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Assessing the taxonomic identity of white and orange specimens of *Cantharellus*: occasional colour variants or independent species?

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Abstract – Species of *Cantharellus* contain carotenoid pigments, which produce yellow, orange and red colours. As microscopic characters are of limited value to separate species, colour has always been an important taxonomic character for species delimitation in *Cantharellus*. Entirely white *Cantharellus* or specimens lacking yellow pigments are occasionally reported from Europe, but it is unclear whether these represent independent species or are simply unusual colour variants of otherwise yellow species. The main objective of this study is to assess the taxonomic identity of such white and orange specimens using molecular data. In the context of an ongoing 4-gene phylogeny of European *Cantharellus*, an ITS2-LSU dataset representing all the European taxa was assembled, including 9 white and 3 orange specimens. Bayesian analyses revealed that white specimens may occasionally occur in *C. amethysteus*, *C. cibarius*, *C. ferruginascens*, *C. pallens* and *C. romagnesianus*, whereas orange specimens are found in *C. cibarius* and *C. pallens*. We therefore associate white specimens with an albinism phenomenon due to a possible absence of carotenoids. Accordingly, the names *C. cibarius* var. *inodorus* and *C. cibarius* f. *pallidus* are neotypified and synonymized with *C. cibarius*, while *C. gallaecicus* is considered a synonym of *C. romagnesianus* based on sequences from a paratype specimen of the former. Likewise, the name *Cantharellus cibarius* var. *salmoneus* is neotypified and falls in synonymy with *C. cibarius*.

Albinism / Barcoding / Cantharelloid clade / Carotenoids / ITS

INTRODUCTION

Cantharellus species, popularly known as chanterelles, are commercially important mushrooms harvested in large quantities around the world (Watling, 1997; Pilz *et al.*, 2003). The economic interest in *Cantharellus* is reflected in extensive

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research on ecology, physiology, cultivation and screening for bactericide compounds for medicinal applications and other aspects (e.g. Cieniecka-Roslonkiewicz *et al.*, 2007; Danell & Camacho, 1997; Danell & Flygh, 2002; Daniewski *et al.*, 2012; Kim *et al.*, 2008; Tibuhwa, 2014), but species delimitation in *Cantharellus* is still controversial. Molecular data has been implemented to achieve a better insight on species diversity in a few studies centered on Africa (Buyck *et al.*, 2012), Madagascar (Buyck *et al.*, 2015) and North America (Buyck *et al.*, 2013; Foltz *et al.,* 2013), but molecular data remain unavailable for most European, Australian and Asian chanterelles. Buyck *et al.* (2013) provided the first worldwide phylogeny of *Cantharellus* and proposed an infrageneric classification based on molecular and morphological characters.

Species of *Cantharellus* show a low variation of microscopic characters. The wall thickness of pileipellis hyphae has been used to define subgenera (Eyssartier & Buyck, 2001), but it is rarely informative to recognize individual species. Spore size can be used to separate a few species pairs (Olariaga, 2009; Buyck *et al.*, 2013), but is highly overlapping for most *Cantharellus*. Mycologists have therefore largely relied on macroscopic characters for species delimitation, such as the presence of a coating on the pileus, the tendency to stain when handled, and especially, the colour of pileus and hymenophore (Eyssartier & Buyck, 2000).

Carotenoid pigments, rarely present in Basidiomycota, are responsible for the yellow, orange and red colours in *Cantharellus* species (Arpin & Fiasson, 1971). The few *Cantharellus* studied for pigments contain a mixture of bicyclic carotenoid pigments, including α-carotene, β-carotene and canthaxanthin (Velíšek & Cejpek, 2011). Canthaxanthin appears to be the main pigment in orange-red-coloured species (Haxo, 1950). Carotenoids intervene in responses to light in some fungi (Carlile, 1970) and their synthesis may thus be influenced by light, as suggested by the fact that unexposed parts of chanterelles exhibit paler colours (Pilz *et al.*, 2003). This phenomenon has been largely overlooked and some taxa have been described solely based on colour differences. Orton (1969), for example, described *C. ferruginascens* P.D. Orton primarily based on a paler pileus and hymenophore as compared to *C. cibarius* Fr: Fr., whereas *Cantharellus cibarius* var. *salmoneus* L. Corb. was characterized as a distinctly more coloured, orange-pink variety (Corbière, 1929). In the absence of additional diagnostic characters, the intraspecific variability of colour remains difficult to evaluate. It is likewise unknown whether each species has a unique and characteristic carotenoid assemblage, or whether differences in colour merely correspond to different proportions of the same assemblage of carotenoids.

The sporadic occurrence of entirely white or orange basidiomata in otherwise yellow *Cantharellus* species is a known phenomenon. White specimens have been named as *Cantharellus pallens* Pilát (Pegler *et al.*, 1997) and *Cantharellus alborufescens* (Malençon) Papetti & S. Alberti (Pérez-De-Gregorio, 2003) or have been attributed to *C. cibarius* var. *pallidus* R. Schulz (Eyssartier & Buyck, 2000) or *Cantharellus* sp. (Roffler, 1999), using the white colour as a diagnostic character. Likewise, *Cantharellus gallaecicus* (Blanco-Dios) Olariaga, very close to *Cantharellus romagnesianus* Eyssart. & Buyck but lacking yellow-orange tones, is treated as an independent species, although both taxa co-exist in the same localities (Blanco-Dios, 2004; Olariaga, 2009). Of interest, few authors have posed the question as to white specimens respond to an albinism phenomenon (Corbiére, 1929; Persson & Mossberg, 1994; Watling & Turnbull, 1998). Likewise, orange specimens of *C. cibarius* are usually attributed to its var. *salmoneus* (Corbiére, 1929; Eyssartier & Buyck, 2000) in Europe, but their taxonomic status has been questioned as orange specimens occur mixed with typical-coloured spots of *Cantharellus cibarius* Fr.: Fr. (Olariaga, 2009).

In order to evaluate the taxonomic identity of white and orange specimens of *Cantharellus*, we utilize molecular characters to infer phylogenetic affinities of white and orange specimens, as part of an ongoing 4-gene phylogeny to resolve species limits of European *Cantharellus* (Olariaga *et al.*, in prep). Molecular data has been used in *Cantharellus* to a lesser extent than in other fungi, probably due to the fact that the ITS region, especially the ITS1, is extremely long (Feibelman *et al.*, 1994) and shows a low amplification success with the general fungal-specific primers (Buyck & Hofstetter, 2011). The ITS2 region and the LSU, albeit offering medium-low molecular support, have been employed when describing new *Cantharellus* (Kumari *et al.*, 2009; Foltz *et al.*, 2003; Shao *et al.*, 2014).

In this study we set the following objectives: i) to evaluate the intraspecific variability of the colour and the taxonomic status of white and orange specimens in European chanterelles, ii) to clarify the interpretation of names described for white and orange-pink taxa by proposing pertinent neotypifications.

MATERIALS AND METHODS

White and orange specimens examined

Cantharellus amethysteus – *White specimens*. Spain: Navarre, Artikutza, Usku, under *Fagus sylvatica* on acidic soil, 29 Sept. 2008, A. Felipe & I. Olariaga, BIO-Fungi 12922; BIO-Fungi 12923. ***Cantharellus cibarius*** – *White specimens*. Spain: Asturias, Nueva de Llanes, under *Betula*, 19 Sept. 2004, E. Fidalgo, BIO-Fungi 12777. Bizkaia, Zeanuri, Jondegorta, under *Fagus sylvatica*, 29 Aug. 2009, J. Fernández, J. R. Undagoitia, F. Hidalgo & M. Oyarzabal, JAFDEZ 2009082904; 3 Aug 2010, J. Fernández, M. Oyarzabal & F. Hidalgo, JAFDEZ 2010080313. Sweden: Södermanland, Lerbo sn, på gränsen mot St. Malm sn, invid torpet Björklunda, in *Picea* forest on sandy ground, 1 Sept. 1958, UPS. United Kingdom: England, Devon, Bovey Tracey, Tradbere Down, on the ground near *Betula*, 3 Oct. 1992, N.W. Legon, K(M)22132 [as *Cantharellus pallens*]. Scotland, Perthshire, Blairgowrie, on soil, 22 Sept. 2008, C. Wegner, K(M)159714 [as *Cantharellus cibarius* var. *albidus*]. *Orange specimens*. Norway, Hedmark, Sølendet, on acidic soil among *Betula nana*, 15 Aug. 2006, K. Hjördis, BIO-Fungi 11714. Spain, Madrid, Navacerrada, "las siete revueltas", *Pinus sylvestris* forest with *Vaccinium myrtillus*, *Pteridium* and mosses, 19 June 2005, J.C. Zamora, BIO-Fungi 12731. ***Cantharellus ferruginascens*** – *White specimens*. Spain: Bizkaia, Barrika, Gainibis, under *Quercus robur*, 15 Sept. 2005, A. Meléndez, BIO-Fungi 11697; 15 Sept. 2006, A. Meléndez & K. Ugartetxe, BIO-Fungi 11700. Asturias, Valbúcar, ruta de los Molinos del Profundo, Villaviciosa, under *Quercus robur*, 18 Aug. 2007, E. Rubio, ERD-4202 (AH). ***Cantharellus gallaecicus*** – *White specimens*. Spain: Cantabria, Lamadrid, under *Castanea sativa* and *Eucalyptus*, 11 July 1998, J.L. Alonso, BIO-Fungi 12298; 14 June 2003, BIO-Fungi 12299. Gipuzkoa, Astigarraga, Santiagomendi, 29 Aug. 1993, ARAN-Fungi 6255 [as *C. cibarius* var. *albidus*]. Pontevedra, Sanxenxo, Nantes, mixed forest with *Pinus pinaster*, 25 Oct. 1997, J.B. Blanco-Dios, LOU-Fungi 18010 [holotype]; 16 Nov. 1997, LOU-Fungi 18012 [paratype]. ***Cantharellus pallens*** – *White specimens*. Spain: Araba, Manurga, under *Quercus faginea*, 24 Oct. 2004, R. Picón, BIO-Fungi 10725. Cantabria, Ucieda, La Jaya Cruza, under *Quercus robur*, J. Fernández & M. Oyarzabal, 19 Aug 2010, JAFDEZ 2010081914; JAFDEZ 2010081915. Girona, Baix Empordà, Sant Cerbrià de Lledó, Cruïlles, under *Quercus* *suber*, M.À. Pérez-De-Gregorio, 3 Oct. 1999, PG031099 (SCM). Girona, Fitos, Solius, M.À. Pérez-De-Gregorio, 1 Nov 1998, PG011198 (SCM). Navarre, Erro, Espinal, under *Fagus sylvatica*, 9 Aug. 2004, J.M. Lekuona, ARAN-Fungi A5019040. Sevilla, Constantina, Carretera del Águila 0.400, under *Eucalyptus* and scattered *Quercus suber* plants, among the leaves, 10 Jan 2011, *J. Mariñas*, AH44800. *Orange specimens*. Spain: Guadalajara, Arroyo de las Fraguas, under *Quercus pyrenaica* and *Erica arborea*, 17 June 2007, L. Rubio Casas, AH44785.

Taxon sampling for the phylogenetic study

Nine white *Cantharellus* specimens, and 3 orange specimens were selected among the material examined. Four of these white specimens have previously been reported in the literature, namely K(M)22132 (Pegler *et al.*, 1997, as *Cantharellus pallens*), PG031099 (Pérez-De-Gregorio 2003, as *Cantharellus alborufescens*), LOU-Fungi 18012 (Blanco-Dios, 2004; isotype of *Cantharellus gallaecicus*), and ERD-4202 (Rubio, 2007; as *Cantharellus ferruginascens*). For comparison with these white and orange specimens, 26 specimens representing all European species were sequenced, as well as a specimen of *Cantharellus formosus* from Canada (Table 1).

Table I. Voucher information and GenBank accession numbers of ITS and LSU sequences of *Cantharellus* used in the phylogenetic analyses. Unusually coloured variants in bold. **W** and **OR** refer to white and orange specimens, respectively

Identification	*Locality*	*Voucher no*	*GenBank no (ITS)*	*GenBank no (LSU)*
C. alborufescens	Spain, Mallorca, Campanet	BIO-Fungi 12025	KR677491	KR677529
C. alborufescens	France, Gard, Frouzet	AH 44783	KR677492	KR677530
C. alborufescens	Spain, Mallorca, Inca	JLS2880 (AH)	KR677493	KR677531
***C. alborufescens* (W)**	Spain, Girona, Baix Empordá	PG031099	KR677496	KR677534
C. altipes	USA	337/07.115 (PC)	JN944018	JN940599
C. amethysteus	Spain, Gipuzkoa, Aia	AH44796	KR677512	KR677550
C. amethysteus	Spain, Navarre, Goizueta	BIO-Fungi 12921	KR677513	KR677551
***C. amethysteus* (W)**	Spain, Navarre, Goizueta	BIO-Fungi 12923	KR677514	KR677552
C. amethysteus	Slovakia	349/07/284 (PC)	JN944020	JN940589
C. cascadensis (holotype)	USA	OSC 75975	AY041183	AY041163
C. cascadensis	USA	OSC 75908	AY041181	AY041160
C. cibarius	Sweden, Uppland, Nåsten	BIO-Fungi 10986	KR677501	KR677539
***C. cibarius* (W)** (neotype of *C. cibarius* var. *inodorus*)	Spain, Asturias, Nueva de Llanes	BIO-Fungi 12777	KR677502	KR677540
C. cibarius	France, Landes, Onesse	BIO-Fungi 10780	KR677503	KR677541
C. cibarius	Spain, Gipuzkoa, Oieleku	BIO-Fungi 12701	KR677504	KR677542
C. cibarius	Switzerland, Valais, Orsieres	BIO-Fungi 12684	KR677505	KR677543
C. cibarius	Spain, Pontevedra, Cangas	AH44779	KR677506	KR677544
C. cibarius	Spain, Madrid, Navacerrada	AH44778	KR677507	KR677545
C. cibarius	Spain, Madrid, Condemos de Abajo	AH44780	KR677508	KR677546
C. cibarius	Slovakia	351/07/300 (PC)	JN944019	JN940598

Identification	*Locality*	*Voucher no*	*GenBank no (ITS)*	*GenBank no (LSU)*
C. cibarius	Sweden	OSC 76031	AY041176	AY041156
C. cibarius	Sweden	OSC 75940	AY041177	AY041157
***C. cibarius* var. *salmoneus* (OR)**	Spain, Guadalajara, Arroyo de las Fraguas	AH44785	KR677500	KR677538
***C. cibarius* var. *salmoneus* (OR)** (neotype)	Norway, Hedmark, Sølende	BIO-Fungi 11714	KR677510	KR677548
***C. cibarius* var. *salmoneus* (OR)**	Spain, Madrid, Navacerrada	BIO-Fungi 12732	KR677511	KR677549
C. cinnabarinus	USA	341/07.120 (PC)	JN944016	JN940601
C. ferruginascens	Spain, Gipuzkoa, Aia	AH44794	KR677485	KR677523
C. ferruginascens	Spain, Gipuzkoa, Aia	BIO-Fungi 12651	KR677487	KR677525
C. ferruginascens	France, Gard, St-Laurent le Minier	AH44782	KR677488	KR677526
***C. ferruginascens* (W)**	Spain, Asturias, Valbúcar	ERD-4202 (AH)	KR677489	KR677527
C. ferruginascens	Spain, Navarre, San Juan Xar	ARAN A50120121	KR677490	KR677528
***C. ferruginascens* (W)**	Spain, Bizkaia, Barrika	BIO-Fungi 11700	KR677486	KR677524
C. flavus	USA	CH5	JX030457	JX030430
C. flavus	USA	C068	JX030468	JX030436
C. formosus	Canada, Vancouver, Kildonan	DAOM 220712	KR677515	KR677553
C. formosus	USA	OSC 76054	AY041184	AY041165
C. friesii	Spain, Gipuzkoa, Oiartzun	ARAN A3020106B	KR677483	KR677521
C. friesii	Spain, Gipuzkoa, Aia	AH44798	AH44798	KR677522
***C. gallaecicus* (W)**	Spain, Cantabria, Lamadrid	BIO-Fungi 12299	KR677478	KR677516
***C. gallaecicus* (W)** (paratype)	Spain, Pontevedra, Lourizán	LOU-Fungi 18012	KR677482	KR677520
C. lewisii	USA	314/07.003 (PC)	JN944021	JN940597
***C. pallens* (W)** (neotype of *C. cibarius* var. *pallidus*)	United Kingdom, Devon, Tradbere Down	K(M)22132	KR677509	KR677547
C. pallens	Spain, Girona, Viladrau	BIO-Fungi 11150	KR677494	KR677532
C. pallens	Sweden, Uppland, Vaksala	BIO-Fungi 10988	KR677495	KR677533
***C. pallens* (W)**	Spain, Navarre, Erro-Espinal	ARAN A5019040	KR677497	KR677535
C. pallens	Spain, Gipuzkoa, Andoain	AH44799	KR677499	KR677537
C. pallens	Spain, Madrid, Canencia	AH44784	KR677498	KR677536
C. phasmatis	USA	C076	JX030466	JX030425
C. phasmatis	USA	CH2	JX030458	JX030428
C. platyphyllus	Tanzania	Tibuhwa 1078.2007	JQ976947	JQ976978
C. pseudoformosus	India	SMR-2009a	HM776721	GU237071
C. romagnesianus	Spain, Gipuzkoa, Bilabona	ARAN A3007090A	KR677479	KR677517
C. romagnesianus	Spain, Gipuzkoa, Usurbil	BIO-Fungi 9933	KR677480	KR677518
C. romagnesianus	Spain, Pontevedra, Cangas	AH44788	KR677481	KR677519
C. roseocanus	USA	OSC 67634	AY041174	AY041154
C. tabernensis	USA	333/07.064 (PC)	JN944012	JN940608
C. tabernensis	USA	325/07.042 (PC)	JN944014	JN940596
C. tabernensis	USA	323/07.040 (PC)	JN944013	JN940609

DNA extraction, PCR amplification and sequencing

DNA was extracted from dried material or from fresh material stored in 1% SDS extraction buffer. The extraction method follows Hansen *et al.* (1999). Material was ground in eppendorf tubes using a plastic pestle and after adding a few sand particles. For material stored in SDS buffer, the 5.8S-ITS2-LSU regions were amplified in one piece using the primers ITS3C-LR5 (Vilgalys & Hester, 1990; Tibuhwa *et al.*, 2012). When extracting dried material, the 5.8S-ITS2 and LSU regions were amplified separately using primers ITS3C-ITS4 (White *et al.*, 1990) and LR0R-LR5 (Vilgalys & Hester, 1990), respectively. In a few cases in which the LSU failed to amplify primers LR0R-LR3 and LR3R-LR5 were employed. PCR products were purified using ExoSAP-IT® (USB, Cleveland, OH, USA). The amplicons were sequenced in both directions.

Sequences were edited and assembled using Sequencher 4.1.4 (Gene Codes Corporation Ann Arbor, Michigan, USA) and were deposited in GenBank. The alignment was done with MAFFT v6.864b under the anysymbol option (Katoh *et al.*, 2005) and was optimized manually in MacClade (Maddison & Maddison 2003).

Phylogenetic analyses

Specimens for phylogenetic analyses were selected based on a more inclusive 4-gene phylogeny and representing the whole diversity of European *Cantharellus* (Olariaga *et al.*, in prep.) (Table 1). *Cantharellus platyphyllus* (JQ976947-JQ976978) was selected as outgroup, based on the multigene phylogeny by Buyck *et al.* (2013). The dataset was analyzed employing a Bayesian approach and analyzed using Metropolis-coupled Markov Chain Monte Carlo (MCMCMC) in MrBayes v.3.2.1 (Ronquist *et al.*, 2012). Data were divided into 3 partitions: 5.8S, ITS2 and LSU. Ambiguous regions were excluded manually. The substitution model was sampled across the GTR space by the MCMC analysis. Two parallel analyses of four MCMC chains were run for 10M generations, starting from a random tree, sampling a tree every 100^{th} generation. To check if the chains had converged, to determine if the mixing was adequate and to choose an appropriate burnin, log-likelihood values were plotted against the time generation using Tracer v. 1.5 (Rambaut & Drummond, 2007). Stationarity was assumed when average standard deviation of split frequencies fell below 0.01. A burnin sample of 25000 trees was discarded from each run. To assess branch confidence, a 50% majority rule consensus tree was computed with the remaining 150000 trees using the sumt command of MrBayes. Bayesian PP values ≥ 95% were considered to be significant.

RESULTS

Macromorphological observations on white and orange gatherings

White and orange specimens occurred in groups of several basidiomata and grew exposed to sunlight. White specimens were collected in the immediate vicinity of typical basidiomata of *C. amethysteus* (BIO-Fungi 12923), *C. cibarius* (BIO-Fungi 12777), *C. ferruginascens* (BIO-Fungi 12700), and *C. pallens* (ARAN-Fungi

Fig. 1. White specimens of *Cantharellus*. **a.** White specimen with pink coating on the pileus (BIO-Fungi 12923) growing near typical *Cantharellus amethysteus*. **b.** Typical specimen of *C. amethysteus* (BIO-Fungi 12921), collected near white white specimens in fig. 1a. **c.** White specimen with pink coating on the pileus (BIO-Fungi 11700) growing near typical *Cantharellus ferruginascens* basidiomata. **d.** White specimen (BIO-Fungi 12777) growing near typical *Cantharellus cibarius* basidiomata. **e.** White specimen (on the left side, JAFDEZ 2001008914) growing near typical *Cantharellus pallens*. **f.** Typical specimen of *Cantharellus gallaecicus* (BIO-Fungi 12299). Photos: A. Meléndez (c), E. Fidalgo (d), J. Fernández (e), J.L. Alonso (f).

A5019040). *Cantharellus romagnesianus* has also been reported in the same locality where one of the specimens of *C. gallaecicus* (LOU-Fungi 18012) was collected (Blanco-Dios, 2004). White specimens had a pure white to pale flesh-coloured pileus and they strongly stained reddish brown when bruised on the stipe and pileus margin (Fig. 1). In two putative white specimens of *C. amethysteus* (BIO-Fungi 12923) and *C. ferruginascens* (BIO-Fungi 11700), a conspicuous lilac-pink coating was present (Fig. 1) on the pileus, over a white background colour. *Cantharellus gallaecicus* specimens showed a pale brown coating instead. Orange-coloured basidiomata,

Fig. 2. Orange specimens of *Cantharellus*. **a.** Orange specimen (BIO-Fungi 11714) growing near typical *Cantharellus cibarius*. **b.** Orange specimen (BIO-Fungi 12731) growing near typical *C. cibarius*. **c.** Comparison between a typical basidioma of *C. cibarius* (on the left, BIO-Fungi 12732) and an orange basidioma of *C. cibarius* (on the right, BIO-Fungi 12731). **d.** Orange specimen (AH44785) growing near typical *Cantharellus pallens*. Photos: J. C. Zamora (b, c), L. Rubio Casas (d).

devoid of yellow tones, were found in the neighbourhood of normal-coloured *C. cibarius* and *C. pallens* and varied markedly in comparison with typical basidiomata of *C. cibarius* and *C. pallens* (Fig. 2).

Phylogenetic analyses

Thirty eight 5.8S-ITS2-LSU sequences were generated in this study (Table 1) and were aligned with 20 sequences downloaded from GenBank. The nucleotide alignment, excluding ambiguous regions, consisted of 1058 characters. The 50% majority rule consensus tree obtained from the analysis is showed in Fig. 3. Regarding European species, well-supported clades were obtained for all species but *C. cibarius*, *C. pallens* and *C. ferruginascens*. All the clades of European species accepted here are strongly supported in our forthcoming 4-gene phylogeny (Olariaga *et al.*, in prep.).

Albino specimens previously attributed to *C. amethysteus* (BIO 12923), *C. cibarius* (BIO 12777), *C. ferruginascens* (ERD-4202, BIO 11700) and *C. pallens* (ARAN A5019040) were part of these respective clades together with normal coloured yellow specimens. Specimen K(M) 22132, published by Pegler *et al.* (1997) as *C. pallens*, is in the *C. cibarius* clade, whereas PG031099, published as *C. alborufescens* (Pérez-De-Gregorio, 2003), nests in the *C. pallens* clade. The *C. romagnesianus* clade encompasses all the specimens that had been identified as

C. gallaecicus, including a paratype specimen of this taxon (LOU-Fungi 18012). Orange specimens identified as *Cantharellus cibarius* var. *salmoneus* nest in both the *C. cibarius* clade (BIO-Fungi 11714, BIO-Fungi 12731) and *C. pallens* clade (AH44785).

DISCUSSION

Colour variants in Cantharellus

We demonstrate here that white specimens have been erroneously assigned to species names that explicitly refer to pale taxa, such as *C. pallens* (Pegler *et al.*, 1997) or *C. alborufescens* (Pérez-De-Gregorio, 2003). We also show here that white colour variants exist within several European species of *Cantharellus*, viz. in *C. amethysteus*, *C. cibarius*, *C. ferruginascens*, *C. pallens* and *C. romagnesianus*, therefore suggesting that white specimens correspond to a phenomenon of albinism, a rarely accepted view (Rangel-Castro *et al.*, 2002). Albino *Cantharellus* are probably devoid of carotenoid pigments. Regrettably, our efforts to investigate the presence and composition of carotenoids in dried albino specimens were unsuccessful, as carotenoids were degraded during the desiccation process (S. Seoane, pers. comm.).

Adopting the idea that albinism occurs in some European species has taxonomic implications. At least three taxa have been described based on white specimens of *Cantharellus* in Europe: *C. cibarius* var. *inodorus* Velen., *C. cibarius* f. *pallidus* R. Schulz and *C. gallaecicus* Blanco-Dios. The former was described as a taxon reminiscent of *C. cibarius* in shape and size, but being entirely white and staining red when bruised (Velenovský, 1939). In the absence of any original specimen (J. Holec, pers. comm.), we consider *C. cibarius* var. *inodorus* to be an albinistic form of *C. cibarius*, and we thus propose a neotype specimen studied and sequenced by us (BIO-Fungi 12777) corresponding to *C. cibarius*. As for *C. cibarius* f. *pallidus*, it was described as being pale yellow or white (Michaël, 1923), suggesting likewise a phenomenon of albinism. Eyssartier & Buyck (2000) compared this taxon to *C. alborufescens* (Malençon) Papetti & S. Alberti, a strictly Mediterranean species (Malençon & Bertault, 1975; Olariaga *et al.*, in prep.) as confirmed by our analyses (Fig. 3). Rather, we interpret *C. cibarius* f. *pallidus* as an albinistic *C. cibarius*, and we accordingly propose a neotype specimen following this view (K(M)22132). A third name, *C. gallaecicus*, is here reduced to a synonym of *C. romagnesianus*, based on ITS-LSU sequences of paratype material of *C. gallaecicus*. The spore differences between *C. gallaecicus* and *C. romagnesianus* proposed by Olariaga & Salcedo (2007) seem to be an artefact of undersampling as only 4 specimens of *C. gallaecicus* had been measured. A fourth name equally refers to albino specimens of *Cantharellus*: *C. cibarius* var. *albus*, but we were not able to trace its original description. Rea (1922) ascribed *C. cibarius* var. *albus* to "Fr.", but provided no full reference. Subsequently, Corner (1966) provided a full reference in his monograph: "*C. cibarius* var. *albus* Fr., Syst. Mycol. I (1821) 318", but no reference to *C. cibarius* var. *albus* was made on that page, nor was *C. cibarius* var. *albus* cited in the Index of Systema Mycologicum (Fries, 1832). A possible explanation is that *C. cibarius* var. *albus* was mistaken for *C. albidus* Fr.: Fr., described on the next page (Fries, 1821: 319), which has also later been referred to white specimens of *Cantharellus* (Corbière, 1929). The name *C. albidus* has long been applied to *Cantharellopsis*

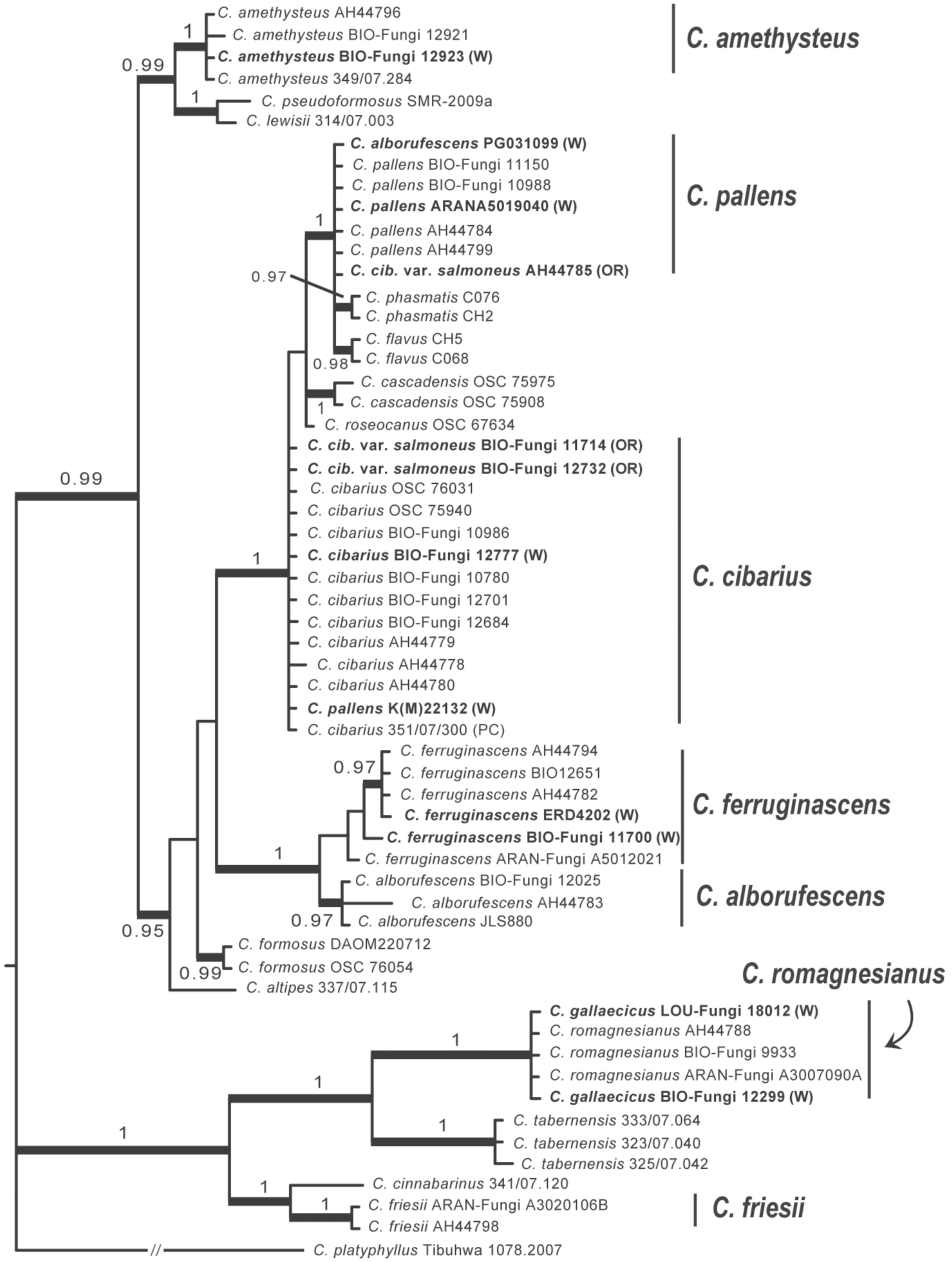

Fig. 3. Bayesian inference 50% majority rule consensus phylogram from 5.8S-ITS2-LSU sequence data in *Cantharellus*. Bayesian Posterior probabilities (≥ 95%) are present by nodes. W and OR refer to white and orange specimens.

prescotii (Weinm.) Kuyper, as pointed out by Redhead (1984). The plate cited by Fries under *Cantharellus albidus* (Hornemann, 1805: tab. 1293) represents in our opinion, an albinistic gathering of a *Craterellus* species, probably *C. lutescens* (Fr.: Fr.) Fr. The thin-fleshed umbilicate pileus, suggesting a hollow stipe, are typical features of species of *Craterellus* Pers.: Fr. Further, a branched stipe producing smaller pilei, as depicted in the plate cited by Fries, is rather often seen in several *Craterellus* species. It is clear from this that much taxonomic and nomenclatural confusion has prevailed with regard to albinistic specimens of *Cantharellus*.

This study shows also that orange colour variants are not uncommon in the *C. cibarius* species complex where they exist in at least two European species (*C. cibarius* and *C. pallens)* and have been described for at least one American species, *Cantharellus tenuithrix* Buyck & V. Hofstetter (Buyck *et al.*, 2011). As with albinistic specimens, these orange basidiomata occur in the immediate vicinity of normal, yellow-coloured basidiomata of *C. cibarius* and *C. pallens* under the same light exposure. This pigmentation pattern might be due to either to the presence of different carotenoids or to different relative amounts of identical carotenoids in different specimens.

This study substantiates the idea that at least some species of *Cantharellus* show high infraspecific variability in basidioma colour (Petersen, 1979; Buyck *et al.*, 2015). We demonstrate that albino specimens in *Cantharellus*, hitherto questioned as distinct taxa, occur in a number of European species, and we predict that albino variants will be discovered in extra-European taxa as well. When molecular approaches are not possible, additional characters such as spore-size (permitting distinction between species in a few cases), presence of an additional coating on the pileus surface (pink to purple in *C. amethysteus* and sometimes also in *C. ferruginascens*) or type of oxidation reaction with $FeSO_4$ crystals can be used to guide the identification of unusual colour variants of chanterelles. Future investigations employing pigment chromatography will contribute to better understand the carotenoid composition changes occurring in albino specimens of *Cantharellus*.

Taxonomic and nomenclatural summary

Cantharellus cibarius Fr., *Syst. Mycol*. 1: 318. 1821: Fr., ídem.
≡ *Cantharellus cibarius* var. *inodorus* Velen., *Nov. Mycol.*: 36. 1939, syn. nov.
Type: Not designated; no original material is known. Neotype (designated here): Spain, Asturias, Nueva de Llanes, under *Betula*, 19 July 2004, E. Fidalgo, BIO-Fungi 12777 (!). MycoBank MBT201370.
≡ *Cantharellus cibarius* f. *pallidus*, R. Schulz in Michaël, *Führ. Pilzfr.* 1: no. 82. 1923, syn. nov.
Type: not designated; no original material is known. Neotype (designated here): United Kingdom, England, Devon, Bovey Tracey, Tradbere Down, on the ground near *Betula*, 3 Oct. 1992, N.W. Legon, K(M)22132 (!). MycoBank MBT201371.
≡ *Cantharellus cibarius* var. *salmoneus* L. Corb., *Mém. Soc. Sci. Nat. Math. Cherbourg* 10: 123. 1929 “1924-1929” , syn. nov.
Type: not designated; no original material is known. Neotype (designated here): Norway, Hedmark, Sølendet, on acidic soil among *Betula nana*, 15 Aug. 2006, H. Lundmark, BIO-Fungi 11714 (!). MycoBank MBT201372.
Missaplied names: *Cantharellus albidus* Fr.: Fr. sensu L. Corb., *Mém. Soc. Sci. Nat. Math. Cherbourg* 10: 123. 1929 “1924-1929”; *Cantharellus pallens* sensu Pegler,

P. Roberts & Spooner, *Brit. Chanterelles Tooth Fung.*: 24. 1997; *Cantharellus* sp. sensu Roffler, *Schweiz. Z. Pilzk.* 77(4): 71. 1999.

Cantharellus pallens Pilát, *Omagiu Traian Săvulescu*: 600. 1959.
Holotype: Czech Republic, Bohemia, Přeštice, in piceto nudo ad terram, 10 Sept. 1957, A. Pilát 655551 (PRM!).
Missaplied name: *Cantharellus alborufescens* sensu Pérez-De-Greg. *Bolet. Catalunya* 22: no 1056. 2003.

Cantharellus romagnesianus Eyssart. & Buyck, *Cryptog. Mycol.* 20(2): 108. 1999.
Holotype: France, Dordogne, environs de Notre Dame de Sanilhac, dans auiguilles de *Pinus pinaster*, 26 Sept. 1974, H. Romagnesi 74.268 (PC0085043) (!).
≡ *Cantharellus cibarius* var. *gallaecicus*, Blanco-Dios, *Bol. Soc. Micol. Madrid* 28: 181. 2004, syn. nov.
≡ *Cantharellus gallaecicus* (Blanco-Dios) Olariaga in Olariaga & Salcedo, *Anales Jard. Bot. Madrid* 64(2): 222. 2007, syn. nov.
Holotype: Spain, Sanxenxo, Nantes, 29TNG1597, 50 m, en bosque de *Pinus pinaster*, 25 Oct 1997, J.B. Blanco-Dios, LOU-Fungi 18010 (!).

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