Cryptogamie, Mycologie, 2016, 37 (3): 405-417

Setting the record straight on North American *Cantharellus*

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Abstract – The authors assembled for the first time a sequence dataset representative of all 29 presently described North American *Cantharellus* species, including not only all six newly described North American species presented in this special issue, but very importantly, also newly obtained partial ITS and LSU sequence data from the type specimens of *C. camphoratus* and *C. septentrionalis*, two species that supposedly had never been recollected in the United States since their original description. As such, they hope to put the record straight for future research on *Cantharellus* in North America and to allow for a more precise identification and appreciation of newly collected, sequenced specimens.

***Cantharellus septentrionalis* / *Cantharellus camphoratus* / ITS2 / LSU / phylogeny / taxonomy**

INTRODUCTION

Molecular phylogenies have revolutionized the morphological classification of fungi. They have demonstrated the impressive flexibility in the overall habit of fungi and the existence of many convergences shared by different fungal groups (Pine *et al*. 1997; Dentinger & McLaughlin 2006). When taking family Russulaceae for example, the name Elasmomycetaceae as a separate family for gasteroid Russulales has been abandoned and so were all of the genera adopted for various secotioid-gasteroid or pleurotoid members of this family in the same way such morph-genera have been abandoned in other ectomycorrhizal groups (Peintner *et al.* 2001). The traditional agaricoid genera in Russulaceae are very well characterized in the field because of their brittle context, but at subgeneric level, several convergent

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doi/10.7872/crym/v37.iss3.2016.405

features have been overemphasized in classifications: e.g. species with unequal gills in *Russula* are no longer confined to subgenus *Compacta* but occur instead within three different subgenera in *Russula* (Hongsanan *et al*. 2015). On finer levels (i.e. sectional, subsectional and below), the impact of molecular phylogenies has been much more limited as the impressive diversity of macro- and microscopic features in the genus allow for a rather correct grouping of closely related species (Miller & Buyck 2002).

Compared to the easily recognizable genus *Russula* that offers an impressive microscopic diversity, *Cantharellus* offers an example of the opposite scenario: traditionally ill-defined by the presence of veins instead of well-developed gills, the majority of the earlier names for *Cantharellus* species are accommodated now in no less than 40 different genera and nine different orders of Hymenomycetes (Buyck *et al*. 2014). Because of the monotony of its microscopic features, the genus also lacked any significant infrageneric classification before the advent of molecular phylogenetic approaches. *Cantharellus,* as currently circumscribed, has no known gasteroid-secotioid representatives, but was recently emended to include also a pleurotoid (Buyck 2014) and even a cyphelloid species that is easily taken for a tiny discomycete (Suhara & Kurogi 2015). In the absence of sufficient microscopic variation, the general field habit remained very important in descriptions as well as in the general identification of species and this was responsible for the description of many superfluous taxa in Europe (Olariaga *et al*. 2015, 2016).

In North America, the number of described chanterelles (excluding those that are apparently members of sister genus *Craterellus*) has more than doubled over the past five years, with species recognition mainly based on a combination of morphological and molecular criteria (Arora & Dunham 2008, Dunham *et al*. 2003, Foltz *et al*. 2013, Leacock *et al*. 2016; Buyck *et al* 2011, Buyck & Hofstetter 2011, Buyck *et al*. 2010, Buyck *et al*. 2016a,b,c this issue). The influence of macroscopic features in most species definitions is nevertheless still very important and maintains a certain degree of negligence of microscopic features. The latter are rarely illustrated by American authors despite allowing sometimes for a much more reliable species recognition compared to macroscopic features. Confronted with the impressive variation in form, color, size and hymenophore development among American chanterelles, some mycologists estimate the extant biodiversity of *Cantharellus* in North America to be in excess of 50 species (T.Volk pers. comm.). We think that such an estimation is somewhat too optimistic, not only because form, color, size and hymenophore development can be incredibly variable within a single species (see Buyck *et al*. 2016b, this issue), but also because some recently described species are based on very slight molecular differences (Buyck *et al*. 2016c, this issue). On the other hand, we have to admit that the description of new American species is booming (e.g. the six new species described in this issue) and that more new species await description (Buyck, unpubl.). At the same time, however, the precise identity of some chanterelles described several decennia ago has never been molecularly investigated.

With the recent shift from morphological features to molecular sequence data in defining species concepts, one might think that all of the earlier described species would be rapidly rediscovered through sequencing of new collections and older type material. Nevertheless, three species remain a complete enigma up to the present day, even though the microscopic features of their type specimens were reexamined and illustrated (Buyck *et al*. 2010, 2011, Eyssartier 2001), viz. *C. camphoratus* R.H.Petersen, *C. septentrionalis* A.H. Sm. and *C. persicinus* R.H. Petersen. The first two species remained most likely ignored because they were attributed an exceptional field characteristic, but the third species was misinterpreted ever since a misidentified LSU sequence had been deposited on GenBank (see Buyck *et al*. 2016c, this issue).

In this paper, the authors thus assembled for the first time a sequence dataset representative of all 29 presently described North American *Cantharellus* species. Our dataset not only includes all new species presented in this special issue, but importantly, includes also newly obtained partial ITS and LSU sequence data from the type specimens of *C. camphoratus* and *C. septentrionalis*, two species that supposedly had never been recollected in the United States since their original description. Sequencing efforts for the holotype of *C. persicinus* were unsuccessful so far (and might require cloning), but a morphological comparison suggests rather convincingly that it is an earlier name for *C. spectaculus* (see Buyck *et al*. 2016c, this issue). With this paper, we hope to put the record straight for future research on *Cantharellus* in North America and to allow for a more precise identification and appreciation of newly collected, sequenced specimens.

MATERIALS AND METHODS

Morphological data. – All newly sequenced collections (with the exception of the older types) were gathered by the first author and collaborators in the past few years. All cited specimens are deposited at the mycological herbarium of the Paris' Natural History Museum (PC) unless indicated otherwise. Microscopic features were examined and sketched by B. Buyck using a camera lucida setup. Original drawings for all elements of the hymenium or pellis were made at × 2400. All microscopic observations and measurements were made in ammoniacal Congo red, after a short aqueous KOH pretreatment to improve tissue dissociation and matrix dissolution. Measurements of basidiospores cite length, width and length/width ratio (Q) in the following format: (minimum measured) mean minus stand.dev. – *mean value* – mean plus stand.dev. (maximum measured); spore measurements are based on 20 spores/collection.

Molecular data. – *Molecular data and phylogenetic analyses* – The analysed data set includes sequence data for the partial 5.8S, ITS2 and partial LSU obtained from 63 collections representing all 29 presently recognized American *Cantharellus* species together with a few European or Asian species belonging to the same subgenera (Table 1). *Cantharellus luteostipitatus* from subg. *Afrocantharellus* has been chosen as outgroup (Buyck *et al*. 2014, Shao *et al.* 2014). Nucleotide sequences were newly produced for 23 collections of *Cantharellus* and additional ITS and LSU sequences were downloaded from Genbank.

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). The 5.8S-ITS2 and the LSU regions were amplified using primers ITS3C-ITS4 (White *et al*. 1990) and LR0R-LR5 primers (Vilgalys & Hester, 1990), respectively. Sequences were assembled and edited using the software package Sequencher 3.0 (Gene Codes Corp., USA). The 62-specimen alignment was analysed using Bayesian (MB) and Maximum Likelihood (ML) phylogenetic inferences. Several basal nodes that received significant support in the 4-gene worldwide phylogeny by Buyck *et al*. (2014) were constrained in our analyses

Table 1. Voucher table providing specimen list used for the phylogenetic analyses together with their extraction and collector numbers, as well as GenBank deposit numbers for used sequences. Newly generated sequences are in bold. The letter "T" refers to holo-, neo- or epitype collections.

Species	*Extraction no*	*Voucher*	*GenBank ITS*	*GenBank LSU*
C. alborufescens	–	AH44783	KR677492	KR677530
C. altipes	1080	JJ NC-cant-6	**KX896772**	**KX896787**
C. altipes	1315	BB 14.032	**KX896770**	–
C. altipes	1337	BB 14.063	**KX896771**	–
C. aff. *altipes*	1071	JJ AR-cant-7	**KX896769**	**KX896786**
C. amethysteus	349	BB 07.284	JN944020	JN940589
C. amethysteus T	–	AH44796	KR677513	KR677550
C. appalachiensis	1084	JJ MO-cant-3	**KX896759**	**KX896777**
C. californicus T	–	OSC 122878	**KX828768**	**KX828795**
C. camphoratus T	–	TENN38025	**KX896773**	**KX896788**
C. cascadensis	–	OSC 75908	AY041181	AY041160
C. cascadensis	–	OSC 75975	AY041183	AY041163
C. chicagoensis	–	PRL8332	KP639200	KP639214
C. chicagoensis	–	PRL8916	KP639201	KP639218
C. cibarius	–	AH44780	KR677508	KR677546
C. cibarius T	–	BIO10986	KR677501	KR677539
C. cinnabarinus T	312	BB 07.001	–	KF294624
C. coccolobae T	1065	RC 11.025	**KX896757**	**KX907624**
C. corallinus T	1083	JJ/MO-cant-2	**KX896758**	–
C. corallinus	1086	JJ/MO-cant-5	–	**KX896776**
C. deceptivus T	1074	JJ/WI-cant-1	**KX896761**	**KX896779**
C. deceptivus	1079	JJ/NC-cant-5	**KX896760**	**KX896778**
C. ferruginascens	–	AH44782	KR677488	KR677526
C. ferruginascens	–	AH44794	KR67785	KR677523
C. flavolateritius	1076	JJ NC cant-2	**KX896766**	**KX896783**
C. flavus	–	CH5	JX030457	JX030430
C. flavus	–	C068	JX030468	JX030436
C. formosus	–	OSC 76054	DQ898686	AY041165
C. formosus	–	DAOM220712	KR677515	KR677553
C. friesii	–	AH44798	KR677484	KR677522
C. friesii	–	ARANA3020106B	KR677483	KR677521
C. iuventateviridis T	1309	BPL 523	**KX896762**	**KX896780**
C. lateritius	332	BB 07.062	**KX896767**	**KX896784**
C. lewisii T	314	BB 07.003	JN944021	JN940597
C. minor	313	BB 07.002	–	**KX907625**
C. minor	329	BB 07.057	–	**KX907626**
C. pallens	–	AH44799	KR677499	KR677537
C. pallens	–	BIO11150	KR677494	KR677532
C. persicinus	1085	JJ MO-cant-4	**KX896775**	**KX896790**
C. persicinus	1685	MH15.001	–	**KX896791**
C. phasmatis	–	C076	JX030466	JX030425
C. phasmatis	–	C057	JX030464	JX030431
C. luteostipitatus T	1044	BB 11.044	JQ976947	JQ976978
C. pseudoformosus	–	SMR-2009a	HM776721	GU237071
C. quercophilus T	636	BB 07.097	–	KF294644
C. romagnesianus	–	AH44788	**KX828784**	**KX828807**
C. roseocanus	–	DAOM220723	**KX828787**	**KX828810**
C. septentrionalis T	–	Smith67052 (MICH)	**KX896768**	**KX896785**
C. sp.(aff. *versicolor*)	–	C117	LC085386	LC085419
C. sp.(aff. *versicolor*)	–	C106	LC085384	LC085418
C. spectaculus T	–	C081	–	JX030421
C. subalbidus	1196	BB 13.014	**KX896764**	**KX896781**
C. subalbidus	1197	BB 13.014b	**KX896765**	**KX896782**
C. tabernensis	323	BB 07.040	JN944013	JN940609
C. tabernensis	325	BB 07.042	JN944014	JN940596
C. tabernensis	333	BB 07.064	JN944012	JN940608
C. tenuithrix T	343	BB 07.125	JN944017	JN940600
C. texensis T	317	BB 07.018	JN944016	KF294626
C. velutinus T	1321	BB 14.038	**KX896774**	**KX896789**
C. velutinus	1326	BB 14.045	**KX896763**	–

(marked * in Fig. 1). A maximum likelihood (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 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) and consisted in two independent runs to ensure stationary and convergence to the same log-likelyhood level. We sampled one of 100 trees during 15M generations and the last 75 001 trees sampled from each run were used to build the majority-rule consensus tree. Branch support was considered significant when Bayesian posterior probabilities (BPP) were ≥ 0.95.

RESULTS

Phylogeny

The full alignment included 1400 characters (1-110 5.8S; 111-553 ITS2; 554-1400 LSU), after exclusion of ambiguous regions. The most likely tree inferred by ML analysis of the *TEF*-1 dataset (-lnL = 4837.525749) exhibited a quite similar supported topology as the Bayesian majority-rule consensus tree shown in Figure 1. Standard deviation of split frequencies was 0.0052 when the Bayesian analysis finished.

Basal nodes within *Cantharellus* subg. *Cantharellus* lack support, but a few groups of species are encompassed on supported clades. The core clade corresponding to *C.* sect. *Cantharellus* is supported (MLbs = 96%, BPP = 1), and encompasses *C. cascadensis*, *C. cibarius*, *C. flavus*, *C. pallens*, *C. phasmatis*, *C. roseocanus*, *C. subalbidus* and *C. tenuithrix*. *Cantharellus persicinus* is in another supported clade in the ML analysis (MLbs = 92%) together with *C. amethysteus, C. lewisii* and *C. pseudoformosus*. The type of *C. camphoratus* nests in a supported clade in the ML analysis (MLbs = 81%), together with *C. formosus* and an undescribed species from Japan, and appears distinct from both. The type of *C. septentrionalis* clusters in the *C. altipes* clade (MLbs = 99%, BPP = 1) which does not show affinity to any other clade within *C.* subg. *Cantharellus*. Most terminal nodes corresponding to species are supported in the ML analysis, but less so in the Bayesian analysis. Nevertheless, within sect. *Cantharellus*, *C. flavus* and *C. roseocanus* did not receive support from either analysis. Branches are considerably longer in *C.* subg. *Cinnabarinus* and subg. *Parvocantharellus*, and their species have in general more divergent sequences among each other.

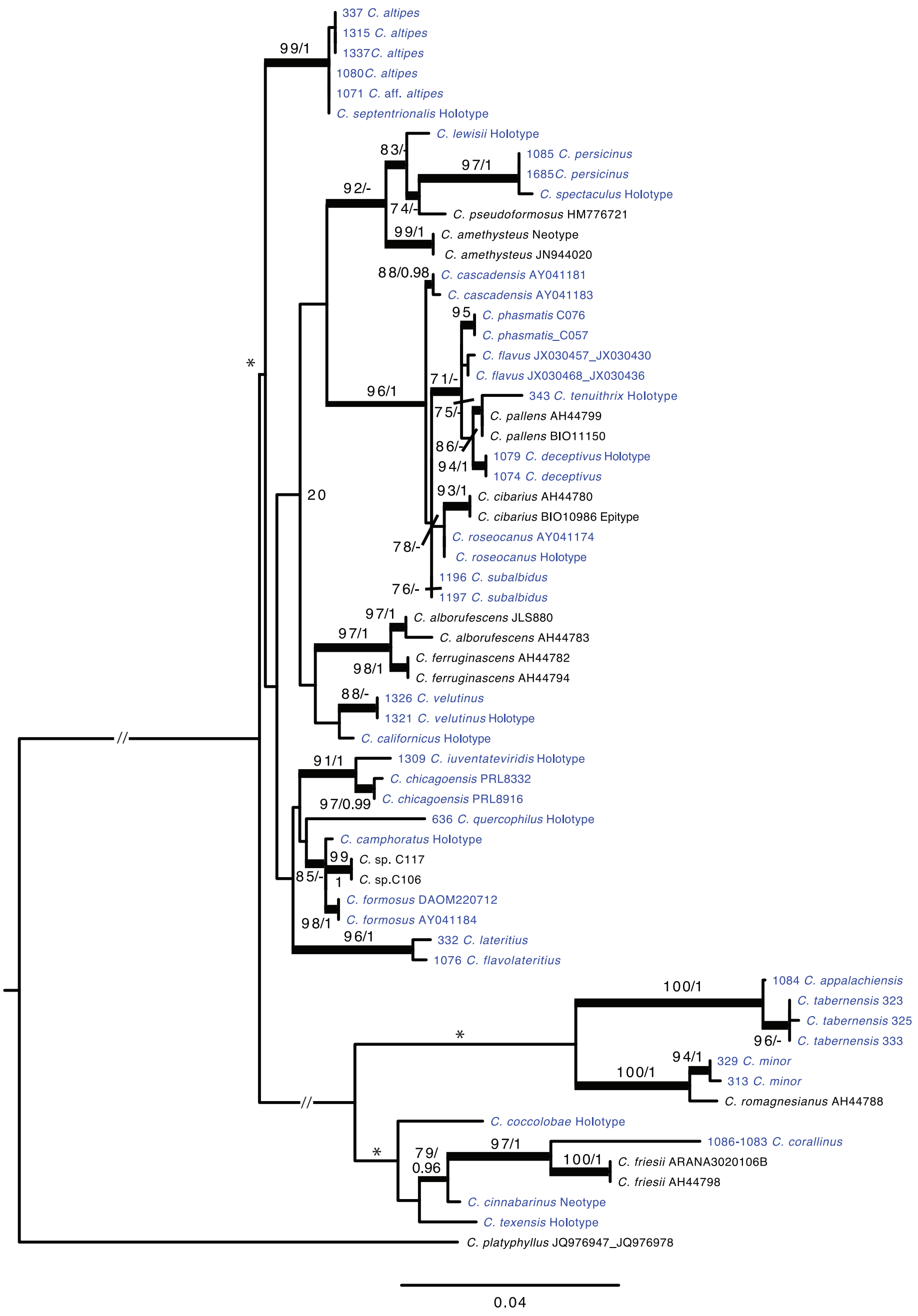


Fig. 1. Most likely tree from the Maximum Likelihood analysis of the ITS and LSU regions of all known taxa of *Cantharellus* in North America. Sequences from North American specimens are marked in blue. Branches that received BPP ≥ 0.95 or MLbs ≥ 70% are in bold and ML and BPP values are reported along the branches respectively. Asterisks (*) indicate nodes that were implemented as backbone constraints in phylogenetic analyses.

DISCUSSION

Our phylogenetic analyses (Fig. 1) show little problems for the molecular recognition of the various orange-pink-red species in subg. *Cinnabarinus* in spite of their macroscopic similarity. In subg. *Parvocantharellus*, the molecular recognition of *C. minor* poses no problem as sole American species in a subclade that comprises the European *C. romagnesianus* (see Olariaga *et al*. 2015, 2016) and several Asian chanterelles of strongly reduced size (Das *et al.* 2015). However, unpublished sequence data (Buyck unpubl.) suggest that the situation in North America is more complex, comprising one or more undescribed relatives of *C. minor*. The same observation applies to the already closely related sister-pair *C. tabernensis*-*C. appalachiensis* for which preliminary analyses also indicate a more complex situation in North America (Buyck unpubl.).

In subg. *Cantharellus* (the third and only other subgenus represented in North America out of the six presently recognized subgenera worldwide), our analyses suggests the existence of several distinct subclades although not all obtain significant support (Fig. 1). The well-supported core clade (MLbs = 96%, BPP = 1) comprises the European *C. cibarius* and *C. pallens.* It is the most species-rich subclade in North America with seven closely related, described taxa, two of which have still a strictly western distribution (*C. subalbidus* and *C. cascadensis*). Within this core clade, the *C. tenuithrix* complex receives significant support (MLbs = 71%), but it is composed of very closely related species (see Buyck *et al*. 2016c, this issue), e.g. *C. flavus* is here not significantly supported. Our ITS-LSU analyses might have better discriminated species in *C*. sect. *Cantharellus* if the regions, that were here excluded because they are not alignable with species in *C.* subg. *Cinnabarinus* and *C.* subg. *Parvocantharellus*, would have been included. Yet, an analysis based on a more comprehensive sampling in the case of the *C. tenuithrix* complex might again annihilate this effect for the concerned species as existing differences merely represent a few base pairs in the whole alignment.

A second well-supported subclade (MLbs = 92%) is composed of the species belonging in sect. *Amethystini* Buyck & V. Hofstetter, represented in North America by *C. lewisii* and *C. persicinus* (= *C. spectaculus*). Together with *C*. sect. *Sublaeves* Buyck & V. Hofstetter, in North America represented by the monophyletic (MLbs = 96%, BPP = 1) *C. lateritius* and *C. flavolateritius*, this section comprises known tropical representatives, contrary to *C*. sect. *Cantharellus* (see Buyck *et al*. 2014).

Our analysis places *C. camphoratus* for the first time in a genus phylogeny. *Cantharellus camphoratu*s was described in much detail by its author (Petersen 1979) as a chanterelle that looks somehow like the European *C. cibarius*, but was reported to differ most notably from all other known chanterelles in its unique odor reminiscent of the smell of *Lactarius camphoratus*. Since then, existing identication keys for North American *Cantharellus* (Eyssartier 2001, Kuo 2015) overemphasize this unusual smell as main distinguishing character at the expense of other important features (such as spore size). We doubt that the ‘camphoratus’smell is a good feature to identify *C. camphoratus* and it might be due, in our opinion, to the nearby presence of a plant or other fungus that “contaminated” the specimens or the adhering soil with this particular smell.

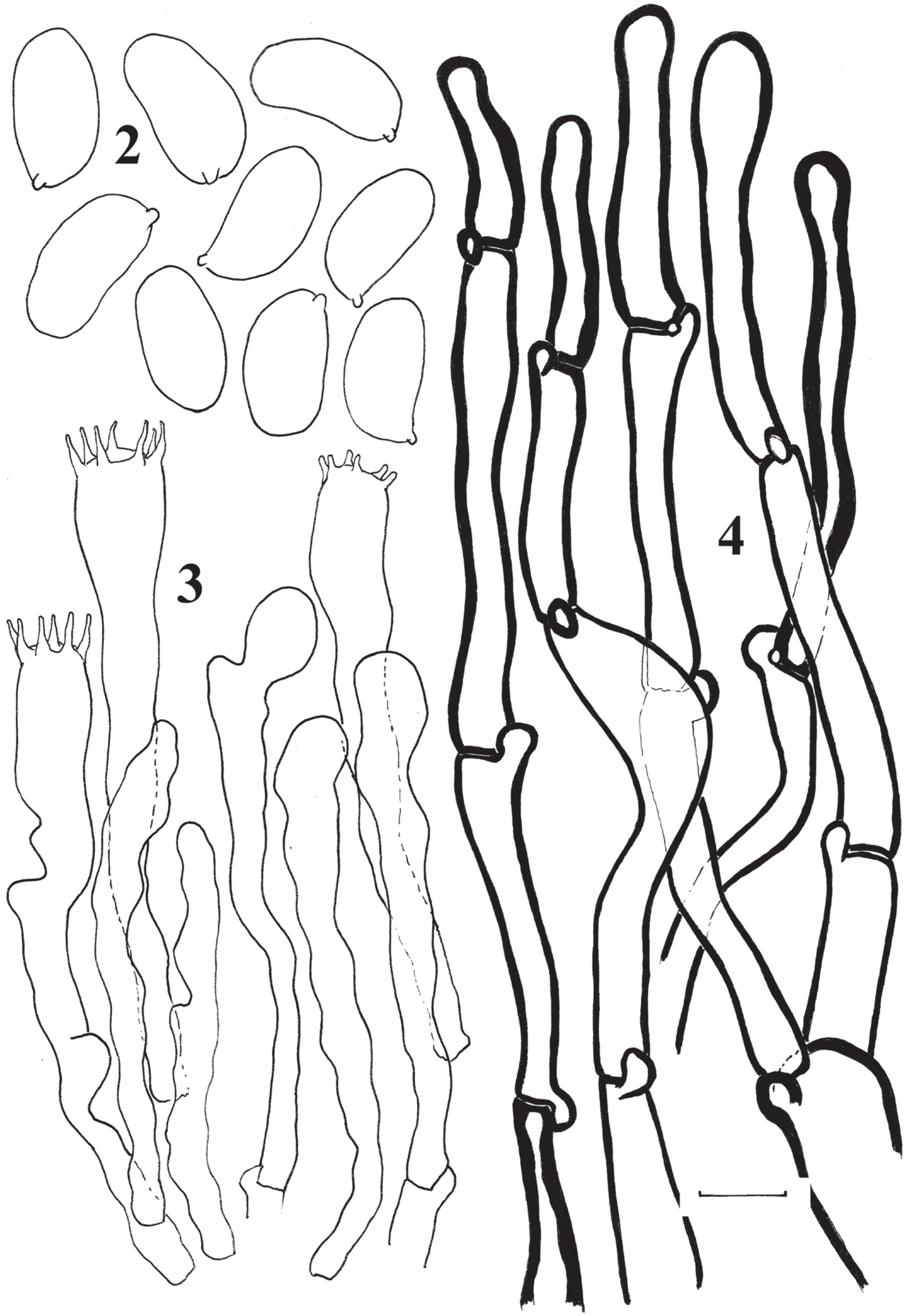
Cantharellus camphoratus, a species originally described from Nova Scotia (Canada), appears to be monophyletic with significant support (MLbs = 85%) with a still undescribed Japanese species that is apparently related to the Chinese *C. versicolor*, and also with *C. formosus*, a chanterelle so far only known from the

Pacific Northwest. This relationship, together with the fact that we never collected *C. camphoratus* in the nearly 15 years that we have been collecting in the more southern states of the United States, suggests a restricted northeastern distribution for *C. camphoratus*, most likely in association with conifers, acting as some kind of eastern counterpart for *C. formosus* which associates with similar host trees in the Pacific Northwest. Both species are principally yellowish to yellowish brown, have often a distinctly squamulose pileus, possess often poorly developed gill folds and have very similar microscopic features (Figs 2-4). Our microscopic analysis confirms the observations made by Petersen (1979) and Eyssartier (2001), viz. quite long, 4-5(6)-spored basidia that are mostly irregularly undulate-sinuate in outline, large spores [(8.5)9.2-*9.78*-10.3(11.0) × (4.6)4.8-*5.15*-5.4(5.8) µm, Q = (1.64)1.77-*1.91*-2.04(2.18)], abundant and very obvious clamp connections in all tissues and distinctly [1(-2) µm] thick-walled hyphal terminations in the pileipellis, 5-10(15) µm diam., with often a rather short or more or less clavate terminal cell, some hyphae with transversal, zebroid incrustations.

Cantharellus altipes, possibly a synonym of *C. septentrionalis*, occupies a surprisingly isolated position within subg. *Cantharellus* (MLbs = 99%, BPP = 1) considering its ordinary field habit. The here suggested possibility of a co-identity between *C. septentrionalis*, described from Michigan, and *C. altipes* Buyck & V. Hofstetter, very common in the states bordering the Gulf Coast, came as a real surprise. Indeed, *C. septentrionalis* was described (Smith 1968) as having a rather short and stout stipe, a convex cap and a strongly yellowing context becoming rapidly orange tan upon handling while producing watery lilac tinges in the upper stipe. These features taken together picture a chanterelle that should be at the opposite of *C. altipes* when it comes to general field habit (see Buyck & Hofstetter 2011). Yet, both the description for *C. altipes* and the one for *C. septentrionalis* refer to a yellowish, quite small species having more or less thick-walled hyphal extremities in the pileipellis and producing large spores [mean values: *9.39* × *5.46* µm. Q = *1.72* for the holotype of *C. septentrionalis* (fide Eyssartier 2001) versus *9.40* × *4.90* µm, Q = *1.87* for *C. altipes*].

The only identification key (Eyssartier 2001) that comprises *C. septentrionalis* has emphasized a single, quite uncommon feature within the genus: the presence of the lilac tinge in the upper stipe, something we never observed in *C. altipes*. In this respect, it is interesting to note that specimen 1071, mentioned as *C. aff. altipes*, is a specimen possessing a clear pinkish hymenium (see fig. 6) and this collection is molecularly distinct from all other specimens, including from the *C. septentrionalis* type. However, these differences – impossible to align together with the species of the other subgenera – have been excluded from our alignment. We assume that the type of *C. septentrionalis* might have been a collection with an untypical field habit for *C. altipes* (compare figs. 5-7), but molecularly they seem to correspond to this species (see fig. 1). *Cantharellus septentrionalis* thus suddenly becomes another example of an eastern species with a very wide distribution (see Buyck *et al.* 2016c, this issue) although being far more common in the southern states as deduced from the absence of additional records for either species (i.e. including *C. altipes*) from more northern states since their original description.

The phylogenetic position of the few remaining species remains unresolved except for the monophyly of the species pair *C. iuventateviridis*-*C. chicagoensis* (MLbs = 91%, BPP = 1). Our analyses suggest, although without support, a close relationship between the Western, oak-associated *C. californicus* and the southeastern *C. velutinus* (see Buyck *et al.* 2016b, this issue). It is for the first time that a possible close relationship with other American chanterelles is suggested for this Californian



Figs 2-4. *Cantharellus camphoratus* (holotype). **2.** Spores. **3.** Basidia and basidiola. **4.** Terminal elements of the pileipellis. Scale bar = 10 µm but 5 µm for spores (drawings B. Buyck).

Fig. 5. Untypical, but molecularly similar collection for *C. altipes* (Jay Justice NC-cant-6) showing specimens with less depressed cap and strongly staining context. (photo Jay Justice)

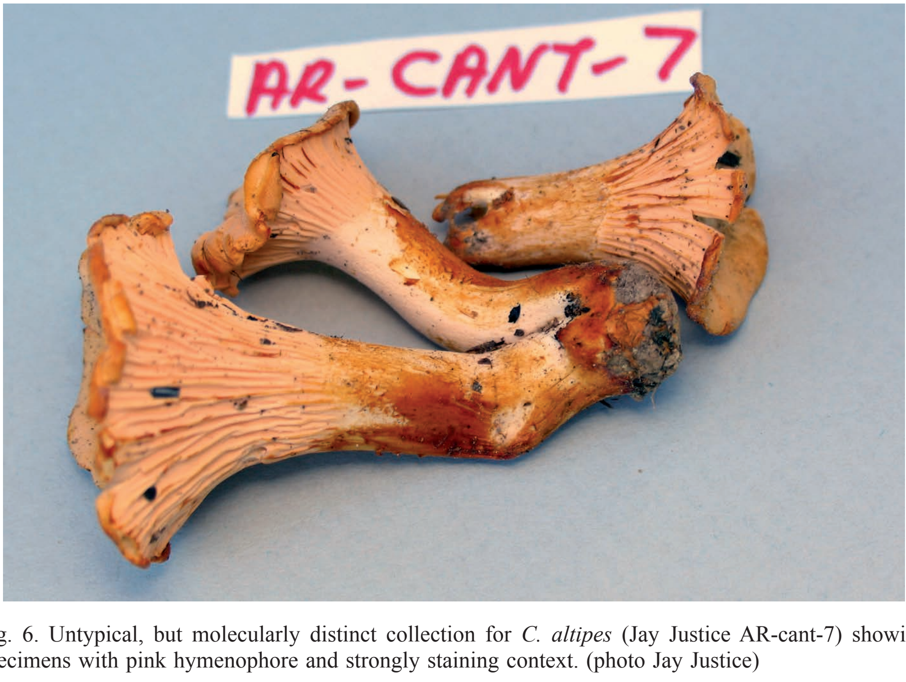


Fig. 6. Untypical, but molecularly distinct collection for *C. altipes* (Jay Justice AR-cant-7) showing specimens with pink hymenophore and strongly staining context. (photo Jay Justice)

Fig. 7. Typical collection of *C. altipes*, showing the long stipe, poorly staining context and depressed pileus. (photo B. Buyck)

species, as the original paper (Arora & Dunham 2008) only compared it to other Western chanterelles. This species pair is again suggested without support to be sister to the well-supported (MLbs = 91%, BPP = 1) European species pair composed of *C. ferruginascens* + *C. alborufescens*. This makes some sense from a morphological point of view as the latter species produces sometimes fruiting bodies that are very reminiscent of *C. californicus*, especially those, more robust, growing under Meditteranean evergreen oaks, previously considered a separate species (*C. ilicis* – see Olariaga *et al*. 2016).

Acknowledgements. We extend our thanks to the Curators of TENN and MICH for providing the type specimen of American chanterelles, thee first author thanks in particular D.P. Lewis and family for travel and accommodation in Texas. Travel to the USA was made possible through several grants to the senior author by the Paris' Museum Pluriformation programm «Etat et structure phylogénétique de la biodiversité actuelle et fossile» (Dir. Ph. Janvier). The U.S. Department of the Interior national Park Service is thanked for delivering a collecting permit for the Big Thicket National Preserve; the Big Thicket Association (Saratoga, TX) is acknowledged for funding the collecting trip to the BTNP. Steve Trudell, the Daniel E. Stuntz Memorial Foundation and M. Berbee (UBC) for inviting me over to the Pacific Northwest, as well as numerous persons for hospitality and help during travel; A. Bazzicaluppo (UBC) is thanked for assisting with collecting and travel. Stephen Harsch (LA) and Mike Hopping (NC) are acknowledged for providing additional collections for *C. iuventateviridis* and *C. persicinus* respectively. Scott Redhead is thanked for sharing his expertise on nomenclatural aspects. The first author would also like to acknowledge the "Service de Systématique Moléculaire"

(USM2700) of the National History Museum of Paris for assistance with sequencing procedures. The curator of DEWV is acknowledged for the loan of specimens. Jay Justice is acknowledged for providing specimens and photographs.

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