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The fungal genus *Tricholomopsis* (Agaricales) in New Zealand, including *Tricholomopsis scabra sp. nov.*

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Abstract

The status of the genus *Tricholomopsis* (Agaricales) in New Zealand is reviewed. *T. rutilans* is a species described from the northern hemisphere and recorded from plantations of exotic *Pinus radiata* in New Zealand. Historical collections identified as *T. rutilans* were subjected to morphological and phylogenetic analysis. The results show that most of these collections refer to *T. ornaticeps*, originally described from New Zealand native forests. The presence in New Zealand of *T. rutilans* was not confirmed. Collections of *Tricholomopsis* from native forests and bush also include a newly described species, *T. scabra*, which is characterised by a distinctly scabrous pileus. The new species is phylogenetically and morphologically distinct but related to *T. ornaticeps*. *T. ornaticeps* and *T. scabra* are currently known only from New Zealand and the former has extended its habitat to include exotic conifer plantations.

Keywords: conifer plantations, *Pinus radiata*, Southern Hemisphere, *Tricholomopsis rutilans*, Agaricales

Introduction

Tricholomopsis Singer (1939: 56) is a genus of saprophytic agaricoid fungi with yellow lamellae, a fibrillose or squamulose dry pileus with red or yellow tones, and it is usually associated with decaying wood. The spores are smooth and inamyloid, the hyphae are clamped, and the lamellae have a sterile edge and prominent cheilocystidia. Thirty-four species are accepted in the genus on the basis of the current literature (see supplementary materials). A number of recent phylogenetic studies have included some species from Europe (Holec & Kolařík 2012, Olariaga *et al.* 2015), Asia (Razaq *et al.* 2012) and North America (Saar & Voitk 2015). Species from the Southern Hemisphere have not been included in any analyses to date.

Recent phylogenetic studies have not fully resolved the higher classification of *Tricholomopsis* (type species *T. rutilans* (Schaeff.) Singer (Singer 1939)). Lodge *et al.* (2014) found *Tricholomopsis rutilans* and *T. decora* (Fr.) Singer (Singer 1939), together with *Typhula phacorrhiza* (Reichard) Fr., *Macrotyphula fistulosa* (Holmsk.) R.H. Petersen, *Pleurocybella porrigens* (Pers.) Singer and *Phyllotopsis sp.,* within a clade basal to the hygrophoroid group. *Typhula phacorrhiza* is the type species of *Typhula* (Persoon) Fries (1818: 296), suggesting this clade may represent the Typhulaceae. This clade has been recovered in a number of studies (Dentinger *et al.* 2006, Lawrey *et al.* 2009, Matheny *et al.* 2006). The affiliation of *Tricholomopsis* to the Typhulaceae and the hygrophoroid clade informed our choice of comparative sequenced species and outgroup for the phylogenetic analysis.

Two species of *Tricholomopsis* have previously been recognised in New Zealand. *T. rutilans* has been recorded as an introduced species associated with decaying wood in exotic *Pinus radiata* plantations (Horak 1971, Taylor 1981, Hood 1992, Ridley 2006, NZFUNGI2 2016). *Tricholomopsis ornaticeps* (G. Stev.) E. Horak (Horak 1971) was described as an indigenous fungus and has been recorded from native beech and podocarp forests (Stevenson 1964, NZFUNGI2 2016). Differences in texture and ecology have been used to separate the species (Hood 1992). However, a painting of material identified as *T. rutilans* in New Zealand (Taylor, 1981, Fig. 3) shows a pileus colouration and texture different to typical European specimens of *T. rutilans*. In addition, morphological examination of collections identified as *T. ornaticeps* in the national fungarium (PDD) indicated the name was being used for two different taxa. Hood (1992) also noted variability in this species. This study, using morphological and phylogenetic data, was carried out to verify New Zealand collections of *T. rutilans* in order to establish the true identity of *T. ornaticeps*.

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Material & Methods

Seventeen collections of *Tricholomopsis* species from New Zealand were examined (Table 1).

TABLE 1. Material examined.

Original identification	Revised identification	Fungarium accession	Collector's number	Collector	Substrate/habitat	Locality	Date
T. rutilans	*T. ornaticeps*	PDD 57441		P.K. Buchanan	*Pinus radiata* wood	New Zealand	4 May 1990
T. rutilans	*T. ornaticeps*	PDD 82501		G. Ridley	*Pinus radiata* wood	New Zealand	2005
T. rutilans	*T. ornaticep*	PDD 84216	GMT 536	L. Taylor	Nothofagaceae wood	New Zealand	1970
T. rutilans	*T. ornaticeps*	PDD 86173	GMT 151	L. Taylor		New Zealand	3 Sep. 1963
T. rutilans	*T. ornaticeps*	PDD 31126		R.F.R. McNabb	*Larix decidua* wood	New Zealand	12 May 1970
T. rutilans	*T. ornaticeps*	PDD 84171	GMT 433	G.M. Taylor	*Pinus radiata* wood	New Zealand	14 Apr. 1968
T. ornaticeps	*T. ornaticeps*	PDD 90602		T. Aldridge	*Lophozonus menziesii* wood	New Zealand	8 Mar. 1981
T. ornaticeps	*T. ornaticeps*	PDD 72909	ZT8735	E. Horak	Nothofagacae forest	New Zealand	24 Mar. 2000
T. ornaticeps	*T. ornaticeps*	PDD 102517	PL19509	P. Leonard	*Fuscospora fusca* wood	New Zealand	2 May 2009
T. ornaticeps	*T. ornaticeps*	PDD 102769	PL 1110	P. Leonard	*Lophozonus menziesii* wood	New Zealand	13 Jan. 2010
Tricholoma. ornaticeps (Holotype)	*Tricholomopsis ornaticeps*	K(M) 177251	GS 237	E. Cone		New Zealand	20 Apr. 1947
T. rutilans	*T. rutilans*	PDD 24163		D. Reid		UK	3 Oct. 1962
T. rutilans	*T. scabra*	PDD 78235		P. White	*Kunzea* wood	New Zealand	9 May 2003
T. rutilans	*T. scabra*	PDD 34860		J.M. Dingley	*Leptospermum* scrub	New Zealand	26 May 1976
T. ornaticeps	*T. scabra*	PDD 81264	CSAK155	C. Shirley	*Kunzea* wood	New Zealand	2 Jun. 2004
Tricholomopsis	*T. scabra*	PDD 102100	CSAK385	C. Shirley	Podocarp forest	New Zealand	10 Jul. 2010
Tricholomopsis	*T. scabra* (Holotype)	PDD 102579	CSAK379	C. Shirley	*Leptospermum* scrub	New Zealand	8 May 2011

Morphological studies:—Colours for *T. scabra* are based on standard plates (Kornerup 1978). Spore dimensions are provided as the mean and standard deviation of a stated number of measurements. Standard deviation statistics from spore measurements of different fruitbodies/gatherings were averaged using standard formulae. Dried fungarium material was re-hydrated and mounted in 10% potassium hydroxide (KOH) or Melzer's reagent. Material was hand-sectioned. Some micrographs were obtained under differential interference contrast (DIC) illumination. All New Zealand material is deposited in the New Zealand Fungarium (PDD). Additional images, field notes and annotations associated with all New Zealand collections are available online through the Systematic Collection Data (SCD 2016) website of Landcare Research, New Zealand.

Sequence analysis protocols:—Sequence data were obtained for the rDNA internal transcribed spacer (ITS) region for 9 collections, and the D1–D2 domains of the 28S rDNA large subunit (LSU) for 8 collections (Table 2). A small amount of fruitbody material was ground to a fine powder with a sterile steel ball. Total genomic DNA was extracted from each sample above using the DNeasy 96 Plant kit, using QIAcube HT system (Qiagen Inc., USA). The standard primer pairs ITS1F/ITS4 and LR0R/LR5 were used for polymerase chain reaction (PCR). The PCR conditions for ITS and LSU were 3 min at 94°C, then 35 cycles of 94°C for 30 s, 52°C for 30 s, 72°C for 40 s, and then 7 min at 72°C. DNA sequences were obtained in both directions on an Applied Biosystems 3500 × l genetic analyser using BigDye v3.1 chemistry.

Additional sequences of *Tricholomopsis* species were downloaded from GenBank (see supplementary materials). Sequences from *Hygrophorus pudorinus* were used as the outgroup. Sequence data management was carried out using Geneious version 9.1.5 (Kearse *et al.* 2012). Sequence alignments were obtained using MAFFT v7.222 (Katoh *et al.* 2002), using default settings within Geneious. A concatenated alignment of ITS + LSU was generated. We used the CIPRES Science Gateway (Miller *et al.* 2010) to perform the phylogenetic analysis. A maximum likelihood analysis was carried out using RAxML v. 8.2 (Stamatakis 2014) with a GTRGAMMA model and 1000 bootstrap replicates to assess branch support.

Results

Morphological and phylogenetic analysis (Fig. 1) indicates that two New Zealand species are represented by the sequenced samples: *T. ornaticeps* and the newly described *T. scabra*. In the phylogenetic analysis these species are distinct and are grouped with an undescribed species from northern Australia. The newly described *T. scabra* is morphologically distinguished from all other described species in the genus by its very scabrous pileus and its habitat in indigenous tea-tree scrub (*Kunzea spp.* and *Leptospermum spp.*) and podocarp forests in New Zealand. The data show *T. ornaticeps* is present in both indigenous southern beech forests (*Fuscopora* and *Lophozonus spp*.) and exotic plantations of *Pinus radiata*. *Tricholomopsis ornaticeps* has a less densely scabrous pileus and is distinguished from *T. rutilans* by the pileus scale colour being predominantly reddish-brown rather than plum-coloured, and minutely scaly rather than fibrillose. Both New Zealand species are not always found on rotting wood but are also recorded as terrestrial. In addition, the shape and size of cheilocystidia and spores easily separate *T. ornaticeps* and *T. scabra* from *T. rutilans* (see Key). Our study did not confirm the presence of *T. rutilans* in New Zealand, although one poorly preserved collection may represent this species (PDD 36529). The current data do not rule out the presence of *T. rutilans* in New Zealand conifer plantations but do show that the majority of existing collections have been misidentified.

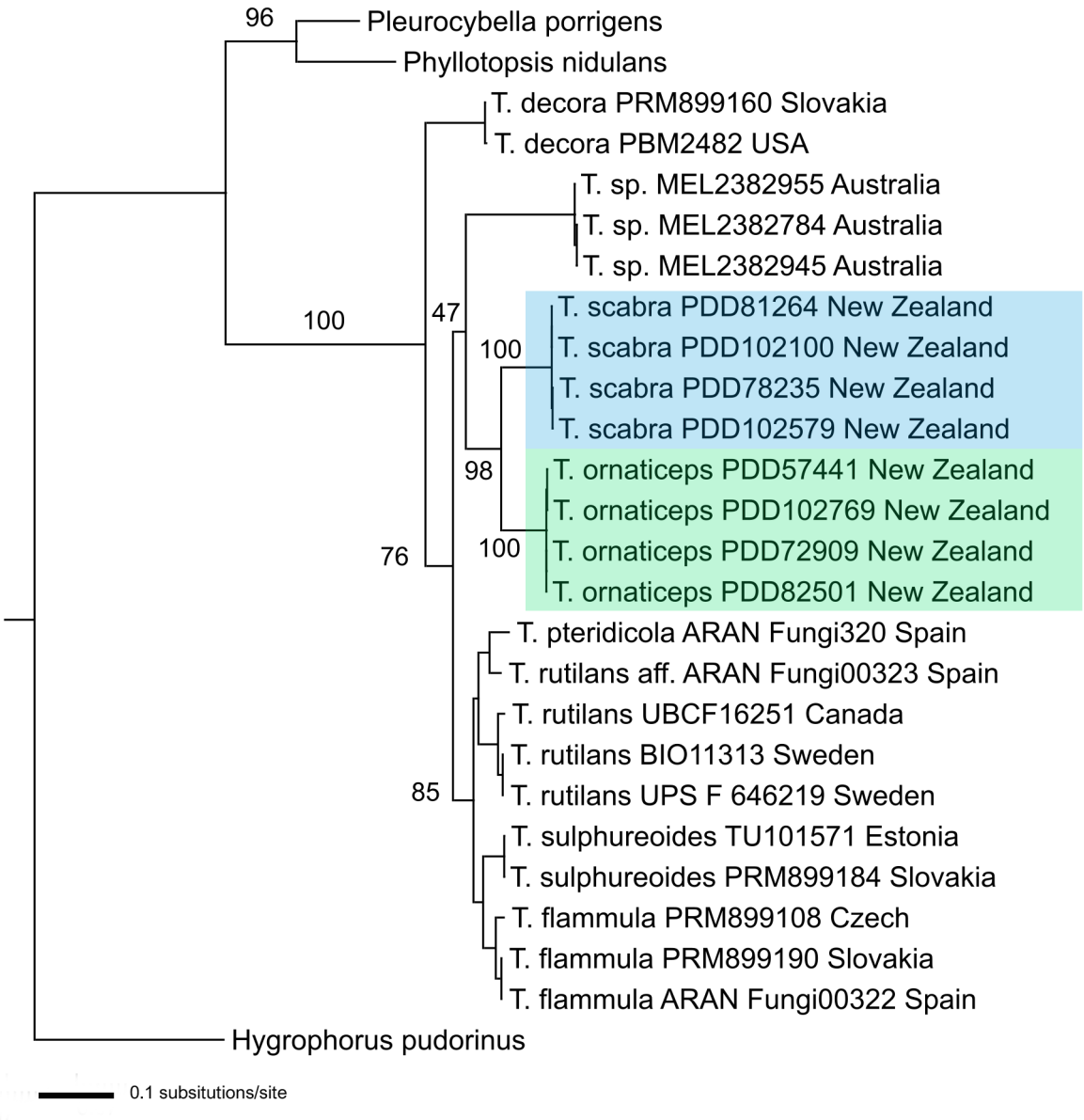

FIGURE 1. Best maximum likelihood phylogenetic tree for *Tricholomopsis* species using concatenated ITS + LSU dataset. Bootstrap support is indicated for relevant branches. Outgroup *Hygrophorus pudorinus*.

Discussion

The majority of existing collections identified as *T. rutilans* from New Zealand exotic pine plantations in the PDD fungarium refer to *T. ornaticeps*. This raises the question of the origin of *T. ornaticeps*. Is this an indigenous fungus that has taken advantage of a new niche in New Zealand exotic conifer plantations, or is it an introduced fungus that has invaded both indigenous beech forest and exotic conifer plantations? There are existing examples of saprophytic indigenous fungi present in New Zealand exotic plantations; for example, *Singerocybe clitocyboides* (Cooke & Massee) Zhu L. Yang, J. Qin & Ratkowsky and *Pholiota multicingulata* E. Horak (NZFUNGI2 2016). In addition, New Zealand *Pinus radiata* plantations have exotic ectomycorrhizal fungi from both North America, e.g. *Suillus pungens* Thiers & A.H. Smith (syn. *S. subacerbus*) and Europe, e.g. *Tricholoma terreum* (Schaeff.) P. Kumm. (NZFUNGI2 2016).

The phylogenetic data presented for *Tricholomopsis*, based on relatively poor sampling of species in the genus, show a clade with New Zealand and Australian taxa. The clade is poorly supported in the current analysis, but may indicate an Australasian origin for *T. ornaticeps* and *T. scabra*. However, 8 species of *Tricholomopsis* species have been described from Asia (see supplementary materials). These species are not represented by any available sequence data. Their phylogenetic relationship with Australasian samples may prove informative in resolving the origin of New Zealand species, either as a recent introduction through anthropogenic means, or through historical natural dispersal.

Conclusion

Most historical collections of *T. rutilans* in New Zealand exotic pine plantations are shown to be misidentifications of *Tricholomopsis ornaticeps*, originally described from New Zealand beech forest. The species is present in both indigenous and exotic forests. The origin of *T. ornaticeps* remains uncertain, but it is likely to be an indigenous species which has invaded pine plantations. A distinct and newly described species, *T. scabra*, has been confused with *T. ornaticeps* and is present in indigenous tea-tree and podocarp forests.

Taxonomy

Tricholomopsis scabra J.A. Cooper *sp. nov*. (Fig. 2)

IndexFungorum IF552507

Holotype PDD 102579. New Zealand, North Island. ITS KY010823. LSU KY010832.

Etymology:—scabra, referring to the pileus, which is covered in coarse scaly tufts of agglutinate hyphae.

Diagnosis:—Distinguished from all other species of *Tricholomopsis* by the degree of scabrosity of the pileus and habitat in tea-tree scrub and podocarp forests of New Zealand.

Macro-morphology:—Pileus 60–100 mm diam., convex becoming concave, with lightly inrolled margin. Base colour light orange (6A5) to orange (6A6) overlaid with a dense covering of radially arranged erect fibrous scales, dull red (8C4) to reddish brown (8E7 to 9F8) in colour. Stipe 80–120 mm × 7–12 mm, orange (6A6) to reddish brown (8E8), with coarse, longitudinally arranged surface fibrils. Lamellae pale orange (5A4 to 5A5), edge entire, with lamellulae. Spore print white. Gregarious in litter on the ground and associated with base of standing dead trees.

Micro-morphology:—Spores broadly ellipsoid, neither amyloid nor dextrinoid, hyaline, with refractive wall, with hilar appendage, length 6.6 µm ($\sigma = 0.34$) × 5.0 µm ($\sigma = 0.31$), Q = 1.30 ($\sigma = 0.10$), n = 20. Average of 5 collections: 6.3 µm ($\sigma = 0.39$) × 5.3 µm ($\sigma = 0.32$), Q = 1.24 ($\sigma = 0.08$), n = 5 × 20. Basidia 25–35 × 6–8 µm, 4-spored. Lamella edge sterile. Cheilocystidia cylindrical to clavate, 50–80 × 6–12 µm, 1- or 2-septate, occasionally with yellow plasmatic pigment. Clamp connections present in all tissue. Pleurocystidia absent. Pileipellis a cutis of loosely woven hyphae about 5 µm diam.; scales of loose to dense aggregations of erect hyphae, 5–10 µm diam., brown in KOH.

Material examined:—NEW ZEALAND. North Island, Katikati, Aongatete, on root of dead standing tree of *Kunzea*, 9 May 2003, P. White, PDD 78235. NEW ZEALAND. North Island, Waitakere Ranges, Clark Bush Track, on bark at base of *Leptospermum* tree, 26 May 1976, J.M. Dingley, W.S.M. Versluys, PDD 34860. NEW ZEALAND. North Island, Manukau, Murphy's Bush, 2 June 2004, C. Shirley (CS AK155), PDD 81264. NEW ZEALAND. North

Island, Manukau City, Wairere Road, Totara Park, on ground, 10 July 2007, C. Shirley (CS AK385), PDD 102100. NEW ZEALAND. North Island, Waitakere, Upper Nihotupu Dam track, Piha Rd, in litter associated with *Leptospermum sp*., 8 May 2011, C. Shirley (CSAK379), PDD 102579 (Holotype).

Habitat and distribution:—in tea-tree scrub (*Kunzea spp*. & *Leptospermum spp*.), and podocarp-dominated forest in New Zealand.

Comments:—*T. scabra* (Fig. 2) is macroscopically more similar to *T. rutilans* than to *T. ornaticeps* because it often shows a dominant reddish-brown colouration to the pileus, which is absent in *T. ornaticeps*. The 2 species are easily distinguished by the degree of pileus scabrosity in *T. scabra*, its smaller stature, much smaller cheilocystidia, and habitat.

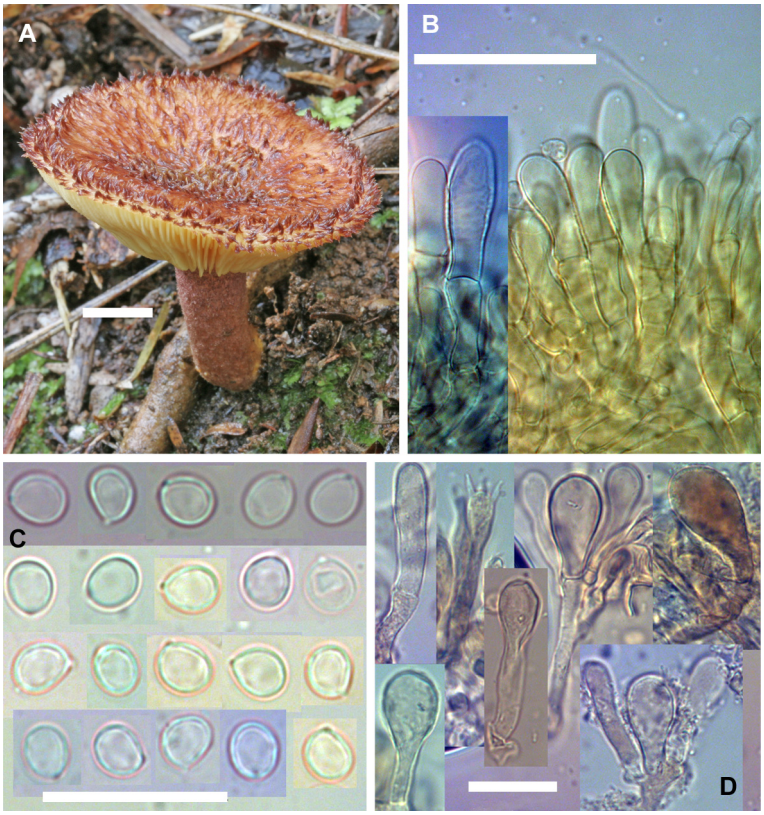

FIGURE 2. *Tricholomopsis scabra*. A) fruitbody, PDD 102579 (holotype), scale = 15 mm; B) cheilocystidia (composite image), PDD 102579 (holotype), scale = 40 µm; C) spores (composite image), PDD 102579 (holotype), scale = 20 µm; D) cheilocystidia and basidium (composite image), PDD 102100, scale = 20 µm. Photos: A by Clive Shirley, B, C, D by Jerry Cooper.

Tricholomopsis ornaticeps (G. Stev.) E. Horak

The following description is emended from Stevenson (1964), Horak (1971), and examination of New Zealand collections, including the holotype, enumerated in Table 1.

Macro-morphology:—Pileus 70–80 mm diam., convex with down-rolled margin becoming centrally depressed, ochraceous to saffron yellow, thickly covered with minute brown fibrillose scales. Lamellae moderately distant, attachment sinuate, yellow, staining brown at edges. Stipe 30 × 10 mm, creamy above, ochraceous at base, fibrillose-striate. Context creamy yellow in pileus and continuous with stipe. Spore print white. Gregarious on ground and associated with decaying wood.

Micro-morphology:—Spores oval to subcylindrical, neither amyloid nor dextrinoid, hyaline, thin-walled, with hilar appendage, length 8.3 µm (σ = 0.54) × 4.3 µm (σ = 0.32), Q = 2.0 (σ = 0.16), n = 20. Basidia 20–40 × 8–10 µm, narrowly clavate, 4-spored. Lamella edge sterile. Cheilocystidia conspicuous, thin-walled, some with yellow plasmatic pigment in KOH, 30–100 µm long × 10–30 µm diam., multi-septate, constricted at septa and often appearing like chains, terminal cells obovoid to broadly cylindrical. Clamp connections present in all tissue. Pleurocystidia absent. Pileipellis a cutis of loosely woven hyphae about 5 µm diam.; scales are aggregations of parallel hyphae 3–5 µm diam., with thickened walls which are rusty brown in transmitted light.

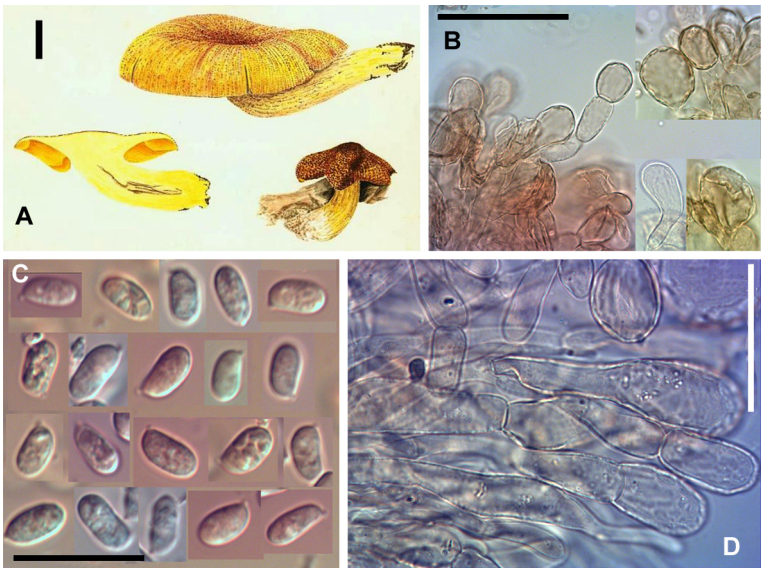

FIGURE 3. *Tricholomopsis ornaticeps*. A) water colour (G.M. Taylor), PDD 84171, scale 15 mm; B) cheilocystidia (composite image), PDD 82501, scale = 75 µm; C) spores (composite image), PDD 84171, scale = 20 µm; D) cheilocystidia, PDD 102517, scale = 40 µm. Photos: B, C, D by Jerry Cooper.

Habitat and distribution:—occasional in North Island and upper South Island in native beech forest, and in exotic conifer plantations of *Pinus radiata* and *Larix spp*.

Comments:—T. ornaticeps (Fig. 3) is easily distinguished microscopically by its elongate spores and cheilocystidia often appearing to be chained. Macroscopically it is distinguished from *T. rutilans* by the lack of plum colours, and from *T. scabra* by its less scabrous pileus and occurrence in beech forest and plantations.

TABLE 2. Sequences generated for the analysis.

Name	Country	Voucher	ITS GenBank/Unite accession	LSU GenBank accession
T. ornaticeps	New Zealand	PDD 57441	KY010816	KY010825
T. ornaticeps	New Zealand	PDD 82501	KY010820	KY010827
T. ornaticeps	New Zealand	PDD 72909	KY010817	KY010826
T. ornaticeps	New Zealand	PDD 102769	KY010824	KY010828
T. ornaticeps	New Zealand	PDD 102517	KY010822	
T. scabra	New Zealand	PDD 102579	KY010823	KY010832
T. scabra	New Zealand	PDD 102100	KY010821	KY010831
T. scabra	New Zealand	PDD 78235	KY010818	KY010829
T. scabra	New Zealand	PDD 81264	KY010819	KY010830

Tricholomopsis rutilans (Schaeff.) Singer

The following description of European material after T. Boekhout & M.E. Noordeloos in Bas *at al*. 1999 and material enumerated in Table 1.

Macro-morphology:—Pileus 20–160 mm, convex, expanding applanate, usually with low, broad umbo and undulating marginal zone when old, purplish-reddish-brown at centre, golden yellow towards margin, covered with purplish-reddish fibrils or minute squamules, dry. Lamellae crowded, adnate or sinuate, pale yellow to yellow, brownish edge. Stipe 25–85 × 3–25 mm, cylindrical or clavate, usually connate, solid finally fistulose, pale yellow at apex, golden yellow below, with purplish-red fibrillose covering. Context yellow-white in pileus and apex of stipe, pale golden yellow in basal part of stipe. Smell rather weak, pleasant. Taste mild or somewhat astringent. Spore print white. Solitary or caespitose on freshly cut or decayed wood of conifers, causing white rot.

Micro-morphology:—Spores broadly ellipsoid to ellipsoid with hilar appendage, hyaline, thin-walled, neither amyloid nor dextrinoid, length 6.5 µm (σ = 0.28) × 4.9 µm (σ = 0.26), Q = 1.32 (σ = 0.06), n = 21. Basidia 35–45 × 6.0–8.0 µm, narrowly clavate, 4-spored. Lamella edge sterile. Cheilocystidia 40–120 × 12–25 µm, clavate, often with brown, intracellular pigment. Pleurocystidia absent or scarce. Pileipellis a cutis with transitions to a trichoderm, made

up of clavate terminal elements, 5.0–15 µm wide. Pigment purplish-brown, intracelluar in pileipellis and stipitipellis. Stipitipellis a cutis with transitions to a trichoderm, made up of inflated hyphae, 4.0–16 µm wide. Caulocystidia abundant, 20–80 × 4.0 µm, with brown, intracellular pigment. Clamp-connections present in all tissues.

Habitat and distribution:—Apparently widespread throughout Europe, North Africa, and North America.

Comments:—*T. rutilans* may be present in New Zealand conifer plantations. It can be distinguished from *T. scabra* and *T. ornaticeps* by its plum colours in combination with elliptical spores and voluminous cystidia.

Key

1.	Spores Q > 1.8	*Tricholomopsis ornaticeps*
-	Spore Q < 1.5	2.
2.	Cheilocystidia 12–25 µm diam. Pileus not densely scabrous	*Tricholomopsis rutilans*
-	Cheilocystidia 6–12 µm diam. Pileus very densely scabrous	*Tricholomopsis scabra*

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