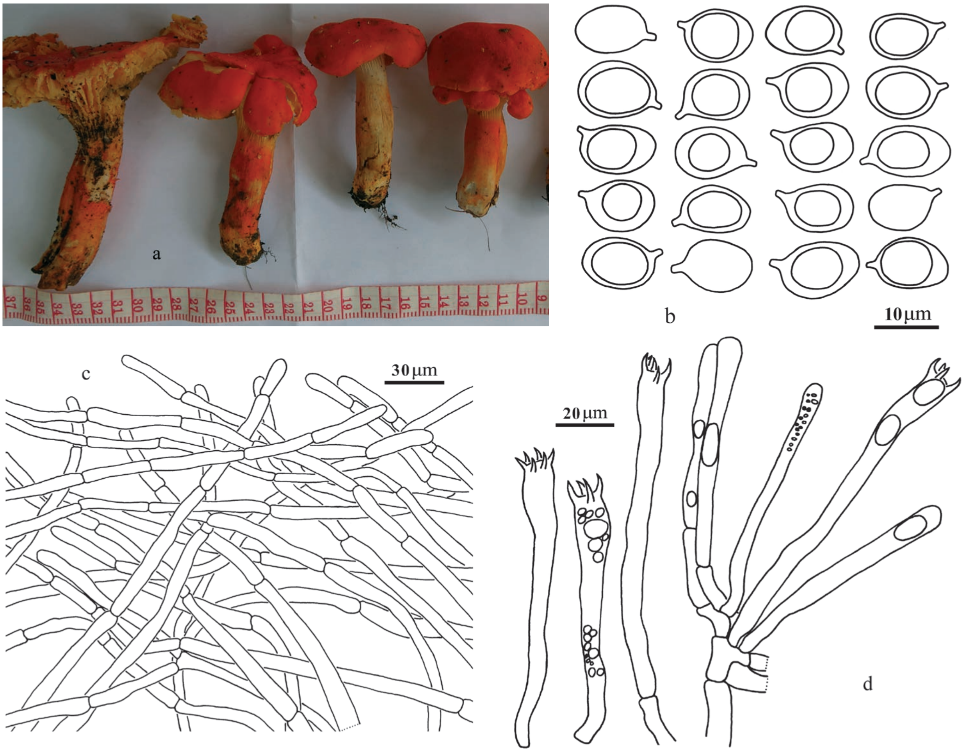

Fig. 2. *Cantharellus hygrophorus* (HKAS 80614, holotype): **a.** Basidiomata. **b.** Spores. **c.** Terminal elements of the pileipellis**. d.** Basidia.

Habit, habitat and distribution: caespitose, under shadeway of tropical rain forest with dominant tree species *Mayodendron igneum* (Bignoniaceae) *Annona squamosal* and *Miliusa tenuistipitata* (Annonaceae), *Terminalia myrio*carpa (Combretaceae) and *Mangifera siamensis* (Anacardiaceae), frequent understory species were *Prismatomeris connate* (Rubiaceae), *Ardisia* sp. (Myrsinaceae), *Pometia pinnata* (Sapindaceae) and *Pittosporopsis kerrii* (Icacinaceae).

Specimens examined: CHINA. Yunnan Prov., Xishuangbanna city, alt. 570 m, 23 July 2013, S. C. Shao hyg1 (HKAS 80614, holotypus); ibid., S. C. Shao hyg 2 (HKAS 80615, paratypus).

DISCUSSION

The new species strongly reminds of the genus *Hygrophorus* because of its well-differentiated, thick gill folds, but can be distinguished from it by flesh texture, thickening hymenium, and molecular evidence. In the field, the Chinese specimens could easily be mistaken for the African *C. splendens* Buyck (1994) from which it differs microscopically only by its distinctly longer basidia (76-137 µm versus 60-80(-90) µm for *C. splendens*) and more voluminous, broader spores ((9.5-)10-12.0(-12.5) × (6.0-)6.5-8.0(-8.5) µm, Qm = 1.50 versus 8-9.5-11 × 5-5.25-6 µm, Qm = 1.8). In addition, unlike the African *C. splendens*, the Chinese specimens never stain hands upon handling.

Both *C. splendens* and *C. hygrophorus* belong in subgenus *Afrocantharellus* Eyssart. & Buyck, a subgenus in which all presently known species are medium-sized to large, have moderately to very well-developed gill folds, a high proportion of four-spored basidia, lack clamp connections and have thin-walled hyphal extremities at the cap surface (Buyck *et al.*, 2014). All species are tropical in distribution and hitherto only known from Africa (Buyck 1994, Buyck *et al.*, 2013), Madagascar (Buyck *et al.*, 2014) or Malaysia (Eyssartier *et al.*, 2009). Nevertheless, none of these characters are unique to this subgenus. Absence of clamps also characterizes the entire subgenus *Rubrinus*, presently only known from Africa. The latter subgenus contains also a subclade with a considerable number of orange-red species (sect. *Heinemannianus* Eyssart. & Buyck), but these are typically much smaller. Also subgenus *Rubrinus* has some species with both very well-developed gills folds (especially in sect. *Isabellinus* Eyssart. & Buyck *emend*. Buyck & V. Hofstetter 2014) and thin-walled extremities in the pileipellis, and it includes even exclusively four-spored taxa. For these reasons Buyck *et al.* (2014) already expressed concerns about the recognition of *Cantharellus* subgen. *Afrocantharellus* at generic level by Tibuhwa *et al.* (2012). Our phylogeny of nucLSU sequences (Fig. 1) now clearly supports these concerns as the neotropical *C. guyanensis* Montagne, a species having clamp connections at all septa, is basal to the rest of the genus, including subgenus *Afrocantharellus*, which can thus no longer be considered to represent a separate genus.

Together with its African look-alike, *C. splendens,* and two Malayan species (*C. cutirellus* Corner and *C. cerinoalbus* Eyssart. & Walleyn), *C. hygrophorus* belongs in sect. *Cutirellus* Corner (Fig. 1) for species that have more or less vertically oriented hyphae in the pileipellis instead of a cutis as in nearly all other chanterelles (Buyck *et al.*, 2014). Both Malayan species are very similar under the microscope but quite different in general aspect from the previous two species and do not resemble *C. hygrophorus* in the field (compare illustrations in Eyssartier *et al.*, 2009). The remaining species in subgenus *Afrocantharellus,* all restricted in distribution to Africa or Madagascar, constitute sect. *Afrocantharellus* and are very similar in general habit and coloration. *Afrocantharellus fistulosus* sensu Tibuhwa *et al.*, (2012), which seems to be closely related (or identical?) to *C. symoensii* Heinem. is clearly a misapplication of *C. fistulosus* as originally published in Tibuhwa *et al.* (2008). Tibuhwa's collections for *Afrocantharellus splendens* also seem to involve misidentifications (although nucLSU offers no significant support to back this up) as the original material for *C. splendens* clusters in section *Cutirellus*, where it fits also morphologically next to *C. hygrophorus*, whereas Tibuhwa's collections are suggested to be part of subgenus *Afrocantharellus*, section *Afrocantharellus*.

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