

Molecular systematics of *Craterellus*: cladistic analysis of nuclear LSU rDNA sequence data

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Considerable taxonomic confusion exists regarding many species of *Cantharellus*. Several taxa have been classified in either *Cantharellus* or *Craterellus* depending on which morphological characters were emphasised. Recent phylogenetic studies based on sequence analyses suggest that some species now classified in *Cantharellus* should be in *Craterellus*. We extracted DNA from dried herbarium specimens and amplified, sequenced and cladistically analysed approximately 650 bp of the 5' end of the nuclear large subunit ribosomal DNA gene. Our data confirm earlier results and provide molecular evidence for the classification of additional *Cantharellus* species (*Ca. ignicolor* and *Ca. lutescens*) within *Craterellus*. Furthermore, the data enable us to predict that all *Leptocantharellus*-like species currently classified within *Cantharellus* are more accurately classified within *Craterellus*. The species complexes of *Cr. tubaeformis* and *Cr. cornucopioides* were also investigated. These analyses did not support the monophyly of *Ca. tubaeformis* but the hypothesis that colour varieties of *Cr. cornucopioides* represent separate species was rejected.

INTRODUCTION

Chanterelles are highly appreciated edible wild mushrooms that are divided into two genera in Europe and North America: *Cantharellus* and *Craterellus* (*Pseudocraterellus* is *Craterellus* according to Feibelman *et al.*, 1997). Chanterelles form a significant part of the wild mushroom harvest (Molina *et al.*, 1993; Rowe, 1997; Persson & Mossberg, 1998; Liegel, Pilz & Love, 1998), with the world market for chanterelles estimated at £1 billion per year (Watling, 1997). Commercially, *Craterellus* species are collected less often than those of *Cantharellus*. Fresh and dried *Craterellus* species are, however, commonly sold in Europe and North America. Prices for fresh *Craterellus* (= *Cantharellus tubaeformis*) in Sweden can be around £10 per kilo, and dried £25 per kilo. Although *Craterellus* species are generally considered to be as tasty and flavourful as *Ca. cibarius*, they are often overlooked due to their less attractive appearance. Recent success in cultivating chanterelles (*Ca. cibarius*) (Danell & Camacho, 1997) has opened possibilities for commercial cultivation. Such techniques might be important as species of *Cantharellus* and *Craterellus* and other ectomycorrhizal species have shown a significant decrease of fruitbody formation in Europe over the last decades (Arnolds, 1995).

The economical importance and the evolutionary significance of the *Cantharellaceae* has resulted in considerable research on their ecology, physiology and phylogenetics (e.g. Danell & Eaker, 1992; Danell, Alström & Ternström, 1993;

Homola, 1993; Danell, 1994*b*, 1997; Feibelman, Bayman & Cibula, 1994; Norvell, 1995; Amaranthus & Russel, 1996; Feibelman, Bennet & Cibula, 1996; Hibbett *et al.*, 1997; Redhead, Norvell & Danell, 1997; Hibbett & Thorn, in press; Pine, Hibbett & Donoghue, 1999). Such studies rely on the ability to accurately identify species of *Cantharellus* and *Craterellus*. Chanterelles belong to the *Cantharellaceae*, which was originally placed in the *Aphylllophorales* (Donk, 1964; Corner, 1966; Jülich, 1984). Some more recent studies have classified species of *Craterellus* and *Cantharellus* in separate families (*Craterellaceae* and *Cantharellaceae*, respectively) within the *Cantharellales* (Hawksworth *et al.*, 1995; Pegler *et al.*, 1997). These two genera are, however, superficially similar and several of the species have been transferred at least once between them (Corner, 1966; Donk, 1969; Pegler, Roberts & Spooner, 1997). In other studies, all species of the *Cantharellaceae* have been merged into *Cantharellus* (Kühner & Romagnesi, 1953).

In the traditional classification (Fig. 1), species with clamp connections belong to *Cantharellus*, and species without clamp connections belong to *Craterellus* (e.g. Corner, 1966; Hansen & Knudsen, 1997; Pegler *et al.*, 1997; Phillips, 1991). *Craterellus* possesses thin, funnel-shaped basidiocarps with a hollow stipe that may also be highly reduced (Petersen, 1971). *Cantharellus* species which possess thin basidiocarps and hollow stipes were grouped together in subgenus *Leptocantharellus*, and the well-developed, fleshy basidiocarps with a solid stipe were placed in subgenus *Cantharellus* (Corner, 1966). Pigment contents indicate similarities between dark *Craterellus* and *Leptocantharellus* since they both contain large amounts of

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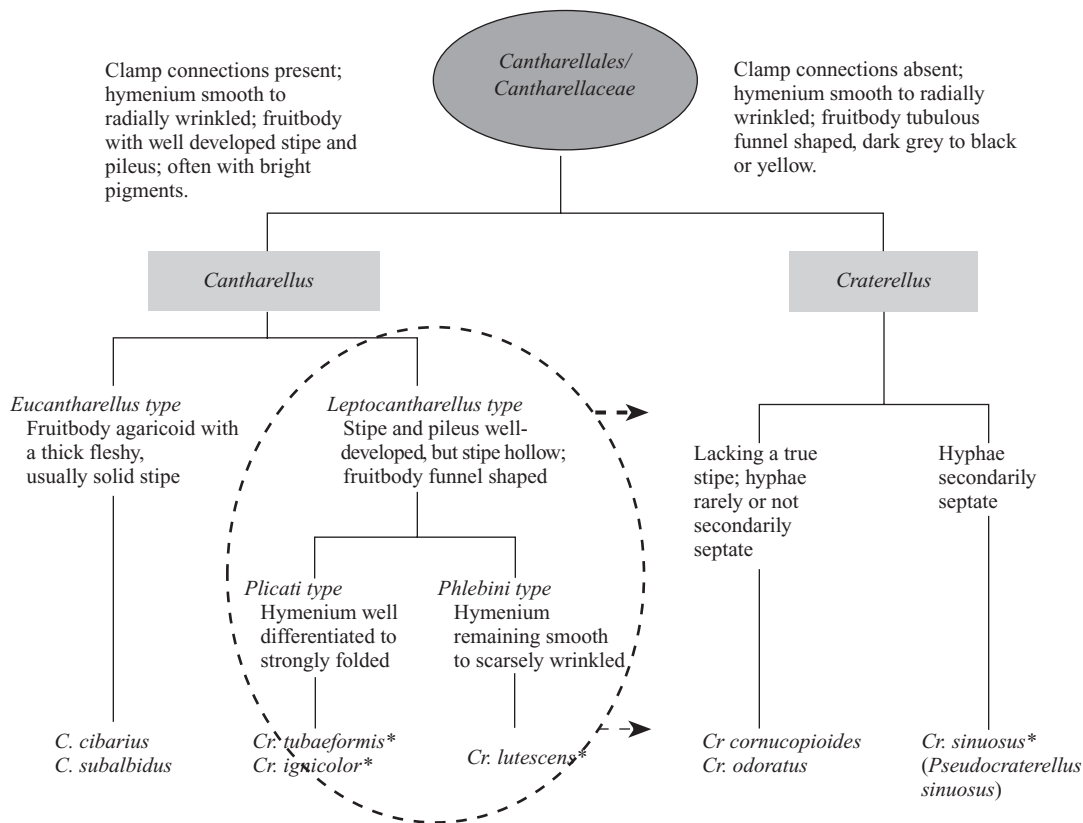


Fig. 1. Traditional classification based on morphological characters (Corner, 1966; Donk, 1969; Hansen & Knudsen, 1997; Pegler *et al.*, 1997). * Names according to this study and Feibelman *et al.* (1997).

neurosporene (7,8-dihydro- ψ - ψ -carotene), whereas β -carotene is more common in *Cantharellus* and yellow *Craterellus* (Fiasson *et al.*, 1970; Arpin & Fiasson, 1971; Gill & Steglich, 1987).

Recent phylogenetic studies from sequence analyses suggested that *Ca. tubaeformis*, a hollow-stiped species, should be placed in *Craterellus* (Feibelman *et al.*, 1997; Pine *et al.*, in press). The classification of Feibelman *et al.* (1997) has not been accepted in recent literature (Watling & Turnbull, 1998), illustrating the considerable taxonomic confusion regarding generic and species circumscriptions for several *Cantharellus* and *Craterellus* species. Two of the more problematic taxa are the *Cr. tubaeformis* and *Cr. cornucopioides* species complexes. The present study aimed to examine species circumscriptions for these complexes, and to test contrasting placements of subgenus *Leptocantharellus* in both *Cantharellus* and *Craterellus*.

MATERIAL AND METHODS

Taxa and sequences

Specimens for DNA analysis were selected to include numerous morphological taxa and to cover a wide geographical range (Table 1). Special emphasis was made on colour variants with allopatric and sympatric distributions. Sequence data from additional taxa were included from sequences available from GenBank and from unpublished data (Table 1). Where possible, at least two samples of each taxon were included. Specimens studied from personal collections are now deposited at the Botanical Museum, Uppsala (UPS).

We chose to study the nuclear LSU rDNA sequence because Feibelman *et al.* (1997) showed that it was useful for distinguishing species of *Cantharellus* and *Craterellus* and data from appropriate outgroup taxa were available.

DNA extraction, amplification and sequencing

DNA was extracted from dried herbarium specimens using a modified CTAB protocol (Gardes & Bruns, 1993; Danell, 1994a). Samples of 10–40 μ g of dried fruitbody fragments were homogenized with a plastic pestle in a microcentrifuge tube (1.5 ml) with 750 μ l lysisbuffer (100 mM Tris-HCl pH 9; 1.4 M NaCl; 20 mM EDTA; 2% cetyltrimethylammonium-bromide (CTAB); 0.2% mercaptoethanol) and incubated in 65 $^{\circ}$ C for 1 h, 600 μ l chloroform was added and the tube was briefly vortexed and centrifuged for 15 min. The aqueous phase was removed to a new tube, purified either by ethanol/isopropanol precipitation or GeneClean no. III (BIO 101, Inc. La Jolla, CA) and resuspended in 50 μ l ddH₂O. The DNA extracts were diluted 1:1–1:100 for use in the PCR reactions.

The 5' end of the nuclear-encoded large subunit ribosomal DNA (LSU rDNA) was amplified with primers LR0R and LR3 (Vilgalys & Sun, 1994). Primers were purchased from Oligos Etc. Inc. (Wilsonville, OR). Reaction mixtures comprised 1 μ l of diluted DNA in a 50 μ l mastermix containing 125 nM dNTP, 200 nM of each primer, 1.5 mM MgCl₂, 2.5 U of *Taq* DNA polymerase and 5.0 μ l PCR buffer 50 μ l reaction. The amplifications were conducted in a MJ Research PTC100 Thermocycler as follows: (1) 94 $^{\circ}$, 3 min; (2) 5 cycles of: (1)

Table 1. Sequenced taxa. Names according to collectors.

	Herbarium/GenBank accession no.	Geographic origin	Collector
<i>Cr. cornucopioides</i> (yellow form)	UPS F-11787/AF105296	Sweden (Norrtälje)	E. Danell <i>et al.</i>
<i>Cr. cornucopioides</i> (black form)	UPS F-11792/AF105297	Norway (Oslo)	G. Gulden
<i>Cr. cornucopioides</i> (black form)	UPS F-11800/AF105298	U.S.A. (NC)	E. Danell
<i>Cr. cornucopioides</i> (black form)	UPS F-11801/AF105299	U.S.A. (Monterey County, CA)	—
<i>Cr. konradii</i> × <i>cornucopioides</i>	HbO 53303/AF105300	Norway (Oslo)	G. Gulden
<i>Cr. konradii</i>	HbO 53302/AF105301	Norway (Oslo)	G. Gulden
<i>Ca. lutescens</i>	UPS F-11789/AF105302	Sweden (Brunskog, Värmland)	M. Dahlman
<i>Ca. lutescens</i>	UPS F-11790/AF105303	Sweden (Västerås)	E. Danell
<i>Ca. lutescens</i>	UPS F-11791/AF105304	Spain (Pinós, Lleida)	E. Florit <i>et al.</i>
<i>Cr. fallax</i>	UPS F-11798/AF105305	U.S.A. (MS)	E. Danell
<i>Cr. fallax</i> ^a	—	—	S. Rehner
<i>Cr. odoratus</i>	UPS F-11799/AF105306	U.S.A. (MS)	E. Danell
<i>Cr. odoratus</i> ^b	TF 1852/U87990	U.S.A. (MS)	T. Feibelman
<i>Ca. tubaeformis</i>	UPS F-11793/AF105307	Sweden (Uppsala)	E. Danell
<i>Ca. tubaeformis</i>	UPS F-11795/AF105308	U.S.A. (NC)	E. Danell
<i>Ca. tubaeformis</i>	OSC 49915/AF105309	U.S.A. (WA)	T. O'dell
<i>Ca. tubaeformis</i>	UPS F-11796/AF105310	U.S.A. (Oak Ridge, OR)	E. Danell
<i>Ca. tubaeformis</i>	UPS F-11797/AF105311	U.S.A. (Washburn, OR)	E. Danell
<i>Ca. infundibuliformis</i>	SFSU, DED 3406/AF105312	U.S.A. (NC)	D. E. Desjardin
<i>Ca. infundibuliformis</i>	OSC 41280/AF105313	U.S.A. (WA)	J. Trappe
<i>Ca. ignicolor</i>	UPS F-11794/AF105314	U.S.A. (NC)	E. Danell
<i>Ca. cf. cibarius</i> ^c	—	U.S.A. (OR)	S. Dunham
<i>Ca. cibarius</i> ^b	—/U87985	U.S.A.	T. Feibelman
<i>Ca. formosus</i>	—	U.S.A. (OR)	S. Dunham
<i>Ca. subalbidus</i>	—	U.S.A. (OR)	S. Dunham
<i>Ca. subalbidus</i> ^d	—	U.S.A. (OR)	A. Camacho
<i>Clavulina cristata</i>	—	U.S.A. (OR)	J. Spatafora
<i>Hydnum umbilicatum</i>	—	U.S.A. (OR)	J. Spatafora
<i>P. sinuosus</i> ^b	TF1802/U8799-	U.S.A.	T. Feibelman

^a Sequence received from S. Rehner.

^b GenBank sequence.

^c Sequence received from S. Dunham.

^d Sequence received from A. Camacho.

94°, 1 min; (II) 45°, 1 min; (III) 72°, 1 min; (3) 30 cycles of: (I) 94°, 1 min; (II) 50°, 1 min; (III) 72°, 1 min; (4) 72°, 5 min; (5) hold at 4°. PCR products were purified with Qiagen QIAquick PCR Purification spin columns (Qiagen Inc., Chatsworth, CA). PCR products were quantified by electrophoresis on a 1.0% agarose gel with ethidium bromide.

Approximately 650 bases at the 5' end of the nuclear ribosomal DNA were sequenced on both strands using primers LR0R and LR3 on an ABI 373 or 377 automated sequencer at the Central Service Laboratory at Oregon State University. Sequences included in the study have been submitted to the Genome Sequence Data Base (Table 1).

Alignments and analyses

Sequence assemblies and alignments were performed by direct examination using SeqApp version 0.6 (Gilbert, 1992). The final alignment included 547 bp. Maximum parsimony analyses were performed using the test version of PAUP* 4.0d64 (Swofford, 1998). *Clavulina cristata* and *Hydnum umbilicatum* were defined as outgroup taxa based upon the results of

Hibbett *et al.* (1997) and used for rooting the ingroup. Heuristic searches were conducted with the following settings: (i) stepwise random sequence addition; (ii) 100 replications of tree bisection-reconnection (TBR) branchswapping algorithm; and (iii) collapsing zero-length branches and saving all minimal-length trees (MULPARS). Both maximum parsimony and generalized (weighted) parsimony analyses were performed. Generalized parsimony analyses employed a step matrix to weight transversions twice that of transitions. Topological support was estimated *via* 500 bootstrap replications (Felsenstein, 1985) with the above setting except that MULPARS was inactivated. Alignment gaps were treated in two different ways: (i) gaps treated as missing data; and (ii) selected gap positions coded as a fifth character state 'I'. Alternative phylogenetic hypotheses that represented conflicting classifications were tested via the Kishino-Hasegawa test (1989) as implemented in PAUP* 4.0d65. The gap positions selected for recoding as a fifth character state were either unambiguously aligned across all taxa or were unambiguously aligned within *Craterellus*. In the latter case, corresponding positions were coded as missing in *Cantharellus*

and outgroup taxa (Bruns *et al.*, 1992). A new character 'I' was inserted to designate an insertion/deletion (indel) event of multiple bases (Alignments are available from J.W.S.)

RESULTS

The final LSU rDNA sequence alignment included 564 characters, of which 190 were potentially phylogenetically informative. Sixteen most parsimonious trees of 359 steps were inferred using maximum parsimony analyses with gaps treated as missing. The consistency index (CI) of these trees was 0.889 and the retention index (RI) was 0.950. Generalized parsimony analyses with gaps treated as missing resulted in four most parsimonious trees with CI and RI of 0.889 and 0.950, respectively. These trees were also 359 steps in length when measured with the unweighted characters. Alternative gap coding did not have a major effect on tree topology.

In the maximum parsimony analyses the basal node of *Craterellus* was not resolved, but in the generalized parsimony analyses all major polytomies occurring between species of *Craterellus* were resolved (Fig. 2). The four trees recovered in the generalized parsimony analyses were a subset of the 16 trees inferred in the maximum parsimony analyses and received the best $-\ln$ likelihood values in the Kishino-

Hasegawa test (Table 2). Those nodes that were not resolved in the maximum parsimony analyses but were in the generalized parsimony analyses did not receive strong bootstrap support and are denoted by an asterisk in Fig. 2.

Results from these analyses strongly support the reclassification of *Ca. tubaeformis*, *Ca. lutescens* and *Ca. ignicolor* within *Craterellus*. Kishino-Hasegawa tests were performed to test four alternative phylogenetic hypotheses that place the following taxa as members of *Cantharellus*: (i) *Ca.* subgenus *Leptocantharellus*, (ii) *Ca. tubaeformis*, (iii) *Ca. ignicolor*, and (iv) *Ca. lutescens*. In all cases, the constraint topologies received significantly worse $-\ln$ likelihood values and were rejected as significantly worse phylogenetic hypotheses with *P* values of < 0.05 (Table 2). Furthermore, these data do not support the recognition of *Cr. fallax* and *Cr. konradii* as unique species. Rather, we suggest that these species should be synonymized with *Cr. cornucopioides*. In contrast, the specimens sampled from the *Ca. tubaeformis* (= *Ca. infundibuliformis*) did not form a monophyletic group (Fig. 2). Two *Ca. tubaeformis* clades are represented in our analyses, one comprising specimens from Europe and eastern North America and one comprising specimens from the Pacific northwest (PNW) of North America. Based on these results together with earlier presented molecular data (Feibelman *et al.*, 1997) and supporting

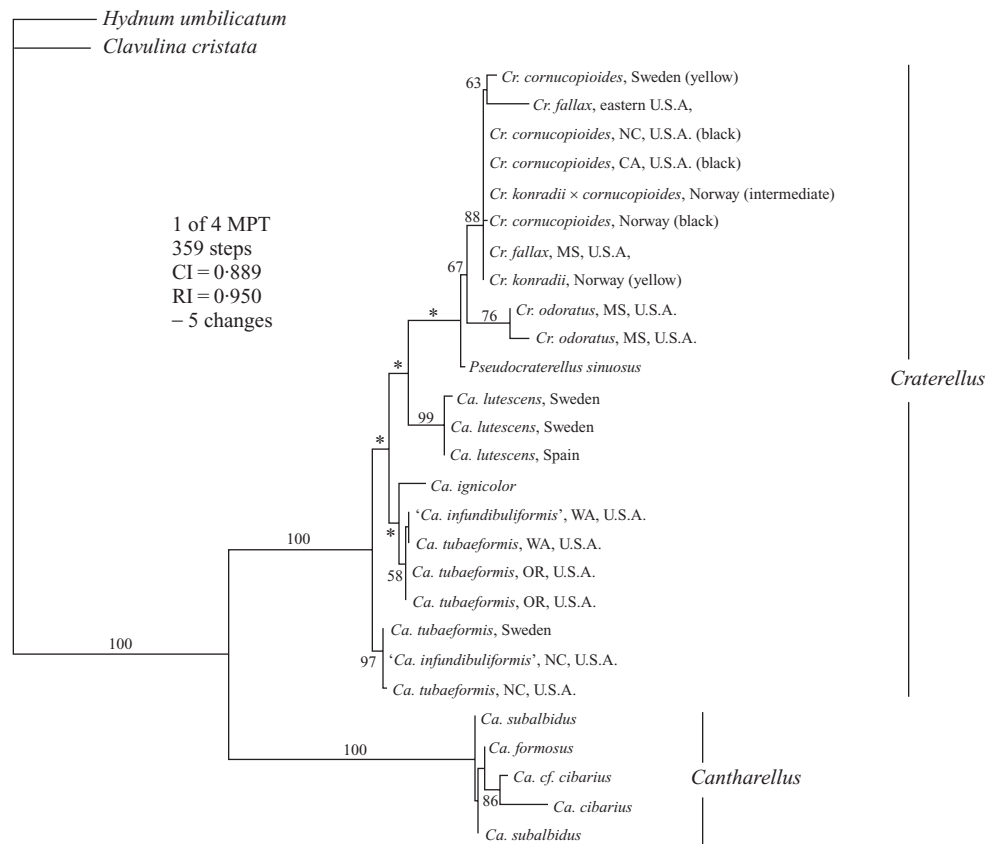


Fig. 2. Phylogenetic tree based on weighted (Tv:Ts) parsimony analyses of nuclear LSU rDNA sequence data (359 steps, CI = 0.889 and RI = 0.950). The tree shown here is one of the four most parsimonious trees; all polytomies were restricted to infraspecific rearrangements within the *Cr. cornucopioides* and the eastern N. American–European *Ca. tubaeformis* clades. Initial maximum parsimony analyses resulted in sixteen most parsimonious trees of 359 steps. The four trees from the weighted parsimony analyses were a subset of the maximum parsimony trees. Branches that collapse in the strict consensus of the maximum parsimony trees are designated by asterisks. Bootstrap values of $> 50\%$ from 500 replications are shown on respective nodes. Names are according to collector or herbarium label.

Table 2. Results from Kishino-Hasegawa tests of topological constraints of *Craterellus*–*Cantharellus* species relationships

Constraint	Trees (no.)	Tree length	RC	–ln likelihood	P value
Maximum parsimony ¹	16	359	0.844	2466.37–2470.20	1.000–0.6037
Tv:Ts parsimony ²	4	359	0.844	2466.37	1.000
<i>Leptocantharellus</i> – <i>Cantharellus</i>	12	383	0.767	2494.18–2500.62	> 0.05
<i>Ca. tubaeformis</i> – <i>Cantharellus</i>	4	383	0.767	2494.23	> 0.05
<i>Ca. ignicolor</i> – <i>Cantharellus</i>	48	386	0.757	2494.19–2506.48	> 0.05
<i>Ca. lutescens</i> – <i>Cantharellus</i>	166	385	0.760	2490.36–2500.8	> 0.05

¹ Most parsimonious trees from maximum parsimony analyses with gaps treated as missing.

² Most parsimonious trees from generalized parsimony analyses with gaps treated as missing and transversions weighted twice that of transitions.

morphological aspects, we formally propose the following taxonomic revision:

Craterellus lutescens (Pers.: Fr.) Fr. (Fries, 1838).

Synonyms: *Agaricus aurora* (Batsch, 1783), *Cantharellus aurora* (Kuyper, 1990), *Ca. xanthopus* (Duby, 1830), *Ca. lutescens* (Fries, 1821).

Craterellus ignicolor (R. H. Petersen) Dahlman, Danell & Spatafora, **comb. nov.**

Basionym: *Cantharellus ignicolor* R. H. Petersen, *Beihefte Nova Hedwigia* **51**: 183 (1975).

Craterellus tubaeformis (Fr.) Quél. (Quélet, 1888).

Basionym: *Cantharellus tubaeformis* (Fries, 1821).

Synonyms: *Ca. infundibuliformis* (Fries, 1838), *Cr. infundibuliformis* (Quélet, 1888).

Craterellus cornucopioides (L.: Fr.) Pers. (Persoon, 1825).

Synonyms: *Craterellus konradii* (Bourdot & Maire, 1930), *Cr. fallax* (Smith, 1968).

DISCUSSION

Two major clades corresponding to *Cantharellus* and *Craterellus* were inferred in these analyses (Fig. 2). *Craterellus* comprised five major lineages that included the *Cr. cornucopioides* complex, *Cr. odoratus*, *Ca. lutescens*, *Ca. tubaeformis* specimens from western and eastern North America and Europe and *Ca. ignicolor*. All taxa sampled in this study, which were morphologically grouped into the subgenus *Leptocantharellus*, displayed a phylogenetic affinity with *Craterellus* rather than with *Cantharellus*. These results are consistent with those of Feibelman *et al.* (1997), who placed *Ca. tubaeformis* in *Craterellus*. In addition to *Ca. tubaeformis*, this study indicates that *Ca. lutescens* and *Ca. ignicolor* should be reclassified in *Craterellus* as well. From these results and those of Feibelman *et al.* (1997) we predict that all *Leptocantharellus* species currently classified within *Cantharellus* are more accurately classified within *Craterellus*. The presence of clamp connections is not restricted to *Cantharellus* but also occurs in *Craterellus*. The hollow stipe seems to be a synapomorphy for *Craterellus*. A species such as *Ca. melanoxeros* might, however, belong to *Craterellus* in spite of its solid stipe, as indicated by its umbilicate or infundibuliform cap and dark pigments (Corner, 1966; Gill & Steglich, 1987; Pegler *et al.*, 1997; Persson & Mossberg, 1997). Judging from our phylogenetic tree, the

amount of β -carotene produced does not seem to be a useful character for separating *Cantharellus* from *Craterellus* since *Ca. cibarius*, *Cr. fallax* and *Cr. odoratus* contain large amounts in contrast to *Cr. cornucopioides* (Gill & Steglich, 1987).

The *Craterellus tubaeformis* complex

The distinction between *Cr. tubaeformis* and *Cr. infundibuliformis* has long been disputed. Both epithets were coined by Fries (1821, 1838). They have been considered separate by some (e.g. Corner, 1966; Smith, 1968), while others, including several of the most contemporary publications (Donk, 1969; Bigelow, 1978; Thiers, 1982; Ryman & Holmåsén, 1984; Pegler *et al.*, 1997; Persson & Mossberg, 1997), consider the two species to be synonymous. Following the latter treatment of conspecificity, the older name is *Cr. tubaeformis* and has priority over the name *Cr. infundibuliformis* (Donk, 1969). This decision of nomenclatorial priority was also the conclusion of Kuyper (1990).

Herbarium specimens labelled as *Cr. tubaeformis* or *Cr. infundibuliformis* were sampled from western and eastern North America and Europe. *Craterellus tubaeformis* and *Cr. infundibuliformis* specimens from the Pacific North West America form a distinct clade separate from the clade comprising *Cr. tubaeformis* and *Cr. infundibuliformis* specimens from Europe and eastern North America. These results do not support the grouping of taxa under the names *Cr. tubaeformis* and *Cr. infundibuliformis*. Rather, they support unique clades that are correlated with geographic distributions. The name *Cr. tubaeformis* is most accurately applied to the Europe/eastern North America clade since it was originally described from Sweden. If future research confirms a distinct species in western North America, then a new name will be required. As *Cr. infundibuliformis* is considered a synonym of *Cr. tubaeformis* that name should not be used.

Also it is noted that Pegler *et al.* (1997) used the name *Cantharellus tubiformis*, but the epithet *tubiformis* is an orthographic error. The correct epithet is *tubaeformis* according to Art. 73 (orthography of names and epithets, cf. Recommendation 73.G I(b)), (Kuyper, 1990).

The *Craterellus cornucopioides* complex

White, pink, yellow and greyish variants of *Cr. cornucopioides* exist, and have been reported from e.g. North America (Arora,

1986), Sweden (Persson & Mossberg, 1995), Norway (Gulden & Høiland, 1989), Italy (Apicella & Vizzini, 1994) and France (Maire, 1930; Heim, 1960). Taxonomically they have either been treated as varieties of *Cr. cornucopioides* or as distinct species (e.g. *Cr. konradii*, a pale yellow form).

This study does not support the recognition of species of the *Cr. cornucopioides* complex based on colour variation or geographic distribution. Rather, *Cr. cornucopioides* is recognized as a morphologically heterogeneous species that includes colour variants that have been classified as *Cr. konradii* and *Cr. fallax*. This concept is in accordance with observations by Apicella & Vizzini (1994) who found intermediate stages between *Cr. cornucopioides* and *Cr. konradii* at one single spot. Additionally, no geographic subdivision across North America was detected but other sequences should be studied to further elucidate occurrence of species and populations.

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