Fungal Diversity (2014) 64:101–121
DOI 10.1007/s13225-013-0272-3

A multilocus phylogeny for worldwide *Cantharellus* (Cantharellales, Agaricomycetidae)

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Received: 15 July 2013 / Accepted: 13 November 2013 /

Abstract After a short historical overview of past systematic studies on *Cantharellus*, discussing delimitation and species diversity of the genus as well as previous, morphology-based, infrageneric classifications, this paper presents the first molecularly-based infrageneric classification of this genus using a multigene phylogenetic approach (nucLSU, mitSSU, RPB2 and *tef-1*) on a dataset that covers approximately halve of the described chanterelles worldwide, including many type specimens. Six subgenera are recognized and the recognition of subgenus *Afrocantharellus* as a separate genus is not accepted. The taxonomic value of individual morphological features is discussed as challenged by this new multigene phylogeny which comprises five new sections, one new subgenus and many emendations for previously recognized infrageneric groups. The paper discusses the observed discrepancy in biodiversity of *Cantharellus* when comparing between studies that focus either on below- or above-ground presence. A preliminary biogeographic hypothesis suggests an 'out of Africa' Gondwanan origin as a result of vicariance and subsequent migrations.

Keywords Biogeography · Ectomycorrhiza · Gondwana · mitSSU · nucLSU · *RPB2* · *tef*-1 · Systematics

Introduction

Short historical overview of the study of *Cantharellus*

The name *Cantharellus* Adans.: Fr. is derived from the French word "chanterelle" for which we find the first published records in the middle of the 17th century (Bauhin and Cherler 1651). As pointed out by Eyssartier and Buyck (2000), the first use of the name "Chanterel" at the generic level was not by de Jussieu (1789) as often assumed, but by the French botanist Adanson (1763). His concept and genus name was later adopted - and as such sanctioned - by Fries (1821) with the current, latinized orthograph.

The generic concept of *Cantharellus* has evolved considerably over time. Persoon (1797) accepted *Cantharellus* and *Craterellus* Pers.:Fr. for a short time as two smaller, separate, but closely related genera, but then transferred both genera (Persoon 1801) to the much larger genus *Merulius* Fr. which grouped most fungi that had a veined hymenophore but were often morphologically very different in general habit (including e.g. *Serpula* (Pers.) Gray). *Cantharellus*, *Craterellus* and look-alikes constituted then together "*Cantharellus*", one of four main subgroups recognized in *Merulius*. Fries (1838) interpreted *Craterellus* and *Cantharellus* again as separate genera but his generic concept was still much wider than today and Fries' circumscription of *Cantharellus* applied to all fungi that morphologically resemble a chanterelle. Fries (1838) also introduced a systematical gap between craterelles and chanterelles, classifying the former in his "*Auricularini*"—which he

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later renamed "*Thelephorei*" (Fries 1874)—side by side with other fungi with a primarily smooth hymenophore, such as *Stereum* Hill ex Pers. or *Thelephora* Ehrh. ex Willd., for example.

During the second half of the 19th century, the introduction of microscopic features in fungal descriptions allowed for a more refined definition of *Cantharellus*. Léveillé (1843) followed Persoon's classification when describing and illustrating for the first time the microscopic features of "*Merulius cantharellus*" with basidia bearing more than 4 sterigmata. Léveillé (1837) introduced the term 'cystidium' in mycology and noted their complete absence in *Cantharellus*, whereas he described the form of the spores as resembling "wheat grains". Within the next 30–40 years, nearly all of the microscopically important features of *Cantharellus* and *Craterellus* were discovered: homomorphic trama (Forquignon 1886), related to 'Agaricinae' (Patouillard 1887), long basidia, similarities with Hygrophoraceae (Fayod 1889), stichic basidia (Juel 1898), evolutionary hypothesis based partly on absence-presence of clamps (Maire 1902). As such, at the dawn of the 20th century, all of the important "modern" features of *Cantharellus* had already been described, but progress on Cantharellaceae then stagnated for nearly a century. In fact, progress took a step back in Europe when, under the influence of some of the major identification works (e.g. Kühner and Romagnesi 1953), *Craterellus* was abandoned as a separate genus and included within *Cantharellus* at the rank of either section or subgenus.

Before the advent of molecular biology, *Cantharellus* and *Craterellus* were considered to be part of the "Aphyllophorales" in Friesian classifications, i.e. they were part of those fungi that lack true gills. This concept seemed justified for European taxa or, more in general, for the majority of northern hemisphere taxa and was never questioned, not even when numerous chanterelles with well-developed gill folds were described from subtropical and tropical parts of the world. With the arrival of molecular techniques, taxonomic progress on *Cantharellus* shifted from Europe to America. In general terms, molecular contributions towards a better understanding of *Cantharellus* and the cantharelloid clade can be situated at two levels.

A first series of contributions was directly interested in the genus *Cantharellus* and its delimitation from *Craterellus*, an interest that was probably triggered by the discovery that ITS sequences of *Craterellus* and *Cantharellus* differ significantly in length (Feibelman et al. 1994). Although Feibelman et al. (1997) demonstrated convincingly that *Pseudocraterellus* Corner and *Craterellus* did not belong in *Cantharellus*, it was Dahlman et al. (2000) who finally recombined some species of *Cantharellus* subgenus *Leptocantharellus* Corner into *Craterellus,* thereby circumscribing *Cantharellus* to its present day concept. With the natural concept of *Cantharellus* finally established, most of the recent descriptions of new, individual chanterelles continue nevertheless to be principally based on morphology (e.g. De Kesel et al. 2011; Tibuhwa et al. 2008; Tian et al. 2012; Wartchow et al. 2012a, b; Buyck and Randrianjohany 2013), although for some of the more important papers of the last 2–3 years, support from molecular data is now common practice, e.g. for chanterelles from the United States (Buyck et al. 2011; Buyck and Hofstetter 2011; Foltz et al. 2013), the Guyana shield (Wilson et al. 2012), East Africa (Buyck 2012; Buyck et al. 2013a; Tibuhwa et al. 2012) and Madagascar (Buyck et al. 2013b).

A second series of molecular papers focused on the frequent occurrence of convergence among different architectural forms of the fungal fruit body within the older concept of "Hymenomycetes". Some of these papers contributed therefore indirectly to a better understanding of the relationships beween *Cantharellus* and some of the other groups within the 'cantharelloid clade'. Since neither polyporoid (Hibbett and Donoghue 1995), cyphelloid (Bodensteiner et al. 2004), nor gasteroid fungi (Hibbett et al. 1997) have been demonstrated to exist within the cantharelloid clade, the first study that discussed in detail the modern delimitation of the cantharelloid clade was a paper that focused on the development of the hydnoid-clavarioid fruit body in hymenomycetes (Pine et al. 1999). In this paper, the phylogenetic importance of the stichobasidium was underlined when pointing out the close relationship between *Hydnum* L., *Multiclavula* R.H. Petersen, *Craterellus* and *Cantharellus*. In the past two decennia, a considerable number of papers dealt with the distribution of the resupinate architecture of the fungal fruit body (for discussions see Binder et al. 2005; Larsson 2007). These papers confirmed the placement of *Botryobasidium, Ceratobasidiaceae* and a polyphyletic *Sistotrema* within the cantharelloid clade, whereas continuing inventories of the neotropics have demonstrated the existence of resupinate forms in a morphologically suprisingly diverse *Clavulina* (Henkel et al. 2011; Uehling et al. 2012). In the most recently published paper that focused specifically on the delimitation of the cantharelloid clade, Moncalvo et al. (2007) confirmed the unexpected relationship with the heterobasidiomycetous *Tulasnellales,* already suggested by Hibbett and Binder (2002), and documented the extreme evolutionary rate heterogeneity in the nuclear ribosomal RNA genes of *Tulasnella*, *Cantharellus* and *Craterellus*. Consequently, Hibbett et al. (2007) proposed Cantharellales, with the provisional inclusion of *Tulasnella,* as the official nomenclatural rank for the cantharelloid clade.

Species diversity

The economically and commercially very important genus *Cantharellus* has drawn surprisingly little interest from taxonomists in the past. Part of the explanation resides very likely in the difficulty to recognize good species with the limited variation of the few morphological features available. Indeed, under the microscope, chanterelles exhibit a discouraging monotony: they have no cystidia (Léveillé 1837), their spores lack any type of ornamentation and vary little in size and form, and also hyphal endings in the pileipellis offer little variation in form and size, as well as—with rare exceptions—in their general orientation. The recognition of *Cantharellus* as a genus can be especially difficult in the tropics and some of the smaller species are nearly impossible to assign to genus in the field. Even careful microscopic examination may leave the morphologist in doubt, particularly in those rare cases where a *Cantharellus* has dull colors, predominantly unequal gills that do not fork, as well as regularly four-spored basidia (e.g. the Malagasy *C. paucifurcatus*) or even two-spored basidia (e.g. the African *C. croceifolius*). In this sense, Corner's monograph (1966) which treated all fungi with a cantharelloid habit as a single artificial concept is a very understandable approach.

Given the limited micromorphological variation, it is comprehensible that *Cantharellus* was never easily distinguished from other, morphologically similar genera. After a revision of all 346 species names through detailed examination of available type specimens, Eyssartier (2001) retained merely 59 good and valid species in *Cantharellus* out of a total of 418 published names (346 specific and 72 infraspecific taxa, 35 of which were related to C. *cibarius*).

Apart from the long lasting confusion with species in its sister-genus *Craterellus*, many of the older *Cantharellus* names have been synonymized with such diverse genera as *Guepinia* (Auriculariales), *Dacryopinax* (Dacrymycetales), *Arrhenia, Camarophyllus, Campanella, Cantharellula, Clitocybe, Cotylidia, Cuphophyllus*, *Cyphella, Gerronema, Haasiella, Hohenbuehelia, Hydropus, Hygrocybe, Hygrophorus, Leptoglossum, Marasmiellus, Marasmius, Merulius, Merismodes, Micromphale, Mniopetalum, Mycena, Omphalina, Rimbachia, Tetrapyrgos, Trogia* (Agaricales), *Afrocantharellus, Goossensia, Pterygellus, Pseudocraterellus* (Cantharellales), *Podoserpula* (Atheliales), *Hygrophoropsis, Paxillus* (Boletales), *Gomphus, Gloeocantharellus* (Gomphales), *Faerberia, Lentinus* (Polyporales) and even *Lactarius* (Russulales).

Since the revision by Eyssartier (2001), already a total of 40 new species have been published in *Cantharellus* s.s., mainly from Mediterranean, subtropical and tropical areas (Arora and Dunham 2008; Blanco-Dios 2004, 2011; Buyck 2012; Buyck et al. 2010, 2011, 2013a, b; Buyck and Hofstetter 2011; Buyck and Randrianjohany 2013; Contu et al. 2009; De Kesel et al. 2011; Ducousso et al. 2004; Eyssartier et al. 2009; Foltz et al. 2013; Hermitte et al. 2005; Kumari et al. 2011; Olariaga and Salcedo 2007, 2008; Redhead 2012; Sasia et al. 2003; Shao et al. 2011; Tian et al. 2012; Tibuhwa et al. 2008; Wartchow et al. 2012a, b). Yet, a quick analysis of deposited sequences in the GenBank is enough to realize that a large number of sequenced collections represent undescribed species and many more species of *Cantharellus* are going to be described over the next years. In the senior author's estimation, *Cantharellus* will account worldwide for at least some 200 to 300 species.

Some of the older literature on chanterelles suffered from conservative species concepts that resulted most often in the description of new varieties and forms of European species or in the extension of their distributions to other continents. Previously considered to be widely distributed, *C. cibarius* is probably one of the most eloquent examples, and recent data seem to suggest its distribution might be limited to the northern parts of Europe (perhaps also to northern parts of Asia and North America, although modern studies are lacking there). Recent molecular studies of the *C. cibarius*-complex in the United States have resulted in the description of eight new species over the past 5 years (Arora and Dunham 2008; Buyck et al. 2010; Buyck and Hofstetter 2011; Foltz et al. 2013) and this seems only the beginning (Buyck unpubl.). Also in Europe, the publication of a new identification key for European chanterelles (Eyssartier and Buyck 2000) has triggered a renewed interest in *Cantharellus* which rapidly resulted in the description of six new, principally Mediterranean species in the *C. cibarius* complex, although all still exclusively based on morphological and ecological features (Blanco-Dios 2004, 2011; Hermitte et al. 2005; Sasia et al. 2003; Olariaga and Salcedo 2007, 2008; Contu et al. 2009). Surprisingly, molecular studies focusing on European *Cantharellus* are still lacking, but this shortcoming should be repaired soon.

Infrageneric classification

Molecular studies have confirmed the clear separation between *Craterellus* and *Cantharellus*, and also allowed for a more precise placement of *Cantharellus* within the broader context of a monophyletic "Cantharellales", but they did not have the slightest impact on the infrageneric classification of *Cantharellus* itself. Nor did tropical inventories of the twentieth century have any substantial impact on the systematics of this genus until recently (Eyssartier and Buyck 2001b). Indeed, the infrageneric classification of *Cantharellus* has remained very rudimentary for a very long time (Table 1), and this notwithstanding the description, during the second half of the 20th century, of many tropical species with often surprising features.

Whereas all the recent new taxa from the temperate northern hemisphere conform well to the classical concept of *Cantharellus*, the situation in the tropics and southern hemisphere is quite different. During the 50's and 60's, Heinemann (1958, 1959, 1966) and Corner (1966) described and illustrated a number of very original chanterelles from Central Africa, respectively Malaysia. Many of these tropical chanterelles

Table 1 Past infrageneric classifications proposed for *Cantharellus*

Heinemann 1958	Corner 1966		Eyssartier and Buyck 2001a, b		Present genus concept
	Subg. *Cantharellotus*				*Rimbachia*
Sect. *Infundibuliformes*	Subg. *Phaeocantharellus*				*Craterellus*
Sect. *Congolenses*			Subg. *Afrogomphus*		*Cantharellus*
	Subg. *Cantharellus*	Sect. *Cutirellus*	Subg. *Cantharellus*	Sect. *Cutirellus*	
Sect. *Cibarii*		Sect. *Cantharellus*		Sect. *Isabellinus*	
				Sect. *Heinemannianus*	
				Sect. *Cantharellus*	
			Subg. *Rubrinus*		
			Subg. *Pseudocantharellus*		
			Subg. *Afrocantharellus*		
Sect. Tenues			Subg. *Parvocantharellus*		

lack clamps for example, a fact that seems to have been ignored by many mycologists up to the present day. Many recent publications on chanterelles still present the presence of clamps as an important diagnostic feature to separate *Cantharellus* from *Craterellus* (Hansen and Knudsen 1997; Pegler et al. 1997; Watling and Turnbull 1998; Lindahl 2000; Pilz et al. 2003), something that seems justified only in a strictly temperate northern hemisphere context. Notwithstanding the impressive diversity of true *Cantharellus* in the paleotropics, most of the earlier recognized subdivisions at infrageneric level (see Table 1) concerned the opposition of true *Cantharellus* versus species that are now accepted in either *Craterellus* or *Rimbachia* (Redhead 1983). The considerable diversity in tropical *Cantharellus* resulted merely in a few small, mainly monotypic, infrageneric groups. These split-offs had no other reason than to allow for a more practical and easier identification: the monotypic subgenus *Cutirellus* (Corner 1966) for the then unique species with a trichoderm-like pileipellis, the equally monotypic section *Congolenses* (Heinemann 1958) for a single, African chanterelle with intensely blackening context, and section *Tenues* (Heinemann 1958) for some extremely small, tropical African species.

A detailed morphological revision of all available type material for *Cantharellus* worldwide finally resulted in the first argumented subdivision of *Cantharellus* species in six subgenera based on macro- and micromorphological features (Eyssartier and Buyck 2001a, b), proposing two diagnostic microcharacters as taxonomically most informative features for a subgeneric division : (1) absence/presence of clamps, a feature still widely believed to be informative solely to distinguish between *Craterellus* and *Cantharellus*, and (2): absence/presence of thick-walled, hyphal terminations on the cap surface.

The objective of the present paper is to test the latest morphology-based hypotheses for a subgeneric division of *Cantharellus* using a multigene phylogenetic approach (nucLSU, mitSSU, RPB2 and *tef-1*) on a dataset that covers approximately half of the described chanterelles worldwide and includes type specimens whenever possible.

Materials and methods

Molecular data

Taxon sampling, sequence data, new primers and dataset assembling

Nucleotide sequence data were generated for 82 fungal collections and four loci (Table 2). Taxon sampling consisted of 80 *Cantharellus* collections representing 46 species (not accounting for additional subspecies and five provisional ID's labeled as 'aff' or 'cf') and two outgroup taxa, *Craterellus tubaeformis* and *Hydnum* cf. *repandum*, following Moncalvo et al. (2007). Our sampling is representative of all subgenera proposed in the latest infrageneric classification of the genus (Eyssartier and Buyck 2001a, b). DNA was isolated from fresh material stored in cetyl-trimethyl-ammonium-bromide buffer or from dried fruit bodies. Data produced in this study were as described in Hofstetter et al. (2002) for ribosomal genes: part of the nuclear large subunit (nucLSU) and part of the mitochondrial small subunit (mitSSU). The primers used for amplification and sequencing of part of the transcription elongation factor 1-alpha (*tef*-1) gene were those published by Morehouse et al. (2003), with the exception of a few species for which these primers did not work. For those species, the primer pair *tef*-1Fcanth: 5′- AGCATGGGTDCTYGACAAG -3′ and *tef*-1Rcanth: 5′- CCAATYTTRTAYACATCYTGGAG -3′ was designed. New primers were also designed to amplify region 5–7 of the second largest subunit of the RNA polymerase II (*RPB*2) within Cantharellales (*RPB*2-5FCanth: 5′-GAAWGCTATTCCGRAAGCTCAC-3′and *RPB*2-

7cRCanth: 5′-ATGCCCAGAATCATRCTTGGRTG-3′). These newly designed *RPB*2 primers were used together or alternatively with the primers designed by Liu et al. (1999) for this region (f*RPB*2-5F [or 6F] and f*RPB*2-7cR). As these newly designed *RPB*2 primers were not well adapted to sequencing conditions, PCR products were cloned using pSTBlue-1 AccepTor Vector^{TM} Kit (Novagen). Sequencing used the M13F and M13R vector primers and reagents and conditions of the *BibDye®Terminator v3.1 Cycle sequencing Kit* and an automated capillary sequencer ABI 3700 DNA analyzer (Perkin Elmer, Applied Biosystems, Foster City, CA, USA).

A total of 213 sequences were newly produced for this study: 74 nucLSU, 65 mitSSU, 73 *RPB*2 and 1 *tef*-1 (Table 2). We also used published sequences already available in Genbank (Table 2) from previous studies (Buyck et al. 2011, 2013a; Buyck and Hofstetter 2011; Moncalvo et al. 2007; Schoch et al. 2012). Sequences were assembled and edited using the software package Sequencher 3.0 (Gene Codes Corp., USA).

The combined alignment of these four genes totaled 6,674 characters (nucLSU: 1,447 characters; mitSSU: 3, 163 characters; *RPB*2: 1,200 characters; *tef*-1: 864 characters). After removal of introns and unalignable regions, the final data set contained 3,201 characters (mitSSU: 66 taxa, 488 characters; nucLSU: 79 taxa, 1, 107 characters; *RPB*2: 78 taxa, 977 characters; *tef*-1: 70 taxa, 629 characters).

Phylogenetic analyses

To test for topological incongruence among loci we used the program compat3 (available at www.lutzonilab.net/downloads). For each individual locus of the combined data set, 500 bootstrap replicates (Felsenstein 1985) were generated with RAxML 7.2.7 (Stamatakis 2006; Stamatakis et al. 2008) and all pairwise comparisons between the four loci were performed with compat3. A conflict between two loci was assumed when a clade was supported as monophyletic with bootstrap support (BS) ≥70 % in one tree, but supported as non-monophyletic in another (Mason-Gamer and Kellogg 1996).

Phylogenetic searches were carried out implementing Maximum Likelihood (ML) and Bayesian analyses. All analyses were run on the computer cluster of the Nano + Bio Center (University of Kaiserslautern, Germany). For the ML analyses the combined data set was partitioned into eight partitions: mitSSU, nucLSU, *RPB2* 1st position, *RPB2* 2nd position, *RPB2* 3rd position, *tef*-1 1st position, *tef*-1 2nd position, and *tef*-1 3rd position. The ML analyses were carried out using RAxML 7.2.1 (Stamatakis 2006), implementing a GTR model of nucleotide substitution (Rodríguez et al. 1990) with a gamma shape distribution and a proportion of invariable sites, and searching for the most likely tree with 500 heuristic replicates. Bootstrap frequencies (Felsenstein 1985; Stamatakis et al. 2008) were estimated with 500 replicates. For the Bayesian analyses, the combined data sets were partitioned as described above. Three independent runs with 10,000,000 generations, and four independent chains each were started with MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003) for each data set, sampling every 500th tree. The burn-in fraction of sampled trees was estimated both by eye with ln-likelihood plots and using AWTY (Nylander et al. 2008). Only nodes that received posterior probabilities (PP) ≥ 0.95 and ML-bootstrap support values (MLBS) ≥ 70 % were interpreted as significantly supported.

Morphological data

This paper is principally based on material collected by the senior author over the past 20 years. All cited specimens are deposited at the mycological herbarium of the Paris' Natural History Museum (PC) unless otherwise stated. All sequenced specimens were microscopically examined in ammoniacal Congo red after a short pre-heating in KOH, at a magnification of ×1,000. Drawings and measurements of individual elements were made for every specimen at a magnification of ×2,400 using a camera lucida. Part of these observations is summarized in Fig. 2. Species concepts are based on the re-examination of all existing type material for *Cantharellus* (Eyssartier 2001).

Results and discussion

Phylogenetic analyses

Our ML approach for combinability detected significant conflicts within 3 of the 6 possible pairwise comparisons of single locus bootstrap analyses. NucLSU conflicts with *RPB*2 and *tef*-1 for the placement of one of the two collections of *Cantharellus platyphyllus* subsp. *bojeriensis* (*nr. 458*), that is supported as sister species of *C. symoensii* by BS analysis of the nucLSU (MLBS=80 %) while *RPB*2 and *tef*-1 single gene BS analyses both support it as monophyletic with *C. platyphyllus* subsp. *bojeriensis* (*nr. 459*) and *C. platyphyllus* (respectively with MLBS=92 % and MLBS=98 %). BS analysis of nucLSU supports the monophyly of *C. subpruinosus* with *C. tenuithrix* (MLBS=84 %) while *RPB*2 supports its monophyly with *C. cibarius* (MLBS= 90 %). Finally *RPB*2 and *tef*-1 BS analyses conflict for the placement of *C. densifolius* that clusters with significant support with *C. albidolutescens* (*nr. 457*) based on *RPB*2

Table 2 Voucher table. List of species names with corresponding DNA extraction numbers, collector and collector number, herbarium accession numbers, geographical origin and GenBank accession numbers for the respective genes

Taxon	Voucher Extraction nr/coll. Nr.	Herb. Acc.Nr.	Origin	nucLSU	mitSSU	*RPB*2 (5–7)	*tef*-1
Genus *Cantharellus*							
C. addaiensis	495/BB 98.033 neotype	PC0084717	Tanzania	KF294667	KF294592	KF294745	JX192992*
C. addaiensis Henn. 1898	267/BB 98.057	PC0084718	Tanzania	KF294621	KF294550	KF294695	JX192976
C. afrocibarius	497/BB 96.236	PC0084125	Zambia	KF294669	KF294594	KF294747	JX192994
C. afrocibarius Buyck & V. Hofstetter 2012	496/BB 96.235 holotype	PC0084124	Zambia	KF294668	KF294593	KF294746	JX192993
C. albidolutescens	457/BB 08.070 holotype	PC0084751	Madagascar	KF294646	KF294577	KF294723	JX192982*
C. albidolutescens Buyck & V. Hofstetter 2014	456/BB 08.057	PC0084750	Madagascar	KF294645	KF294576	KF294722	KF294752
C. altipes	344/BB 07.162 paratype	PC0084090	USA	KF294636	KF294567	KF294713	GQ914945
C. altipes Buyck & V. Hofstetter 2011	318/BB 07.019 holotype	PC0084085	USA	KF294627	KF294556	KF294702	GQ914939
C. ambohitantelyensis Buyck & V. Hofstetter 2014	475/BB 08.336 holotype	PC0084754	Madagascar	KF294656	KF294582	KF294733	JX192989*
C. amethysteus	352/BB 07.309	PC0084071	Slovakia	KF294642	KF294573	KF294719	GQ914954
C. amethysteus (Quél.) Quél.1888	349/BB 07.284	PC0084070	Slovakia	KF294639	KF294570	KF294716	GQ914953
C. appalachiensis	GRSM 77088	–	USA	DQ89869	DQ898646	DQ898748	–
C. appalachiensis R.H. Petersen 1971	342/BB 07.123	PC0084075	USA	KF294635	KF294565	KF294711	GQ914979
C. cerinoalbus Eyssart. & Walleyn 2009	487/AV 06.051 isotype	PC0084743	Malaysia	KF294663	KF294590	KF294741	–
C. cibarius	479/GE 07.025	PC0084088	France	KF294658	KF294585	KF294736	GQ914949
C. cibarius Fr. :Fr. 1821	351/BB 07.300	PC0084077	Slovakia	KF294641	KF294572	KF294718	GQ914950
C. cinnabarinus	326/BB 07.053	PC0084093	USA	KF294630	KF294559	KF294705	GQ914984
C. cinnabarinus (Schwein.) Schwein. 1834	312/BB 07.001 neotype	PC0084094	USA	KF294624	KF294552	KF294698	GQ914985
C. congolensis	512/BB 98.058	PC0084776	Tanzania	KF294673	KF294599	–	JX192996
C. congolensis aff.	66/BB 06.176	PC0084078	Madagascar	KF294606	KF294538	KF294680	JX192967
C. congolensis aff.	69/BB 06.197	PC0084076	Madagascar	KF294608	KF294541	KF294683	GQ914982
C. congolensis Beeli 1928	247/BB 98.039	PC0084123	Tanzania	KF294609	KF294542	–	JX193015
C. conspicuus Eyssart., Buyck &Verbeken 2002	501/GE 99.560 isotype	PC0084809	Zimbabwe	–	KF294598	KF294751	–
C. cuticulatus Corner 1966	486/DS 06.283	PC0084742	Malaysia	KF294662	KF294589	–	–
C. decolorans aff.	466/BB 08.243	PC0084733	Madagascar	KF294653	–	KF294730	JX192987
C. decolorans aff.	57/BB 06.146	PC0084757	Madagascar	KF294603	–	KF294677	JX192964
C. decolorans Eyssart. & Buyck 1999	469/BB 08.278 epitype	PC0084098	Madagascar	KF294654	–	KF294731	GQ914968
C. densifolius Heinem. 1958	258/BB 98.013	PC0084126	Tanzania	KF294616	–	KF294690	JX193014
C. diminutivus Corner 1969	485/DS 06.033	PC0084739	Malaysia	KF294661	KF294588	KF294740	–
C. ferruginascens P.D. Orton 1969	348/BB 07.283	PC0084099	Slovakia	KF294638	KF294569	KF294715	GQ914952
C. fistulosus Tibuhwa & Buyck 2008	517/DT 43 isotype	PC0084738	Tanzania	KF294674	KF294600	–	JX192992
C. friesii Quél. 1872	481/GE 07.077	PC0084719	France	KF294659	KF294586	KF294737	–
C. gracilis Buyck & V. Hofstetter 2012	251/BB 98.234 holotype	PC0084737	Tanzania	KF294612	–	KF294686	JX192970
C. heinemannianus Eyssart. & Buyck 1998	491/BB 96.307	PC0084720	Zambia	KF294665	–	KF294743	–
C. humidicolus Buyck & V. Hofstetter 2012	493/BB 98.036 holotype	PC0084724	Tanzania	KF294666	–	KF294744	JX193005*
C. ibityensis	463/BB 08.203 paratype	PC0084722	Madagascar	KF294651	–	KF294728	JX192985
C. ibityensis Buyck & V. Hofstetter 2014	462/BB 08.196 holotype	PC0084109	Madagascar	KF294650	–	KF294727	GQ914980
*C. isabellinus var. parvispo*rus	256/BB 98.020 holotype	PC0084753	Tanzania	KF294614	–	KF294688	JX192972
*C. isabellinus var. parvispo*rus *Eyssart. & Buyck 2000*	249/BB 98.037 paratype	PC0084100	Tanzania	KF294611	–	KF294685	GQ914966
C. lateritius	330/BB 07.058	PC0084105	USA	KF294633	KF294562	KF294708	GQ914959
C. lateritius (Berk.) Singer 1949	320/BB 07.025 epitype	PC0084103	USA	KF294628	KF294557	KF294703	GQ914957
C. lewisii	314/BB 07.003 holotype	PC0084074	USA	JN940597	KF294554	KF294700	GQ914962
C. lewisii Buyck & V. Hofstetter 2011	301/BB 02.197 paratype	PC0084073	USA	KF294623	KF294551	KF294697	GQ914961
C. lilacinopruinatus Hermitte, Eyssart. & Poumarat 2005	347/BB 07.221	PC0084106	Slovakia	KF294637	KF294568	KF294714	GQ914951
C. minor	329/BB 07.057	PC0084721	USA	KF294632	KF294561	KF294707	JX192979*
C. minor Peck 1872	313/BB 07.002	PC0084747	USA	KF294625	KF294553	KF294699	JX192978*
C. miomboensis Buyck & V. Hofstetter 2012	255/BB 98.021 holotype	PC0084748	Tanzania	KF294613	KF294544	KF294687	JX192971

Table 2 (continued)

Taxon	Voucher Extraction nr/coll. Nr.	Herb. Acc.Nr.	Origin	nucLSU	mitSSU	*RPB*2 (5–7)	*tef*-1
C. paucifurcatus. Buyck & V. Hofstetter 2014	474/BB 08.320 holotype	PC0084729	Madagascar	KF294655	–	KF294732	JX192988
C. platyphyllus	262/BB 98.126 epitype	PC0084723	Tanzania	KF294620	KF294549	KF294694	JX192975
C. platyphyllus Heinem. 1966	259/BB 98.012	PC0084108	Tanzania	KF294617	KF294546	KF294691	GQ914969
C. platyphyllus subsp. bojeriensis	459/BB 08.160	PC0084740	Madagascar	KF294648	KF294579	KF294725	JX192984
C. platyphyllus subsp. bojeriensis Eyssart. & Buyck 1999	458/BB 08.158	PC0084741	Madagascar	KF294647	KF294578	KF294724	JX192983
C. pseudominimus Eyssart. & Buyck 1999	477/JV 00.663	PC0084725	Portugal	KF294657	KF294584	KF294735	JX192991*
C. quercophilus Buyck, Lewis, Eyssart. & V. Hofstetter 2010	636/BB 07.097 holotype	PC0084726	USA	KF294644	KF294575	KF294721	JX192981
C. romagnesianus Eyssart. & Buyck 1999	482/GE 07.031	PC0084735	France	–	–	KF294738	–
C. sebosus	465/BB 08.234 holotype	PC0084736	Madagascar	KF294652	KF294581	KF294729	JX192986
C. sebosus Buyck & V. Hofstetter 2014	460/BB 08.162 paratype	PC0084079	Madagascar	KF294649	KF294580	KF294726	GQ914981
C. sp. ined. (eucalyptus)	68/BB 06.180	PC0084130	Madagascar	JN940604	KF294540	KF294682	JX192969
C. sp. ined. (eucalyptus)	67/BB 06.179	PC0084129	Madagascar	KF294607	KF294539	KF294681	JX192968
C. splendens	499/BB 96.199	PC0084730	Zambia	KF294671	KF294596	KF294749	–
C. splendens Buyck 1994	498/BB 96.306 epitype	PC0084731	Zambia	KF294670	KF294595	KF294748	–
C. subamethysteus Eyssart. & Stubbe 2009	488/DS 06.218 isotype	PC0084744	Malaysia	KF294664	KF294591	KF294742	–
C. subcyanoxanthus aff	257/BB 98.014	PC0084745	Tanzania	KF294615	KF294545	KF294689	JX192973
C. subcyanoxanthus Buyck, Randrianjohany & Eyssart. 2012	476/BB 00.1137 holotype	PC0084746	Madagascar	–	KF294583	KF294734	JX192990*
C. subincarnatus subsp. rubrosalmoneus	13/BB 06.080 holotype	PC0084727	Madagascar	KF294601	KF294536	KF294675	JX192962
C. subincarnatus subsp. rubrosalmoneus Buyck & V. Hofstetter 2014	55/BB 06.096 paratype	PC0084755	Madagascar	KF294602	KF294537	KF294676	JX192963
C. subpruinosus Eyssart. & Buyck 2001	484/GE 07.080	PC0084734	France	KF294660	KF294587	KF294739	–
C. symoensii	261/BB 98.113 epitype	PC0084756	Tanzania	KF294619	KF294548	KF294693	JX192974
C. symoensii Heinem. 1966	260/BB 98.011	PC0084113	Tanzania	KF294618	KF294547	KF294692	GQ914970
C. tabernensis	340/BB 07.119	PC0084116	USA	KF294634	KF294563	KF294709	GQ914976
C. tabernensis Feibelman & Cibula 1996	328/BB 07.056	PC0084115	USA	KF294631	KF294560	KF294706	GQ914974
C. tanzanicus aff.	60/BB 06.149	PC0084128	Madagascar	KF294605	–	KF294679	JX192966
C. tanzanicus aff.	59/BB 06.148	PC0084127	Madagascar	KF294604	–	KF294678	JX192965
C. tanzanicus Buyck & V. Hofstetter 2012	268/BB 98.040 holotype	PC0084728	Tanzania	KF294622	–	KF294696	JX192977
C. tenuithrix	343/BB 07.125 holotype	PC0084084	USA	JN940600	KF294566	KF294712	GQ914947
C. tenuithrix Buyck & V. Hofstetter 2011	322/BB 07.035 paratype	PC0084087	USA	KF294629	KF294558	KF294704	GQ914946
C. texensis	341/BB 07.120 paratype	PC0084096	USA	JN940601	KF294564	KF294710	GQ914987
C. texensis Buyck & V. Hofstetter 2011	317/BB 07.018 holotype	PC0084097	USA	KF294626	KF294555	KF294701	GQ914988
C. tomentosus	500/BB 98.060 holotype	PC0084732	Tanzania	KF294672	KF294597	KF294750	JX192995
C. tomentosus Eyssart. & Buyck 2000	248/BB 98.038 paratype	PC0084121	Tanzania	KF294610	KF294543	KF294684	GQ914965*
Genus *Craterellus*							
Cr. tubaeformis(Fr.) Quél.	350/BB 07/293	PC0084122	Slovakia	KF294640	KF294571	KF294717	GQ914989
Genus *Hydnum*							
H. cf. *repandum L.*	356/BB 07.341/ MTS3757	PC0084749	Slovakia	KF294643	KF294574	KF294720	JX192980

The * in the *tef*-1 GenBank accessions numbers indicates sequences obtained with the newly designed primers

Collectors abbreviated as *BB* Bart Buyck, *AV* Annemieke Verbeken, *DS* Dirk Stubbe, *DT* Donatha Tibuhwa, *GE* Guillaume Eyssartier, *JV* Jan Vesterholt

(MLBS=85 %) but clusters with the other *C. albidolutescens* (*nr. 456*) based on *tef*-1 (MLBS=100 %). Each of these three conflicts takes place among very closely related species based on morphology and might consequently result from saturation at the 3rd position of protein-coding genes. Therefore we ignored them and combined the data.

Combining 4 loci for 82 taxa, the best ML tree estimated with RAxML (ln likelihood= −19908.132327) is shown in Fig. 1. Bootstrap proportions (MLBS) and bayesian posterior probabilities (PP) are shown along the branches. The three independent runs of MrBayes plateaued at the same likelihood

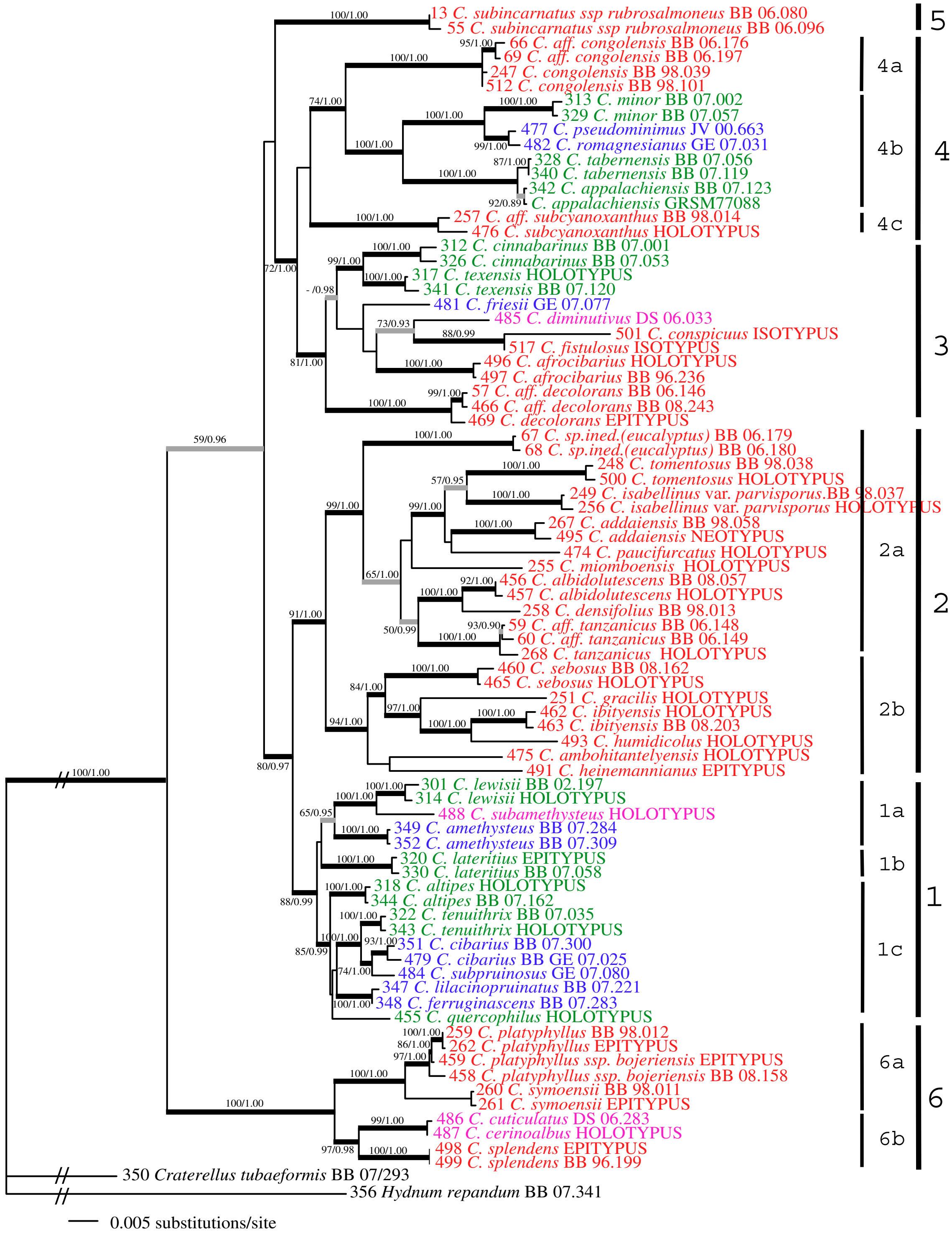

Fig. 1 ML best tree inferred from the analysis of four loci for 82 specimens. Branches that received both bootstrap support (MLBS)≥70 and Bayesian posterior probabilities (PP)≥95 % are in *bold*; branches supported by either bootstrap or PP are in *gray*. Both values (MLBS/PP) are reported along the branches. Names of African-Malagasy chanterelles are in *red font*, Malayian chanterelles are in *lilac* and North American and European chanterelles are in *green and blue* respectively. Outgroups are in *black lettering*. Numbers on the right refer to the recognized clades as discussed in the Results section

levels, and after discarding the first 5.000.000 generations as burnin (50 %), the last 10,000 trees of each run were used to calculate the posterior probabilities for internal branches.

Commented tree topology

The following paragraphs depict and discuss the six major clades that are here obtained and accepted at subgeneric levell (see Fig. 1). The morphological characters of the sampled species referred to below are mapped on the phylogeny (Fig. 2).

Clade 1 (subgenus Cantharellus)

This clade (MLBS=88 %; PP=0.99) is defined by the presence of the type species of the genus, *C. cibarius*, and thus corresponds to subgenus *Cantharellus*. All of its constituant species have abundant clamps and, with the exception of *C. quercophilus* and to a lesser degree also *C. tenuithrix*, all of the sequenced species in this subclade possess distinctly thick-walled hyphal extremities in the pileipellis. Both features were considered the main characters allowing for the morphological subdivision of the genus (Eyssartier and Buyck 2001a, b). This clade is entirely composed of northern hemisphere taxa. Most of the species are yellow, but this color is sometimes mixed with greenish, brownish, vinaceous to lilac-purple pigments. Some species have a squamulose cap, although the squamulae are less developed and more appressed compared to the majority of species in clade 2. Clade 1 consists of variously supported subclades. The well-supported subclade 1c (MLBS=85 %, PP=0.99) contains *C. cibarius* and most of its northern temperate look-alikes. The smooth chanterelle, *C. lateritius,* constitutes subclade 1b. Amethyst chanterelles constitute subclade 1a in which the European *C. amethysteus* is sister to the Malayian *C. subamethysteus*, a species that clusters with maximum

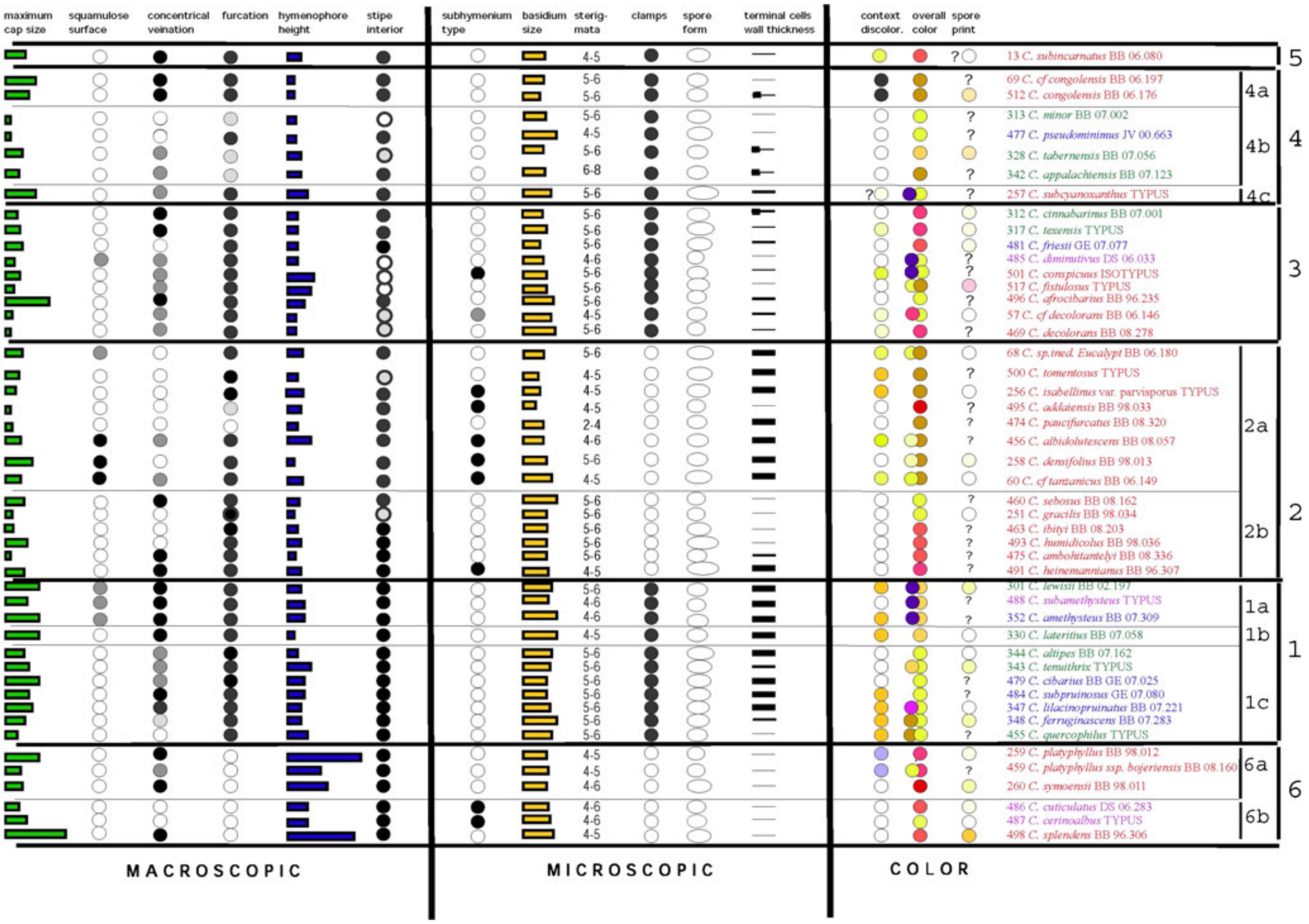

Fig. 2 Mapping of various morphological characters for the studied taxa as revealed by original descriptions or recent examination of type specimens by either Bart Buyck (BB) or Guillaume Eyssartier (GE). Taxa are presented as they appear in the phylogeny, with *horizontal lines* and numbers on the right referring to the clades discussed in the Results section. From left to right, columns of mapped characters correspond to: MACROSCOPIC FEATURES: maximum cap size, squamulose aspect of the cap surface, presence of concentrical veination-anastomosing in between the radial veins or gill-folds, forking of the radial veins or gill-folds, height of the hymenophore, compact (*white*) or fistulose (*black*) stipe interior; MICROSCOPIC FEATURES: filamentous (*white*) or cellular (*black*) subhymenium type, maximum basidium length (not accounting for extreme values), number of sterigmata for majority of basidia, absence (*white*) or presence (*black*) of clamp connections, mean length/width ratio for spores, thickening of hyphal endings on the cap surface, with signs baring one-ended thickenings corresponding to species that have occasional thickened cell walls for terminal cells only. Unless specified otherwise above, *black*, *gray* and *white dots* correspond to strong, weak or absent respectively for character states; COLORS: discoloration of the context (*black*, *blue*, *bright yellow*, *rusty*), main overall color of the fruit body (*lilac*, *bluish purple*, *red-pink*, *yellow*, *brown*), color of the spore print (*ochre-yellow*, *cream*, *pale pinkish*, *white*)

support (MLBS=100 %, PP=1.0) with the North American *C. lewisii*. The monophyly of 1a+1b received only significant support in Bayesian analysis (MLBS=65 %, PP=0.95). As both the/*amethysteus* and/*lateritius* clades include known representatives from the tropics, contrary to clade 1c, these have here been accepted as individual entities.

Clade 2 (subgenus Rubrinus)

The strongly supported Clade 2 (MLBS=91 %, PP=1.00) is sister to the previous clade with significant support (MLBS=80 %, PP=0.97). Clade 2 is here proposed as separate subgenus (instead of section *Isabellinus* Eyssart. & Buyck, type species *C. isabellinus*) because of strong geographical and morphological differences with its sister clade: it is for the moment exclusively composed of tropical species of African or Malagasy origin and all species completely lack clamps in their tissues. Clade 2 is subdivided in two highly supported subclades: subclade 2a (MLBS=99 %, PP=1.0) for predominantly medium-sized to large, yellowish-brownish, often strongly squamulose chanterelles, and subclade 2b (MLBS=94, PP=1.00) for very small to medium-sized, smooth, yellowish orange to red species, corresponding to section *Heinemannianus* Eyssart. & Buyck.

In subclade 2a the Malagasy, eucalypt-associated *C. sp.ined* is clearly separated from the other species nested in that subclade (MLBS=100 %, PP=1.00). Near maximum support (MLBS=99 %, PP=1.00) is recovered for the monophyly of the African *C. tomentosus*, *C. isabellinus* var. *parvisporus*, *C. addaiensis* and the Malagasy *C. paucifurcatus*. Resolved as sister to these species, however without support, the African *C. miomboensis* occupies an isolated position. Several species in this subclade possess very small basidia (Fig. 2). One of those, the very small *C. addaiensis* (= *C. floridulus* sensu auct., see Buyck 2012), differs from the other, closely related taxa in its bright red color and thin-walled hyphal extremities. Two other terminal relationships received maximal support: the monophyly of *C. albidolutescens* with *C. densifolius* and the monophyly of *C. aff tanzanicus* with *C. tanzanicus*. Both species groups are suggested to be monophyletic but this relationship is only supported by Bayesian analysis (MLBS=50 %, PP=0.99).

Subclade 2b contains *C. heinemannianus*, type species of the hitherto monotypic section *Heinemannianus,* previously placed in subgenus *Cantharellus* (Eyssartier and Buyck 2001a, b). All of its members lack the squamulose surface of pileus and stipe, most lack also distinctly thick-walled hyphal endings, while half of the species are very small (1–2[3] cm diam.). In this subclade, *C. heinemannianus* and *C. ambohitantelyensis* are resolved, but not supported, as sister species and are clearly separated from a strongly supported subclade (MLBS=84 %, PP=1.00) including *C. sebosus* (a relatively small, yellow *cibarius* look-a-like from the *Uapaca* woodlands in Madagascar (MLBS=100 %, PP=1.00) and a well resolved and strongly supported (MLBS=97 %, PP=1.00) species group including *C. gracilis* and a monophyletic Malagasy *C. ibityensis* and African *C. humidicolus* (MLBS=100 %, PP=1.00).

Clade 3 (subgenus Cinnabarinus)

This well-supported clade (MLBS=81 %, PP=1.00) contains predominantly small species that are mostly orange, pink or red, while some have also purplish tints. All possess abundant clamps and nearly all have thin-walled hyphal ends at the cap surface (Fig. 2). *Cantharellus afrocibarius*, a medium-sized to large, fleshy, yellow-capped and often caespitose species that grows in the miombo woodlands and resembles *C.cibarius,* is the odd exception in this group. The monophyly of the Malagasy species pair *C. aff. decolorans* (eucalypt-associated) + *C. decolorans* received maximum support (MLBS=100 %, PP=1.00). The remainder of the species form a sisterclade only resolved with Bayesian support as monophyletic (MLBS<50 %, PP=0.98). Within the latter subclade, only the terminal relationships are supported: the African *C. conspicuus* + *C. fistulosus* (MLBS=88 %, PP=0.99) and the North American *C. texensis* + *C. cinnabarinus* (MLBS=99 %, PP=1.00).

Clade 4 (subgenus Parvocantharellus)

This clade is suggested to be monophyletic and sister, however without support, to clade 3. All species nested in this clade possess abundant clamps and have predominantly thin-walled hyphal ends at the cap surface.

Morphologically and phylogenetically distinct from the other species of clade 4, the Malagasy *C. subcyanoxanthus* and a morphologically similar African specimen constitute subclade 4c (MLBS=100, PP=1.00). Both specimens belong to the *C. cyanoxanthus* species complex (see Buyck 2012), exclusively known from Madagascar and tropical Africa, with species possessing very strong, blue-violet-lilac to vinaceous colors on the fruit bodies and a yellowing context (particularly in the stipe base). Rather than leaving this clade orphan because of the lack of bootstrap support, we accept it provisionally as part of a larger clade 4 as resolved by the analyses.

Two more subgroups are resolved and significantly supported as monophyletic within this clade (4a and 4b; MLBS=74 %, PP=1.00) and with strongly supported internal relationships (MLBS=87–100 %). Subclade 4a is composed of several collections of a single species (taken *sensu lato*) possessing a strongly blackening context and reacting strongly with most macrochemical reagents: the Malagasy, eucalypt-associated *C. aff. congolensis* and the African *C. congolensis*, type species of the monospecific subgenus *Afrogomphus* Eyssart. & Buyck. Subclade 4b comprises several, small to very small taxa that have a northern hemisphere distribution and range in color from yellow-orange to brown: the North American species pair *C. tabernensis* + *C. appalachiensis* is sister to a subclade in which the North American *C. minor* is again sister to the European species pair *C. pseudominimus* + *C. romagnesianus*, the type species of subgenus *Parvocantharellus*, name here adopted for this clade.

Clade 5 (subgenus Pseudocantharellus)

This monospecific clade consists of two specimens of the recently described Malagasy *C. subincarnatus* subsp. *rubrosalmoneus* (MLBS=100 %, PP=1.00), a taxon that is morphologically very close to the very rare Central African type variety and the nearly identical *C. rhodophyllus* Heinem. (see Buyck et al. 2013b). *Cantharellus ruber* Heinem., type species of subgenus *Pseudocantharellus* Eyssart. & Buyck, is a species occurring in the Zambezian woodlands with discoloring fruit bodies and nearly identical morphological features. It should, therefore, be very closely related. We were unable to obtain good sequences from our *C. ruber* collections, but a preliminary analysis of partial LSU data for this species (Tibuhwa et al. 2012), suggest indeed a close relationship to our Malagasy collections of *C. subincarnatus.* We therefore identified clade 5 as subgenus *Pseudocantharellus* until additional sequences of *C. ruber* allow for a well supported placement.

The reasons for this clade being genetically so different from the rest of the genus are for the moment impossible to understand as *C. subincarnatus* and allies are morphologically completely ‘normal’ chanterelles. Notwithstanding the lack of distinctly thick-walled cells in their pileipellis, Eyssartier and Buyck (2001a, b) had even placed *C. subincarnatus* in the core-group of the genus (subgenus *Cantharellus* section *Cantharellus*, corresponding to clade 1 in our phylogeny) because of the typical *cibarius*-like habit and abundant clamps.

Clade 6 (subgenus Afrocantharellus)

This highly supported clade in our phylogeny (MLBS=100 %, PP=1.00), corresponds to subgenus *Afrocantharellus* Eyssart. & Buyck (type species: *C. symoensii*). Its sister position to the rest of the genus obtained only weak support from Bayesian inference (PP=0.96). All species have a high proportion of four-spored basidia, lack clamp connections and have thin-walled hyphal extremities at the cap surface. All taxa are tropical, with a distribution that is presently limited to Africa + Madagascar and Malaysia.

This clade contains two fully resolved and supported subclades: the first (6a: MLBS=97 %, PP=0.98) places *C. splendens* sister with high support to *C. cuticulatus* + *C. cerinoalbus,* two very closely related Malayan species. *Cantharellus cuticulatus* had been set apart from the rest of the genus in the monotypic section *Cutirellus* Corner because of the trichodermal structure of the pileipellis, a feature shared with the African *C. splendens*. The second subclade (6b: MLBS=100 %, PP=1.00) is comprised of taxa lacking the trichodermal structure in the pileipellis. The African *C. platyphyllus* and its Malagasy subspecies *bojeriensis*, both remarkable because of their sometimes distinctly bluish context, are clearly different from the African *C. symoensii*, which lacks this bluish context and has different spores (Fig. 2).

General discussion

Phylogenetics versus morphology

When one realizes the limited extent of morphological variation in the genus, especially at the microscopic level (Fig. 2), it is surprising to see that our multigene analysis (Fig. 1) corresponds in several respects rather well to the latest morphological classification proposed by Eyssartier and Buyck (2001a, b). This classification introduced for the first time as main criteria for an infrageneric division the presence/absence of clamps in combination with the presence/absence of thick-walled hyphal extremities in the pileipellis and, as secondary characters, some general macroscopic features (size, context discoloration, general coloration, etc.…) as taxonomic informative characters for the recognition of six major subdivisions in the genus. In the following paragraphs we will discuss the taxonomic value of these individual morphological features as challenged by our multigene phylogeny.

> *Clamp connections*. − Our phylogeny clearly confirms that, just as in sister-genus *Craterellus*, the genus *Cantharellus* is divided in a number of strongly supported groups of species that either lack or possess distinct clamps at virtually all septa. As this feature is perfectly stable within each of the six main clades that result from our phylogenetic analyses, its importance as a taxonomically informative character is hereby confirmed. Interestingly, clamps are absent in those clades that lack northern hemisphere representatives (clades 2 and 6), with the exception of the monospecific clade 5 for *C. subincarnatus*.
>
> *Hyphal terminations*. – The presence of thick-walled hyphal extremities in the pileipellis was considered to be of great importance (Eyssartier and Buyck 2001a, b) and to be characteristic for subgenus *Cantharellus* sensu Eyssart. & Buyck (corresponding to clades 1+2), although with some exceptions, e.g. *C. cyanoxanthus*, *C. friesii*, *C. subincarnatus* which were placed in subgenus *Cantharellus* on the basis of their general morphology,

notwithstanding the fact that these species had hardly thickened terminal cells. Our phylogenetic analyses now place these species in different subgenera which might give the impression that this feature is more waterproof than previously thought. However, some additional, more recently described species with irregularly thickened to thin-walled hyphal endings have since been suggested as close relatives to *C. cibarius* in analyses based on the protein coding gene *tef-1* (Buyck et al. 2010; 2013a, 2013a, b; Buyck and Hofstetter 2011) and these are now indeed confirmed as good species of subgenus *Cantharellus*: e.g. *C. quercophilus, C. tenuithrix*. Also the monotypic section *Heinemannianus* (clade 2b) has recently been extended to embrace a number of species with thin-walled hyphal extremities, leaving *C. heinemannianus* as sole thick-walled species in this section, although its sister-species, *C. ambohitantelyensis,* does have some dispersed, slightly thickened hyphae at the cap surface. According to Eyssartier (2001), the thickness of the hyphal endings in *C. heinemannianus* varies among collections.

On the other hand, our analyses now show that thick-walled extremities also occur outside clades 1+2, viz. in clade 3, where *C. cinnabarinus* has distinctly thickened hyphal terminations (see Buyck et al. 2011), but in this case the thickening of the cell wall is more irregular, more variable and often restricted to the last one or two terminal cells, not to five or more subterminal cells as is often the case in clades 1 and 2. The closely related *C. friesii* was also described by Eyssartier (2001) as having only slightly thickened, ‘refringent’ hyphae, and we have observed similar refringent walls in *C. decolorans* and *C. afrocibarius*. Absence of distinctly thick-walled hyphal endings remains a good feature for clades 4, 5 and 6.

We can therefore conclude that the presence of distinctly thick-walled (>1 μm) hyphal endings in the cap is less clear-cut than previously suggested, but remains a valuable indication for the systematic position of a chanterelle. Example given, Fig. 2 clearly shows that a chanterelle with distinctly thickened hyphal endings in the northern hemisphere (clamps always present), belongs in subgenus *Cantharellus* (clade 1) when it is yellowish-brownish or has violet tinges, or belongs in subgenus *Cinnabarinus* (clade 3) when it is reddish-orange. If one collects such a species in the southern hemisphere (necessarily without clamps if it has thickened cell-walls), then it belongs in subgenus *Rubrinus* sect. *Isabellinus* (clade 2a) if it is yellowish-brownish, or in subgenus *Rubrinus* sect. *Heinemannianus* (clade 2b) if it is orange-red.

Finally, the form of the terminal cell of hyphal endings at the cap surface is not informative for the placement of a species, but can certainly be a useful feature for identification. Most chanterelles have more or less cylindrical terminal cells, but in some cases the terminal cells are often clavate (e.g. *C. cinnabarinus, C. tabernensis*) or either strongly undulate or repetively constricted near the apex (e.g. *C. sebosus, C. tomentosus, C. paucifurcatus*).

General size. − The general size of the basidiomata has been used in past morphology-based classifications for the delimitation of some infrageneric groups (e.g. sect. *Tenues*, subgenus *Parvocantharellus* – see Table 1). From a practical point of view, we can group species in categories with respect to the cap diameter: very small (mostly ca 1 cm diam), small (2–4 cm diam.), medium-sized (4–10 cm diam.), large (10–20 cm diam.) and very large (20–30 cm diam.). One the one hand, our phylogeny suggests indeed that size matters as small to very small species tend to group together within clades 4b (sect. *Flavobrunnei*), 3 (subg. *Cinnabarinus*) and 2b (sect. *Heinemannianus*) for example. On the other hand, conspicuously small taxa are absent from clades 1, 5 and 6.

Stipe. − The stipe of chanterelles is generally believed to be solid and firm as opposed to the hollow stipe that perforates the cap in *Craterellus*. Nevertheless, several of the very small chanterelles have a fistulose, although not perforate stipe (e.g. *C. fistulosus, C. minor*).

Hymenophore configuration. − The configuration of the hymenophore has been used previously to delimit clade 6 (subgenus *Afrocantharellus*) in which some of the African species have the appearance of a *Cuphophyllus* (Hygrophoraceae) because of their exceptionally well-developed gill-folds (Eyssartier and Buyck 2001a, b). Our phylogeny gives maximum support to this subgenus which is in our dataset now extended to encompass also two species from Malaysia (Eyssartier et al. 2009). These Malayan species have nevertheless much less well-developed gill-folds and, for example, *C. cuticulatus* had been placed in subgenus *Cantharellus* by Eyssartier and Buyck (2001a, b).

At the other extreme of this morphological range, clade 1 (subgenus *Cantharellus*) is the only clade that includes a species with a constantly (nearly) smooth hymenophore in our phylogeny (*C. lateritius,* clade 1b). This subgenus exhibits undoubtedly the weakest overall hymenophore development between species. Apart from *C. lateritius* and the Chinese *C. vaginatus*, which also belongs in clade 1 (Shao et al. 2011), the hymenophore of the other species ranges from low gill-like folds to a hardly perceptible veination that is usually intensily anastomosing and abundantly forked.

In the other clades, the hymenophore configuration is more variable, with several species having well-developed gill-folds, in some cases accompanied by a near absence of both furcations and insterstitial anastomoses. Although there are no species other than *C. lateritius* in our sampling that have a constantly 'smooth' hymenophore, occasional specimens of *C. sebosus* or *C. ambohitantelyensis* (both in sect. *Heinemannianus*, clade 2), come quite close to *C. lateritius* in terms of (absence of) hymenophore development (see Buyck et al. 2013b).

Our analyses suggest that hymenophore development may show clear tendencies in some major clades, but is not taxonomically informative. Hymenophore development can even be extremely variable within a single species or even within a single collection.

Hymenium composition. − The constituant elements of the hymenium are in theory limited to basidia in various stages of their development since distinct types of cystidia are reputedly absent throughout the genus. Nevertheless, in several species we observed cells that were unlikely to develop into mature basidia because of their (sometimes much larger) size and different form. Therefore, leptocystidia taken in the broadest sense, i.e. thin-walled, sterile cells that are not going to develop into basidia, do occur in the hymenium of chanterelles. In our opinion, such cells represent aborted basidia and their presence seems not taxonomically informative. We have found unexpectedly high numbers of such leptocystidia in some African species, e.g. certain specimens of *C. splendens, C. heinemannianus* or *C. humidicolus.* (Fig. 3).

Basidia. − *Cantharellus* is reputed for producing very long and narrow basidia and this character is often claimed to be a generic feature. Yet, there is considerable variation in the size of basidia (Fig. 2) and this character seems to have some phylogenetic signal. Whereas most *Cantharellus* have basidia that are on average ca. 80 μm long, the African chanterelles of clade 2a*,* for example, include several species with extremely short basidia (some basidia measuring only 25 μm), up to five times shorter compared to species having the longest basidia (up to 120–140 μm) in the genus. The latter are mostly found in clade 1, especially sections *Sublaeves* and *Amethystini*, as well as many of the chanterelles that have a poorly developed hymenophore (apart from *C. lateritius*, also for example *C. afrocibarius, C. sebosus, C. solidus*, etc.…). Length of basidia is not correlated with the size of the fruit bodies and one of the smallest European chanterelles, *C. pseudominimus*, has particularly long basidia.

The number of spores per basidium is most frequently five to six (publications citing regularly two- to four-spored basidia for *Cantharellus* are generally based on inaccurate observations: e.g. Buyck 1994; Eyi Ndong et al. 2011). There exist nevertheless exceptions to this rule. In clade 4b, the north American *C. appalachiensis* may produce predominantly seven to eight-spored basidia (Buyck et al. 2010; Shao et al. 2011), whereas in the African clade 2a there is a clear tendency towards basidia with less spores. In subgenus *Afrocantharellus*, several taxa show a remarkably high percentage of four-spored basidia, but these are always mixed with five and six-spored basidia. Exclusively two-spored basidia have so far only been confirmed for two tropical African species of still uncertain systematic position (not represented in our phylogeny): the recently described *C. solidus* (De Kesel et al. 2011) and the unsufficiently known *C. croceifolius* as confirmed by the holotype examination (Eyssartier 2001).

Spores. – Size and form of spores vary too little to be relevant for the systematic position of the species but may nevertheless be important for the identification of certain species. Example given: they constitute the single distinctive character to distinguish between frequent lookalikes of *C. platyphyllus* and *C. symoensii* (clade 6).

Spore print color varies from white to yellow or pinkish salmon. Yet, good spore deposits that are sufficient for a precise appreciation of spore color are more difficult to obtain for chanterelles: unlike most gilled hymenomycetes, they form long-lived fruit bodies that start to produce spores from the very first primordial stages and continue to do so over much longer periods but apparently at a much slower pace (Reijnders 1963; Eyssartier 2001). As a consequence, information on spore print color in descriptions of new taxa is rare, whereas a good color evaluation of the obtained spore print remains difficult.

Presently available data on spore print color for known chanterelles (see Fig. 2) does not allow for a sufficient appreciation of the evolution of spore print color in *Cantharellus*, but our analyses do not seem to suggest that different subgenera may be characterized by differences in spore print color.

In some instances, spore print color has been used to differentiate between some very closely related species, e.g. in the *C. cibarius* complex (Petersen 1969; Foltz et al. 2013).

Subhymenium. – The subhymenium is rarely given much attention in descriptions of chanterelles, but the senior author distinguishes two main types of subhymenia: (1) 'filamentose' subhymenia (subhymenial cells have a similar diameter as the basidium base and are often long and cylindrical), and (2) a more 'cellular' type of subhymenium (with subhymenial cells that are considerably more inflated and wider than any part of the basidium itself). Both types occur in small or large species, and in species with or without clamp connections, but the cellular type is much less common in the genus (Fig. 2). Both types can occur in closely related species: in clade 2 (subgenus *Rubrinus*), for example, the two closely

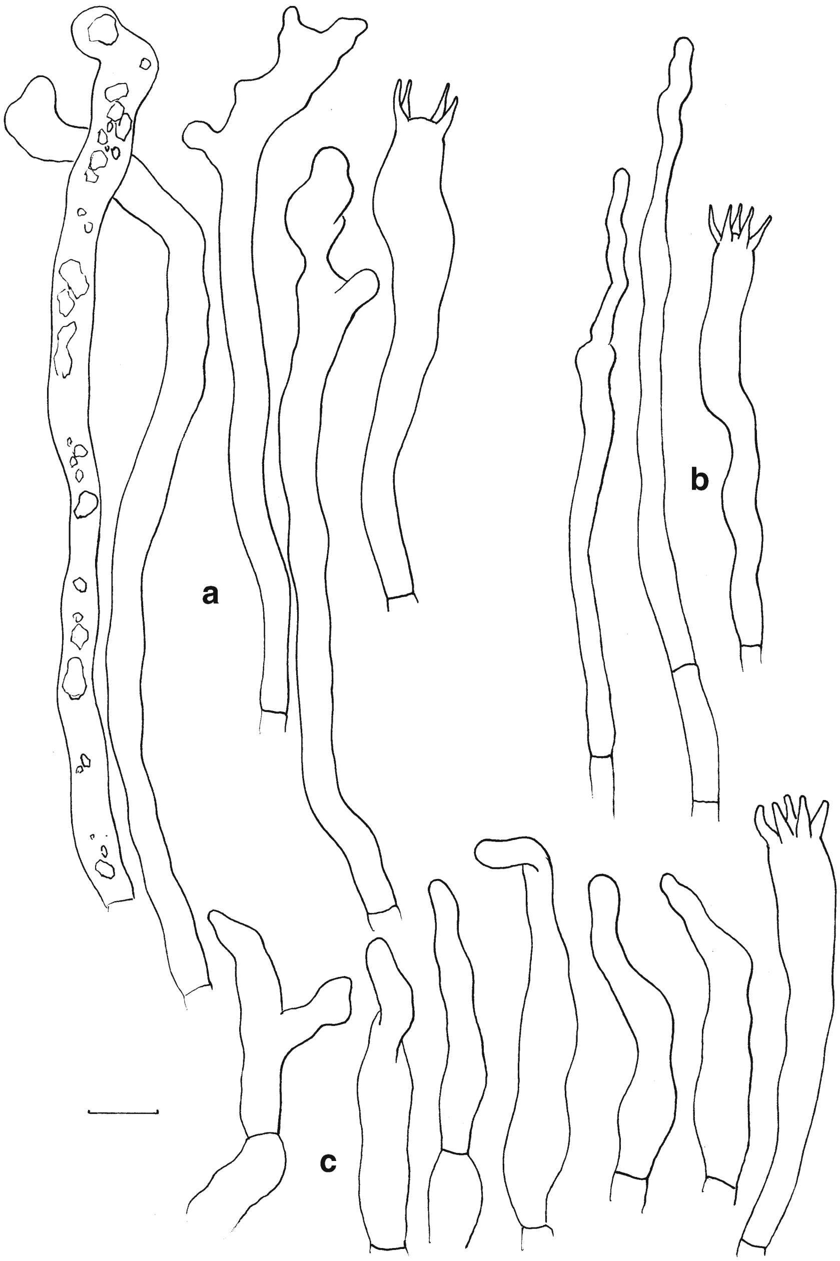

Fig. 3 Occasional cystidioid elements in the hymenium of *Cantharellus*. a. *C. splendens*, b. *C. humidicolus*, c. *C. heinemannianus*. For every species, an average-sized basidium is represented for comparison. Scale bar equals 10 μm. Drawings B. Buyck

related species that have the smallest basidia in the genus, *C. tomentosus* and *C. addaiensis*, have different types of subhymenia (filamentose in the former, cellular in the latter), even between the extremely close *C. tanzanicus* and *C. aff. tanzanicus*, the latter differs from the former by its strongly filamentose subhymenium. In clade 6b (subgenus *Afrocantharellus* sect. *Cutirellus*), the Malayan *C. cerinoalbus* and *C. cuticulatus* have a cellular subhymenium, whereas the African *C. splendens* has not. On the other hand, in species with very long basidia (>80 μm) we never observed a cellular subhymenium.

Pileipellis structure. − The structure of the pileipellis is generally a cutis or trichocutis, exceptionally a trichoderm regularly constituted of vertically oriented hyphal endings only known so far from two species in section *Cutirellus* of subgenus *Afrocantharellus* (clade 6).

Another structural character of the pileipellis is the disruption of the upper layer into squamae that are more or less concentrically arranged. This feature is especially well-developed (although much less than in some *Craterellus*) in many yellowish brown species within Clade 2a (subgenus *Rubrinus* section *Isabellinus*), but occasional squamulose species are also found in other subgenera, e.g. *C. conspicuus* (clade 3) or/*amethysteus* subclade (clade 1).

One or two genera?

The question whether subgenus *Afrocantharellus* deserves recognition as a separate genus as recently proposed by Tibuhwa et al. (2012) has already been discussed by Buyck et al. (2013a). In fact, apart from the more developed gill folds for some of the African species, nothing distinguishes *Afrocantharellus* from other chanterelles. As discussed above, the Malaysian species in subgenus *Afrocantharellus* have much less developed gill folds. None of the morphological arguments invoked by Tibuhwa et al. (l.c.) to justify the distinction of two separate genera, is supported by factual data. Species in subgenus *Afrocantharellus* are neither more variegated, nor are the gill folds more widely spaced than in some other groups of the genus. Tibuhwa et al. (2012) interpret *Afrocantharellus* as 'mostly lacking clamps' as opposed to the rest of the genus where clamps are "usually present". The present phylogeny clearly shows that the complete absence of clamps is a feature that characterizes the large majority of all chanterelles in Africa: it is a diagnostic feature for both subgenus *Rubrinus* and subgenus *Afrocantharellus*, representing together more than 70 % of the African chanterelles. The presence of *A. fistulosus*, the only species with clamps in *Afrocantharellus* sensu Tibuhwa et al. is one of several identification problems in the latter paper. Both the phylogenies presented by Tibuhwa et al. and our-selves use sequence data (presumably) obtained from the type specimen. Yet, whereas our sequence data place this species in subgenus *Cinnabarinus* where it is morphologically similar to closely related species, the phylogenetic analyses by Tibuhwa et al. place *C. fistulosus* with full support in *Afrocantharellus*, a group of morphologically completely different taxa. The presumed *A. fistulosus*-sequences produced by Tibuhwa et al. (l.c.) are indeed clearly related to the other species in *Afrocantharellus,* but can impossibly correspond to the specimen on which the original description was based.

As discussed above, *Afrocantharellus* is sister to the rest of the genus with very weak support (MLBS=59 %, PP=0.96) and lacks morphological characters to support its segregation from *Cantharellus*. We think it is therefore unwarranted to split the genus at this time as we may deal here with a problem of unsufficient sampling in the southern hemisphere. Interestingly, the nucLSU analysis that was recently published by Wilson et al. (2012) places the South American *C. guyanensis* as sister to African representatives of *Afrocantharellus*, but when introducing these same nucLSU sequences in our nucLSU dataset (not shown), the resulting consensus tree places *C. guyanensis* as sister to [*Afrocantharellus* + the rest of *Cantharellus*], which would imply that, if one accepts Tibuhwa's viewpoint, *C. guyanensis* represents in this case yet another genus for a species that is, morphologically speaking, a completely 'normal' chanterelle.

Preliminary observations on the evolutionary history of Cantharellus

When looking at our phylogeny (Fig. 1), there is a striking tendency of clades to be of predominantly northern or southern hemisphere composition. Whereas some of the major clades entirely lack northern hemisphere taxa, the reverse is not true: all clades contain at least a few tropical representatives. The sister relationship between major (sub)clades of restricted geographical distribution suggests ancient separation events followed by evolution in isolation. Interestingly, as one of the most basal clades in Homobasidiomycetes (Binder et al. 2005), Cantharellales might have been present well before the breakup of Gondwana, whereas the ectomycorrhizal nutritional mode that characterizes the whole family Cantharellaceae (as well as Clavulinaceae, Hydnaceae and part of *Sistotrema*) may indeed be responsible for very limited long distance dispersal, if any at all (see discussion below). A vicariance-migration scenario seems, therefore, the most logical explanation since it is independent of far-fetched hypotheses that have to account for long distance dispersal events of these ectomycorrhizal symbionts. Transatlantic presence (Western Europe, USA) of *C. cibarius* and *C. amethysteus* has recently been proven inaccurate for example (Buyck et al. 2011; Buyck and Hofstetter 2011; Foltz et al. 2013), and also the islands of oceanic origin in the Mascarenes and Comores have never been colonized by African or Malagasy ECM fungi and their hosts notwithstanding millions of years of history. In the case of *Cantharellus*, there is another element that argues against long distance dispersal: *Cantharellus* is known to produce predominantly uninucleate spores (Horton 2006) which would virtually exclude successful establishment by long distance dispersal. Not only would two spores of compatible mating type need to arrive within mm distance of each other in order to allow primary mycelia to form a secondary mycelium, they also need to arrive in near contact with fine roots or germinating seeds of a compatible host. However, the fact that most of the tropical African chanterelles lack clamps with some showing a clear tendency to a reduced number of spores - unlike the North American species examined by Horton (l.c.)—calls for caution before generalizing this for the whole genus.

The distribution of afibulate clades

Africa and Madagascar are not only characterized by a very high species diversity, but also by a very high percentage of chanterelles that lack clamp connections (clade 2 and 6), unlike on other continents. With the exception of the few afibulate species described by Eyssartier et al. (2009) from Malaysia (all placed by our phylogeny in clade 2=subgenus *Afrocantharellus*), the sole other afibulate chanterelle from outside Africa was described from New Zealand: *C. elsae*

(G. Stev.) Horak. This apparently rare species, collected under *Nothofagus*, but able to grow with *Kunzea/Leptospermum* (Myrtaceae), is an entirely pinkish chanterelle with widely spaced gills. It lacks clamp connections and does have predominantly 5–6 spored basidia (Eyssartier 2001), contrary to what is mentioned in the original description and the redescription of the type by McNabb (1971), both of which report 4-spored basidia. *Cantharellus elsae* therefore is most likely a good species of *Cantharellus* and should not belong in *Craterellus* as suggested by Petersen and Mueller (1992), a recombination motivated at the time probably precisely because of the lack of clamp connections. The fact that it was first published as a *Hygrophorus* is a possible indication that it is very similar to species in subgenus *Afrocantharellus*.

Our phylogeny does not include species from either Australia or South America, but published descriptions of chanterelles from South America and Australia all indicate the complete absence of species without clamps, a typical feature of the two dominant subgenera in Africa and Madagascar (*Rubrinus* and *Afrocantharellus*). The same is true for chanterelles collected in New Caledonia (Ducousso et al. 2004; Buyck unpubl.) and the Indian Himalaya (Deepika et al. 2011), where all collected species so far have clamps and share morphological similarities with northern temperate taxa.

The discrepancy between studies focusing on below- and above-ground presence

The very high species diversity in African and Madagascan chanterelles stands in sharp contrast to the poor representation of *Cantharellus* in the rest of the southern hemisphere, at least in the case of Australia and South-America. This discrepancy is not an artifact due to differences in the fungal inventory. The intensely studied ectomycorrhizal forests of the Guyana shield in tropical America are rich in Clavulinaceae, but poor in Cantharellaceae, and particularly so in species of *Cantharellus*.

The few studies on African below ground ECM fungal communities do not reflect this high above-ground species diversity of the genus and principally report on the diversity of Clavulinaceae (Ba et al. 2012; Diédhiou et al. 2010; Tedersoo et al. 2011; Jairus et al. 2011), the latter remaining nevertheless less diverse compared to South America (Wilson et al. 2012; Smith et al. 2013; Moyersoen 2006, 2012). Studies on below-ground ECM fungi in worldwide dipterocarp forests reviewed by Brearley (2012) also report a poor below-ground presence of Cantharellaceae, although the latter publication contains several serious inaccuracies with respect to Cantharellaceae (the six taxa of/Cantharellaceae associated with *Vateriopsis* in the Seychelles should in fact read as a single/Clavulinaceae (Tedersoo et al. 2007), the 22/Clavulinaceae associated with the southamerican Parakaraima should read as 2/Clavulinaceae, and the four/Cantharellaceae and three/Clavulinaceae from Thai dipterocarp forests (Poshri et al. 2012) are in reality three/Cantharellaceae (all *Craterellus*) and two/Clavulinaceae). Judging from described taxa, *Cantharellus* is nevertheless much more diverse in Asia when compared to e.g. South-America (Wartchow et al. 2012a) or Australia (Eyssartier and Buyck 2001a). Preliminary data for Asia, but based on fruit bodies, indicate that chanterelles are quite more common and diverse in dipterocarp dominated forests and exhibit close affinities with the African species (Corner 1966; Eyssartier et al. 2009; Buyck unpubl.). Yet, nearly all Asian Cantharellaceae detected on root-tips correspond to *Craterellus* and not *Cantharellus*.

This high discrepancie between above- and below ground diversity is very likely related to two aspects of the unusual ITS of *Cantharellus*. Indeed, the exceptional length of the ITS of most *Cantharellus* may bias PCR reactions that are known to favor the amplification of short fragments over longer ones (Ihrmark et al. 2012; Quist and Chapela 2001; Sagerström et al. 1997; Suzuki and Giovannoni 1996), whereas the hypervariability of the ITS in *Cantharellus* may be responsible for mismatches with the applied primers. In any case, our phylogeny shows *Cantharellus* to be clearly more diverse in tropical ecosystems compared to temperate ecosystems and, in this particular case, contradicts the hypothesis of Tedersoo and Nara (2010), based on studies of below-ground diversity, according to which ectomycorrhizal groups are less diverse in tropical ecosystems compared to temperate ones.

Host associations of early *Cantharellus*

Whereas the clampless *C. elsae* may shed some doubt as to whether or not some of the more ancient *Cantharellus* were associated with *Nothofagus*, remarkably few chanterelles are associated with this host tree genus. Of the three reported chanterelles that do so, both *C. elsae* and the New Caledonian *C. garnierii* appear to be host generalists (Ducousso et al. 2004), whereas the very small *C. nothofagorum* R. H. Petersen & Mueller is only known from the type collection in Argentina. Based on morphology, both latter chanterelles would seem to fit in subgenus *Cinnabarinus* or *Parvocantharellus*.

Our data do not suggest that conifers have played an important role in the early history of *Cantharellus*. In our sampling, conifers are known host trees for a few individual terminal taxa in subgenus *Cantharellus*, and potentially (although data on precise host associations are lacking) in subgenus *Parvocantharellus*. Our dataset also suggests that the northern hemisphere species in these subgenera may have evolved from tropical representatives, but unfortunately our sampling is too restricted and lacks confidence for some of the basal relationships. In the case of subgenus *Cantharellus*, there is a clear need for more sampling and sequencing of both the/*lateritius* and/*amethysteus* clades (see Buyck and Hofstetter 2011; De Kesel et al. 2011) to document the link between tropical and temperate taxa in this subgenus. In particular the/*lateritius* clade seems to have a worldwide distribution with the exception of Europe where it may have become extinct during recent glaciation periods. Branch lengths leading to terminal taxa are on average shorter in clade 1, composed of northern hemisphere taxa, compared to its sister-clade (clade 2), composed of African and Malagasy species. These longer terminal branches are a general phenomenon for tropical taxa in our phylogeny. As African chanterelles have been collected and studied for many decennia and have been fairly well sampled in our phylogeny, the absence of a "broom" effect for terminal taxa in our tree (pointing to a recent radiation) seems therefore to reflect a reality. This suggests that these tropical taxa may have been subjected for a very long time to more or less stable, environmental conditions. In contrast, the shorter branch lengths for the northern temperate species could point to a more recent origin for these taxa and the reduced sampling almost certainly hides terminal "broom" effects due to more recent diversifications (possibly coinciding with the Pinaceae-Fagales migrations). The *C. cibarius* complex, accounting in the United States alone approximately 15 different species (Buyck unpubl.), is a good example.

Our phylogeny suggests also a possible secondary colonization of the southern hemisphere by northern hemisphere taxa in clade 3 (subgenus *Cinnabarinus*): *C. friesii* is resolved, although without support, as basal to a number of Malayian and African species. Also here more sampling and sequencing is needed.

Although our sampling does not contain Australian chanterelles, the phylogeny suggests that Myrtaceae were equally not associated with early *Cantharellus* as the morphology of the few Australian species suggests affinities to northern temperate species. The only eucalypt-associated taxa in our phylogeny (*C. aff. congolensis, C. aff. decolorans, C. sp. ined.* (eucalyptus) and *C. aff. tanzanicus*) were collected in exotic plantations in Madagascar and seem to be the result of a recent host shift (Buyck unpubl.).

A provisional biogeographic working hypothesis

As a provisional, biogeographic working hypothesis, we suggest that the earliest *Cantharellus* may not have been in contact with the most southern parts of Gondwana when *Nothofagus* was common there (although there still is the enigmatic *C. elsae*), but that its present distribution is the result of an 'out of Africa' history when the genus was associated with ancestors of the extant Phyllantaceae, Caesalpiniaceae, and particularly Dipterocarpaceae and Sarcolaenaceae, using the Indian plate to arrive in Asia where very similar and phylogenetically close taxa are indeed associated with extant dipterocarps (Eyssartier et al. 2009), to then disperse east and west in the northern hemisphere where they may have radiated migrating together with Pinaceae and Fagales in the more temperate climates of the Eocene-Oligocene transition as already suggested for other ectomycorrhizal fungal groups (Bruns et al. 1998). Whether the few chanterelles in neotropical lowland (where Clavulinaceae are much more diverse), such as *C. guyanensis*, are the result of an even older vicariance, as already suggested for their host trees (Moyersoen 2006), remains to be investigated. Yet, the sister-relationship between some African *Inocybe* and those recovered from root tips of neotropical dipterocarps (Moyersoen 2012) is consistent with our preliminary analysis of existing LSU data for *C. guyanensis* that puts this neotropical chanterelle sister to the rest of the genus (not shown). The general vicariance and migration hypothesis for *Cantharellus* parallels therefore the evolutionary hypothesis for their host trees (Moyersoen 2006). The latter hypothesis was recently supported by Dutta et al. (2011), who concluded, based on fossil resin chemistry and palynological data from 53 Myr old sediments in Western India, that Dipterocarpaceae must have originated in Gondwana and migrated from India into the SE Asian region from the middle Eocene onwards. The palynological assemblage accompanying these 53Myr old dipterocarps suggested a warm, humid, tropical climate that still characterizes extant dipterocarps (Dutta et al. 2011). The early history of *Cantharellus* therefore seems completely different from that suggested for Hysterangiales, another ancient group of Agaricomycetidae (Hosaka et al. 2008), where basal clades appear to have been associated primarily with Myrtaceae. Hysterangiales are also very diverse on those continents where *Cantharellus* is poorly represented (i.e. South America and Australia). Early Hysterangiales thus seem to have been associated with sclerophyllous vegetation in the southern part of Gondwana, whereas the early *Cantharellus* of Western Gondwanaland may well have been primarily associated with lowland rain forests as suggested by their presence in all of the important rain forest blocks where Dipterocarpaceae (and related Sarcolaenaceae in the case of Madagascar) are still present or dominant.

Conclusion

Proposal for a new infrageneric arrangement

Cantharellus Adans.: Fr.

Fruit bodies growing individual or in groups, rarely clustered at the base, long-lived compared to other gilled fungi, gymnocarpic, growing on soil, rarely fruiting on dead wood. Cap of very variable size (30 cm to <1 cm diam.), smooth to strongly squamulose, of very variable color, with parietal to vacuolar pigments of the bicyclic carotenoid type (particularly ß-carotène et ketonic derivatives). Hymenophore varying from nearly smooth, over veined to distinctly lamellate, with gills mostly distinctly forked in varying degrees or polydymous, concolorous or not to the rest of the fruit body; hymenium (always?) accrescent. Stipe central or excentric, not lateral, smooth to strongly squamulose, solid, although in some smaller species often rapidly fistulose, but without perforating the cap center as in *Craterellus*, concolorous or not with cap and/or hymenophore. Context very variable in thickness, in many species characteristically discoloring and yellowing, browning, blueing or blackening, either entirely or in certain parts of the fruit body. Odor mostly distinctly fruity (apricots). Taste slightly acrid to mild. Spore print white to yellow or salmon pink. Pileipellis poorly differentiated, a cutis or trichocutis, rarely a trichoderm, hyphal terminations thin- to thick-walled. Basidia (always ?) stichic, very variable in length between species, bearing mostly (2–4)5–6(7–8) sterigmata, exceptionally regularly 2- or 4-spored. Cystidia of a particular type not differentiated, but leptocystidia (in the broadest sense) and aborted basidia sometimes present. Spores ovoid, ellipsoid, reniform to shortly cilindrical, inamyloid, not dextrinoid, not cyanophilous, smooth, thin-walled. Clamp connections absent or present. Ectomycorrhizal, neither lichenicolous nor saprotroph. Type species: *Cantharellus cibarius* Fr.: Fr.

Subgenus *Cantharellus emend*. Buyck & V. Hofstetter: Fruit bodies fleshy, medium sized to large; hymenophore veined with blunt, mostly strongly forking-anastomosing ridges, rarely smooth or nearly so; cap and stipe usually smooth, sometimes with appressed squamae; hyphal endings mostly thick-walled; clamp connections abundant everywhere. Automatic type: *C. cibarius* Fr.:Fr.

Section *Cantharellus*: Fruit bodies yellow to whitish, or with brownish, greenish or pinkish lilac tones. Automatic type: *C. cibarius* Fr.:Fr.
Section *Amethystini* Buyck & V. Hofstetter sect. nov. — MycoBank MB 806113; Fruit bodies developing clear lilac-purple colors on either hymenophore or cap and sometimes also on stipe; cap often with appressed squamae. Type: *C. subamethysteus* Eyssart. & Stubbe
Section *Sublaeves* Buyck & V. Hofstetter sect. nov. — MycoBank MB 806114; Fruit bodies yellow to orange, hymenophore with poorly developed veins to smooth. Type: *C. lateritius* (Berk.) Singer

Subgenus *Rubrinus* Eyssart. & Buyck *emend*. Buyck & V. Hofstetter: Fruit bodies variably fleshy, large to very small; hymenophore very variable, from nearly smooth to producing well-developed gill-folds, forking-anastomosing or not; cap and stipe smooth to strongly squamulose; hyphal endings thick- to thin-walled; clamp connections absent. Type: *C. floridulus* Heinem.

Sect. *Isabellinus* Eyssart. & Buyck: Fruit bodies fleshy, medium-sized to large, off-white, yellowish to grayish brown, exceptionally red; cap and also stipe often strongly squamulose from disruption of the outer layer, forming more or less dressed squamae; hymenophore usually producing well-developed gill-folds, with furcations and anastomoses often poorly developed to absent; hyphal endings mostly thick-walled, basidia sometimes very small. Type: *C. isabellinus* Heinem.
Sect. *Heinemannianus* Eyssart. & Buyck *emend*. Buyck & V. Hofstetter: Fruit bodies medium-sized to very small and yellow, orange, pink or red; hymenophore variable, nearly smooth, veined or with more or less well-developed gill folds. Hyphal endings thin- (mostly) to thick-walled. Type: *C. heinemannianus* Eyssart. & Buyck

Subgenus *Parvocantharellus* Eyssart. & Buyck *emend*. Buyck & V. Hofstetter: Fruit bodies thick- or thin-fleshed, medium-sized to very small and then often with a slender stipe that may become fistulose, yellowish to brownish, sometimes with lilac-purple stains, context yellowing, rarely strongly blackening. Hyphal endings usually thin-walled, sometimes slightly thickened. Clamp connections abundant everywhere. Type: *C. romagnesianus* Eyssart. & Buyck

Sect. *Flavobrunnei* Buyck & V. Hofstetter sect. nov. — MycoBank MB 806115; Fruit bodies (very) small to hardly medium-sized, usually thin-fleshed and with a long stipe, yellowish to brownish. Type species: *C. romagnesianus* Eyssart. & Buyck
Sect. *Congolenses* Heinem. Fruit bodies medium-sized, fleshy, strongly and intensily blackening. Type: *C. congolensis* Beeli.
Sect. *Cyanomaculati* Buyck & V. Hofstetter sect. nov. — MycoBank MB 806116; Fruit bodies medium-sized, fleshy, yellow but in places distinctly lilac-purple to almost bluish, context slightly yellowing. Type species: *C. subcyanoxanthus* Buyck, Randrianjohany & Eyssart.

Subgenus *Cinnabarinus* Buyck & V. Hofstetter subgen. nov. — MycoBank MB 806117; Fruit bodies fleshy or not, mostly quite small, yellow, orange, pink or red, sometimes with lilac-purple or brownish tones, particularly in the cap center, smooth or with appressed squamules; hymenophore strongly veined to lamellate; thick-walled hyphal endings either absent or rare and then mostly limited to terminal cells; clamp connections abundant everywhere. Type species: *C. cinnabarinus* (Schwein.) Schwein.

Subgenus *Afrocantharellus* Eyssart. & Buyck: Fruit bodies mostly brightly colored, yellow, orange to red, sometimes with grayish to bluish hues, often with stipe, cap and hymenophore of different color, fleshy, medium-sized to large; hymenophore with (sometimes very) well-developed gill folds, interstitial veination-anastomoses absent or present; hyphal extremities thin-walled, clamp connections absent. Type species: *C. symoensii* Heinem.

Sect. *Afrocantharellus* Buyck & V. Hofstetter sect. nov. — MycoBank MB 806118; Pileipellis without a tendency towards trichodermal structure, gill folds very well developed. Type species: *C. symoensii* Heinem.

Sect. *Cutirellus* Corner. Pileipellis structure often trichodermal, gill folds not always very well developed. Type species: *C. cuticulatus* Corner

Subgenus *Pseudocantharellus* Eyssart. & Buyck *emend*. Buyck & V. Hofstetter: Fruit bodies medium-sized to large, fleshy, pink, pinkish orange to reddish pink or red. Hyphal endings thin-walled. Clamp connections abundant everywhere. Type species: *C. ruber* Heinem.

Acknowledgments We are grateful to the curators of the herbaria AD, BR, DAR, K, MICH, MPU, PMR and TENN for access to type specimens. Part of the sequencing for this study was performed by A. Couloux at the Genoscope or "Consortium National de Recherche en Génomique" near Paris (France) as part of the agreement n°2005/67 on the project "Macrophylogeny of life" between the Genoscope and the "service de systématique moléculaire" (CNRS IFR 101) of the Muséum national d'histoire naturelle. For sequencing, this study also received continuing support from the ATM-project "Barcode of life" of the Muséum national d'histoire naturelle (Dirs. L. Legall and S. Samadi).

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