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Wisconsin chanterelles revisited and first indications for very wide distributions of *Cantharellus* species in the United States East of the Rocky Mountains

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Abstract – The authors discuss and illustrate several American collections of *Cantharellus* that are in one way or another related to species that have previously been reported or described from Wisconsin. These new collections indicate that the potential distribution area of many of these chanterelles may be much larger than generally assumed. *Cantharellus deceptivus* sp. nov. is described as new cryptic look-alike of *C. phasmatis* and problems related to the narrow species concept of *C. flavus* and *C. phasmatis* are discussed; *C. iuventateviridis* sp. nov. is described as closest southern relative to *C. chicaoensis*. Microscopic features of *C. chicaoensis* and *C. flavus* are illustrated for the first time. *Cantharellus spectaculus* is considered a later synonym of *C. persicinus* on morphological criteria.

***Cantharellus deceptivus* sp. nov. / *Cantharellus iuventateviridis* sp. nov. / *Cantharellus persicinus* / phylogeny / TEF-1**

INTRODUCTION

In recent years, the taxonomy of American chanterelles is in a flux. Several native American species have been described as a result of purely morphological criteria (Buyck *et al.* 2010, Wartchow *et al.* 2012a,b; Nascimento *et al.* 2014) or

combined morphological-molecular analyses (Foltz *et al.* 2013, Buyck *et al.* 2011, 2016a-c, this issue; Buyck & Hofstetter 2011; Leacock *et al.* 2016).

All new species treated in this contribution belong to *Cantharellus* subg. *Cantharellus*. They are supported molecularly by sequence data of the *tef-1* gene, which was proposed as best choice for the molecular characterization of the various species in replacement of the extremely variable and long ITS, which poses problems with amplification and sequencing (Buyck *et al.* 2011).

With the description of *C. quercophilus* (Buyck *et al.* 2010), shortly after followed by the descriptions of *C. lewisii*, *C. tenuithrix* and *C. altipes* (Buyck *et al.* 2011) – all four described from Texas – it became soon clear that North America harbored a more diverse native species diversity in *Cantharellus* subg. *Cantharellus* compared to Europe (Olariaga *et al.* 2016). Hardly two years later, Foltz *et al.* (2013) described three more new species in the same subgenus, but now from Wisconsin, close to the Canadian border. Yet another new chanterelle, *C. chicagoensis*, has just been published based on multiple collections from the Midwest, including Wisconsin (Leacock *et al.* 2016) and more publications on new chanterelles are presently being prepared for the Newfoundland area (Thorn & Voitk, 2011).

As a result of recent collecting, we report here on a number of collections that are in one way or another related to the various chanterelles reported from Wisconsin.

MATERIAL AND METHODS

Morphological study

All newly sequenced specimens reported in this paper have been collected by the first author and collaborators and are deposited in the Mycological Herbarium of the Paris' Natural History Museum unless indicated otherwise (Table 1). Macroscopic descriptions are based on notes and photographs taken in the field or from fresh material. Microscopic study follows the protocols and methods as described in Buyck *et al.* (2011).

Taxon sampling, molecular data and phylogenetic analyses

Our taxon sampling includes 102 collections representative of the major clades presently recognized in the genus. Sequences of the translation elongation factor 1-alpha (*TEF-1*) were newly produced for 45 specimens in for this study and deposited in GenBank (Table 1). Already published *TEF-1* sequences representative of known American chanterelles species were selected from GenBank (Buyck *et al.* 2011, 2013, 2014; Foltz *et al.* 2013; Leacock *et al.* 2016). *Cantharellus luteostipitatus* of *Cantharellus* subg. *Afrocantharellus* was used as outgroup (Buyck *et al.* 2014, Shao *et al.* 2014).

DNA was isolated from fresh material stored in CTAB 1x buffer or from dried basidiocarps following the protocol described in Hofstetter *et al.* (2002). *TEF-1* amplification and sequencing used the primers and conditions of Morehouse *et al.* (2003). Sequences were assembled and edited with the software package Sequencher 3.0 (Gene Codes Corp., USA). The 102-specimen alignment was analysed using Bayesian (inference) and maximum likelihood (ML) phylogenetic

Table 1. Voucher table listing 45 newly sequenced specimens with collector and collector number, herbarium number and GenBank accession numbers for newly deposited *TEF*-1 sequences, both in this study and Buyck *et al.* 2016b, this issue). Abbreviations for authors are BB: Bart Buyck, BL: Brian Looney; DM: Donna Mitchell, EC: Emanuele Campo; JJ: Jay Justice; MH: Mike Hopping; SH: Stephen Harsch; WR: William Roody. Herbarium abbreviations follow Index Herbariorum

995	<i>C. pallens</i>	BB 09.392/441	PC 0084788	KX857013
996	<i>C. pallens</i>	BB 09.409	PC 0084811	KX857014
1066	<i>C. velutinus</i>	JJ/AR-CANT-1	PC 0142426	KX857022
1067	<i>C. velutinus</i>	JJ/AR-CANT-2	PC 0142427	KX857023
1068	<i>C. flavolateritius</i>	JJ/AR-CANT-4	PC 0713850	KX857024
1073	<i>C. chicaoensis</i>	JJ/MO-CANT-1	PC 0142428	KX857025
1074	<i>C. deceptivus</i>	JJ/WI-CANT-1	PC 0142430	KX857026
1076	<i>C. flavolateritius</i>	JJ/NC-CANT-2	PC 0713851	KX857027
1077	<i>C. flavus</i>	JJ/NC-CANT-3	PC 0142433	KX857028
1078	<i>C. flavolateritius</i>	JJ/NC-CANT-4	PC 0713852	KX857029
1079	<i>C. deceptivus</i>	JJ/NC-CANT-5	PC 0142429	KX857030
1083	<i>C. corallinus</i>	JJ/MO-CANT-2	PC 0713846	KX857031
1085	<i>C. persicinus</i>	JJ/MO-CANT-4	PC 0142431	KX857033
1086	<i>C. corallinus</i>	JJ/MO-CANT-5	PC 0713849	KX857034
1196	<i>C. subalbidus</i>	BB 13.014	PC 0713862	KX857037
1197	<i>C. subalbidus</i>	BB 13.014B	PC 0713863	KX857038
1198	<i>C. formosus</i>	BB 13.015	PC 0713859	KX857039
1201	<i>C. subalbidus</i>	BB 13.045	PC 0142443	KX857040
1206	<i>C. formosus</i>	BB 13.108	PC 0713860	KX857041
1207	<i>C. formosus</i>	BB 13.120	PC 0142444	KX857042
1211	<i>C. formosus</i>	BB 13.153	PC 0713861	KX857043
1216	<i>C. cascadiensis</i>	BB 13.251	PC 0713864	KX857044
1306	<i>C. tenuithrix</i>	BB 14.008	PC 0142197	KX857045
1307	<i>C. tenuithrix</i>	BB 14.009	PC 0142198	KX857046
1309	<i>C. iuventateviridis</i>	BPL 523	PC 0142425	KX857046
1310	<i>C. tenuithrix</i>	BB 14.010	PC 0142199	KX857047
1321	<i>C. velutinus</i>	BB 14.038	PC 0142227	KX857049
1323	<i>C. velutinus</i>	BB 14.042	PC 0142231	KX857050
1325	<i>C. velutinus</i>	BB 14.044	PC 0142233	KX857051
1326	<i>C. velutinus</i>	BB 14.045	PC 0142234	KX857052
1353	<i>C. tenuithrix</i>	BB 14.098	PC 0142287	KX857053
1354	<i>C. tenuithrix</i>	BB 14.099	PC 0142288	KX857054
1359	<i>C. velutinus</i>	BB 14.104	PC 0142293	KX857055
1360	<i>C. velutinus</i>	BB 14.105	PC 0142294	KX857056
1366	<i>C. velutinus</i>	BB 14.111	PC 0142299	KX857057
1367	<i>C. velutinus</i>	BB 14.112	PC 0142300	KX857058
1383	<i>C. flavus</i>	BB 14.132	PC 0142321	KX857059
1542	<i>C. iuventateviridis</i>	SH13/7/2012	PC 0713848	KX857063
1543	<i>C. iuventateviridis</i>	SH14/7/2012	PC 0713847	KX857064
1573	<i>C. velutinus</i>	WR WV04.695	DEWV5391	KX857065
1575	<i>C. velutinus</i>	WR WV04.284	DEWV5575	KX857066
1579	<i>C. velutinus</i>	WR WV05.1326	DEWV7759	KX857067
1581	<i>C. velutinus</i>	WR WV07.074	DEWV8944	KX857068
1582	<i>C. velutinus</i>	WR WV04.64	DEWV9938	KX857069
1583	<i>C. velutinus</i>	DM WV13.36	DEWV10727	KX857070
1685	<i>C. persicinus</i>	MH15.001	PC0142432	KX857080

inferences. Several basal nodes that received support in the 4-gene worldwide phylogeny by Buyck *et al.* (2014) were constrained in our analyses (marked with * in Fig. 1). A ML analysis was implemented via CIPRES Science Gateway (Miller *et al.*, 2010), employing the “RAxML HPC2 on XSEDE” tool (Stamatakis 2006), with the GTRMIX model and gamma distribution, starting from a random tree and leaving the remaining options as default. Bootstrap proportions were based on 1000 replicates of ML bootstrapping (MLbs) from RaxML with same settings as for the tree searches. ML bootstrap values were considered significant only when ≥ 70 .

For the Bayesian analysis, the substitution model was sampled across the GTR space. Bayesian Metropolis coupled Markov Chain Monte Carlo (B-MCMCMC) as implemented in MrBayes (3.2.3) (Ronquist *et al.* 2012) consisted in two independent runs to ensure stationary and convergence to the same log-likelihood level. We sampled one out of every 100 trees during 5M generations and the last 2,501 trees sampled from each run were used to build the majority-rule consensus tree. Branch support was considered significant only when Bayesian posterior probabilities (BPP) were ≥ 0.95 .

RESULTS

Phylogenetic analyses

The full alignment included 1111 characters. After exclusion of ambiguous regions, consisting in four spliceosomal introns, the final alignment included 637 characters. The most likely tree inferred by ML analysis of the *TEF*-1 dataset ($-\ln L = 4096.582373$) exhibited a quite similar supported topology as the Bayesian majority-rule consensus tree shows in Figure 1. Most terminal relationships in subg. *Cantharellus* received significant support, with exceptions such as for the internal relationships within the *C. flavus*-*C. phasmatis*-*C. tenuithrix* clade or within the *C. cibarius* – *C. roseocanus* clade.

TEF-1 sequences produced for the two new species described in the present study, *C. iuventateviridis* and *C. deceptivus*, show no intraspecific variability, respectively. *Cantharellus iuventateviridis* (MLbs = 91%, BPP = 1) is monophyletic (MLbs = 91%, BPP = 1) and sister species with *C. chicaoensis* (MLbs = 97%, BPP = 0.99). *Cantharellus deceptivus* nests in a monophyletic clade (MLbs = 86%, BPP = 0.99) including *C. pallens* (MLbs = 65%, BPP = 1) and four other species (*C. flavus*, *C. phasmatis*, *C. tenuithrix* plus a not yet identified species [*C. sp.*]). The branch separating *C. deceptivus* from the other species within that clade is significantly supported (MLbs = 86%, BPP = 0.96). However, relationships between, *C. deceptivus*, *C. pallens*, and the other species of that clade are not resolved as well as the relationships within the subclade including *C. flavus*, *C. phasmatis* and *C. tenuithrix*, which appear to be not distinguishable from each other based on this *TEF*-1 phylogeny.

Taxonomy

Cantharellus chicaoensis Leacock, J. Riddell, Rui Zhang & G.M Muell.,
Mycologia 108:767. 2016 **Figs 2-4**

Examined material: UNITED STATES. **Missouri.** Meramec State Park, near hardwoods, 2010, J. Justice Mo-Canth1 (PC0142428).

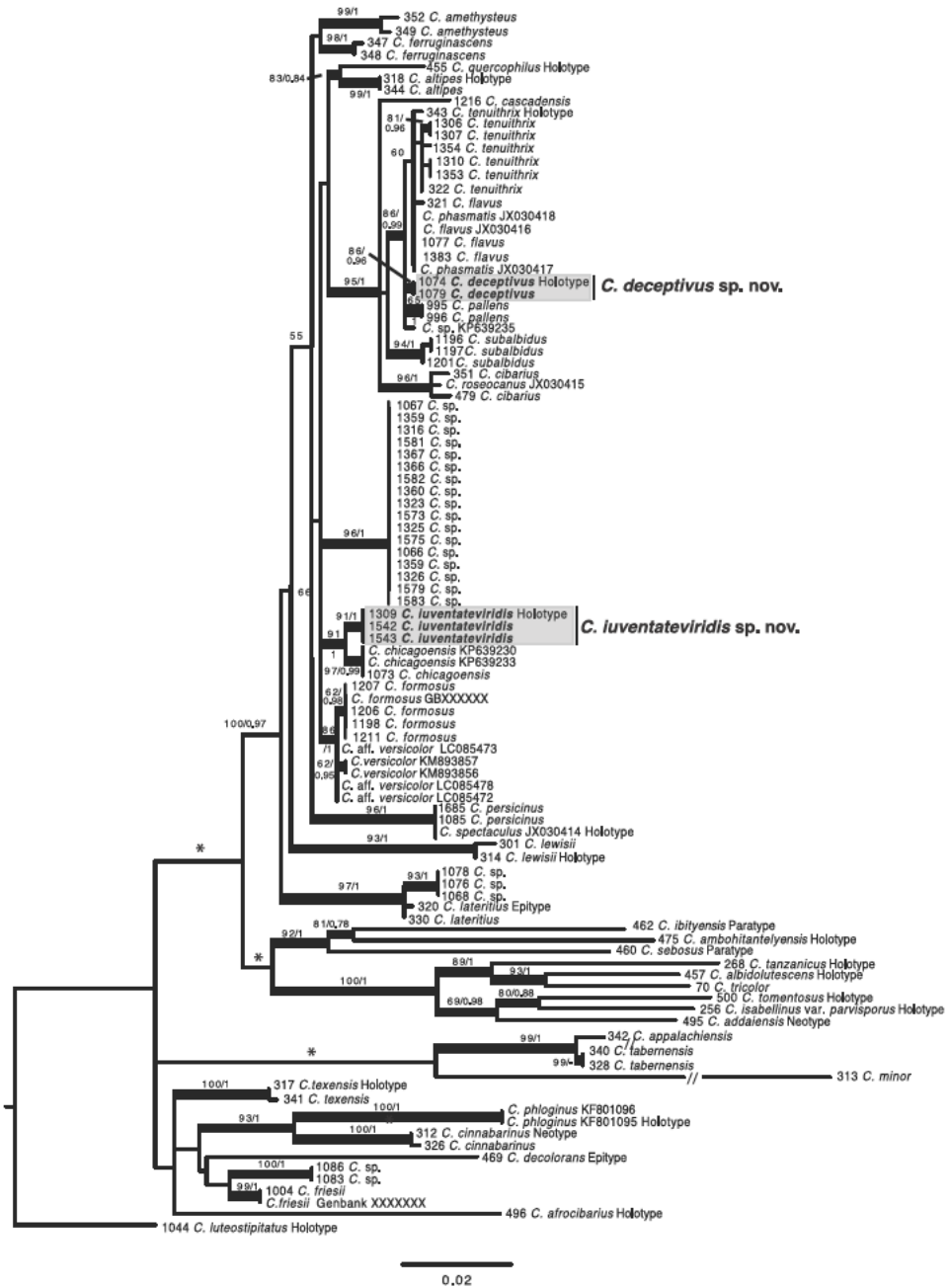
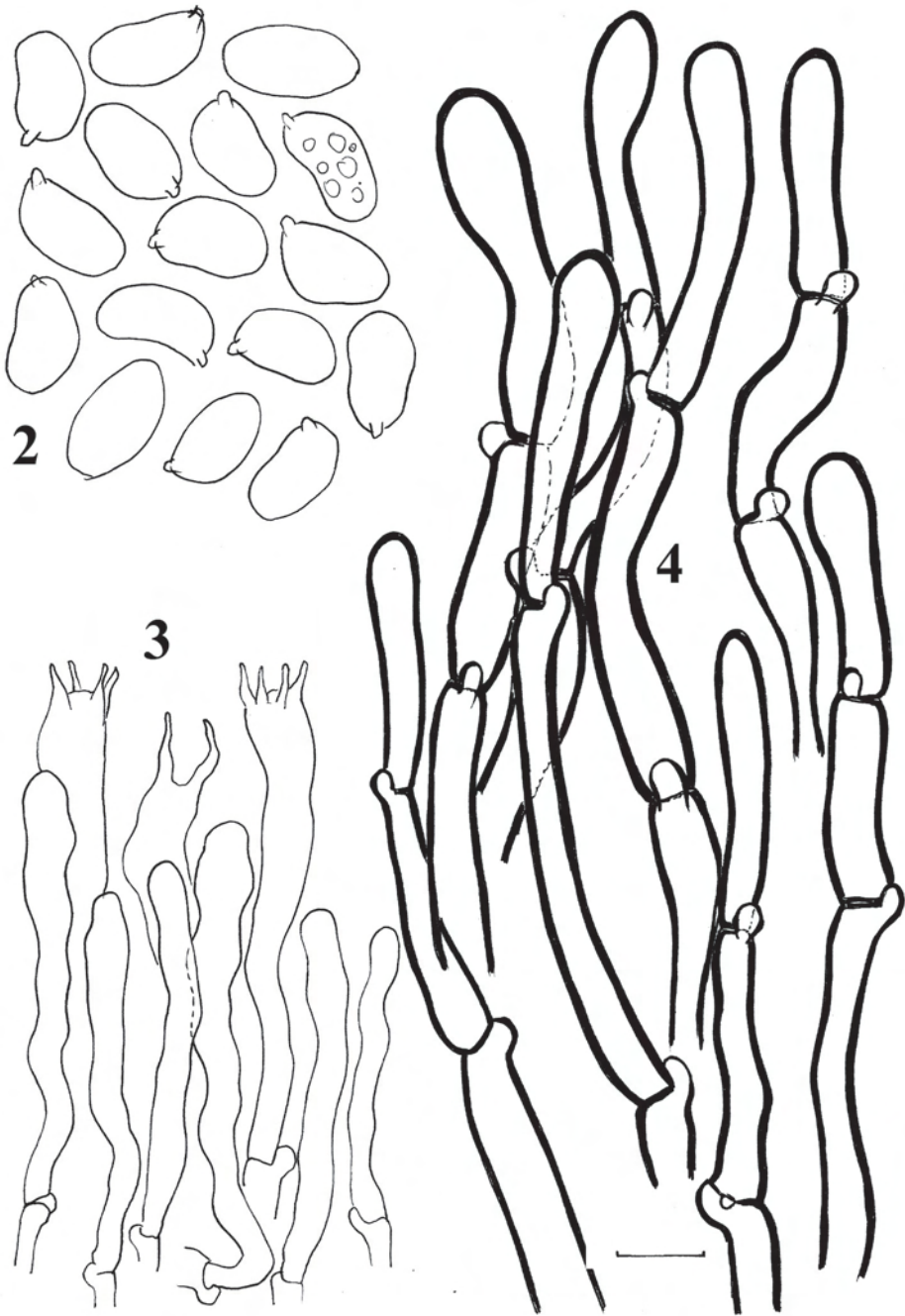


Fig. 1. Most likely tree from the maximum likelihood (ML) analysis of the *TEF-1* region of selected taxa of *Cantharellus*. Branches that received both MLBs $\geq 70\%$ and BPP ≥ 0.95 are in bold and MLBs and BPP values are reported along the branches respectively. Asterisks (*) indicate nodes that were implemented as backbone constraints in phylogenetic analyses.



Figs 2-4. *Cantharellus chicagoensis* (JJ MO cant-1). 2. Spores. 3. Basidia and basidiola. 4. Hyphal extremities of the pileipellis. (Scale 10 μ m, 5 μ m for spores). Drawings B. Buyck.

Commentary: The recently described *C. chicagoensis* (Leacock *et al.* 2016) is here recovered with significant support as sister to a new clade of three southern collections that appear to represent its more southern counterpart. This new clade is described below as a new species (*C. iuventateviridis*) and it shares with *C. chicagoensis* the ephemeral presence of greenish tints near the cap margin.

Our Missouri collection of *C. chicagoensis* extends its distribution more to the south, as this species was only reported from northern Indiana, northern Illinois and Wisconsin (Leacock *et al.* l.c.). The analysis of the microscopic features of our *C. chicagoensis* collection confirm data supplied by Leacock *et al.* (l.c.), including near-identical spore size for the Missouri specimen [(6.7)6.9-7.44-7.9(8.9) × (3.7)4.0-4.31-4.6(5.0) μm, Q = (1.5)1.6-1.73-1.8(2.0)]. As Leacock *et al.* did not illustrate the microscopic features of their new species, we provide here microscopic drawings (Figs 2-4) for the Missouri collection to compare it with features of *C. iuventateviridis*.

Cantharellus deceptivus Buyck, Justice & V. Hofstetter *sp. nov.* **Figs 5-7, 17-20**

Mycobank: MB 818373

Diagnosis: Differs from *Cantharellus phasmatis* in the *TEF-1* sequence data and from *C. tenuithrix* and *C. flavus* in its less brightly colored hymenophore.

Holotype: UNITED STATES. **Wisconsin.** Lost Lake, under hardwood trees including paper birch (*Betula papyrifera*) and big toothed aspen (*Populus grandidentata*), 24 July 2010, 1074/Jay Justice JJ13 / WI-CANT-1 (PC0142430).

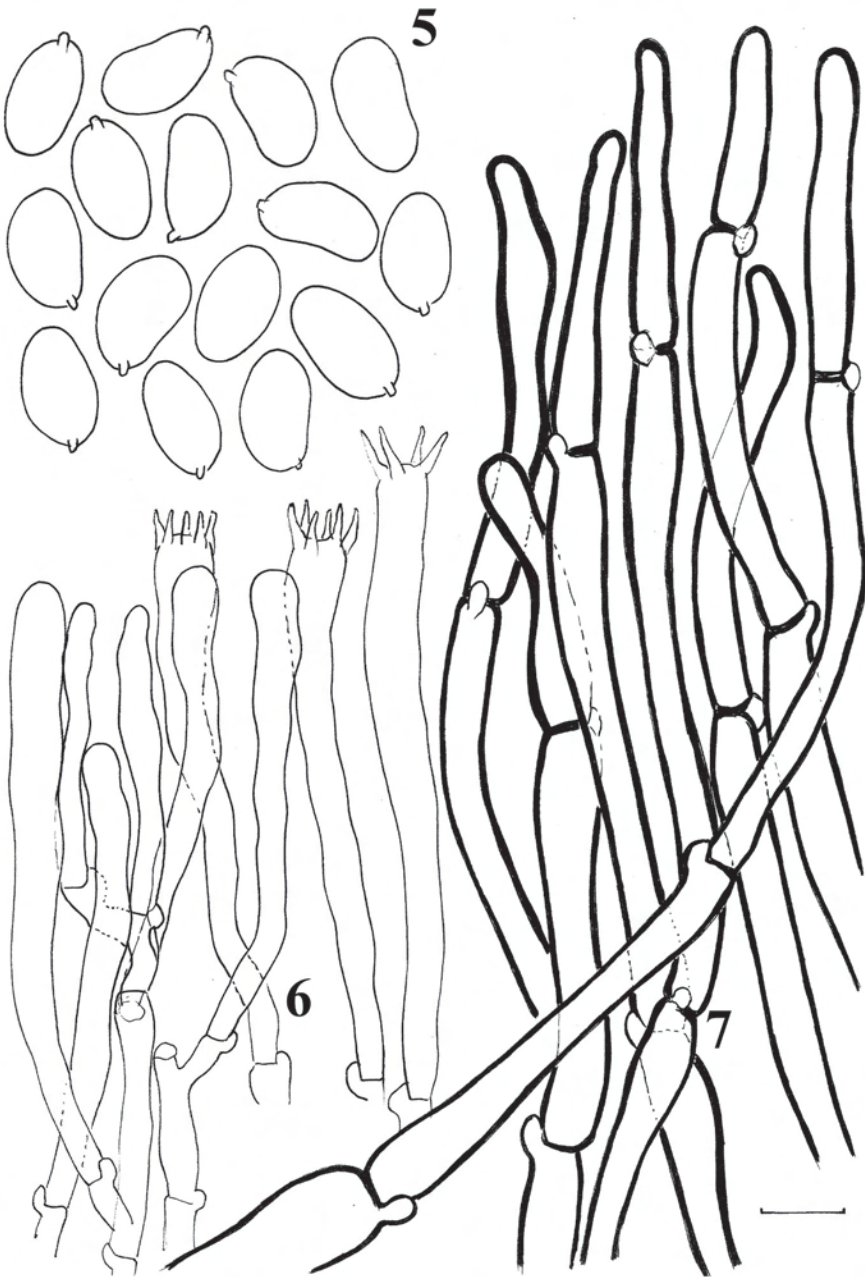
Etymology: refers to its deceptive overall habit making it impossible to distinguish this species in the field from *C. phasmatis*.

Cap medium-sized to large, first plane-convex, then rapidly slightly depressed in the center, sometimes becoming funnel-shaped at maturity. 70-150 mm diam., funnel-shaped, smooth to weakly scaly, a velvety, bright yellow (4AB8), **Hymenophore** strongly decurrent, with quite well-differentiated, dense gill folds, abundantly forking, weakly interveined, either a paler or deeper yellow than the cap surface or with golden yellow tones, developing a clear pinkish hue at maturity. **Stipe** up to 50 mm long, cylindrical, light yellow, massive, darkening on handling. **Context** white to cream or flesh-colored, slightly yellowing with age. **Spore print** distinctly yellowish.

Spores ellipsoid to narrowly ellipsoid, (6.7)7.5-8.09-8.7(9.4) × (4.2)4.4-4.75-5.1(5.4) μm; Q = (1.4)1.5-1.71-1.9(2.0), n = 20), often somewhat reniform, thin-walled, smooth. **Basidia** slender, mostly 70-85 × 6-8 μm, slightly undulate, clavulate, mostly 5-6-spored. **Cystidia** none. **Subhymenium** filamentous. **Hyphal extremities of the pileipellis** very long and slender, aggregated in bundles lying on the cap surface, with distant septa, composed of long, regular, mostly subcylindrical cells, measuring 6-10(15) μm diam., moderately thick-walled, with cell walls only in few terminal cells ca. 1 μm thick; the terminal cell measuring mostly 30-50(80) μm long, subcylindrical or sometimes slightly inflated above the septum, obtuse-rounded at the tip. **Clamp connections** everywhere.

Additional specimens examined: UNITED STATES. **North Carolina.** Standing Indian campground, south of entrance of Long Branch trail, 35° 04.268' / 083° 31.510, 1079/Jay Justice NC-CANT-5 (PC0142429).

Commentary: Together with the European *C. subpruinosis* Eyssartier & Buyck (recently synonymized with *C. pallens* Pilát, see Olariaga *et al.* 2016), we have here yet another species that is member of the *flavus-phasmatis-tenuithrix* complex, a group of several uncomfortably close American “species”. In our *TEF-1* analysis (Fig. 1), the European *C. pallens* and the here newly described *C. deceptivus*



Figs 5-7. *Cantharellus deceptivus* (holotype). 5. Spores. 6. Basidia and basidiola. 7. Hyphal extremities of the pileipellis. (Scale 10 μ m, 5 μ m for spores). Drawings B. Buyck.

are the only taxa that received significant support. Published *TEF-1* sequences for *C. flavus* and *C. phasmatis* are not significantly supported as being different from our *C. tenuithrix* as spliceosomal introns have been excluded from our analysis. When including these four introns in the analyses (see De Kesel *et al.* 2016, this issue), all species of this complex do obtain significant support based on *TEF-1* phylogenetic inference, but this may be different when using a more extended sampling for each species as the differences are really minimal.

Species recognition within this group becomes now even more complex as *C. deceptivus*, for which the holotype was also collected in Wisconsin, is morphologically identical to *C. phasmatis* when mature, yet is molecularly distinct from all other species in this complex. The identical aspect of cap and stipe surfaces of both species is evident when comparing our picture (Fig. 18) with the one published for *C. phasmatis* in Foltz *et al.* (2013, fig. 1B). However, young fruiting bodies of *C. phasmatis* have a white hymenophore, and then develop pinkish buff to yellowish tinges (Foltz *et al.* l.c.). Our figs 17-20 for *C. deceptivus* depict mature specimens having a yellowish hymenophore with distinct pinkish hues as described for mature *C. phasmatis*. As we collected only mature specimens of *C. deceptivus*, we don't know whether its hymenophore was equally white when young. The yellow color of the spore print noted for our species was based on a dried spore print. This potentially does not exclude the presence of pinkish tinges in the fresh spore print of our species because pink spore prints are known to fade to yellow after drying (Petersen 1985), especially considering the identical pinkish hues of the mature hymenophore of both species. Because of the pinkish hues in the hymenophore, our species can also be compared to *C. persicinus* Petersen (= *C. spectaculus*, see below), but the latter species has a hymenophore that is entirely and distinctly salmon pinkish, and nests outside this species complex.

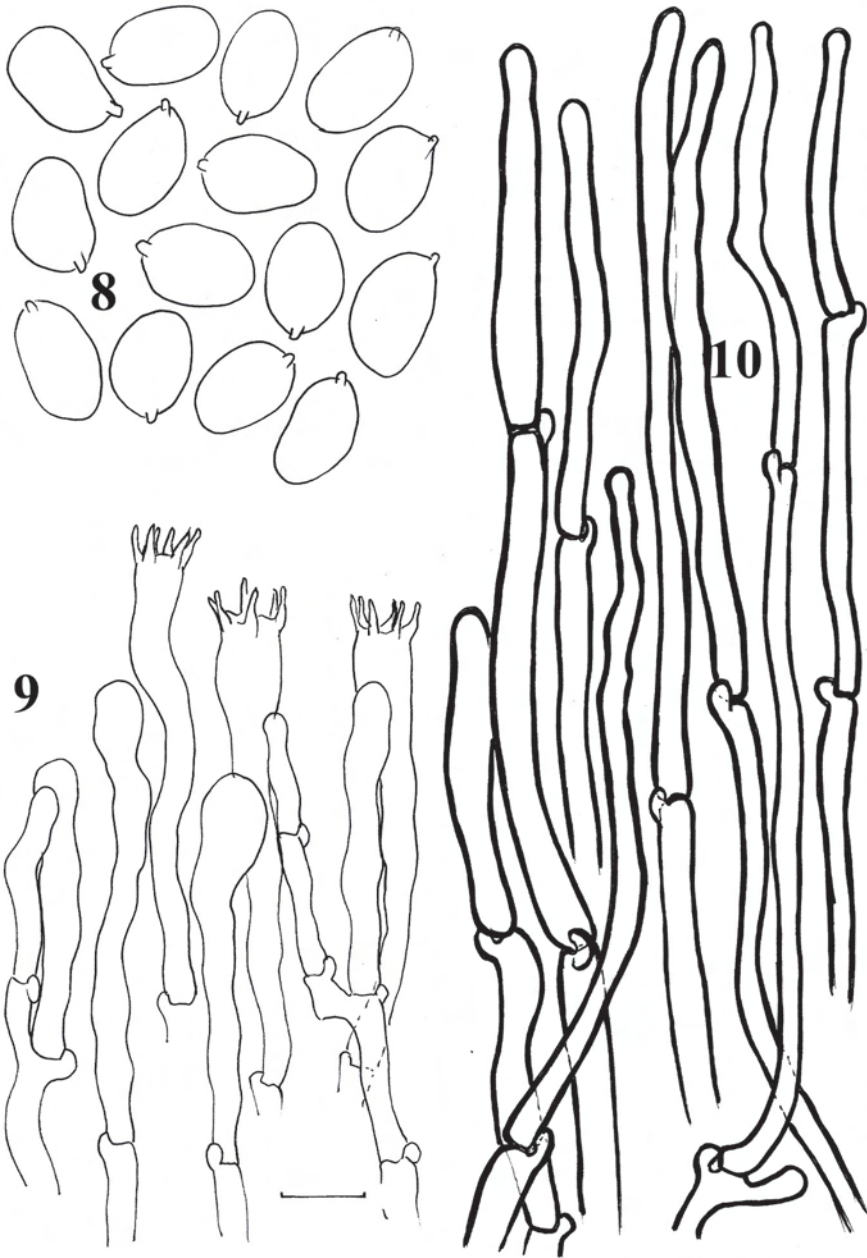
Both *C. flavus* and *C. tenuithrix* are easily distinguished in the field from *C. deceptivus* and *C. phasmatis* as they have a hymenophore of a much more intense yellow that never develops any pinkish hues, and both share the yellow spore print. In the field, however, the first author admits he is incapable of distinguishing between the two species in each species pare.

Our material of *C. deceptivus* demonstrates that its wide distribution stretches at least from North Carolina to Wisconsin. The North Carolina collection resembles the holotype in spore size [(7.1)7.5-7.72-8.0(8.1) × (4.2)4.6-4.94-5.3(5.4) μm, Q = (1.4)1.5-1.57-1.7(1.9)] but this is also within the (wide) range given for spore size for *C. phasmatis*. The pileipellis of our new species has less slender hyphal terminations with shorter terminal cells compared to both *C. tenuithrix* (see Buyck & Hofstetter 2011) and *C. flavus*. Illustrations of microscopic features for *C. phasmatis* have not yet been provided.

***Cantharellus flavus* M.J. Foltz & T.J. Volk, Mycologia 105: 458. 2013 Figs 8-10, 23**

Examined material: UNITED STATES. **North Carolina.** Nantahala Nat. Forest, under hardwoods along trail near Standing Indian campground, GIS: 35. 04488 / 083.31699, 3 Aug. 2010, 1077/Jay Justice NC-Cant-3 (PC0142433). **Texas.** Newton Co., Site 7 at Toledo Bay Reservoir, oak-hickory forest on sandy soil, 20 July 2007, Buyck 321/07.027 (PC0084091); Polk Co., Big Thicket National Preserve, Big Sandy Creek Unit, Big Sandy trail, 4 July 2014, N 30.62648-W 094.64516, 80-90 m alt., pine uplands, 1409/BB 14.167 (PC 0142356).

Notes: The original diagnosis for *C. flavus* reads as follows: “*Pileus yellow; hymenium yellow; stalk yellow; spore print yellow. Molecular data from ITS and TEF1 loci distinguish this species from all other Cantharellus*”. This diagnosis



Figs 8-10. *C. flavus* (1077/JJ NC-Cant-3). 8. Spores. 9. Basidia and basidiola. 10. Hyphal extremities of the pileipellis. (Scale 10 μ m, 5 μ m for spores). Drawings B. Buyck.

therefore defines this entirely yellow species on the basis of the distinctiveness of its ITS and *tef-1* sequences from other yellow chanterelles which, in view of the minimal differences between sequences of the various taxa in this complex, seem to us somewhat of an overstatement. *Tef-1* sequences are actually identical in their coding parts and the differences are equally thin when comparing the available ITS sequences among these species (Buyck *et al.* 2016c, this issue). As such, the perfect quality of sequence reads becomes a major issue for correct identification.

Another problem, however, is that neither the ITS nor the *tef-1* sequences produced by Foltz *et al.* (2013) were retrieved from the designated holotypes (i.e. *C. flavus*: specimen CO66; *C. phasmatis*: specimen CO73) and both holotypes have only been associated with LSU sequences which are identical for all species in the *C. tenuithrix*-complex (including European taxa) and do not contribute to species-level identification. Both diagnoses (i.e. for *C. flavus* and *C. phasmatis*) are, therefore, still in need of verification, but this fact seems not to invalidate both names (fide S. Redhead, pers. comm.).

Foltz *et al.* (2013) associate with *C. flavus* one specimen, that was previously included by Buyck & Hofstetter (2011) as representing their newly described *C. tenuithrix*, [BB 07.027, noted as 321 *C. flavus* in Fig. 1]. Both this specimen, which is not the type of *C. tenuithrix*, as well as the here cited collections from North Carolina (1077, fig. 1) and Texas (1383, fig. 1), have a white stipe (Fig. 23) and stipe color appears to be variable in both species. While *C. flavus* is impossible to distinguish from *C. tenuithrix* in the field, it is genetically closer to *C. phasmatis*. A multigene analysis comprising multiple collections of these species will be required to correctly delimit these taxa. When including introns for *Tef-1* in the analyses of a limited number of samples (De Kesel *et al.* 2016, this issue), the results nevertheless seem to support the distinction of separate taxa.

Microscopic features were not illustrated in the original description of *C. flavus* and are here provided for our collection from North Carolina (Figs 8-10). Our microscopic observations on this specimen conform to the original description in having very slender hyphal extremities in the pileipellis, but this character is shared with *C. tenuithrix* and to a lesser degree also with the other species in this complex. Our specimens have shorter basidia, measuring mostly $50\text{--}65 \times 7\text{--}9 \mu\text{m}$ compared to $(63)75\text{--}80(84) \times 7\text{--}9(10) \mu\text{m}$ in the original description of *C. flavus*.

Spore size of *C. flavus* was given in the original description as $(7.5)8\text{--}10(11) \times (4)4.5\text{--}6 \mu\text{m}$, which is near identical to the spore size given for *C. phasmatis* [$(7)7.5\text{--}10(11) \times 4\text{--}6(7) \mu\text{m}$]. Interestingly, when applying statistics on spore measurements, our data reveal considerably wider spores for *C. flavus* compared to *C. tenuithrix*:

C. flavus: $(6.2)7.2\text{--}7.77\text{--}8.3(8.8) \times (4.6)4.8\text{--}5.17\text{--}5.5(5.8) \mu\text{m}$, $Q = (1.2)1.4\text{--}1.51\text{--}1.6(1.7)$
C. tenuithrix: $(6.9)7.0\text{--}7.72\text{--}8.4(9.8) \times (3.5)3.74\text{--}4.05\text{--}4.4(4.8) \mu\text{m}$, $Q = 1.6\text{--}1.86\text{--}2.1(2.5)$

Cantharellus iuventateviridis Buyck, Looney, Harsch & V. Hofstetter *sp. nov.*

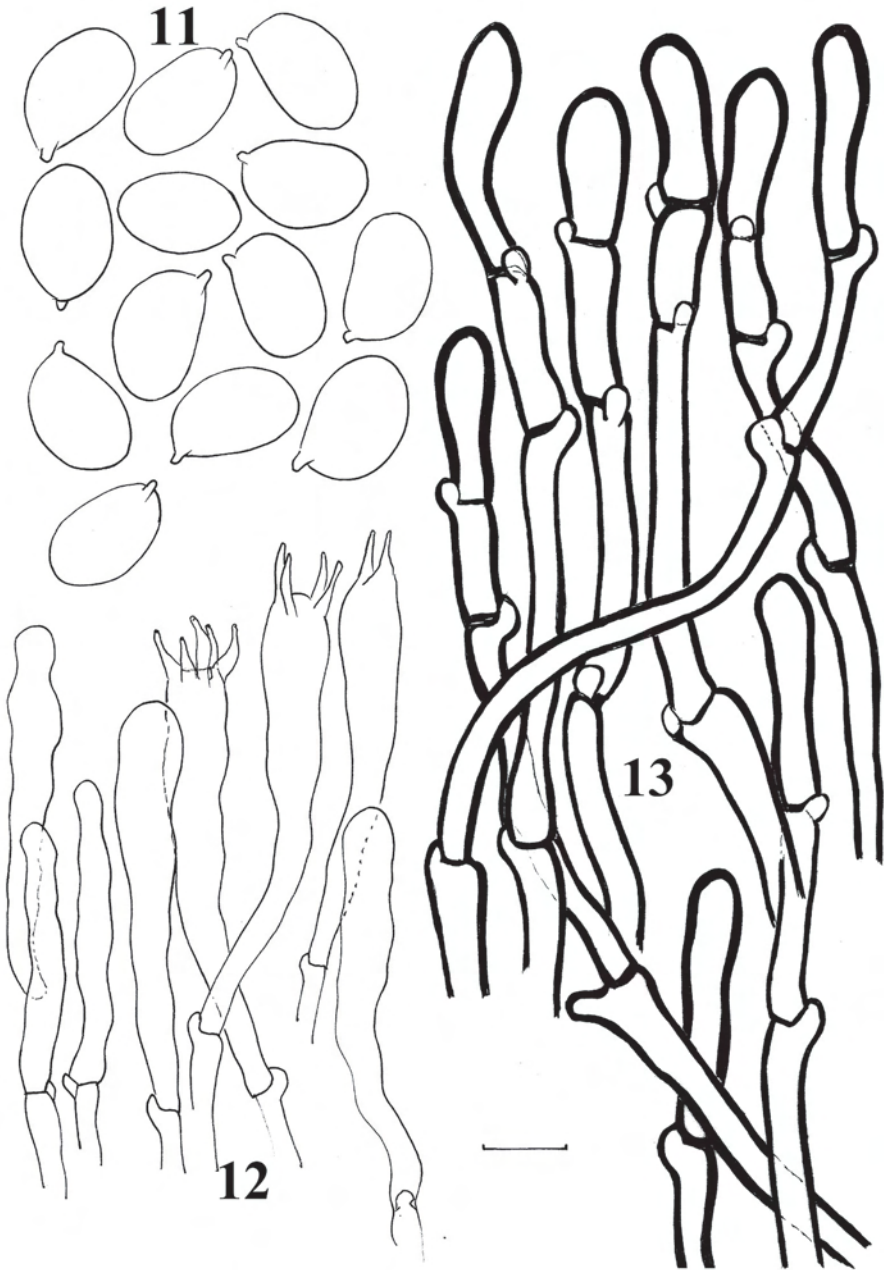
Figs 11-13, 21-22

Mycobank: MB 818374

Diagnosis: Differs from *C. chicaoensis* in its apparently more southern distribution, its slightly wider spores (mean width $> 5 \mu\text{m}$) and sequence data obtained for *TEF-1* and ITS.

Etymology: Latin name refers to the distinct green margin color when young (*iuventas* = youth, *viridis* = green).

Holotype: **Mississippi**. Mississippi Welcome Center, along I-20 westbound, near Meridian, $32^{\circ}24'39''\text{N } 88^{\circ}32'00''\text{W}$, elev. 119m, scattered and gregarious in



Figs 11-13. *C. iuventateviridis* (holotype). 11. Spores. 12. Basidia and basidiola. 13. Hyphal extremities of the pileipellis. Scale bar = 10 μ m, but only 5 μ m for spores. Drawings B. Buyck.

bare, muddy, clay-rich soil in small runoff gulch, on bottom and under earthy overhangs near *Pinus* and *Quercus*, 10 July 2014, BP Looney 523 (PC0142425, isotype TENN070197).

Pileus 12-47 mm diam., convex at first, but rapidly becoming depressed in center to infundibuliform, dull, near-glabrous to radially and minutely hairy-velutinous, becoming pubescent at margin, bumpy in center and there often scaly-squamulose-fibrillose in older specimens, becoming thin at margin and fraying when expanded; margin strongly in-rolled at first, later sometimes irregularly undulate-lobed, frequently crenate; when young 4C6-7 on surface, 3D7 on margin with a distinct olive green pigment strongest at the very edge, but sometimes the entire cap with olivaceous tints; becoming 4B7-8 towards edges, 5D4 in center, 3C6-B6 on inrolled margin at maturity and rapidly fading olivaceous tones, in age turning more brownish (5B7, 4A5, 5D7). **Hymenophore** decurrent, composed of relatively well-differentiated gill folds or thick veins, quite regularly forking and in some specimens also transversely anastomosing in between although never strongly so, from the very beginning already pale yellow, rapidly more bright yellow, peachy-yellow, (4A8, 5A6). **Stipe** 40-10 × 3-11 mm, quite variable in form, when young sometimes terete to flattened, but also firm and obclavate, equal to tapering towards base, often curving in lower half, with yellowish-brown tinges and distinctly paler than the cap, 4A6, 4B5, 4A4; stipe surface reacting gray-green to FeSO₄, producing red fibrils with KOH. **Context** in the cap center relatively thick and firm considering the small cap size, brown-gray and off-white streaked, sometimes extending all the way to margin, faintly yellowing on handling. **Odor** weakly fruity-nutty when cut. **Taste** none. **Spore print** a very pale cream (IIa on Romagnesi scale for *Russula*).

Spores ellipsoid, (7.7)8.1-8.63-9.1(9.4) × (4.4)5.1-5.63-6.1(6.9), Q-(1.3)1.4-1.54-1.6(1.7), some distinctly wider in the basal part (egg-shaped), smooth. **Basidia** undulate-clavulate but not very long, mostly 55-75 × 7-9 μm, (2)4-5-spored, with often stout sterigmata. **Subhymenium** filamentous, of slender cells, 4-7 μm diam. **Cystidia** none. **Hyphal extremities of the pileipellis** generally with conspicuously thickened cell-walls (ca 0.5-1.2 μm), composed of short chains of a few terminal, often quite short cells, but then with gradually more spaced septa and narrower, not strongly branching; the terminal cell measuring (5)7-9 μm wide and more inflated than the subterminal cells, often remarkably short, mostly 20-30(-40) μm long, subcylindrical to clavulate or sometimes almost ellipsoid, broadly obtuse-rounded. **Clamps** everywhere.

Additional collections studied: UNITED STATES. **Louisiana:** Louisiana Game and Fish Pearl River Game Management Area (Lower Pearl River Delta), near Pearl River, Gravel Road heading South, before dead end, off Old Hwy 11 E., 30.374623 / -89.673493, in old streambed that crosses wide bulldozed trail, about 300 yards down trail in year-round wet to flooded muddy bottom, 13 July 2012, Stephen Harsch s.n. (PC 0713848); ibidem, 14 July 2012, S. Harsch s.n. (PC 0713847).

Commentary: Our description of *C. iuventateviridis* is entirely based on the holotype. This new Gulf coast species appears to be ecologically adapted to nearly bare soil in wet or muddy places. The most likely host in both localities appears to be a southern oak species, *Quercus nigra* L. (wateroak), although *Pinus* and *Carpinus caroliniana* Walt were also noted at proximity of some specimens.

In cap size it seems comparable to the *Pinus*-associated *C. altipes* Buyck & V. Hofstetter, likely a later synonym of *C. septentrionalis* A. H Sm. (see Buyck *et al.* 2016c, this issue), from which it differs notably in the less glabrous cap surface, as well as in its overall dull coloration which is strongly reminiscent of the European *C. ferruginascens*. The latter species shares the less robust aspect, e.g.

compared to *C. cibarius* and close allies, and comes in varying tones of yellow, grayish brown and green, but it turns immediately and strongly rusty-yellow upon handling or when ageing, whereas our species does so only reluctantly.

Spore measurements of the Louisiana collections for *C. iuventateviridis* are very similar although slightly smaller compared to the holotype, i.e. $(6.7)7.2\text{--}7.58\text{--}7.9(8.1) \times (4.8)5.0\text{--}5.18\text{--}5.4(5.6) \mu\text{m}$, $Q = (1.3)1.4\text{--}1.47\text{--}1.5(1.6)$. These spore measurements suggest that *C. iuventateviridis* might be characterized by larger and in particular wider spores and do not overlap with those for *C. chicagoeensis*. Both species share similar, often apically inflated, short terminal cells in the hyphal extremities of the pileipellis, with extremities being larger in the latter species (Fig. 4).

Cantharellus persicinus R.H. Petersen, *Nova Hedwigia* 42: 151–160. 1985

Figs 14–16, 24–27

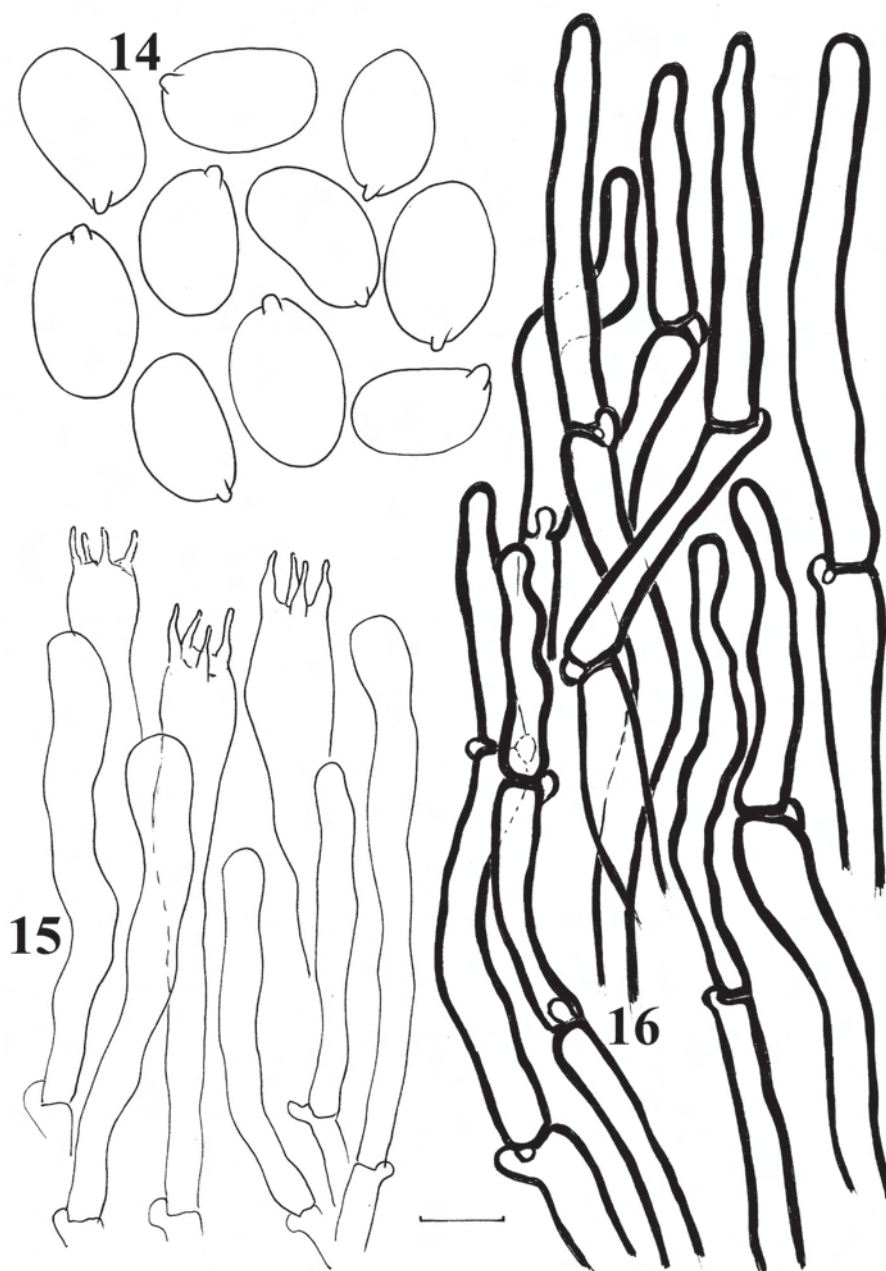
Synonym: *Cantharellus spectaculus*, M.J. Foltz & T.J. Volk, *Mycologia* 105: 458. 2013 **syn. nov.**

Cap up to 30(–45) mm diam., convex to irregularly folded and remaining so at maturity, more rarely becoming slightly depressed in the center, light orange to salmon or yellowish to almost yellowish brown in the center, hygrophanous, near the margin often with a whitish pruina. **Hymenophore** strongly decurrent, composed of unequal or forking, prominent, almost gill-like folds, a beautiful pink, turning to orange-buff with some purplish tinges, abruptly delimited from the sterile stipe surface. **Stipe** 33–45 mm high, up to 4 mm wide, subcylindrical, concolorous with the cap surface, often whitish at the extreme base, not hollowing. **Spore print** distinctly a soft yellow (2–3A2) when dry.

Spores ellipsoid and large, $(9.2)9.6\text{--}10.25\text{--}10.9(11.7) \times (5.8)6.3\text{--}6.73\text{--}7.1(7.3) \mu\text{m}$, $Q=(1.3)1.4\text{--}1.53\text{--}1.6(1.7)$, smooth, with a very obtuse and large apiculus. **Basidia** long, 4(5)-spored. **Subhymenium** filamentous. **Cystidia** none. **Hyphal extremities of the pileipellis** with conspicuously thickened cell-walls, ca $1(1.5) \mu\text{m}$ thick, composed of subcylindrical cells, mostly $5\text{--}12 \mu\text{m}$; the terminal cell often somewhat undulating or narrowing at the apex; the terminal cell mostly ca $25\text{--}55 \mu\text{m}$ long, either obtuse-rounded or slightly narrowing near the apex, not clavate. **Clamp connections** abundant everywhere.

Examined material: UNITED STATES. **Missouri**. St Louis Co., Forest 44, Conservation area, GIS: 38.31620 / 090.31055, 16 July 2011, Jay Justice JJ34 / MO-Cant-4 (PC0142431); **North Carolina**. Buncombe Co., Shope Creek Gamelands, scattered through a trailside bank of moss, under mixed Appalachian hardwoods with Oak and Tulip Poplar, elev. ca 1000 m., 21 July 2015, Mike Hopping 15.001 (PC0142432).

Commentary: This relatively small chanterelle was characterized by Petersen (1985) as “*Receptacula ad 8 × 4.5 cm. Pileus convexus ad planus, laevis, salmoneus ad persicinus. Stipes solidus, salmoneus ad persicinus. Lamellae pallido-salmoneus. Gustu nullo/ odor ut C. cibarius. Hyphae fibulatae; basidia 80–100 × 10 μm. Sporae in cumulo pallide-incarnata, 10.4–11.5 × 5.8–7.2 μm.*” and Petersen observed that this species had probably been mistaken for *C. cinnabarinus* in the past. Buyck *et al.* (2011a) published illustrations of the microscopic features of the holotype, thereby confirming that they were clearly different from both *C. cinnabarinus* and the then newly described *C. texensis* Buyck & V. Hofstetter, in particular because of the remarkably large spores and distinctly thick-walled hyphal terminations.



Figs 14-16. *C. persicinus* (JJ MO-Cant-4). 14. Spores. 15. Basidia and basidiola. 16. Hyphal extremities of the pileipellis. Scale bar = 10 μ m, but only 5 μ m for spores. Drawings B. Buyck.



Figs 17-18. *Cantharellus deceptiveus* sp. nov. (holotype). **17.** Detail of gills. **18.** Cap and stipe. (Photos J. Justice)



Figs 19-20. *Cantharellus deceptiveus* sp. nov. (paratype). **19.** Detail of gills. **18.** Cap. (Photos J. Justice)

The here newly reported specimens (Figs 24-27) conform very well to the original description of *C. persicinus* including its rather small size, similar to *C. cinnabarinus*, with a cap < 40 mm diam having a convex to plane shape. The microscopical features (Figs 14-16) of our specimens are near identical to those given for the *persicinus* holotype: the extremities of the pileipellis conform to those illustrated for the type collection in Buyck *et al.* (2011a); the basidia of the holotype of *C. persicinus* were described as 4-spored (Petersen, l.c.), and as 4(-5) spored by Eyssartier (2001), and also applies to our specimens which have mainly four-spored basidia. Finally, a comparison of spore measurements demonstrated extremely similar values:

- holotype (Eyssartier 2001): (9)9.5-10.73-11.5(13) × 6-6.68-7(7.5) μm, Q = 1.38-1.61-1.88,
- NC specimen: (9.2)9.7-10.45-11.2(11.7) × (5.4)5.9-6.30-6.7(7.3) μm, Q= (1.4)1.6-1.66-1.8(1.9),
- MO specimen: (9.2)9.6-10.25-10.9(11.7) × (5.8)6.3-6.73-7.1(7.3) μm, Q= (1.3)1.4-1.53-1.6(1.7).

Cantharellus persicinus is quite often referred to in the literature and even illustrated on the internet (Kuo 2015). Unfortunately, ever since a misidentified LSU sequence was deposited on GenBank (Dunham *et al.* 2003), the name has been misapplied to a different taxon (see *C. velutinus* in Buyck *et al.* 2016b this issue) with quite smaller spores. The *TEF*-1 sequence for the holotype of *C. spectaculus*



Figs 21-22. *Cantharellus iuventateviridis* (holotype). **21.** General view of holotype Scale: one square = 0.5×0.5 cm. (Photo B. Buyck). **22.** Fresh basidiomata in the field. (Photo B. Looney)

(Genbank JX030414) is identical (including all four introns!) with the sequences obtained for the specimens that we here identified as *C. persicinus*. Given, on the one hand, the micro- and macro-morphological similarity of our specimens with the protologue and holotype of *C. persicinus* and, on the other hand, the identical sequences and morphology shared between our collections and *C. spectaculus*, the latter clearly represents a later synonym. Unfortunately, we were as yet unable to obtain sequences from the *C. persicinus* type (but we will try again), but the fact that both have exactly the same, very large spores (the largest among North American chanterelles) and predominantly four-spored basidia leaves little doubt about the correctness of our interpretation.



Figs 23-24. **23.** *Cantharellus flavus* (Jay Justice NC-Cant-3, PC0142433). **24.** *Cantharellus persicinus* (Jay Justice MO-Cant-4, PC0142431). (Photos J. Justice)

It is difficult to understand why both species were not compared in the paper by Foltz *et al.* (2013) as *C. persicinus* and *C. spectaculus* share near identical protologues. Indeed, the original diagnosis of *C. spectaculus* states: “*Pileus orange-salmon; hymenium salmon, sometimes with a purple hue; spore print salmon-pink and larger than C. phasmatis. Molecular data from nLSU and TEF1 loci distinguish this species from all other Cantharellus* (Foltz *et al.* 2013)”. Both descriptions, therefore, define a taxon with salmon tints in cap, hymenophore and also in spore print, and both diagnoses accentuate the very large spores as a diagnostic feature. The more detailed description of *C. spectaculus* cites spore dimensions as 10-12(14) $\times$ 5-7 μm , and thus superimposable with those given in the original diagnosis for



Figs 25-27. *Cantharellus persicinus* (Mike Hopping 15.001). 25. Fresh basidiomata in situ. 26-27. Details of hymenophore, cap and stipe surface. (Photos Mike Hopping)

C. persicinus, and also with the spore measurements cited in the revision of the *persicinus*-holotype by Eyssartier (2001, see above). It is further interesting that both the description of *C. spectaculus* and the few notes taken on the here reported collection from Missouri mention a “purplish” tinge for the hymenophore surface, while the cap surface of the North Carolina collection (a dark yellowish with whitish margin) is near identical to the one illustrated for the Wisconsin holotype for *C. spectaculus* (compare with Foltz *et al.* 2013, fig. 2B).

Spore print color is a very delicate feature in *Cantharellus*, particularly because good spore prints are hard to obtain in this genus. *C. spectaculus* was described as having a salmon spore print. The spore print color of *C. persicinus* was described similarly as “*pallide-incarnata*” in the original diagnosis, but when reading the more detailed description, Petersen (l.c.) reports it as being white in light prints, seashell pink in heavy prints and turning then to deep cream or pale yellow once dry.

The here proposed synonymy between both names implies the existence of considerable variation in general size and coloration in *C. persicinus*, but this is something that concerns most chanterelles (Olariaga *et al.* 2015, 2016). Smaller specimens of *C. persicinus* can not only be confused with *C. cinnabarinus* in the field, as indicated by Petersen, but because of the distinctly pink hymenophore and yellowish overall color, smaller specimens of this species are highly similar to *Cantharellus ignicolor* R. H. Petersen, recently recombined into genus *Craterellus* (Dahlman *et al.*, 2000).

DISCUSSION

Given the considerable geographic distance among collections for the same species, in the case of *C. flavus* for example ranging from the Gulf Coast to Wisconsin, it is quite possible that the potential distribution area of many American chanterelles covers the whole area of the United States – and possibly part of Canada – that lies to the east of the Rocky Mountains.

Macroscopic variability within a single chanterelle species appears to be quite impressive compared to the limited genetic variation, particularly in subg. *Cantharellus*. In the case of the *C. tenuithrix* complex, the genetic similarity between the four presently recognized species is > 99.5%, which is much higher than applied thresholds between most other chanterelle species in the world and certainly much higher than thresholds for species delimitation in more ecologically oriented studies that often still apply a cut-off at 97% sequence similarity (Blaalid *et al.* 2013; O’ Brien *et al.* 2005).

Finally, we would also like to make a plea for illustrating precise microscopic features in more detail when describing new species. Specific boundaries between species belonging to genera with very limited microscopy, such as *Cantharellus*, can only be adequately defined using molecular techniques, yet the benefit of precise illustrations remains undeniable. We have always provided detailed microscopic illustrations for the chanterelles we have described, but American tradition appears to be less inclined to do so, e.g. neither Foltz *et al.* (2013), nor Leacock *et al.* (2016) illustrated microscopic features for their new species. Comparing detailed microscopic drawings of the different species resumes their differences and similarities far better than a written description and they provide more reliable identification criteria (particularly mean values for spore size are very helpful and should always be

provided). It is thanks to our drawings of all type specimens of American chanterelles that we were immediately oriented towards *C. persicinus* when identifying our collections as this species clearly has the largest spore size among North American chanterelles. In certain cases, microscopic features of the pileipellis allow to rapidly sort out perfect look-alikes in the field, such as in the case of *C. cinnabarinus* versus its look-alikes, *C. coccolobae* (Buyck *et al.* 2016a, this issue), *C. corallinus* (Buyck *et al.* 2016b, this issue) and *C. texensis* (Buyck *et al.* 2011).

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