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Cantharellus (Cantharellales, Basidiomycota) revisited in Europe through a multigene phylogeny

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Abstract Resolving species delimitation issues of European *Cantharellus* is crucial to correctly name chanterelles around the globe. Thirty names referring to *Cantharellus* s. str. have been described in Europe, some of which are used in other continents. Based on combined analyses of ITS2, LSU, *RPB*2 and *TEF*-1, merely eight species are here recognized in Europe applying the genealogical concordance phylogenetic species recognition criteria, one of which, *C. roseofagetorum*, is described as new. Morphological characters used in species delimitation are mapped and their variability evaluated. The colour of the hymenophore in young specimens is found to be a rather constant morphological character of taxonomic use. European species of *Cantharellus* are morphologically distinguished by unique combinations of characters, such as the presence of a pink pileal coating, pileus and hymenophore colour when young, and in some cases, the mean spore length and ecology. Eighteen type specimens from Europe are sequenced. Based on revised species concepts sixteen novel taxonomic synonyms are here proposed for European chanterelles: *C. alborufescens* (= *C. henrici*, *C. ilicis*, *C. lilacinopruinatus*), *C. amethysteus* (= *C. cibarius* subsp. *squamulosus*, *C. cibarius* var. *umbrinus, C. rufipes*), *C. cibarius* (= *C. cibarius* var. *atlanticus*, *C. parviluteus*), *C. ferruginascens* (= *C. cibarius* var. *flavipes*), *C. friesii* (= *C. ignescens*), *C. pallens* (= *C. cibarius* var. *albidus*, *C. cibarius* var. *bicolor*, *C. subpruinosus*), and *C. romagnesianus* (= *C. pseudominimus*, *C. lourizanianus*, *C. romagnesianus* var. *parvisporus*). The type of *Cantharellus*, *C. cibarius,* is epitypified. Descriptions, colour illustrations and a key to all European species are provided.

Keywords Cantharelloid clade · Cantharellaceae · Epitype · Edible fungi · Genealogical concordance · Species delimitation

Introduction

Chanterelles are popularly known and commercialized fungi that belong to the genus *Cantharellus* Adans.: Fr. *Cantharellus*, as circumscribed by early authors (e.g. Fries 1821, 1874; Fuckel 1870; Quélet 1888), comprised an artificial assemblage of species with veined or folded hymenophore, but this initial broad concept was progressively narrowed down (Buyck et al. 2014) to species in the Cantharelloid clade (Moncalvo et al. 2006), with *Cantharellus cibarius* Fr.: Fr. selected as the type species by Earle (1909). The controversial boundary between *Cantharellus* and *Craterellus* Pers.: Fr. (Corner 1966; Petersen 1971), both classified in *Cantharellaceae,* has been resolved with aid of molecular data (Dahlman et al. 2000;

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Moncalvo et al. 2006). Compared to *Craterellus*, *Cantharellus* is featured by having bicyclic carotenoids and, with few exceptions, basidiomata with a solid stipe (Buyck et al. 2014). *Hydnum* L.: Fr. and *Sistotrema confluens* Pers.: Fr. are sister to *Cantharellaceae* in available phylogenies (Moncalvo et al. 2006). Nevertheless, rates of evolution of nuclear ribosomal RNA genes are higher in *Cantharellus* and *Craterellus* than in other members of the Cantharelloid clade and conflicts exist between single-gene genealogies of ribosomal and protein-coding genes (Moncalvo et al. 2006; Olariaga, unpublished data). Thus, more robust protein-coding phylogenies are needed to propose a solid family delimitation in the core of the Cantharelloid clade.

Little attention was drawn to taxonomy of European species of *Cantharellus* until the dawn of the XXth century. A number of new taxa was published scattered (e.g. Quélet 1883; Maire 1937; Pilát 1959), mostly employing basidioma size and colour as diagnostic characters. The staining of basidiomata upon manipulation (Gillet 1878; Malençon and Bertault 1975) and ecological characters (Orton 1969) have occasionally been taken into consideration as well, but microscopic characters were never used as ultimate diagnostic characters when describing new *Cantharellus* taxa in Europe. The first modern monographic treatment of *Cantharellus* was published by Corner (1966) as part of his worldwide monograph of Cantharelloid fungi. This author provided interpretations for all available *Cantharellus* names, albeit without having examined type material in most cases. Among more recent monographic treatments, the one by Romagnesi (1995) deserves attention, since he proposed the wall-thickness of the pileipellis hyphae as novel taxonomic character.

In the context of a worldwide revision of *Cantharellus* species (Eyssartier 2001), Eyssartier and Buyck (2000) published an exhaustive compilation of accepted European taxa. These authors provided modern interpretations for all European taxa granting taxonomic importance to the staining of basidiomata upon manipulation, the presence of pileal coating and the wall-thickness of surface hyphae in the pileipellis. New combinations, typifications and a new species were also proposed. This study stimulated description of new taxa of *Cantharellus* in Europe (Fernández-Sasia et al. 2003; Blanco-Dios 2004, 2011; Hermitte et al. 2005; Olariaga and Salcedo 2008), but considerable confusion has remained on name interpretations and species boundaries. On the one hand, the paucity of discriminant microscopic characters (Buyck et al. 2014), widely used in species delimitation in Agaricomycetes, hinders most *Cantharellus* species from being identified microscopically. One the other hand, most diagnostic characters (pileus and hymenophore colour, staining) are lost after desiccation and this makes identification of dried material practically impossible. Regrettably, many new taxa of *Cantharellus* were published without good colour illustrations and this complicates name interpretations even upon examination of type material. Even when attempting identification of fresh material, species limits are often unclear and knowledge of intraspecific morphological variability is poor. Some of the diagnostic characters used in species delimitation have been stated to vary during basidioma development, such as the pileal coating, colour, the scaliness (Petersen 1979; Redhead et al. 1997; Buyck et al. 2015; Olariaga et al. 2015) or the staining upon manipulation (Olariaga 2009), but molecular data have not been used to assert these assumptions. Large intraspecific variation is probably due to the long-lived nature of *Cantharellus* basidiomata (Largent and Sime 1995; Norvell 1995). Thus, several issues concerning species delimitation and name interpretation remain unaddressed.

In the last decade, molecular tools have increasingly been used to support new species descriptions and existing species concepts. Several new *Cantharellus* species have been described using ITS molecular data (Feibelman et al. 1996; Dettman et al. 2003), but the use of the ITS, universal barcode of fungi (Schoch et al. 2012), is problematic in *Cantharellus*. The ITS1 region is extremely long (Feibelman et al. 1994), its amplification sometimes unsuccessful, and, due to its multicopy nature (Hillis and Dixon 1991), a single basidioma can contain ITS1 copies diverging in up to 3% between each other (Kumari et al. 2011). Moreover, ITS amplification with the general or fungal specific primers (ITS1 or ITS1F with ITS4) often generates multiple bands due to the presence of endophytic fungi (Buyck et al. in prep.). Ribosomal nuclear large subunit (nucLSU) has also been used to support descriptions of new species (Kumari et al. 2011; Shao et al. 2014), but this region has frequently a too low resolution to discriminate between closely related species in *Cantharellus* (Buyck et al. 2011), particularly in subgenus *Cantharellus*. As an alternative, the translation elongation factor 1-alpha (*TEF*-1) region has been shown to provide phylogenetic signal to resolve species limits in *Cantharellus*, and has been employed alone (Buyck and Hofstetter 2011; Buyck et al. 2011, 2015; Ariyawansa et al. 2015; Liu et al. 2015; Shao et al. 2016) or in combination with the ITS2 and nrLSU regions (Foltz et al. 2013) when describing new taxa. Also, Buyck et al. (2014) utilized the RNA polymerase II second largest subunit (*RPB*2) and the rDNA mitochondrial small subunit (mtSSU) regions to propose an updated infrageneric classification of *Cantharellus*.

Olariaga et al. (2015) generated a few ITS-nucLSU sequences to place albino and orange specimens of some European *Cantharellus* but, while molecular data have become increasingly available for *Cantharellus* in other continents, no study has ever evaluated species boundaries of *Cantharellus* in Europe using molecular data. We estimate that 30 names that refer to *Cantharellus* s. str. have been described in Europe (19 specific, 11 infraspecific; homotypic synonyms disregarded) some of which have been applied to extra-European *Cantharellus* (Redhead et al. 1997). The name *Cantharellus cibarius* has been used for species from outside Europe (Eyssartier 2001; Pilz et al. 2003) and is still being reported from other continents (GBIF 2016, see records later than 2010 in Global Biodiversity Information Facility, accessed via http://www.gbif.org/species/5249504) although—or perhaps because of the fact that—European *Cantharellus cibarius* is not molecularly characterized and lacks a type specimen. Chanterelles are often commercialized under incorrect names, also in Europe. Knowledge of ecology and distribution of European species of *Cantharellus* is vague and confusing. Despite the huge quantities of chanterelles being harvested from wild populations, the conservation status of most *Cantharellus* species remains difficult to evaluate due to the lack of more robust, unambiguous species concepts supported by molecular data. Thus, several European *Cantharellus* are being classified as Data Deficient in Conservation status assessments (M. Ainsworth, pers. comm.).

In this framework, we set the following objectives for this study: (i) To elucidate species limits among European *Cantharellus* employing genealogical concordance phylogenetic species recognition (GCPSR); (ii) to evaluate the variability of morphological characters used in species delimitation; (iii) to provide sequences of type specimens in order to correctly interpret names; (iv) to undertake a nomenclatural revision of European *Cantharellus* applying revised species concepts and proposing pertinent typifications.

Materials and methods

Sampling

This study is based on around 300 specimens revised by I. Olariaga and B. Buyck, representing the entire known diversity of *Cantharellus* in Europe. Initial species identifications were mainly based on Olariaga (2009). To obtain an estimate of the genetic diversity among European *Cantharellus*, 117 specimens were DNA-extracted, and the ITS, LSU or *TEF*-1 was sequenced. From these we selected a subset of 53 collections covering the whole phylogenetic diversity, for which the ITS2 and LSU of the nrDNA, the *RPB*2 and the *TEF*-1 regions were sequenced (Table 1). Five more North American specimens were included for comparison to European species. Material examined is deposited in AH, ARAN, BIO, C, DAOM, K, LOU, OSC, PC, PRM, S and UPS herbaria (Thiers 2016). Abbreviations of private herbaria are BB (Bart Buyck, deposited at PC), EC (Emanuele Campo, PC), GE (Guillaume Eyssartier, PC), RFS (Roberto Fernández-Sasia), PG (Miquel À. Pérez-De-Gregorio) and ERD (Enrique Rubio). Fourteen type specimens of names described from Europe and two from North America were examined.

Morphological study

Colour codes are based on Kornerup and Wanscher (1961). Basidiospores were measured in KOH 5%. Young, anomalous or aberrant basidiospores were disregarded, and only well-developed free basidiospores were measured in lateral view. Spore statistics are based on measurements of 25 spores from each collection: L_m = mean length, W_m = mean width and $Q_m = L_m/W_m$. ‘n’ refers to the number of collections on which the statistics are based. Extreme values are given in parentheses. Thickness of pileipellis hyphae was measured in terminal elements using KOH 5% as mounting medium. The notation ‘!’ indicates that a type specimen or other original material was examined by us.

DNA extraction, PCR amplification, sequencing and alignment

DNA was extracted from dried material, or from fresh material stored in 1% SDS DNA extraction buffer. The extraction method follows Hansen et al. (1999), except that the material was ground in eppendorf tubes using a plastic pestle. The regions amplified were part of the 5.8S, the ITS2, and partial nucLSU (spanning domains D1 and D2), RNA polymerase II (*RPB*2, 5–7 region) and *TEF*-1 regions. The 5.8S-ITS2-LSU regions were amplified together from fresh samples, using primers ITS3C (Tibuhwa et al. 2012) and LR5 (Vilgalys and Hester 1990). When samples were desiccated the 5.8S-ITS2 and the LSU were amplified separately using ITS3C-ITS4 (White et al. 1990) and LR0R-LR3 or LR5, respectively. The *RPB*2 region was amplified using the *Cantharellus*-specific primers *RPB*2-5F-Cth2 (5′-GAYGATMGTGATCATTTCGG-3′), *RPB*2-7R-Cth2 (5′-RCCCATAGCAGATTGATAGGTA-3′), *RPB*2-6R-Cth (5′-GGACAGACCATMCCCCAGTG-3′) and *RPB*2-6F-Cth (5′-CACTGGGGKATGGYCTGTCC-3′); for sequencing the internal primers *RPB*2-5F-Cth-int (5′- AAGAAGCGATTGGATCTGGCT-3′) and *RPB*2-7R-Cth-int (5′-ACTYCTTGGTTATGGTCGGGG -3′) were designed. The *TEF*-1 region was amplified in one piece using *TEF*-1Fcanth (Buyck et al. 2014) and *TEF*-1R primers (Morehouse et al. 2003), or in two parts employing *TEF*-1Fcanth-Efjr-Cth (5′-TCGCGRGTCAGACCGTCC TT-3′) and EfdF-Cth (5′-AAGGACGGTCAGACCCGC

Table 1 Sequenced specimens used in this study, with GenBank accession numbers for ITS2, LSU, *RPB*2 and *TEF-1* regions. Type specimens are marked in bold. Numbers in parentheses following the species names indicate multiple collections of a species. The GenBank accessions of sequences generated in this study are in bold. *ET* epitype, *HT* holotype, *IT* isotype, *NT* neotype, *PT* paratype

Taxon	Voucher no.	Country	GenBank accession number			
			ITS2	LSU	*RPB*2	TEF-*1*
***C. afrocibarius* HT**	**496/BB 96.235**	Zambia	–	KF294668	KF294746	JX192993
***C. albidolutescens* HT**	**457/BB 08.070**	Madagascar	–	KF294646	KF294723	JX192982
***C. alborufescens* HT**	**MPU027371**	Morocco	**KX828764**	–	–	–
C. alborufescens (1)	JLS880 (AH)	Spain	KR677493	KR677531	**KX828735**	**KX828816**
C. alborufescens (2)	1108/BB 12.075	Italy	**KX907209**	**KX929161**	**KX907232**	**KX907243**
C. alborufescens (3)	1109/BB 12.076	Italy	–	**KX907222**	**KX907233**	**KX907244**
C. alborufescens (4)	1006/EC 09.91	Italy	–	KM484687	**KX907231**	**KX907242**
C. alborufescens (5)	AH44783	France	KR677492	KR677530	**KX828736**	**KX828817**
C. alborufescens (6)	BIO-Fungi 11687	Spain	**KX828765**	**KX828793**	**KX828737**	**KX828818**
C. alborufescens (7)	BB.12.088	Italy	–	**KX907223**	**KX907234**	**KX907245**
C. alborufescens (8)	BIO-Fungi 12025	Spain	KR67749	KR677529	–	–
C. alborufescens (9)	BIO-Fungi 11691	Spain	**KX828766**	**KX828794**	–	–
C. altipes (1)	337/BB 07.115	USA	JN944018	JN940599	JN993602	–
C. altipes (2) PT	344/BB 07162	USA	–	KF294636	KF294713	GQ914945
***C. amethysteus* NT**	AH44796	Spain	KR677512	KR677550	**KX828738**	**KX828819**
C. amethysteus (1)	994/Estades 10.454	France	**KX907205**	**KX907214**	**KX907226**	**KX907237**
C. amethysteus (2)	349/BB 07.284	Slovakia	JN944020	KF294639	KF294716	GQ914953
C. amethysteus (3)	352/BB 07.309	Slovakia	–	KF294642	KF294719	GQ914954
C. amethysteus (4)	993/Estades 10.453	France	–	**KX907213**	**KX907225**	**KX907236**
C. amethysteus (5)	1003/EC 09.29	Italy	–	**KX907220**	**KX907230**	**KX907241**
***C. californicus* HT**	**OSC 122878**	USA	**KX828768**	**KX828795**	**KX828739**	**KX828820**
***C. cibarius* ET**	**BIO-Fungi 10986**	Sweden	KR677501	KR677539	**KX828742**	**KX828823**
C. cibarius (1)	AH44780	Spain	KR677508	KR677546	**KX828740**	**KX828821**
C. cibarius (2)	BIO-Fungi 10780	France	KR677503	KR677541	**KX828741**	**KX828822**
C. cibarius (3)	AH44778	Spain	**KX828769**	**KX828796**	**KX828743**	**KX828824**
C. cibarius (4)	BIO-Fungi 12684	Switzerland	KR677505	KR677543	**KX828744**	**KX828825**
C. cibarius (5)	479/GE 07.025	France	**KX907204**	KF294658	KF294736	GQ914949
C. cibarius (6)	351/BB 07.300	Slovakia	–	KF294641	KF294718	GQ914950
C. cibarius (7)	BIO-Fungi 10477	Spain	**KX828770**	**KX828797**	–	–
C. cibarius (8)	BIO-Fungi 12701	Spain	KR677504	KR677542	–	–
***C. cibarius* var. *albidus* NT**	**BIO-Fungi 11150**	Spain	KR677494	KR677532	**KX828745**	–
***C. cibarius* var. *atlanticus* HT**	**PC0142164**	France	**KX828771**	**KX828798**	–	–
***C. cibarius* var. *bicolor* NT**	**BIO-Fungi 11230**	Spain	KX853517	–	–	–
***C. cibarius* var. *flavipes* IT**	9312B2 (Mornand herbarium)	France	**KX828772**	–	–	–
***C. cinnabarinus* NT**	**312/BB 07.001**	USA	–	KF294624	KF294698	GQ914985
***C. decolorans* ET**	**469/BB 08.278 (PC)**	Madagascar	**KX907203**	KF294654	KF294731	GQ914968
***C. ferruginascens* HT**	**E00204187**	United Kingdom	**KX828773**	–	–	–
C. ferruginascens (1)	K(M)180009	United Kingdom	**KX828774**	**KX828799**	**KX828746**	–
C. ferruginascens (3)	AH44782	France	KR677488	KR677526	**KX828747**	**KX828826**
C. ferruginascens (2)	AH44794	Spain	KR67785	KR677523	**KX828748**	**KX828827**
C. ferruginascens (4)	AH44795	Spain	**KX828775**	**KX828800**	**KX828749**	**KX828828**
C. ferruginascens (5)	BIO-Fungi 11700	Spain	KR677486	KR677524	**KX828750**	**KX828829**
C. ferruginascens (6)	347/BB 07.221	Slovakia	–	**KX907212**	**KX907224**	**KX907235**
C. ferruginascens (7)	348/BB 07.283	Slovakia	–	KF294638	KF294715	GQ914952
C. ferruginascens (8)	BIO-Fungi 12651	Spain	KR677487	KR677525	–	–

Table 1 continued

Taxon	Voucher no.	Country	GenBank accession number			
			ITS2	LSU	*RPB*2	TEF-*1*
C. ferruginascens (9)	AH44226	Spain	**KX828776**	**KX828801**	–	–
C. flavus	C067_CH5		JX030467		–	JX030416
C. formosus	SAR220712 (DAOM)	Canada	KR677515	KR677553	**KX828751**	**KX828830**
C. friesii (1)	1004/EC 09.43	Italy	–	**KX857084**	**KX856988**	**KX857016**
C. friesii (2)	AH44798	Spain	KR677484	KR677522	**KX828752**	**KX828831**
C. friesii (3)	1001/EC 09.16	Italy	**KX907208**	**KX857083**	–	–
C. friesii (4)	ARAN-Fungi A3020106B	Spain	KR677483	KR677521	–	–
C. friesii (5)	481/GE 07.077	France	–	KF294659	–	–
C. gallaecicus PT	LOU-Fungi 18012	Spain	KR677482	KR677520	–	–
C. henrici **HT**	**PC0142165**	France	**KX828777**	–	–	–
C. ilicis **HT**	**BIO-Fungi 11689**	Spain	**KX828778**	**KX828802**	**KX828753**	**KX828832**
C. lateritius **ET**	**320/BB 07.025**	USA	–	KF294633	KF294708	GQ914959
C. lateritius (1)	332/BB 07.062	USA	KX896767	–	–	–
C. lewisii **HT**	**314/BB 07.003**	USA	JN944021	JN940597	JN993612	GQ914962
C. lewisii	301/BB 02.197	USA	–	KF294623	KF294697	GQ914961
C. lilacinopruinatus **HT**	**PC0734066**	France	**KX828779**	–	–	–
C. lilacinopruinatus PT	PC0734067	France	**KX828767**	–	–	–
C. lourizanianus **HT**	**LOU-Fungi 19494**	Spain	**KX828780**	**KX828803**	–	–
C. minor (1)	313/BB 07.002	USA	–	KF294625	KF294699	JX192978
C. minor (2)	329/BB 07.057	USA	–	KF294632	KF294707	JX192979
C. nigrescens	66/BB 06.176	Madagascar	–	KF294606	KF294680	JX192967
C. pallens **HT**	**PRM655551**	Spain	**KX853516**	–	–	–
C. pallens (1)	AH44799	Spain	KR677499	KR677537	**KX828754**	**KX828833**
C. pallens (2)	AH39124	Morocco	**KX828781**	**KX828804**	**KX828755**	**KX828834**
C. pallens (3)	996/BB 09.409	Italy	**KX929162**	**KX907215**	**KX929160**	**KX857014**
C. pallens (4)	1110/BB 12.077	Italy	**KX907210**	**KX857091**	**KX856995**	**KX857035**
C. pallens (5)	997/BB 09.418	Italy	**KX907206**	**KX907216**	**KX907227**	**KX907238**
C. pallens (6)	998/BB 09.430	Italy	**KX907207**	**KX907217**	**KX907228**	**KX907239**
C. pallens (7)	999/BB 09.441	Italy	–	**KX907218**	**KX907229**	**KX907240**
C. pallens (8)	AH44784	Spain	KR677498	KR677536	**KX828756**	**KX828835**
C. pallens (9)	1115/BB 12.082	Italy	**KX907211**	**KX857092**	**KX856996**	**KX857036**
C. pallens (10)	BIO-Fungi 10988	Sweden	KR677495	KR677533	–	–
C. parviluteus **IT**	**PC0084799**	Spain	**KX828782**	**KX828805**	–	–
C. phasmatis	C057		JX030464	JX030431	–	JX030417
C. platyphyllus **ET**	**262/BB 98.126**	Tanzania	–	KF294620	KF294694	JX192975
C. quercophilus **HT**	**455/BB 07.097**	USA	–	KF294644	KF294721	JX192981
C. romagnesianus **HT**	**PC0085043**	France	**KX828783**	**KX828806**	–	–
C. romagnesianus (1)	AH44218	Spain	**KX828784**	**KX828807**	**KX828757**	**KX828836**
C. romagnesianus (2)	PC0142170	France	**KX828785**	**KX828808**	–	–
C. romagnesianus (3)	477/JV00663	Portugal	–	KF294657	–	–
C. romagnesianus (4)	1002/EC 09.17	Italy	–	**KX907219**	–	–
C. romagnesianus (5)	BIO-Fungi 9933	Spain	KR677480	KR677518	–	–
C. romagnesianus (6)	AH44788	Spain	KR677481	KR677519	–	–
C. romagnesianus var. parvisporus **HT**	**LOU-Fungi 19504**	Spain	**KX828786**	**KX828809**	–	–
C. roseocanus **HT**	**DAOM220723**	Canada	**KX828787**	**KX828810**	**KX828758**	**KX828837**
C. roseocanus (1)	DAOM220724	Canada	**KX828788**	**KX828811**	**KX828759**	**KX828838**

Table 1 continued

Taxon	Voucher no.	Country	GenBank accession number			
			ITS2	LSU	*RPB*2	TEF-*1*
***C. roseofagetorum* HT**	**AH44789**	Georgia	**KX828789**	**KX828812**	**KX828760**	**KX828839**
C. roseofagetorum	AH44786	Georgia	**KX828790**	**KX828813**	**KX828761**	**KX828840**
***C. rufipes* ET**	BIO-Fungi 12921	Spain	KR677513	KR677551	–	–
C. subalbidus	OSC81782	USA	**KX828791**	**KX828814**	**KX828762**	**KX828841**
C. subamethysteus	**488/DS 06.218**	Malaysia	–	KF294664	KF294742	–
C. tabernensis (1)	333/BB 07064	USA	JN944012	JN940608	JN993600	GQ914975
C. tabernensis (2)	323/BB 07040	USA	JN944013	JN940609	JN993599	GQ914977
***C. tenuithrix* HT**	**343/BB 07.125**	USA	JN944017	JN940600	JN993596	–
C. tenuithrix (1)	322/BB 07.035	USA	–	KF294629	KF294704	GQ914946
***C. texensis* HT**	**317/BB 07.018**	USA	–	KF294626	KF294701	GQ914988
***C. tomentosus* HT**	**500/BB 98.060**	Tanzania	–	KF294672	KF294750	JX192995
***C. umbrinus* HT**	**PC0142168**	France	**KX828792**	**KX828815**	**KX828763**	–
Cr. tubaeformis	350/BB 07.293	Slovakia	–	KF294640	KF294717	GQ914989

GAGCA-3′)-*TEF*-1R, respectively. The *Cantharellus*-specific internal *TEF*-1Fint (5′-TCGACAAGCGTACGA TTGAG-3′) and *TEF*-1R-Cth-int (5′-CCAATCTTATAY ACATCCTGGAG-3′) primers were used for sequencing.

PCR amplifications were performed using Illustra™ Hot Start Mix RTG PCR beads (GE Healthcare, UK) in a 25 µL volume. PCR amplification conditions followed Olariaga et al. (2015) for the 5.8S-ITS2-LSU regions, but annealing temperature was lowered to 50 °C and the amount of cycles risen up to 40 when dealing with problematic samples. For amplification of the *RPB*2 and *TEF*-1 regions we followed O'Donnell et al. (2011). PCR products were cleaned using ExoSAP-IT® (USB, Cleveland, OH, USA). Sequencing was performed by the Molecular Biology service of the University of Alcalá and Macrogen (The Netherlands).

Sequences were edited and assembled using Sequencher 4.1.4 (Gene Codes Corporation Ann Arbor, Michigan, USA). Each sequence was subjected to BLAST to verify its identity. Sequences were aligned in AliView (Larsson 2014) and then adjusted manually. Aminoacid sequences were used for aligning protein-coding loci and to manually delimit introns. Indels from the ITS2 region were coded using SeqState (Müller 2005), following the simple coding method by Simmons and Ochoterena (2000). Two datasets were assembled: (a) COMB dataset, containing ITS2-LSU-*RPB*2-*TEF*-1 sequence data and coded indel characters of the ITS2 region, to infer phylogenetic relationships of European and extra European specimens (Fig. 1); and (b) MAP dataset, including ITS-LSU sequence data of only European specimens for character mapping (Fig. 2). Here we included several specimens excluded from the COMB dataset in order not to increase the amount of missing data. Sequences of *Craterellus tubaeformis* and *C. platyphyllus* were set as outgroups for the COMB and MAP datasets, respectively, following Buyck et al. (2014). Introns of the outgroup sequence were not alignable to the ingroup and were thus set as missing data in the COMB dataset.

Phylogenetic analyses

Phylogenetic reconstructions were performed on the COMB dataset employing Bayesian (MB) and Maximum Likelihood (ML) approaches. Dataset congruence was evaluated by comparing supported nodes in single-gene phylogenies (Mason-Gamer and Kellogg 1996). Each locus was subjected to a Maximum Likelihood bootstrap analysis in the Cipres Science Gateway (Miller et al. 2010), employing the "RaxML HPC2 on XSEDE" tool (Stamatakis 2006) and the GTR + CAT approximation of models for bootstraping. To assess branch confidence 1000 non-parametric bootstraps were performed. We considered that there was conflict when a node that was supported (bootstrap support >75%; Hillis and Bull 1993) in a single-gene tree was contradicted with significant support in another tree. Only the placement of *C. decolorans* is in supported conflict. While *C. decolorans* is in a clade with *C. afrocibarius* (ML-BP 94%) in the LSU tree, *C. decolorans* is another clade together with *C. friesii*, *C. texensis* and *C. cinnabarinus* in *RPB*2 intron 1 (ML-BP 78%). All single-gene alignments were concatenated since this

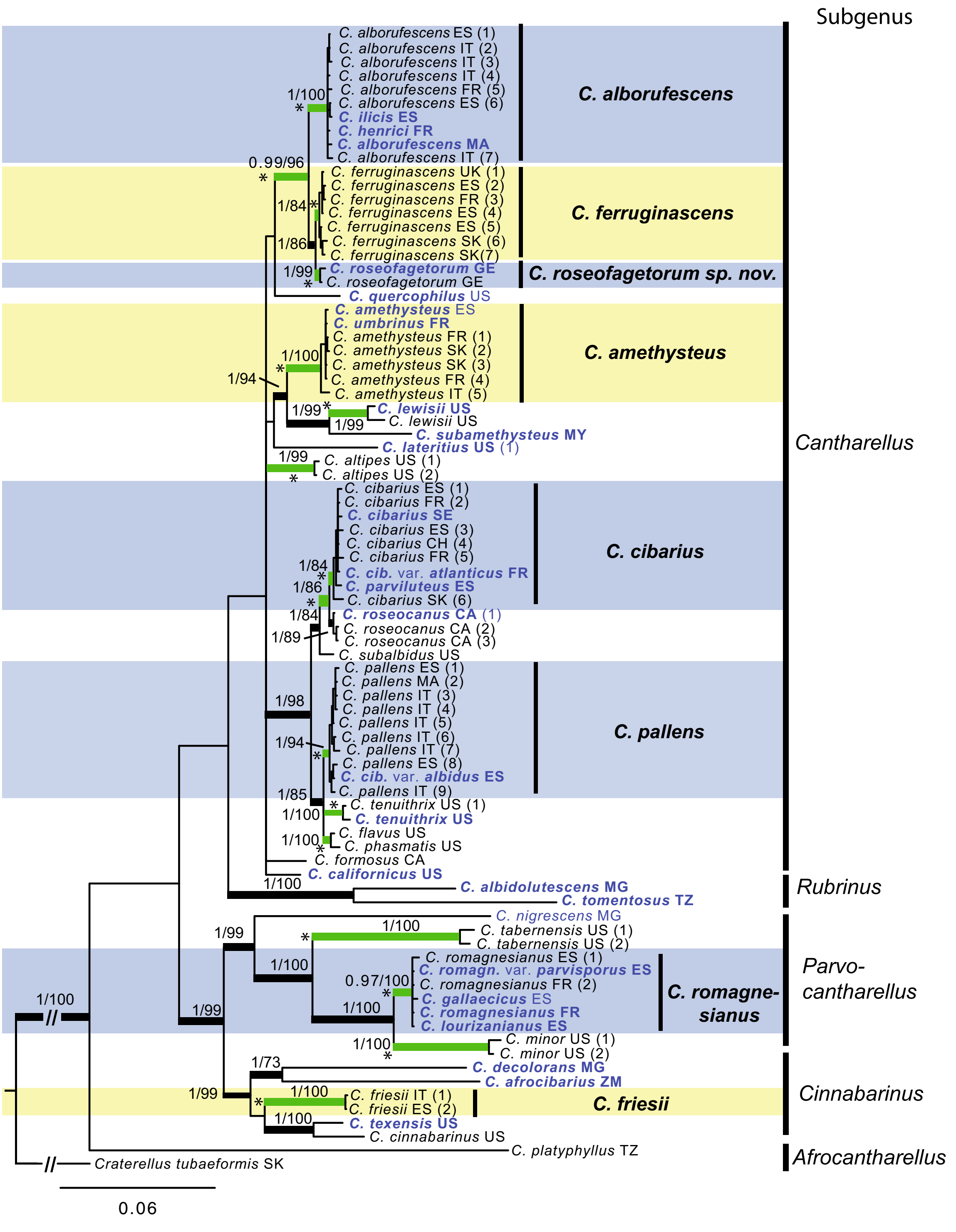

Fig. 1 Bayesian inference 50% majority rule consensus phylogram of *Cantharellus* from ITS2-LSU-*RPB*2-*TEF*-1 sequence data. Bayesian posterior probabilities (PP) ≥0.95/Maximum Likelihood bootstrap values (ML-BP) ≥70% and are shown by nodes, respectively. *Thickened branches* received support by both ML-BP ≥70% and PP ≥95%. *Bold green* branches marked with an *asterisk* represent clades recognized by genealogical concordance phylogenetic species recognition. Type collections are in *blue* and **bold**. Country of origin for each collection is given using two character ISO country codes. Recognized species are indicated by *vertical bars*

conflict does not affect terminal clades corresponding to European species. The binary data subset was included after the nucleotide alignment.

The alignment was split into 13 partitions: 5.8S, ITS2, LSU, *RPB*2, *RPB*2intron1, *RPB*2intron2, *TEF*-1, *TEF*-intron1, *TEF*-intron2, *TEF*-intron3, *TEF*-intron4 and indels.

Fig. 2 Selected morphological characters and possible ectomycorrhizal host mapped on the best Maximum Likelihood tree inferred from the ITS-LSU sequence data. Type collections are highlighted in *bold*. Country of origin for each collection is given using ISO country codes

The MB inference was conducted using Metropolis-coupled Markov Chain Monte Carlo (MCMCMC), as implemented in MrBayes v.3.2.1 (Ronquist et al. 2012). The substitution model was sampled across the GTR space by the MCMC analysis in the nucleotide partitions. The model F81 was used for the binary data partition. Two analyses with four chains were run for 30M generations, starting from a random initial tree. The chains were sampled every

100 generations from the posterior distribution. Stationarity was assumed when average standard deviation of split frequencies fell below 0.01. We further evaluated chain mixing and convergence with Tracer 1.5 (Rambaut et al. 2013). Effective sample size (ESS) values above 200 were considered as indications of optimal convergence. Burnin was set at 50%, and posterior probabilities (PP) were calculated from the remaining 200 002 trees using the sumt command of MrBayes, estimating a 50% majority rule consensus tree. ML analysis was carried out as explained above, with data partitioned as above.

Character coding and mapping

The MAP dataset was subjected to a Maximum Likelihood analysis as specified above. The following characters were put on the tree with highest likelihood score: (1) Young pileus colour, (2) Coating, (3) Colour of young hymenophore, (4) Staining, (5) Ectomycorrhizal partner.

Young pileus colour was coded by observing young basidiomata, or the pileus margin of older basidiomata. Four states were differentiated: (a) Entirely bright orange-yellow, (b) entirely or partially white, (c) citrine yellow to pale ochre-yellow and (d) reddish orange. The presence of coating was also assessed in young basidiomata. Two states were distinguished: (a) At least partially pink or violet and (b) absent. The colour of the hymenophore was evaluated by observing young basidiomata, or the margin of older basidiomata. Five states were specified: (a) Ochre-white to pale ochre, (b) ochre-yellow to orange-yellow, uniform, (c) ochre-yellow to orange-yellow, brighter in the margin, (d) purplish grey to purple and (e) pinkish orange to ochre-orange. The staining was checked in young basidiomata, looking at the change colour of the stipe on bruising. Three states were defined: (a) Not staining, (b) slowly yellow, (c) yellow and rapidly reddish brown. As for the ectomycorrhizal partner, three states were coded: (a) Evergreen Mediterranean *Quercus*, (b) deciduous angiosperms and (c) gymnosperms.

Phylogenetic species recognition by genealogical concordance

We employed genealogical concordance phylogenetic species recognition (GCPSR: Taylor et al. 2000) to assess species limits. Based on Dettman et al. (2003), a clade was recognized as independent evolutionary lineage if, (i) the clade was present and not contradicted in any other single-locus phylogeny, regardless of levels of support, and (ii) the clade was supported as monophyletic in at least one single-locus MB or ML phylogeny (PP $\geq$95% or ML-BP $\geq$70%), and was not contradicted in any other single-locus genealogy at the same level of support. Clades detected as independent evolutionary lineages are marked as bold green branches in Fig. 1.

To determine which independent evolutionary lineages correspond to phylogenetic species, characteristics of lineages in the combined analyses were also considered. Two criteria were followed: (1) To prevent minor tip clades from being recognized, phylogenetic species had to be relatively distinct and well differentiated from other species, and (2) All individuals had to be placed within a phylogenetic species.

Results

Nucleotide sequences

A total of 165 new sequences were generated in this study (41 ITS2, 39 LSU, 44 *RPB*2, 41 *TEF*-1), and were aligned with additional sequences downloaded from GenBank (Table 1). The concatenated COMB matrix comprised 3614 non-ambiguously aligned characters (98 5.8S, 455 ITS2, 906 LSU, 1105 *RPB*2, 875 *TEF*-1, 175 indels) and 83 collections. Of these, 12 collections lack *RPB*2 region and 15 lack *TEF*-1 sequences (Table 1). Sequences of four markers were successfully obtained from 79.5% of the collections.

Spliceosomal intron positions were determined by detecting the conserved dinucleotides (GT-AG) at the intron ends when comparing sequences. Two introns were detected in the *RPB*2, at both ends of the sequenced 5–7 region, the length of which is 67 and ca. 55 nucleotides (not optimally readable in our chromatograms) when aligned, respectively. Four introns are placed throughout the *TEF*-1 region, with length of 70, 74, 66 and 77 nucleotides when aligned.

Genealogical concordance phylogenetic species recognition

The MB and ML analyses recovered trees with a similar topology and no supported conflict. Based on the GCPSR criteria specified above 14 species are recognized here (Fig. 1), eight of which are European and show low sequence divergence and high support values, namely *C. alborufescens* (PP 1, ML-BP 100%), *C. ferruginascens* (PP 0.99, ML-BP 96%), *C. roseofagetorum* (PP 1, ML-BP 99%), *C. amethysteus* (PP 1, ML-BP 100%), *C. cibarius* (PP 1, ML-BP 86%), *C. pallens* (PP 1, ML-BP 98%), *C. romagnesianus* (PP 0.97, ML-BP 100%) and *C. friesii* (PP 1, ML-BP 100%) clades. Two of these clades recognized by GCPSR criteria, *C. ferruginascens* and *C. pallens*, show internal phylogenetic structure. We collapsed the subgroupings within these species as the branches were short and did not correlate to morphological characters. The North American *Cantharellus altipes*, *C. flavus-phasmatis*, *C. lewisii*, *C. minor*, *C. tabernensis* and *C. tenuithrix* are also recognized applying GCPSR criteria. *Cantharellus roseocanus* is supported in the multigene phylogeny, but not recognized by GCPSR criteria (PP 1, ML-BP 89%).

Sequences of 21 type specimens were generated (Table 1; Fig. 1), 18 of which are European. Based on GCPSR, *C. alborufescens*, *C. henrici*, *C. ilicis* are synonyms. In addition, the ITS2 sequence of the type of *C. lilacinopruinatus* is identical to the one of those three, suggesting also synonymy. Sequences from the holotypes of *C. cibarius* var. *umbrinus* and *C. parviluteus* cluster in the *C. amethysteus* and *C. cibarius* clades, respectively. The *C. ferruginascens* and *C. pallens* clades encompass sequences of their respective type specimens. ITS2 sequences of the types of *C. cibarius* var. *flavipes* and *C. ferruginascens* are identical. *Cantharellus lourizanianus, C. romagnesianus* and *C. romagnesianus* var. *parvisporus* are conspecific according to GCPSR criteria. *Cantharellus roseofagetorum* is identified as a new species. Except for the *C. alborufescens*-*C. ferruginascens*-*C. roseofagetorum* clade (PP 0.99, ML-BP 96%), exclusively composed of European specimens, all European taxa form strongly supported clades together with North American taxa.

Infrageneric classification, morphological characterization of clades and species delimitation

Six of the European clades are nested in *Cantharellus* subg. *Cantharellus*, characterized by thick-walled pileipellis hyphae, while *C. friesii* and *C. romagnesianus* are in *Cantharellus* subg. *Cinnabarinus* and *C.* subg. *Parvocantharellus*, respectively (Fig. 1). Within *C.* subg. *Cantharellus*, European species belong to three supported evolutionary lineages: (i) *C. alborufescens-ferruginascens-roseofagetorum* lineage (*C. ferruginascens* group, PP 0.99, ML-BP 96%), characterized by sometimes possessing a pink coating on the pileus, not breaking into scales, having a mostly white hymenophore in young specimens and a grey to reddish grey reaction with iron salts; (ii) *C. amethysteus*-*C. lewisii*-*C. subamethysteus* lineage (PP 1, ML-BP 94%), characterized by a constantly present pink-violet coating on the pileus, often breaking up into concentrically arranged appressed scales, by an ochre-yellow hymenophore and, at least in *C. amethysteus*, by a grey reaction with iron salts, but reddish grey at the stipe base; and (iii) *C. cibarius-pallens* lineage (PP 1, ML-BP 98%), containing also several North American species, characterized by lacking any coating or scales on the pileus, an ochre-yellow to orange-yellow hymenophore (except in *C. subalbidus*), and by having a grey reaction with iron salts, at least in European species.

Mapping of morphological and ecological characters

We have plotted several characters on the best tree obtained from the Maximum Likelihood analysis of the MAP dataset (Fig. 2):

(i) Young pileus colour. Non-albinistic specimens with an entirely or partially white pileus occur in *C. alborufescens, C. pallens* and *C. roseofagetorum* clades, but not all the specimens in those clades have a white pileus when young. Specimens with citrine yellow and reddish orange colour are only present in the *C. ferruginascens* and *C. friesii* clades, respectively;

(ii) Coating on the pileus. A pink or purple coating is present in specimens of *C. amethysteus*, and in some specimens of the *C. alborufescens*-*C. ferruginascens*-*C. roseofagetorum* group. Nevertheless, the intensity of the pileus coating is variable at intraspecific level;

(iii) Colour of young hymenophore. Almost all the specimens of the *C. alborufescens* and *C. ferruginascens* clades have a white to pale ochre hymenophore in young basidiomata. *Cantharellus roseofagetorum* specimens, nevertheless, have a darker orange-yellow-coloured hymenophore. The hymenophore colour also differs among specimens assigned to *C. cibarius* and *C. pallens*, being uniformly coloured in the former, and with a brighter colour near the margin in *C. pallens*. The two specimens coded as having purplish grey or purple-coloured hymenophore nest in the *C. cibarius* (BIO-Fungi 10477) and *C. romagnesianus* clades (LOU-Fungi 19494, holotype of *C. lourizanianus*);

(iv) Staining upon manipulation. Strongly staining specimens occur in the *C. alborufescens*, *C. ferruginascens*, *C. amethysteus* and *C. pallens* clades, but are only predominant in *C. alborufescens* and *C. ferruginascens.* Specimens of *C. pallens* range from non-staining to strongly staining, while staining was moderate to absent in specimens of *C. cibarius* and *C. romagnesianus*, and absent in all specimens of *C. friesii*;

(v) No or low host specificity patterns are observed. *Cantharellus cibarius, C. pallens* and *C. amethysteus*, for instance, occur in pure angiosperm or gymnosperm stands. The species in the *C. ferruginascens* group, however, seem to be exclusively associated with angiosperms, especially Fagaceae, but *C. ferruginascens* has also been found under *Carpinus* (Betulaceae). All specimens of *C. alborufescens* are associated with Mediterranean evergreen oaks, except for specimen BB 12.088 which grew under *Castanea sativa*.

Spore characters

With regard to spore characters, no significant spore shape difference was detected among the European species. Specimens with partially constricted spores were seen in nearly all the species, especially in the larger-spored specimens of each species. Spore-size is highly overlapping among European species, but L_m values appear to be of use to delimit some species, e.g. *C. amethysteus* and *C. pallens*. Nevertheless, spore ranges and statistics provided here are still narrow and will become certainly broader as further measurements are made available from new specimens.

Taxonomy

Key to the European species of Cantharellus

Note: Unusually found albino and orange specimens, treated by Olariaga et al. (2015) are not included in the key.

1. Pileus usually not exceeding 30(50) mm, usually not fleshy; stipe up to 10 mm thick; surface pileipellis hyphae thin-walled or rarely thick-walled (≤1 µm); reaction with iron salts reddish grey………………… 2
1. Pileus up to 130 mm, if less than 30 mm fleshy or with involute margin; stipe up to 20 mm thick; at least some surface pileipellis hyphae thick-walled (≥ 0.8 µm), reaction with iron salts reddish grey or grey……….. 3
2. Pileus pinkish orange to orange-red; not staining upon manipulation; stipe base concolorous, mostly under *Fagus* (if pilepellis hyphae thick-walled see *C. roseofagetorum*)………………………………… ***C. friesii***
2. Pileus orange-yellow to ochre-yellow, sometimes white, sometimes staining upon manipulation; stipe base often red; under angiosperms or conifers……………………………….. ***C. romagnesianus***
3. Hymenophore white or off-white when young, often remaining so near the very pileus margin; growing under angiosperms (*Fagaceae* or *Betulaceae*); reaction with iron salts reddish grey or grey in pileus flesh…………………………………………….…… 4
3. Hymenophore yellow-ochre to orange-yellow when young, at least near the margin, growing under angiosperms or conifers; reaction with iron salts grey in pileus flesh……………………………………….…. 6
4. Typically associated with Mediterranean evergreen *Quercus* on calcareous ground; pileus medium-sized to large, never citrine yellow or with green or brown shades………………………………. ***C. alborufescens***
4. Not associated with Mediterranean evergreen oaks; pileus small to medium-sized, sometimes citrine-yellow or with green or brown shades……………… 5
5. Pileus without a white coating; pileus colour usually citrine yellow in young specimens ……………………………..……………………… ***C. ferruginascens***
5. Pileus with a white coating when young; pileus colour ochre-yellow when the white coating disappears; so far only known from eastern European Georgia under *Fagus orientalis*…………………. ***C. roseofagetorum***
6. Usually with pink to purple coating present on the pileus, remaining almost always in the centre; usually scaly; spores $L_m = 10.1–10.7$ µm, $W_m = 5.2–6$ µm; strongly staining on the stipe upon bruising ……………………………………..……… ***C. amethysteus***
6. Without pink or purple coating on the pileus; usually not scaly; spores $L_m = 7.5–8.9$ µm, $W_m = 4.0–5.3$ µm; staining or not……………………………….... 7
7. Pileus not or at most partially covered with a silvery whitish coating; staining not striking; hymenophore uniformly ochre-yellow to orange-yellow, more common in northern Europe………………… ***C. cibarius***
7. Pileus always partially to entirely white coating when young, later progressively disappearing in patches; hymenophore usually having a distinctly brighter colour near the pileus margin, more common in southern Europe…………………………… ***C. pallens***

Taxonomy

Cantharellus subg. *Cantharellus*

Cantharellus alborufescens (Malençon) Papetti and S. Alberti, Boll. Circ. Micol. G. Carini 36: 26, 1998. Figures 3a, b, and 4a

≡ *Cantharellus cibarius* var. *alborufescens* Malençon in Malençon and Bertault, Trav. Inst. Sci. Chérifien, Sér. Bot. Biol. Vég. 33: 519, 1975

Holotype: Morocco, Moyen Atlas, Azrou, au bas de la forêt a *Quercus ilex*, 22 October 1940, G. Malençon 1036, MPU027371 (!). ITS barcode GenBank: KX828764.

= *Cantharellus henrici* Eyssart. and Buyck, Bull. Soc. Mycol. France 116(2): 120, 2000

Holotype: France, Hérault, Clairac, dans une garrigue, le long d'un sentier, parmi les pierres, 1 November 1974, H. Romagnesi 74.363 (PC0142165!). ITS barcode GenBank: KX828777.

= *Cantharellus lilacinopruinatus* Hermitte, Eyssart. & Poumarat, Bull. Sem. Fed. Assoc. Mycol. Médit. 28(2): 28, 2005

Fig. 3 *Cantharellus alborufescens*. **a** Basidiomata with yellow orange pileus, without pink coating (BIO-Fungi 9968); **b** Entirely white basidiomata, with a faint lilac coating (BIO-Fungi 11691). *Cantharellus amethysteus*. **c** Basidiomata showing variability in presence of a coating and scaliness on the pileus (BIO-Fungi 12921, epitype of *Cantharellus rufipes*); **d** Young basidiomata with a strong coating on the pileus (AH44796, neotype of *C. amethysteus*). *Photos* **a**, **b**, **c**, I. Olariaga; **d** J.L. Teres

Holotype: France, Dordogne, commune du Tursac, La Rastucie, 23 October 2004, M. Rousseau, GE 04-068 (PC0734066!). ITS barcode GenBank: KX828779.

= *Cantharellus ilicis* Olariaga & Salcedo, Revista Catalana Micol. 30: 109, 2009 "2008"
Holotype: Spain, Sigüés, Arroyo de la Tejera, under *Quercus rotundifolia*, *Q. humilis* and *Pinus halepensis* on calcareous soil, 11 October 2006, BIO-Fungi 11689 (!). Isotype: BIO-Fungi 12601 (!). ITS barcode GenBank: KX828778.

Pileus 28–80 mm diam., rather fleshy, very pale ochre white (5A2) or very pale greyish white (5A1) at first, sometimes with a pinkish hue (6A2), sometimes yellow orange (8A1) from the beginning or becoming so in the end, especially in wet weather, often remaining white near the margin or in unexposed parts. Coating often present, pale pink (6A2) to deep pink (7A3), covering the entire pileus or restricted to patches in the margin. Surface smooth, sometimes scaly in the pileus centre of old basidiomata, concentrical, appressed, brownish ochre (5C7). Margin thin and fragile. **Hymenophore** with forked veins, anastomosing afterwards, white to ochre-white (5A1–2) at first, gradually ochre (5A3–5) or orange-ochre (5A7), often strongly staining on manipulation. **Stipe** 20–65 × 5–18 mm, cylindrical, often tapering downwards, initially ochre-white (5A1), gradually pale ochre (5A3) afterwards. Surface smooth or sometimes finely scaly at the apex. **Context** white (5A1), strongly staining in young basidiomata collected in dry weather, white (5A1), pink (9A3) or orange-ochre (5A6) underneath the pileus surface. **Spore print** pale yellowish ochre (5A3–5). Reaction with iron salts reddish grey.
Spores ellipsoid to somewhat reniform, sometimes constricted in the middle, smooth, (8)8.5–11.5(13) × 4.5–6 µm (L_m = 9.2–10.1, W_m = 4.8–5.5; Q_m = 1.71–2.12; n = 7). **Basidia** predominantly 5–6-spored, 82–96 × 8.5–9.5 µm. **Surface pileipellis hyphae** cylindrical, thick-walled (0.8–2 µm), with pale yellow or pale brownish yellow content, 4–7.5 (9.5) µm. Clamps abundant in all tissues.

Specimens examined: FRANCE. **Gard**: Frouzet, under *Quercus ilex* on calcareous ground, 31 October 2012, G. Corriol, AH44783. **Var**: commune de Saint-Cyr-sur-Mer, quartier "La Mûre", 100 m, on calcareous soil, with *Quercus pubescens*, *Viburnum tinus*, *Erica arborea* and *Rosmarinus officinalis*, 26 October 2004, J.-C. Hermitte & G. Eyssartier, GE 04 154 (PC0734067; paratype of *C. lilacinopruinatus*). ITALY. **Prov. Siena**, Fonte Murata, in *Quercus cerris* and *Q. ilex* woodland, 9 November 2012, B.

Fig. 4 Basidiospores of European species of *Cantharellus*. **a** *C. alborufescens* (BIO-Fungi 11691); **b** *C. amethysteus* (AH44796); **c** *C. cibarius* (AH44778); **d** *C. ferruginascens* (AH44794); **e** *C. pallens* (AH44799); **f** *C. friesii* (AH44798); **g** *C. romagnesianus* (AH44218); **h** *C. romagnesianus* (PC0085043, holotype). *Scale bar* 10 μm. Line drawings: I. Olariaga and G. Moreno

Buyck, BB 12.075 (PC); BB 12.076 (PC). Molli, comune di Sovicille (SI), 500 m alt., with *Castanea sativa*, 10 November 2012, B. Buyck, BB 12.088 (PC). **Prov. Pescara**, Colle Romano, commune Penne, 450 m, on calcareous soil, *under Quercus ilex*, 23 October 2009, E. Campo, EC 09.91. SPAIN. **Mallorca**: Campanet, Finca Son Pons, under *Quercus ilex* on basic soil, 28 September 2005, J.S. Siquier, BIO-Fungi 12025; Escorca, Menut, under *Quercus ilex* on calcareous ground, 23 November 2006, I. Olariaga, BIO-Fungi 11687; Inca, under *Quercus ilex*, with presence of *Pinus halepensis*, on calcareous ground, 20 November 2009, J.L. Siquier, JLS 2880 (AH44223); Sa Communa de Bunyola, under *Quercus ilex* on basic soil, 22 November 2006, J.C. Salom & I. Olariaga, BIO-Fungi 11691.

Commentary

Cantharellus alborufescens is a variable species in terms of pileus colour and presence of pink pileal coating. Typical basidiomata of *C. alborufescens* have a white pileus, traces of a pink coating, a white hymenophore and stain strongly when bruised. *Cantharellus alborufescens* differs from close species in almost exclusively occurring in Mediterranean evergreen *Quercus* forests on calcareous soil, but a single collection has been found under *Castanea sativa* (BB 12.088). *Cantharellus alborufescens* was originally described from Morocco and is broadly distributed in Mediterranean Europe.

Specimens with a completely yellow-orange pileus, like the holotype of *C. ilicis* (BIO-Fungi 11689) belong to the same phylogenetic species as the type of *C. alborufescens* following GCPSR criteria (Fig. 1). Basidiomata with an entirely pink pileus occur as well in *C. alborufescens* (AH44783) and these appear to be more frequent in rainy years (J.L. Siquier, pers. comm.). *Cantharellus pallens*, also widespread in the Mediterranean area, has sometimes an entirely white pileus as *C. alborufescens*, but *C. pallens* differs in having typically brighter yellow-orange veins near the margin, smaller spores on average (L_m = 7.5–8.8 µm) and a clear preference for occurring on acidic soil at least in the Mediterranean region.

All the specimens attributed here to *C. alborufescens* had identical ITS2 sequences. Based on GCPSR criteria and sequences from type specimens, we demonstrate here that *C. ilicis*, *C. lilacinopruinatus* and *C. henrici* are later synonyms of *C. alborufescens* (Fig. 1). Further, the examination of the holotype material and the unpublished original colour plate of *C. alborufescens* (at MPU) support this view, as they conform to the material studied here. Nevertheless, much confusion has prevailed over *C. alborufescens* and it has seldom been treated in the correct sense and under its prioritary name (Constantino and Siquier 1996; Papetti and Alberti 1998). *Cantharellus lilacinopruinatus* was separated from *C. alborufescens* on account of the presence of a pink-lilac coating on the cap (Hermitte et al. 2005), a frequent characteristic (Pérez-De-Gregorio and Mir 2006; Becerra and Robles 2009) here proven to be inconstant and thus unreliable. Other reports of *C. alborufescens* are to be referred to *C. pallens* (Anonymous 1989; Roux and Eyssartier 2013) as strongly suggested by the orange-yellow hymenophore margin in their respective photographs.

Cantharellus henrici is presented here as a novel synonym of *C. alborufescens*. *Cantharellus henrici* was described as a small-sized thermophilous species that differed from the holotype of *C. cibarius* var. *tenuis* by possessing thick-walled hyphae on the pileal surface (Eyssartier and Buyck 2000). The Mediterranean affinity of *C. henrici*, the thick-walled pileipellis hyphae and the spore-size (9–12(13) × 4.5–5 µm) conform all to *C. alborufescens*. The small size of the holotype specimen (pileus diameter 23 mm when dry) might be, in our opinion, due to a limited water availability period and is not taxonomically informative in this case.

Cantharellus amethysteus (Quél.) Sacc., Syll. Fung. 5: 482, 1887, Figs. 3c, d, 4b, and 5
≡ *Cantharellus cibarius* var. *amethysteus* Quél., Compt. Rend. Assoc. Franc. Avancem. Sci. 11: 397, 1883 "1882"
= *Craterellus amethysteus* (Quél.) Quél., Fl. Mycol. France: 37, 1888
Type: No type designated. No original material extant. Neotype (designated here): Spain, Basque Country, Gipuzkoa, Aia, Granada erreka, under *Fagus sylvatica* on calcareous ground, 13 September 2013, J. Teres, AH44796. MycoBank MBT372877. ITS barcode GenBank: KR677512.

= *Cantharellus rufipes* Gillet, Champ. France Hyménomyc., pl. suppl. 13: plate "142" (as *Cantharellus rufipes*), 1888, Fig. 5a
= *Cantharellus cibarius* var. *rufipes* (Gillet) Cooke, Hand. Brit. Fungi, ed. 2 (part 3): 339, 1889
Lectotype (designated here) [icon.]: Gillet, Champ. France Hyménomyc. pl. suppl. 13: plate "142" (as *Cantharellus rufipes*), 1888. Epitype (designated here): Spain, Navarre, Goizueta, Usku, under *Fagus sylvatica* on nutrient poor ground, 29 September 2009, A. Felipe & I. Olariaga, BIO-Fungi 12921 (!); MycoBank MBT372878. ITS barcode GenBank: KR677513.

= *Cantharellus cibarius* subsp. *squamulosus* A. Blytt, Skr. Vidensk.-Selsk. Christiana, Math.-Naturvidensk. Kl. 1904(6): 108, 1905 "1904"
= *Cantharellus cibarius* var. *squamulosus* (A. Blytt) Eyssart. and Buyck, Bull. Soc. Mycol. France 116(2): 113, 2000
Type: No type designated. No material extant in O herbarium.

= *Cantharellus cibarius* var. *umbrinus* R. Heim ex Eyssartier and Buyck, Bull. Soc. Mycol. France 116(2): 113, 2000
Holotype: France, Département de la Dordogne, Commune d'Eglise-Neue-de-Vergt, lieu dit "Le Breuilh, au sol dans le lierre et sous chênes, July 1999, G. Eyssartier 99689bis (PC0142168!). ITS barcode GenBank: KX828792.

Pileus 15–95 mm diam., rather fleshy, ochre-yellow (5A5–6) to pale orange-yellow (5A7–8) at first, seldom pale ochre-yellow (5A3) in young unexposed basidiomata. Coating present covering the pileus entirely or when partially, typically remaining in the pileus centre or at the margin, sometimes absent in aged basidiomata, pinkish purple (9B4) to purple (9C2–3), purplish brown (7C4) when weathered. Surface initially smooth, later very often scaly in the entire pileus or only in the centre, scales concentrical, adpressed, of the same colour as the coating.

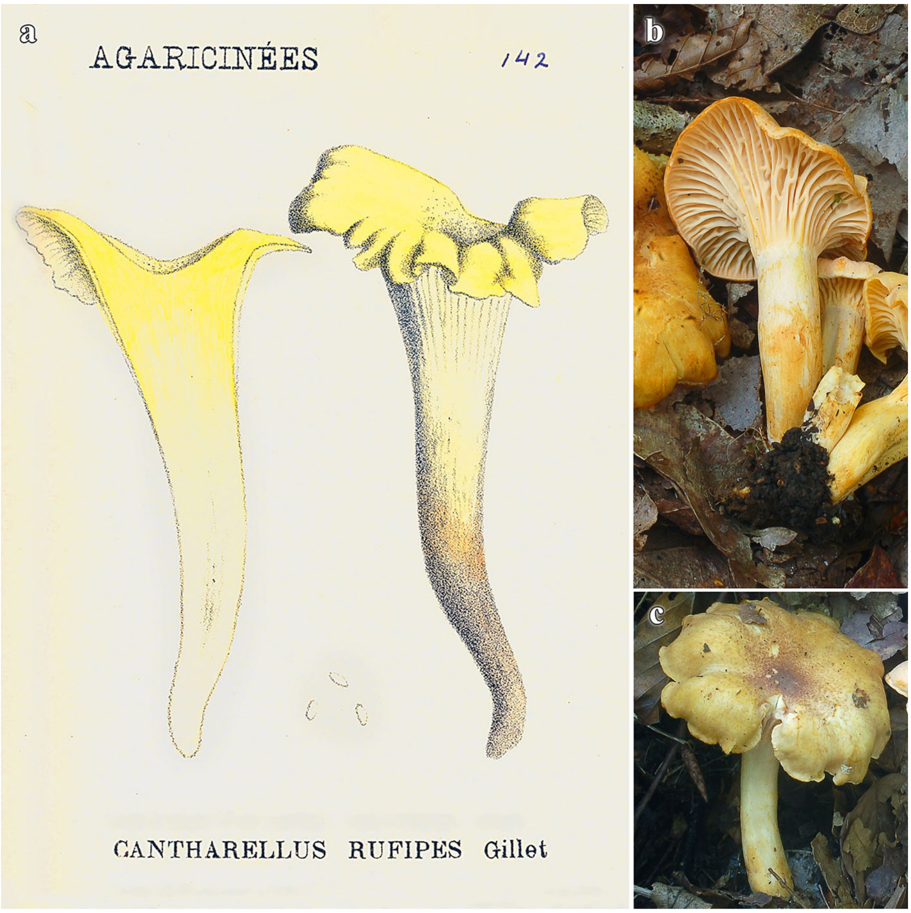

Fig. 5 *Cantharellus amethysteus*. **a** Lectotype plate of *Cantharellus rufipes*; **b** Basidioma showing a stipe surface that stains upon bruising (BIO-Fungi 12921, epitype of *C. rufipes*); **c** Typical basidioma of *C. amethysteus* showing a slightly scaly and pinkish purple pileus as the lectotype (BIO-Fungi 12921, epitype of *C. rufipes*. *Photos* **b**, **c**, I. Olariaga

Margin thin to moderately thick. **Hymenophore** with forked veins, anastomosing afterwards, seldom folded-veined, pale orange-ochre (5A2–3) to pale ochre-yellow (5A1–2) at first, gradually ochre-yellow (5A5–6), sometimes faintly staining on manipulation. **Stipe** 15–55 × 8–12 mm, cylindrical, often tapering downwards, initially ochre-white (5A1–2), gradually pale ochre-yellow (5A4–5) afterwards. Surface smooth. Context white (5A1), staining, especially in young basidiomata, ochre-yellow (5A4) underneath the pileus surface. **Spore print** ochre-yellow (5A3–4). Reaction with iron salts grey; reddish grey at stipe base. **Spores** ellipsoid to somewhat reniform, sometimes constricted in the middle, smooth, (9)9.5–12 × 4.5–6.5(7) µm (L_m = 10.1–10.7, W_m = 5.2–6; Q_m = 1.81–1.93; n = 4). **Basidia** predominantly 4–6-spored, 70-110 × 8-10 µm. **Surface pileipellis hyphae** cylindrical, sometimes somewhat sinuous, thick-walled (0.5–1 µm), sometimes with a 0.5-1.5 µm sheath at the apex, with yellow content, pinkish brown content in areas with coating, 4–7.5 µm. Clamps abundant in all tissues.

Specimens examined: FRANCE. **Dauphiné-Savoie**. Without locality, under *Carpinus*, A. Estades, AE 10.454 (PC); A. Estades, AE 10.453 (PC0084819). ITALY. **Belluno prov.**: Campon, commune Tambre, 1080 m, on calcareous soil, in mixed forest with *Picea abies*, *Abies alba* and *Fagus sylvatica*, 10 September 2009, E. Campo 09.29 (PC). SLOVAKIA. **Banská Bystrica:** Route close to Badinský prales National Reserve, close to Badin village, Kremnické vrchy mountains, 8 September 2007, B. Buyck & S. Adamcik, BB 07.284 (PC0084070). Without locality, 10 September 2007, B. Buyck & S. Adamcik, PC0084071. SPAIN. **Navarre**: Goizueta, Usku, under *Fagus sylvatica* on nutrient poor ground, 29 September 2009, A. Felipe & I. Olariaga, BIO-Fungi 12923 [albinistic].

Commentary

Typical basidiomata of *Cantharellus amethysteus* are characterized by having a pinkish purple coating that very often breaks into scales, by a strong staining upon bruising and by its large spores. Basidiomata devoid of a conspicuous coating and with non-scaly pileus are more difficult to identify, but are recognized by having subtle remnants of coating in the margin, and/or having a flesh-coloured centre. *Cantharellus amethysteus* appears to have a unique reaction with iron salts, being grey in the pileus and stipe context, but distinctly reddish grey at the stipe base. Although we have tested this reaction in one fruitbody, it appears to be constant (S. Serrano, pers. comm.) in most basidiomata and unique among European *Cantharellus*. The name *C. amethysteus* has been consistently applied to this species. The pale egg-yellow colour ("*jaune-d'oeuf pâle*") and the slight flesh-lilac-coloured pileal coating ("*couvert d'un léger duvet incarnat lilacin*") mentioned in the protologue (Quélet 1883) suggest that this interpretation is correct, in spite that no pileal scales are mentioned. As no type specimen is known to be extant (Eyssartier and Buyck 2000), we propose above a neotype specimen of *C. amethysteus* to stabilize this interpretation.

We propose here that *Cantharellus rufipes* is a synonym of *C. amethysteus*. The lectotype plate of *C. rufipes* shows a pale yellow-coloured basidioma with a scaly pileus centre ("*écailleux et jaune carné au centre*") that can hardly refer to any other European species than *C. amethysteus* in our opinion. The date of valid publication of *C. rufipes* is 1878 according to Eyssartier and Buyck (2000) and as listed in public databases (Index Fungorum and Mycobank, viewed 12 Sept 2016) and this would make *C. rufipes* prioritary over *C. amethysteus*. Nevertheless, S. Redhead pointed out to us that *C. rufipes* was not validly published until 1888. Gillet's "Les Hyménomycètes" was published at irregular intervals, the contents of which are not known with precision (Stafleu and Cowan 1976). The text volume was published between 1874 and 1878 but no mention of *C. rufipes* is found there, nor is it found in the "Tableaux analytiques des hyménomycètes de France" (Gillet 1884) which very likely contained all the names published until then. Rather, the name *C. rufipes* appeared in one of the supplementary sets of plates (Saccardo 1912) that were released between 1877 and 1890 (Stafleu and Cowan 1976). According to Cooke (1889), the plate of *Cantharellus rufipes* was distributed in the 13th series, which was released in 1888 (Anonymous 1888, p. 115). Hence, we consider it that the valid publication of *C. rufipes* was in 1888, not in 1878, and that the use of the name *C. amethysteus* for this taxon can be continued as it is the earliest one. The original plate of *C. rufipes* is often referred to as pl. 142, but this number is always handwritten in the original copies we have examined. We thus believe that this plate remained unnumbered until it was assigned no. 142 in the index (page 4) published together with the 16th supplementary series in 1890 (Peltereau 1898; Stafleu and Cowan 1976). This would explain the fact that Cooke did not cite any plate number in 1889. The same plate of *C. rufipes* was numbered otherwise in subsequent reprints of Gillet's "*Les Hyménomycètes*", where plates were arranged alphabetically (Gillet 1897).

Based on the protologue (Rostrup 1905), we propose also *C. cibarius* subsp. *squamulosus* as synonym. The scaly pileus, the brownish red stipe, thus staining, and the fact that *C. amethysteus* is widespread in Norway (Artsdatabanken 2016), where it was originally described from, support this synonymy. Interestingly, *C. cibarius* subsp. *squamulosus* was said to be close to *C. rufipes* in the protologue. *Cantharellus cibarius* var. *umbrinus* is here also considered contaxic with *C. amethysteus* based on molecular data obtained from the holotype.

Cantharellus amethysteus is broadly distributed in Europe, but it is not present in areas of Mediterranean climate with summer drought. Besides the material we have examined, typical material of *C. amethyteus* has been cited in Austria (Ricek 1971), Denmark (Lange 1998), Germany (Krieglsteiner 2000), Norway (Artsdatabanken 2016), Romania (specimen Flora Rom. 5825 (UPS) seen by I. Olariaga), Sweden (UPS F-696927 seen by I. Olariaga), Switzerland (Ricek 1971) and United Kingdom (Pegler et al. 1997).

Cantharellus cibarius Fr., Syst. Mycol. 1: 318, 1821: Fr., idem. Figures 4c and 6a, b

≡ *Agaricus chantarellus* L., Sp. Pl. 2: 1171, 1753

≡ *Merulius chantarellus* (L.) Scop., Fl. Carniol., ed. 2, 2: 461, 1772 "cantharellus".

≡ *Cantharellus flavescens* Lam., Encycl. 1(2): 694, 1785 [nom. nov. based on *Agaricus chantarellus* L.]

≡ *Cantharellus edulis* Pers., Neues Mag. Bot. 1: 106, 1794 [nom. illeg. Art. 52.1]

≡ *Cantharellus vulgaris* Gray, Nat. Arr. Brit. Pl. 1: 636, 1821 [nom. illeg. Art. 52.1]

≡ *Craterellus cibarius* (Fr.: Fr.) Quél., Fl. Mycol. France: 37, 1888

≡ *Alectorolophoides cibarius* (Fr.: Fr.) Earle, Bull. New York Bot. Gard. 5: 407, 1909

Lectotype (icon.): Bulliard, Herb. France 2: pl. 62, 1781–1782, designated by Eyssartier and Buyck (2000). Epitype (designated here): Sweden, Uppland, Uppsala, Nåsten, under *Picea abies*, with *Betula* and *Pinus*, on acidic ground, 23 July 2005, A. Felipe and I. Olariaga (BIO-Fungi 10986!); Isoepitype UPS F-575623; MycoBank MBT372862. ITS barcode GenBank: KR677501.

= *Cantharellus cibarius* f. *pallidus*, R. Schulz in Michaël, Führ. Pilzfr. 1: no. 82, 1923

Neotype: United Kingdom, England, Devon, Bovey Tracey, Tradbere Down, on the ground near *Betula*, 3 October 1992, N.W. Legon, K(M)22132 (!), designated by Olariaga et al. (2015). ITS barcode GenBank: KR677509.

= *Cantharellus cibarius* var. *salmoneus* L. Corb., Mém. Soc. Sci. Nat. Math. Cherbourg 10: 123, 1929 "1924–1929"

Neotype: Norway, Hedmark, Sølendet, on acidic soil among *Betula nana*, 15 August 2006, H. Lundmark, BIO-

Fig. 6 *Cantharellus cibarius*. **a** Typical basidiomata with yellow orange pileus and hymenophore (BIO-Fungi 10986, epitype); **b** Young basidiomata with a silvery coating (AH44778). *Cantharellus ferruginascens*. **c** Typical basidiomata with a citrine yellow pileus (AH44794); **d** Young basidiomata with an unusual pink coating (AH44226). *Cantharellus pallens*. **e** Young basidiomata collected in rainy weather with an almost entirely yellow-orange pileus (BIO-Fungi 11230, neotype of *C. cibarius* var. *bicolor*); **f** Young basidiomata with a orangish white pileus, and showing brighter coloured hymenophore in the margin (BIO-Fungi 11150, neotype of *C. cibarius* var. *albidus*). *Photos* **a**, **e**, **f**, I. Olariaga; **b** L. Rubio Casas; **c** J.L. Teres; **d** J. Martín

Fungi 11714 (!), designated by Olariaga et al. (2015). ITS barcode GenBank: KR677510.

= *Cantharellus cibarius* var. *inodorus* Velen., Nov. Mycol.: 36. 1939.
Neotype: Spain, Asturias, Nueva de Llanes, under *Betula*, 19 July 2004, E. Fidalgo, BIO-Fungi 12777 (!), designated by Olariaga et al. (2015). ITS barcode GenBank: KR677502.

= *Cantharellus cibarius* var. *atlanticus* Romagn., Doc. Mycol. 25(98–100): 421, 1995
Holotype: France, Département de les Landes, Mezos-Capas, sur sol sableux, des plantations de *Pinus pinaster*, 15 May 1981, H. Romagnesi 81.30 (PC0142164!). ITS barcode GenBank: KX828771.

=*Cantharellus parviluteus* Fern. Sas., Pérez-de-Greg. & Eyssart., Bull. Soc. Mycol. France 119(3–4): 262, 2003
Holotype: Spain, Burgos, Agüera de Montija, under *Betula alba*, *Alnus glutinosa* and *Quercus pyrenaica*, 7 September 2002, R. Fernández Sasia, C. Monedero & J.G. Campos, RFS 20907-08 (!). Isotype GE 03059 (PC0084799!). ITS barcode GenBank: KX828782.

Pileus 14–80 mm diam., slender to rather fleshy, orange-yellow (6A7) to bright ochre-yellow (5A7–8), occasionally pinkish orange (6B5–6), pale ochre-yellow (5A5, 6A4–5) in young unexposed basidiomata or when dehydrated, sometimes with a whitish or silvery hue. Coating absent. Surface finely velutinous or smooth, rarely slightly scaly in the centre, scales concolorous. Margin thin to moderately thick. **Hymenophore** with forked veins, anastomosing afterwards, ochre-yellow (5A7–8) to orange-yellow (6A6), occasionally pinkish orange (6B5–6), uniformly coloured, non staining upon manipulation. **Stipe** 35–50 × 8–15 mm, cylindrical, sometimes tapering downwards, initially very pale ochre-white (5A1–2), orange-yellow (5A6–7) afterwards, rarely pale pinkish orange (6A2–3). Surface smooth. **Context** white (5A1), sometimes moderately staining, especially in young basidiomata, ochre-yellow (5A6) or rarely pinkish orange (6A4) underneath the pileus surface. **Spore print** ochre-yellow (5A5–7). Reaction with iron salts grey.

Spores ellipsoid, sometimes somewhat reniform, occasionally constricted in the middle, smooth, (7.5)8–9.5(10) × 4–5.5(6) µm (L_m = 8.4–8.9, W_m = 4.6–5.2; Q_m = 1.74–1.80; n = 7). **Basidia** predominantly 5–6-spored, 76–104 × 8–9.5 µm. **Surface pileipellis hyphae** cylindrical, thick-walled (1–1.5 µm), with yellow content, (3)5–8(10) µm. Clamps abundant in all tissues.

Specimens examined: FRANCE. **Gironde**. Commune de l'Hôpital, sous chênes e châtaigniers en terrain sablonneuse très acide et plutôt humide (*Molinia caerulea*, *Ulex*, *Erica*), 23 August 2007, G. Eyssartier, GE 07.025 (PC0084088). **Les Landes**: Onesse, under *Pinus pinaster* on sandy acidic ground, 20 May 2007, I. Olariaga et al., BIO-Fungi 10780. SLOVAKIA. **Banskobystrický kraj**: near Badínsky prales National reserve, close to Badin village, Kremnicke vrchy mountains, 10 September 2007, B. Buyck, BB 07.300 (PC). SPAIN. **Basque Country**: Biscay, Gernika, Barrutia, under *Quercus robur*, 27 September 2004, R. Picón & I. Salcedo, BIO-Fungi 10477 [violaceous grey hymenophore]. Gipuzkoa, Oiartzun, Oieleku, under *Fagus sylvatica* on acidic soil, 26 June 2008, I. Olariaga, BIO-Fungi 12701. **Castilla La Mancha**: Guadalajara, Condemios de Abajo, under *Pinus sylvestris* on acidic ground, 30 June 2013, B. Rodríguez, AH44780. Condemios de Arriba, turberas del Pelagallinas, under *Pinus sylvestris*, near *Erica arborea*, in wet place near the peatbog, 28 June 2013, D. García, M. Martín & L. Rubio Casas, AH44778. **Galicia**: Pontevedra, Cangas, under *Castanea sativa*, 23 June 2013, L. Rubio Casas, AH44779. **Madrid**: Navacerrada, "las siete revueltas", *Pinus sylvestris* forest with *Vaccinium myrtillus*, *Pteridium* and mosses, 19 June 2005, J.C. Zamora, BIO-Fungi 12731, BIO-Fungi 12732. SWITZERLAND. **Valais**: Orsières, gorges d'Durnand, under *Picea*, *Fagus* and *Pinus*, 26 August 2007, A. Felipe & I. Olariaga, BIO-Fungi 12684.

Commentary

Typical gatherings of *Cantharellus cibarius* are characterized by an orange-yellow pileus, uniform-coloured hymenophore and absence of marked staining upon bruising. Entirely orange-coloured or white gatherings were demonstrated to sporadically occur in *C. cibarius* by Olariaga et al. (2015). Specimens with a silvery coating on the pileus (AH44780; PC0142164, holotype of *C. cibarius* var. *atlanticus*) belong to the same phylogenetic species as *C. cibarius* applying GCPSR criteria (Fig. 1).

Aged and entirely orange-yellow basidiomata of *C. pallens* are strongly reminiscent of *C. cibarius*, but can mostly be separated from the latter by a more robust habit and by a brighter orange-yellow hymenophore near the margin. The North American *C. roseocanus* (Redhead, Norvell & Danell) Redhead, Norvell & Moncalvo is a close sister species of *C. cibarius* (Fig. 1), not recognized as a separate phylogenetic species but supported in the multigene phylogeny. Both form a larger clade that is recognized as a phylogenetic species as well. The yellowish pink hoary coating proposed as diagnostic morphological feature of *C. roseocanus* by Redhead et al. (1997), at least in young stages, has never been observed in European *C. cibarius* specimens, nor has it been mentioned in the literature on European *Cantharellus* (Redhead et al. 1997; Eyssartier and Buyck 2000). Thus, *C. cibarius* and *C. roseocanus* can be recognized morphologically despite being phylogenetically very close and are interpreted here as species that merit distinction.

The name *C. cibarius* has been collectively applied to various orange-yellow *Cantharellus* species in Europe, Africa, Asia and North America (Pilz et al. 2003). Although *C. cibarius* has been consistently interpreted in Europe after the revision by Eyssartier and Buyck (2000), we propose here an epitype specimen of *C. cibarius* in order to allow for a molecular interpretation (Fig. 6a). Based on sequences from type specimens and morphological examination, *Cantharellus parviluteus* and *C. cibarius* var. *atlanticus* are here reduced to synonyms of *C. cibarius* (Fig. 1). *Cantharellus parviluteus* was described as a small-sized *C. cibarius* characterized by a hygrophilous habitat (Fernández-Sasia et al. 2003). Judging from the wider projection (36 mm diam.) of the spore print of the holotype, the fresh pileus was larger than stated in the protologue (22 mm) and within the size range of *C. cibarius*. A hygrophilous habitat is typical for *C. cibarius* close to its south limit of distribution.

Cantharellus cibarius var. *atlanticus* was originally distinguished from *C. cibarius* by having a more vivid colour and a whitish coating on the pileus (Romagnesi 1995), but the latter characteristic is sometimes present in *C. cibarius* as inferred from GCPSR criteria. The material collected in the type locality of *C. cibarius* var. *atlanticus* (BIO-Fungi 10780) and the holotype itself have identical ITS and LSU sequences as the Swedish epitype proposed above. Eyssartier and Roux (2011) considered that *C. cibarius* var. *atlanticus* merited species rank, but did not validly publish the combination (art. 41.5, basionym not cited).

Cantharellus cibarius is broadly distributed in Europe, but not present in areas with Mediterranean climate. In the Iberian Peninsula, and probably elsewhere in South Europe, *C. cibarius* has a clear preference for acid soils and occurs in rainy or locally damp sites, sometimes among *Sphagnum* (BIO-Fungi 12732).

Cantharellus ferruginascens P.D. Orton, Notes Roy. Bot. Gard. Edinburgh 29(1): 83, 1969. Figures 4d and 6c, d
≡ *Cantharellus cibarius* var. *ferruginascens* (P.D. Orton) Courtec., Doc. Mycol. 23 (91): 3, 1993
Holotype: United Kingdom, Norbury Park, Mickleham, Surrey, Druid's Grove (River wood), 20 September 1961, P.D. Orton 2331 (E00204187!). Isotype K(M)34306. ITS barcode GenBank: KX828773.

= *Cantharellus cibarius* var. *flavipes* R. Heim ex Eyssart. and Buyck, Bull. Soc. Mycol. France 116(2): 107, 2000
Holotype: France, Dept. Du Maine-et-Loire, Chaumont d'Anjou, lieu dit Rouchebouet, sous noisetiers, 16 October 1993, J. Boyer (PC). Isotype: pers. herb. J. Mornand (no 9312B2!). ITS barcode GenBank: KX828772.
– *Cantharellus cibarius* var. *neglectus* sensu Michelland, Bull. Féd. Myc. Dauphiné-Savoie 118: 33, 1990

Pileus 18–55 mm diam., not fleshy, citrine yellow (2A7, 3A7) at first, sometimes with olive green (2B8) hue, seldom partially yellowish white (2A2, 3A2) in young unexposed basidiomata, later pale ochre-yellow (4A4–5), often remaining white near the margin. Coating occasionally present, pink (7A3) to pinkish brown (7C4), entirely or partially covering the pileus, usually deeper in the centre. Surface smooth, occasionally scaly in the pileus centre, scales concentrical, adpressed, brown (6A6). Margin thin and fragile, becoming sinuous and lobed in old basidiomata. **Hymenophore** with forked veins, anastomosing afterwards, ochre-white (4A–2) at first, gradually pale ochre-yellow (4A3–4), often remaining white in the very margin, sometimes staining strongly upon manipulation. **Stipe** 15–65 × 5–11 mm, cylindrical, sometimes tapering downwards, initially very pale ochre-white (3A2, 4A2), gradually pale ochre (5A2–3) afterwards. Surface smooth or sometimes finely scaly at the apex. Context white (3A1), strongly staining in young basidiomata collected in dry weather, white (3A1) to citrine yellow (3A3) underneath the pileus surface. **Spore print** not obtained. Reaction with iron salts grey to reddish grey.
Spores ellipsoid to somewhat reniform, sometimes wider in the basal part and constricted in the middle, smooth, (7)8–10.5(11.5) × 4.5–6(6.5) µm (L_m = 8.4–9.7, W_m = 4.6–5.8; Q_m = 1.70–1.96; n = 8). **Basidia** predominantly 5–6-spored, 75–110 × 7–10.5 µm. **Surface pileipellis hyphae** cylindrical to narrowly claviform, thick-walled (0.6–1.5 µm), with pale yellow content, 4–8 (10) µm. Clamps abundant in all tissues.

Specimens examined: FRANCE. **Gard**: St-Laurent le Minier, under *Quercus ilex* and *Castanea* on acidic ground, 31 October 2012, P.-A. Moreau, AH44782. SLOVAKIA. **Banská Bystrica**: Route close to Badinský prales National Reserve, close to Badin village, Kremnické vrchy mountains, 8 September 2007, B. Buyck and S. Adamcik, BB 07.283. **Nitra**: Zuhracka in Sovia dolina valley, Nová Dedina village, Štiavnické vrchy mountains, 4 September 2007, B. Buyck and S. Adamcik, Buyck 07.221 (PC0084106); (PC0084099). SPAIN. **Asturias**: Valbúcar, ruta de los Molinos del Profundu, Villaviciosa, under *Quercus robur*, 18 August 2007, E. Rubio, ERD-4202 (AH). **Basque Country**: Bizkaia, Barrika, Gainibis, under *Quercus robur,* on decalcified calcareous ground, 15 September 2006, A. Meléndez and K. Ugartetxe, BIO-Fungi 11700. Gipuzkoa, Bilabona, Lastur, under *Quercus rubra*, J. Martín, AH44795; 24 September 2013, AH44226. Gipuzkoa, Granada erreka, under *Fagus sylvatica* on calcareous ground, 20 July 2005, J. Teres, BIO-Fungi 12651; 21 August 2013, AH44794. **Navarre**: Igantzi, San Juan Xar, under *Carpinus betulus* on calcareous ground, 16 October 2012, ARAN-Fungi 5012021. UNITED KINGDOM. **England**: North Devon, Tiverton (near), Knightshayes Court, SS960150, on soil, bare ground under a tree, *Quercus ilex*, 3 September 2012, N.W. Legon, K(M)180009.

Commentary
Cantharellus ferruginascens is primarily recognized by its characteristic citrine yellow or pale ochre-yellow pileus in young specimens. Its slender habit and the striking staining in young specimens are additional key features. As judged by GCPSR criteria, specimens with a pink or brown pileal coating belong to the same phylogenetic species as typical *C. ferruginascens* specimens (Fig. 1) like those originally described by Orton (1969). This had been previously interpreted by morphological species recognition (Eyssartier and Buyck (2000). Specimens AH44795 and AH44226 (Fig. 6d), with pale ochre-yellow and pink pileus, respectively, were collected in the same spot and both showed ITS2 sequences almost identical to that of the holotype of *C. ferruginascens*.

Cantharellus cibarius var. *flavipes* is here proposed as synonym of *C. ferruginascens*. The holotype of *C. cibarius* var. *flavipes* shows a pale ochre-yellow colour and a strongly staining stipe (Eyssartier and Buyck 2000, Planche II) that conforms to *C. ferruginascens*. The fact that the ITS2 regions of the types of *C. cibarius* var. *flavipes* and *C. ferruginascens* differ only by a one-nucleotide deletion in *C. ferruginascens* supports this synonymy. Our morphologial study confirms also that *C. ferruginascens* is not conspecific with *C. pallens*, contrary to what Pegler et al. (1997) proposed. *Cantharellus pallens* differs from *C. ferruginascens* by the larger and typically white pileus when young, becoming orange-yellow in patches and by having a brigther orange-yellow hymenophore in the pileus margin.

Cantharellus alborufescens is closely allied to *C. ferruginascens*, but typical basidiomata of *C. alborufescens* are characterized by having an entirely to partially white pileus and never citrine yellow like in *C. ferruginascens*. *Cantharellus alborufescens* and *C. ferruginascens* show clearly different distributional patterns. While *C. alborufescens* is present in areas of Mediterranean climate under various evergreen *Quercus* (*Q. ilex, Q. humilis, Q. rotundifolia*), *C. ferruginascens* occurs in areas of temperate climate without summer drought, and is typically associated with deciduous Fagaceae (*Castanea, Fagus, Quercus*) and Betulaceae (*Carpinus*) on calcareous soil. An interesting collection from the UK and collected under a planted evergreen *Quercus* (K(M)180009), turned out to be *C. ferruginascens*. This suggests that climate is the major factor shaping different distributional patterns in *C. ferruginascens* and *C. alborufescens*, rather than a different host preference. Nevertheless, we are acquainted with a few Mediterranean localities for *C. ferruginascens*, where it is always restricted to locally moist and humid sites under *Quercus suber* (M. Pérez-De-Gregorio, pers. comm.) on acid ground. Hence, *C. ferruginascens* appears to switch its soil pH preference in areas of Mediterranean climate. *Cantharellus ferruginascens* is known from a few localities in central and southwestern Europe (Orton 1969; Eyssartier and Buyck 2000; Olariaga 2009), but it might have been overlooked and more widespread.

Cantharellus pallens Pilát, Omagiu Traian Săvulescu: 600, 1959. Figures 4e and 6e, f
Holotype: Czech Republic, Bohemia, Přeštice, in piceto nudo ad terram, 10 September 1957, A. Pilát (PRM655551!). ITS barcode GenBank: KX853516.

= *Cantharellus cibarius* var. *albidus* Maire, Treb. Mus. Cièn. Nat., Sèr. Bot. 3(4): 49, 1937
Neotype (designated here): Spain, Catalonia, Girona, Viladrau, Montseny, under *Quercus ilex* and *Q. humilis* on acidic soil, 13 October 2005, A. Felipe and I. Olariaga, BIO-Fungi 11150; MycoBank MBT372867. ITS barcode GenBank: KR677494.

= *Cantharellus cibarius* var. *bicolor* Maire, Treb. Mus. Cièn. Nat., Sèr. Bot. 3(4): 49, 1937
Neotype (designated here): Spain, Catalonia, Girona, Sils, L'Esparra, under *Quercus humilis* on acidic soil, 14 October 2005, A. Felipe and I. Olariaga, BIO-Fungi 11230; MycoBank MBT372869. ITS barcode GenBank: KX853517.

= *Cantharellus subpruinosus* Eyssart. and Buyck, Bull. Soc. Mycol. France 116(2): 129, 2000
Holotype: France, dept. Haute-Savoie, bois des Bourguignons, bois mêles de feuillus et d'épicéas, dans la mousse, isolés ou en touffes, 16 July 1997, J.-C. Deiana, GE 99799 (PC).

Pileus 25–95 mm diam., fleshy, very pale orangish white (5A2, 6A2) at first, occasionally pinkish orange (6B5–6), progressively entirely orange-yellow (5A8, 6A6), or sometimes remaining orange-white in unexposed patches or young parts, especially in dry weather. Coating absent. Surface finely velutinous to smooth. Margin thick. **Hymenophore** with forked veins, anastomosing afterwards, ochre-yellow (5A4–6) to orange-yellow (5A8, 6A7–8), almost always brighter-coloured in the margin, sometimes faintly staining upon manipulation. **Stipe** 15–62 × 11–25 mm, cylindrical, sometimes tapering downwards, initially very pale ochre-white (5A1–2), pale ochre-yellow (5A3) afterwards, rarely pale pinkish orange (6A2–3). Surface smooth. Context white (5A1), sometimes strongly staining, especially in young basidiomata collected in dry weather, white (5A1), or ochre-yellow (5A6) underneath the pileus surface. **Spore print** orange-yellow (15B). Reaction with iron salts grey.
Spores ellipsoid, sometimes somewhat reniform, sometimes constricted in the middle, smooth, (7)7.5–9.5(10) × 3.5–5.5(6) µm (L_m = 7.5–8.8, W_m = 4–5.3; Q_m = 1.61–2.10; n = 7). **Basidia** predominantly 5–6-spored, 82–115 × 7–9.5 µm. **Surface pileipellis hyphae** cylindrical, thick-walled (1–2 µm), with yellow content, 4.5–8 µm. Clamps abundant in all tissues.

Specimens examined: ITALY. **Belluno Prov.**: Agordo, Cancellade, 20 July 2009, Buyck 09.418 (PC0084810); Col de Foia, mixed forest, 20 July 2009, B. Buyck, BB 09.409 (PC); Col di Pera, Trichiana, 21 July 2009, B. Buyck, BB 09.430 (PC); Melere, Trichiana, 21 July 2009, B. Buyck, BB 09.441 (PC). **Siena Prov.**: Riciano, commune di Monteriggioni (SI), in *Quercus cerris* and *Q. ilex* woodland, 9 November 2012, B. Buyck, BB 12.077 (PC); Buyck 12.082 (PC). MOROCCO. **Chefchaouen**: Bab Berred, Ketama, under *Quercus canariensis*, 16 November 2010, J.L. Manjón, AH39124. SPAIN. **Basque Country**: Gipuzkoa, Andoain, under *Quercus rubra*, July 2013, J. Martín, AH44799. **Catalunya**: Girona, Baix Empordà, Sant Cerbrià de Lledó, Cruïlles, under *Quercus suber*, M.À. Pérez De Gregorio, 3 October 1999, PG031099 (pers. herb. M.À. Pérez-De-Gregorio). **Madrid**: Canencia, under *Quercus pyrenaica*, 17 June 2013, Mycological Society of Madrid, AH44784. **Navarre**: Erro, Espinal, under *Fagus sylvatica*, 9 August 2004, J.M. Lekuona, ARAN-Fungi A5019040. SWEDEN. **Uppland**: Vaksala parish, Törnby, Ekbacken, under *Corylus*, *Quercus robur* and *Picea abies* on rich soil, 28 August 2005, E. Danell and I. Olariaga, BIO-Fungi 10988.

Commentary

Cantharellus pallens is a very variable species in terms of pileus and hymenophore colour, as suggested by GCPSR criteria (Fig. 1). The ITS2 sequence of the holotype of *C. pallens* is identical to the rest of material assigned to this species here. Typical basidiomata are recognized by an entirely or partially pale orange white pileus and by a distinctly brighter orange-yellow hymenophore near the margin. Nevertheless, aged or water-soaked specimens are devoid of white colour in the pileus (Fig. 6e) and can be mistaken for *C. cibarius*. The hymenophore colour in *C. pallens* ranges from bright orange-yellow to pale ochre-yellow, but is almost always brighter orange-yellow at the very margin. Young basidiomata, especially in dry conditions, stain strikingly, but more mature or water-soaked basidiomata are weakly staining. *Cantharellus pallens* is the *Cantharellus* species with the smallest spores in Europe, but its spore mean length (L_m) overlaps with that of all species except for *C. alborufescens* (9.2–10.1 µm) and C. *amethysteus* (10.1–10.7 µm). Our sampling shows that *C. pallens* is distributed from North Africa (AH39124) to Fennoscandia (BIO-Fungi 10988), albeit showing different ecological preference; typically on forests with rich ground in Fennoscandia (Ryman and Holmåsen 1984) and markedly acidophilous in the Mediterranean area.

Much confusion has prevailed over the correct name for this species. While the name *C. pallens* has been commonly used in northern Europe (Ryman and Holmåsen 1984; Persson and Mossberg 1994; Lange 1998), the name *C. subpruinosus* has been used in southern Europe for the same species. *Cantharellus subpruinosus* was described emphasizing the strong staining and white pileus in young basidiomata but a direct comparison between *C. subpruinosus* and *C. pallens* was not made, as the latter was included among the non-staining species in the key by Eyssartier and Buyck (2000). This characteristic is, nevertheless, shown to be variable and unreliable here, as both markedly staining specimens and weakly staining specimens belong to the same phylogenetic species. We thus consider *C. subpruinosus* a synonym of *C. pallens*. *Cantharellus cibarius* var. *bicolor* Maire and *C. cibarius* var. *albidus* Maire are also reduced to synonyms of *C. pallens* by proposing neotype material collected in their respective type localities, where *C. pallens* grew in abundance when I. Olariaga visited these localities.

Cantharellus roseofagetorum Olariaga, D. Rodríguez, G. Moreno, Manjón, Salcedo, V. Hofstetter, and Buyck **sp. nov.** Figure 7

MycoBank number: MB818285. ITS barcode GenBank: KX828789.

Holotype: Georgia, Ghulelebi, Tbilisi NP, under *Fagus orientalis* on probably calcareous eutric cambisol, 29 July 2012, D. Rodríguez, AH44789 (!).

Etymology: From Latin “roseus” pink, and “Fagus”, beech. The epithet makes reference to a pink pileal coating and association with *Fagus*.

Pileus 10–40 mm diam., rather fleshy, convex-plane, sometimes depressed in the centre, very pale ochre-white (5A1) at first, ochre-yellow (5A5) afterwards, remaining pale ochre-white near the margin or in unexposed parts. Colour dark ochre (5A5, 5B6) when desiccated. Coating present, faint to strong, pale pink (9A2–3) to purple red (9B6, 9C6), covering the centre, or almost the entire pileus. Surface smooth to very finely scaly. Margin thin to moderately thick, initially involute, then straight and becoming undulate with age. **Hymenophore** with forked veins, anastomosing afterwards, ochre-white (5A1–2) at first, soon ochre-yellow (5A5) or orange-yellow (5A7). Colour orange-ochre (6B7) to ferruginous orange (6B7) when desiccated. **Stipe** 10–30 × 6–12 mm, cylindrical, often slightly broader at base, initially ochre-white (5A1), gradually pale ochre-yellow (5A2–3) afterwards. Surface smooth or sometimes finely scaly at the apex. Colour dark ochre (5C7) to ferruginous brown (7C6) when desiccated. Context white (5A1), weakly to moderately staining, white to ochre-yellow (5A6) underneath the pileus surface. **Spore print** not obtained. Reaction with iron salts not tested.

Spores ellipsoid to somewhat reniform, not constricted, smooth, (7)8–10(11.5) × (4)4.5–6 µm (L_m = 8.65–9.3, W_m = 4.9–5.1; Q_m = 1.77–1.85; n = 2). **Basidia** predominantly 5-spored, 82–99 × 8–9 µm. **Surface pileipellis hyphae** cylindrical to narrowly claviform, sometimes sinuous, thick-walled (0.8–1.8 µm), with yellow to pale brown parietal pigment, (4.5)6–9 µm; terminal elements 32–57(93) µm long. Clamps abundant in all tissues.

Specimens examined: GEORGIA. **Region**: Ghulelebi, Tbilisi NP, under *Fagus orientalis*, with scattered *Malus* and *Taxus baccata*, on probably calcareous ground, 29 July 2012, D. Rodríguez, AH44786.

Fig. 7 *Cantharellus roseofagetorum* (AH44786). **a** Basidiomata; **b** Basidiomata. *Cantharellus roseofagetorum* (AH44789, holotype). **c** Basidiomata showing a strong pink coating; **d** Detail of hymenophore; **e** Hymenophore, white in the very margin; **f** Pileipellis hyphae; **g** Basidiospores; **h** Basidium with 5 sterigmata; **i** Basidium. *Scale bar* 10 µm. *Photos* **a**, **b**, **c**, **d**, **e**, D. Rodríguez. Line drawings: I. Olariaga and G. Moreno

Commentary

Cantharellus roseofagetorum forms a distinct phylogenetic species within the *C. alborufescens-ferruginascens* group (Fig. 1) and is morphologically characterized by a white pileus when young and an orange-yellow hymenophore. The strenght of a pink coating is variable in the material examined, as in other species of the *C. ferruginascens* group. The colour of the hymenophore is probably entirely pale in young basidiomata as some basidiomata had cream white hymenophore at younger parts. The hymenophore colour of more aged basidiomata of *C. roseofagetorum* is markedly darker than the colour observed in *C. ferruginascens* and *C. alborufescens*. Nevertheless, further material of *C. roseofagetorum* is needed to obtain a better insight of its morphological variability.

Cantharellus roseofagetorum is closely allied to *C. ferruginascens*, from which it differs in that young basidiomata have a white pileus, and lack the typical citrine yellow colour of young basidiomata of *C. ferruginascens*. *Cantharellus alborufescens* conforms to *C. roseofagetorum* in having a white pileus, but it differs by its paler hymenophore and a restricted Mediterranean distribution. Furthermore, *C. roseofagetorum* and *C. alborufescens* are recognized as different phylogenetic species applying a GCPSR. Blast searches of ITS2 sequences *C. roseofagetorum* did not retrieve highly similar matches either. Judging from ITS2 data of the type of *C. indicus* (HQ270122), described from India (Kumari et al. 2013), this taxon belongs to the *C. ferruginascens* group and is particularly closely related to *C. ferruginascens*. The ITS2 region differs only by a 4-nucleotide insertion in *C. indicus*. In any case, *C. indicus* differs from *C. roseofagetorum* in having a uniformly coloured orange-yellow pileus unlike *C. roseofagetorum*, and a reddish stipe base that does not conform to *C. ferruginascens*. Nevertheless, further material and obtaining molecular data of additional markers of *C. indicus* is desirable to evaluate the limits between *C. indicus* and other taxa within the *C. ferruginascens* group.

Our nomenclatural revision of European *Cantharellus* yielded no name that can be applied to the species described here. Likewise, no other potential synonym was found in the literature of Asian *Cantharellus* (Corner 1966; Eyssartier 2001). We thus describe here *C. roseofagetorum* as a new species to science.

Cantharellus subg. *Cinnabarinus*

Cantharellus friesii Quél., Mém. Soc. Emul. Montbéliard, sér. 2 (5): 215, 1872. Figures 4f, and 8a.

Lectotype (designated here): France, Jura, leg. Quélet, S F-25266 (Bresadola herbarium); MycoBank MBT372875.

= *Cantharellus ignescens* Fayod, Ann. Sci. Nat, sér. 7, Bot. 9: 304, 1889

= *Cantharellus miniatus* Fayod, Ann. Accad. Agric. Torino: 82, 1893 [nom. illeg., Art. 52.1]

Pileus 15–50 mm diam., slender, pinkish orange (6A8, 7A8) to orange-red (8A8), pale orange-white (6A2–3) when young or unexposed. Coating absent. Margin thin. **Hymenophore** with forked veins, sometimes not reaching the margin, very pale pinkish orange (6A2) to pale ochre-orange (6A3), not staining upon manipulation. **Stipe** 10–35 × 3–10 mm, cylindrical, very pale pinkish orange (6A1–2), sometimes with pinkish orange (7A5) patches, especially at apex. Surface smooth. Context white (5A1) to pale orange (6A2), not staining, orange (6A6) underneath the pileus surface. **Spore print** pale orange (6A2–3). Reaction with iron salts reddish grey.

Spores ellipsoid, rarely reniform or constricted in the middle, smooth, (7.5)8.5–11.5(13) × 4.5–5.5(6) µm (L_m = 9.4–10.4, W_m = 5.2–5.4; Q_m = 1.80–2.03; n = 3). **Basidia** predominantly 5-spored, 62–80 × 8–9 µm. **Surface pileipellis hyphae** cylindrical to narrowly claviform, thin-walled (< 0.5 µm), with orange content, 7–10(12) µm. Clamps abundant in all tissues.

Specimens examined: FRANCE. Without locality, G. Eyssartier, GE07.077 (PC). ITALY. **Pordenone prov.:** Ligont-Dardago, commune Budoia, 250 m, on damp soil, with *Carpinus betulus*, *Quercus robur* and *Corylus avellana*, 25 July 2009, E. Campo 09.16 (PC0084812). **Treviso prov**.: Cadolten-Pizzoc, commune Fregona, 1350 m, on calcareous soil, in *Fagus sylvatica* forest, 26 September 2009, E. Campo 09.43 (PC0084815). SPAIN. **Asturias**: Concejo de Ponga, bosque de Peloñu, under *Fagus sylvatica* on acidic ground, 6 November 2004, E. Arbelaitz, M. Gartzia & I. Olariaga, BIO-Fungi 10453; Tarna, under *Fagus sylvatica* on acidic soil, 9 September 2004, I. Olariaga, BIO-Fungi 10450. **Basque Country**: Gipuzkoa, Oiartzun, Oieleku, acidophilous *Fagus sylvatica* forest, 26 September 2007, J.M. Lekuona, ARAN-Fungi A3020106B. Gipuzkoa, Aia, Granada erreka, under *Fagus*, 22 September 2013, J.L. Teres, AH44798.

Fig. 8 *Cantharellus friesii*. **a** Basidiomata with discoloured margin (AH44798). *Cantharellus romagnesianus*. **b** Basidiomata (ARAN-Fungi A3007090A). *Photos* **a** J.L. Teres, **b** J. Martín

Commentary

Cantharellus friesii is readily recognized among European *Cantharellus* because of its bright pinkish orange colour, small size and frequent association with *Fagus*. Microscopically, the pileipellis hyphae with thin-walled hyphae and large spores in comparison to other species are diagnostic. Typical basidiomata of *C. friesii* have a uniformly coloured pileus, but basidiomata with a paler pileus in the margin occur as well (Fig. 8a). *Cantharellus romagnesianus* is reminiscent of *C. friesii* in the slender basidiomata and thin-walled pileipellis hyphae, but its pileus is yellow, or rather often white. The North-American *C. cinnabarinus* (Schwein.) Schwein. and *C. texensis* Buyck and V. Hofstetter differ from *C. friesii* in having a brighter red colour (Buyck et al. 2011b). *Cantharellus roseofagetorum* occurs under *Fagus* like *C. friesii* usually does, but it differs from the latter in having a white pileus when young, an ochre-yellow hymenophore and having thick-walled pileipellis hyphae.

Cantharellus ignescens is considered here a synonym of *C. friesii*, based on the protologue. Fayod (1889) provided a very meagre description of *C. ignescens*, but the small size and "fire colour" mentioned in the protologue strongly suggest the synonymy with *C. friesii*. The later more detailed description by Fayod (1893) as *Cantharellus miniatus*, and including *C. ignescens* as synonym, substantiates this synonymy that has been suggested before (Corner 1966). Although the original description of *C. friesii* by Quélet is meagre and the original figure not optimal, the name *C. friesii* has been consistently interpreted up to date. An original specimen collected by Quélet in the Bresadola herbarium (S-F25266) conforms to the conventional interpretation of *C. friesii*. Although this specimen bears no collection date, the notation "misit Dr. Quélet. Orig. exempl." by Bresadola is considered here as evidence showing that this is one of the specimens upon which Quélet based the description of *C. friesii*. No other original specimen of *C. friesii* is kept in PC (Eyssartier and Buyck 2000). Accordingly, we select the specimen in the Bresadola herbarium as the lectotype of *C. friesii*.

Cantharellus subg. *Parvocantharellus*

Cantharellus romagnesianus Eyssart. and Buyck, Cryptog. Mycol. 20(2): 108, 1999. Figures 4g, h and 8b

≡ *Cantharellus cibarius* var. *tenuis* Romagn., Doc. Mycol. 25(98–100): 422, 1995

Holotype: France, Dordogne, environs de Notre Dame de Sanilhac, dans auiguilles de *Pinus pinaster*, 26 September 1974, H. Romagnesi 74.268 (PC0085043!). ITS barcode GenBank: KX828783.

= *Cantharellus pseudominimus* Eyssart. and Buyck, Cryptog. Mycol. 20(2): 108, 1999 [nom. nov. for *Cantharellus minimus* L.L. Daniel]
= *Cantharellus cibarius* var. *minimus* Bigeard and H. Guill., Fl. Champ. Sup. France 2: 323, 1913 [Art. 58]
= *Cantharellus minimus* L.L. Daniel, Rev. Bretonne Bot. Pure Appl. 7: 2, 1912 [nom. illeg. Art. 53, non *Cantharellus minimus* Vaill. ex Roussel]
Lectotype [icon.]: Daniel, Rev. Bretonne Bot. Appl. 7: Figs. 1, 2, 3, 4, and 5, 1912, designated by Eyssartier et al. (1998).

= *Cantharellus gallaecicus* (Blanco-Dios) Olariaga in Olariaga and Salcedo, Anales Jard. Bot. Madrid 64(2): 222, 2007
= *Cantharellus cibarius* var. *gallaecicus* Blanco-Dios, Bol. Soc. Micol. Madrid 28: 181, 2004
Holotype: Spain, Sanxenxo, Nantes, 29TNG1597, 50 m, en bosque de *Pinus pinaster*, 25 October 1997, J.B. Blanco-Dios, LOU-Fungi 18010 (!).

= *Cantharellus lourizanianus* Blanco-Dios, Tarrelos 13: 8, 2011
Holotype: Spain, Pontevedra, Lourizán, 29TNG2895, 80 m, en talud bajo *Pinus pinaster* y *Quercus robur*, 17 November 2003, J.B. Blanco-Dios, LOU-Fungi 19494 (!). ITS barcode GenBank: KX828780.

= *Cantharellus romagnesianus* var. *parvisporus* Blanco-Dios, Tarrelos 13: 10, 2011
Holotype: Pontevedra, Lourizán, 29TNG2895, 80 m, en talud bajo *Pinus pinaster* y *Q. robur*, 13 November 2008, J.B. Blanco-Dios, LOU-Fungi 19504 (!). ITS barcode GenBank: KX828786.

Pileus 15–30(40) mm diam., slender, orange-yellow (5A7) to ochre-yellow (5A4–5), sometimes entirely grey brown (6B2, 6C3). Coating absent. Margin thin. **Hymenophore** with forked veins, often very spaced, pale yellow-ochre (5A2) to ochre-yellow (5A3–4) at first, sometimes white (5A1), not staining upon manipulation. **Stipe** 2.5–30 × 1.5–5(10) mm, cylindrical, often tapering downwards, pale ochre-yellow (5A2–3), sometimes white (5A1) or tinged orange-red (7A8) at the base. Surface smooth. Context white (5A1), sometimes rather strongly staining, white to ochre-yellow (5A6) underneath the pileus surface. **Spore print** not obtained. Reaction with iron salts reddish grey. **Spores** ellipsoid to reniform, sometimes constricted in the middle, smooth, (8)9–11.5(12.5) × 4–6(6.5) µm (L_m = 9.4–10.9, W_m = 4.7–5.4; Q_m = 1.71–2.28; n = 4). **Basidia** predominantly 5-spored, 70–86 × 9–12 µm. **Surface pileipellis hyphae** cylindrical to narrowly claviform, sometimes sinuous, thin-walled (<0.8 µm), with pale yellow content, 6–8(12) µm. Clamps abundant in all tissues.

Specimens examined: FRANCE. **Dordogne**: Forêt domaniale du Born, under *Picea excelsa*, 25 October 1997, P. Hériveau, EG97955 (PC0142170). Without locality, G. Eyssartier, GE07.031 (PC). ITALY. **Pordenone Prov**.: Ligont-Dardago, commune Budoia, 250 m, on damp soil, with *Carpinus betulus*, *Quercus robur* and *Corylus avellana*, 25 July 2009, E. Campo, EC 09.17 (PC). PORTUGAL. **Viseu**. Beiras, S of river Vouga, E of Arcozelo das Maias, in moss at roadside under *Pinus pinaster* and *Quercus suber*, 14 November 2000, J. Vesterholt, JV00663 (C-F-90396, PC). SPAIN. **Basque Country**: Gipuzkoa, Bilabona, under *Quercus rubra*, 16 June 2011, J. Martín, ARAN-Fungi A3007090A; July 2013, AH44218. Usurbil, Igartzazabal, under *Pinus radiata*, *Frangula alnus* and *Castanea sativa* on acidic soil, 24 May 2005, I. Olariaga, BIO-Fungi 9933. **Galicia**: Pontevedra, Cangas, under *Castanea sativa*, 23 June 2013, L. Rubio Casas, AH44788.

Commentary

Cantharellus romagnesianus shows a large variation in terms of overall habit, pileus colour, staining, colour of the stipe base and spore size, but our specimen sampling showed a very low sequence divergence. Typical basidiomata are recognized by their slender habit, orange-yellow colour, and thin-walled pileipellis hyphae. White albinistic basidiomata are rather frequent and typically found next to normal-coloured basidiomata (Olariaga et al. 2015). Specimens of *C. romagnesianus* with an orange-red stipe base (not as result of manipulation or age) are readily recognized as all other European species have a concolorous stipe base. *Cantharellus romagnesianus* shows a high variability in spore size. The holotype specimen of *C. romagnesianus* (PC0085043, 10–13 µm long) and collection AH44218 (8.5–9.5 µm long), have deviant spores but identical ITS sequences. *Cantharellus romagnesianus* is sister to *C. minor* Peck in our phylogeny (Fig. 1); both belong to *C.* subg. *Parvocantharellus*. Both species are phylogenetically distinct species applying GCPSR criteria.

Several names have been used to refer to *C. romagnesianus*. The specimens sampled here, mostly identified as *C. romagnesianus* or *C. pseudominimus,* showed almost identical sequences (only two insertions of 2 and 1 nucleotides in LOU-Fungi 18012) and this reinforces the idea that specimens attributed to both names belong in fact to a single species notwithstanding considerable variation in overall habit. Indeed, *C. pseudominimus* has been characterized by a small pileus size (up to 15 mm), spaced veins in the hymenophore, a short stipe and not staining flesh, in contrast with the slender habit, a longer stipe and staining flesh in *C. romagnesianus* (Eyssartier and Buyck 2000). The ITS-LSU sequences of the *C. pseudominimus* material reported by Eyssartier et al. (1998, EG97955) and of the type specimen of *C. romagnesianus* are identical. We infer from this that the basidioma habit, stipe length and staining are variable and that this gathering attributed to *C. pseudominimus* is conspecific with the type of *C. romagnesianus*. The lectotype of *C. pseudominimus* selected by Eyssartier et al. (1998) agrees thus with our broadened concept of *C. romagnesianus*. As the names *C. pseudominimus* and *C. romagnesianus* were published simultaneously and have equal priority at species level, we adopt here the name *C. romagnesianus* as prioritary over *C. pseudominimus* (art. 11.5), as the former has a type specimen that has been verified using morphological and molecular characters.

Cantharellus lourizanianus is also proposed here as synonym of *C. romagnesianus* based on examination and ITS-LSU data of the holotype specimen. *Cantharellus lourizanianus* was morphologically characterized by its short stipe and absence of staining upon manipulation and above all, the pink to violet hymenophore composed of very spaced veins. The holotype specimen, very meagre, contains basidiomata that appear not to be optimally developed. As noted above (Fig. 2), specimens with a violaceous grey hymenophore occur at least in *C. cibarius* and *C. romagnesianus*, and this characteristic appears not to be taxonomy informative in European species of *Cantharellus*. See notes on *Cantharellus neglectus* under Excluded and dubious taxa.

Discussion

Morphological and phylogenetic species recognition

The GCPSR approach proved useful for elucidating species boundaries in European *Cantharellus* and our phylogeny yieded strongly supported clades for all the lineages interpreted here as species. The 4-gene phylogeny presented here (Fig. 1) is consistent with the multilocus worldwide phylogeny by Buyck et al. (2013), but the relationships within the species of *C.* subg. *Cantharellus* are not fully resolved in our tree. This is probably due to the fact that our alignment lacks mtSSU sequences, and ITS2 sequences were included unlike in Buyck et al. (2013). The ITS region has been disregarded in a number of studies due to being unalignable across *Cantharellus*. Its suitability as a barcode marker has also been questioned because of the presence of divergent copies within one single genome (Kumari et al. 2011). Nevertheless, in Foltz et al. (2013), the ITS2 provided a good phylogenetic signal that contributed to species discrimination and a strongly supported phylogenetic inference. Phylogenies using ITS2 alone obtain low support for most species (Olariaga, unpublished), but ITS-LSU phylogenies provide supported nodes for some closely allied species (Olariaga et al. 2015). The ITS2 region shows a very low intraspecific variation and was used as a barcode marker to place type specimens in this work.

The phylogenetic knowledge generated here allows for a more objective evaluation of the morphological characters to delimit species. As generally accepted, microscopic characters are of limited use to identify *Cantharellus* (Buyck et al. 2014), but can be used to discriminate between certain sibling species pairs (e.g. Buyck et al. 2011a). This had not been explored for European chanterelles before. The pileal colour, the presence of a pileal coating, the staining upon manipulation and the hymenophore colour are intraspecifically variable characters. Thus, unique macroscopic characters that allow for unambiguous species identification are nearly absent (Fig. 2), but the combination of several characters can be used to guide species identification. For instance, specimens with a strongly white pileus can only be attributed to *C. alborufescens*, *C. roseofagetorum* and *C. pallens*, although not all specimens of those species show a white pileus. A lilac-purple coating is only present in *C. amethysteus* and the *C. alborufescens*-*C. ferruginascens* clade and excludes thus the rest of species. In this study, we found that the colour of the hymenophore of young basidiomata is a more reliable character to discriminate species. Hymenophore colour becomes more similar in aged basidiomata of nearly all species. Also the staining of basidiomata upon manipulation can be misleading, since it depends to a great extent also on basidioma age as well as on degree of tissue hydratation. Aged basidiomata of *C. ferruginascens*, a normally conspicuously staining species, can stain only weakly (AH44782), whereas young specimens of *C. cibarius*, a typically weakly or non-staining species, can stain rather strongly when collected in dry weather (BIO-Fungi 12701). The large variation in pileus and hymenophore colour, in presence of coating and in the degree of staining is largely attributed to the long-lived nature of basidiomata of *Cantharellus*, which have been observed to be able to grow during 90 days (Largent and Sime 1995; Norvell 1995). During such an unusually long period of growth, basidiomata colour and staining are subjected to a progressive development, and more or less influenced by meteorological conditions as well. Old basidiomata show high tendency to become entirely orange-yellow, to lack coating and to stain weakly in most species.

Morphological species recognition of European *Cantharellus* remains being challenging. Ideally, morphological species identification must be based on young and very fresh basidiomata, which are more reliable for undertaking character comparisons between species. Nevertheless, we provide in this study information on the intraspecific variability of the European species and establish more precise species boundaries. In our experience, European species of *Cantharellus* can be morphologically recognized with high certainty in most cases when applying the morphological species concepts proposed here. This study, based on the molecular sampling of 117 specimens, shows that 8 distinct phylogenetic species are present in Europe, in contrast with the 30 names published for European *Cantharellus*. Accordingly, we provide unambiguous interpretations of 18 names based on molecular data from type specimens, along with proposing a revised nomenclature. The reference sequences generated here will hopefully serve as molecular identification tools in the future, contributing to create precise distribution maps, specific information for assessment of *Cantharellus* species in redlisting initiatives and to commercialize chanterelles under their correct scientific name.

Biogeography and speciation

As discussed by Buyck et al. (2014) based on a worldwide phylogeny, the genus *Cantharellus* shows clear phylogeographic patterns. Long debate has existed about the relationships of North American and European *Cantharellus*. European names of *Cantharellus* have long been used in North America, especially *C. amethysteus* and *C. cibarius* (Corner 1966; Redhead et al. 1997; Buyck and Hofstetter 2011). The idea that Europe and the warm-temperate and subtropical parts of North America have species of *Cantharellus* in common, however, has been progressively abandoned (Redhead et al. 1997; Buyck et al. 2011), even though some European and North American species are phylogenetically very close; *Cantharellus cibarius* is sister to *C. roseocanus*, whereas *C. pallens* is sister to a clade encompassing *C. tenuithrix*, *C. phasmatis* and *C. flavus* (Fig. 1).

Species diversity of *Cantharellus* is considerably poorer in Europe compared to North America, where presently 22 species are recognized, without accounting for those that must be transferred to *Craterellus* or for new species in the process of being described (Buyck pers. obs.). This is a well-known phenomenon seemingly related to the presence of east–west oriented mountains that made migration difficult or impossible during recent glaciation periods (Schmitt 2009), but has received poor, if any, attention in fungi so far. We have shown here that *Cantharellus* is represented in Europe and North America by different species from three out of the six presently recognized subgenera (Buyck et al. 2014). Interestingly, chanterelles with a smooth hymenophore and therefore suspected to represent some of the oldest lineages in various subgenera (Buyck 2014) are only absent from Europe. Obtaining multigene data for Asian *Cantharellus* will be of paramount importance to obtain better insights on the dispersal routes and speciation events in the Northern Hemisphere and to obtain a better understanding of the evolutionary history of *Cantharellus*.

Excluded and dubious taxa

The majority of *Cantharellus* names described by early authors do not belong to *Cantharellus* s. str. as currently circumscribed. Providing a comprehensive list of names excluded from *Cantharellus* is therefore beyond the scope of this study. Under this heading we will restrict ourselves to: (a) European *Cantharellus* names of which we cannot provide concise interpretations but which apparently belong to *Cantharellus* s. str., and (b) names described recently in *Cantharellus* but which need to be excluded and transferred to other genera.

Cantharellus atrofuscus Contu, Vizzini, M. Carbone and Setti, Mycotaxon 110: 145 (2009)
Holotype: Italy, Sardegna, prov. Sassari, Tempio Pausania, loc. Baldo, in nemore frondoso acido cum Quercu subere, 26 October 2002, leg. G. Consiglio, AMB (!).

This species was compared to *Craterellus cinereus* (Pers.: Fr.) Maire when described, but it was placed in *Cantharellus* probably due to it having clamp connections (Contu et al. 2009). After examining the holotype, we conclude that it should be placed in *Craterellus* Pers.: Fr. The presence of clamps, the ovoid spores and the ITS molecular sequences obtained from the holotype suggest it is close or conspecific with *Craterellus tubaeformis* (Fr.: Fr.) Quél., to which it should be thoroughly compared.

Cantharellus borealis R.H. Petersen and Ryvarden, Svensk Bot. Tidskr. 65: 399 (1971)
Holotype: Norway, Finnmark, Porsanger, eastern slope of Madercocka, 17 August 1970, Ryvarden 6442 (TENN031663!).

This species should be placed in *Craterellus*. The spore size and the smooth hymenophore suggest it is close or conspecific with *Craterellus lutescens* (Fr.: Fr.) Fr., to which it should be compared.

Cantharellus neglectus (Souché) Eyssart. and Buyck, Bull. Soc. Mycol. France 116(2): 121, 2000.
≡ *Cantharellus cibarius* f. *neglectus* Souché, Bull. Soc. Mycol. 20: 39, 1904
≡ *Cantharellus cibarius* var. *neglectus* (Souché) Sacc., *Syll. Fung*. 17: 34, 1905
Type: No type specimen is known (Eyssartier and Buyck 2000).

Cantharellus neglectus was described as having more slender basidiomata than *C. cibarius*, a paler pileus colour and with emphasis on a distinct violaceous grey hymenophore (Souché 1904). As noted by Eyssartier and Buyck (2000), the colour photo provided by Michelland (1990) conforms to the original description of *C. cibarius* f. *neglectus* and shows a violaceus grey hymenophore as well. Nevertheless, the presence of violaceous tones in the hymenophore is disregarded here as a significant taxonomic character based on two specimens with that characteristic, (BIO-Fungi 10477, holotype of *C. lourizanianus*, Fig. 2), which belong to *C. cibarius* and *C. romagnesianus*, respectively. The examination and sequencing of Michelland's material might shed light on a more solid interpretation of *C. neglectus* in the future. In the meantime, we consider *C. neglectus* a name of doubtful interpretation.

Cantharellus pallidus Velen., České Houby 1: 78, 1920 [nom. illeg. Art. 53.1, non *Cantharellus pallidus* Yasuda in Lloyd, Mycol. Not. 47: 661, 1917]
Type: No type specimen is known (Eyssartier and Buyck 2000)

Based on the protologue, *Cantharellus pallidus* Velen. is probably an older but illegitimate name for *C. pallens* as pointed out by Eyssartier and Buyck (2000).

Cantharellus queletii (Ferry) Corner, Ann. Bot. Mem. 2: 56. 1966
≡ *Craterellus queletii* Ferry, Rev. Mycol. (Toulouse) 14: 81. 1892
Type: No type specimen is known (Eyssartier and Buyck 2000).

This name was coined for a small (pileus 30 mm; stipe 70 mm high), orange-yellow coloured species collected in the French Pyrenees (Ferry 1892). Eyssartier and Buyck (2000) considered that *C. queletii* might be a brighter coloured form of *C. romagnesianus*. Nevertheless, the size of the basidiomata and the height of the stipe appear too large or are in the upper range of size *C. romagnesianus*. The fact that the pileus is convex and slightly umbonate (usually infundibuliform in older specimens of European *Cantharellus*) in the figure, suggests that the basidioma depicted in the figure (pl. 126, Fig. 6) is young, and belongs to a species that becomes larger than that. Typically, the hymenophore in *C. romagnesianus* is also more pale coloured than described for *C. queletii*, and all the specimens studied here were collected at low elevation. Instead, it is here considered that *C. queletii* might be a synonym of *C. cibarius* or *C. amethysteus*, both common in the Pyrenees and producing entirely yellow-orange basidiomata with long stipe, at least sometimes. This view should be further substantiated by freshly collected material from the type locality.

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Compliance with ethical standards

Conflict of interest The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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