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Taxonomy and phylogeny of the basidiomycetous hyphomycete genus *Hormomyces*

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1 new taxon

Abstract: The taxonomy of the genus *Hormomyces*, typified by *Hormomyces aurantiacus,* which based on circumstantial evidence was long assumed to be the hyphomycetous asexual morph of *Tremella mesenterica* (*Tremellales*, *Tremellomycetes*) or occasionally *Dacrymyces* (*Dacrymycetales*, *Dacrymycetes*), is revised. Phylogenies based on the three nuc rDNA markers [internal transcribed spacers (ITS), 28S large ribosomal subunit nrDNA (28S) and 18S small ribosomal subunit nrDNA (18S)], based on cultures from Canada and the United States, suggest that the genus is synonymous with *Tulasnella* (*Cantharellales*, *Agaricomycetes*) rather than *Tremella* or *Dacrymyces.* Morphological studies of 38 fungarium specimens of *Hormomyces*, including the type specimens of *H. callorioides*, *H. fragiformis*, *H. paridiphilus* and *H. peniophorae* and examination of the protologues of *H. abieticola*, *H. aurantiacus* and *H. pezizoideus* suggest that *H. callorioides* and *H. fragiformis* are conspecific with *H. aurantiacus* while the remaining species are unlikely to be related to *Tulasnella*. The conidial chains produced by *H. aurantiacus* are similar to monilioid cells of asexual morphs of *Tulasnella* species formerly referred to the genus *Epulorhiza*. The new combination *Tulasnella aurantiaca* is proposed and the species is redescribed, illustrated and compared with similar fungi. The ecological niche of *T. aurantiaca* and its possible relationship to orchid root endophytes is discussed. A key to asexual genera with similar conidium ontogeny to *T. aurantiaca* is provided.

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INTRODUCTION

The genus *Hormomyces* was introduced by Bonorden (1851) for a single hyphomycetous species, *H. aurantiacus*, collected on old oak (*Quercus* sp.) wood in Germany. The protologue described and illustrated orange, gelatinous sporodochia with branched chains of hyaline, globose conidia; no measurements for microscopic structures were reported (Fig. 1). The location of Bonorden's herbarium is uncertain (Stafleu & Cowan 1976) and no type specimen is known to exist for this species. *Hormomyces*

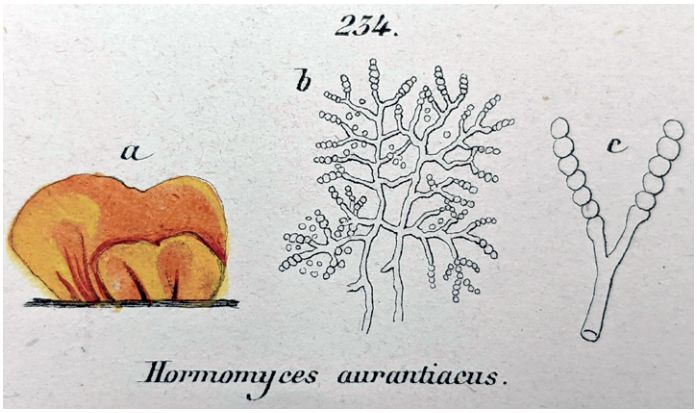

Fig. 1. A copy of the lectotype figure for *Hormomyces aurantiacus,* a reproduction of fig. 234, taf. XI from Bonorden (1851).

is rarely mentioned in modern taxonomic literature (Seifert *et al*. 2011). The only modern study is by Tubaki (1976), who reported on its blastic, acropetal conidium ontogeny and the characters of *H. aurantiacus* in axenic culture based on a strain isolated from a fallen twig of *Tsuga canadensis* collected in New York State, United States. His concept was generally accepted. The colonies of *H. aurantiacus* are conspicuous and distinctive but they may be disregarded as uninteresting "jelly fungi" by those focusing on microfungi, or discarded as a "trivial asexual morph or anamorph" by those interested in macrobasidiomycetes. Despite this lack of academic attention, there are frequent reports by field mycologists, mostly accurately reflecting the Tubaki (1976) concept, *e.g.* Mushroom Observer includes 42 (Wilson *et al.* 2020) and MyCoPortal 180 records (MyCoPortal 2019).

Seven species of *Hormomyces* were described: *H. abieticola*, *H. aurantiacus*, *H. callorioides*, *H. fragiformis, H. paridiphylus*, *H. pezizoideus* and *H. peniophorae* (supplementary table S1). Two were first described in *Hypsilophora* prior to being transferred to *Hormomyces* by Saccardo (1888), namely *Hy. fragiformis and Hy. callorioides*. Saccardo (1888), who mostly compiled descriptions from other mycologists and often did not examine material himself, considered the main distinction among these species to be sporodochial colour: orange for *H. aurantiacus*, purple for *H. fragiformis* and pink for *H. callorioides*. Lloyd (1916) questioned the value of colour to distinguish these species, suggesting that they might be conspecific without formally synonymizing them.

McNabb (1969) synonymized *H. callorioides* under *H. fragiformis*, re-emphasizing their exclusion from *Hypsilophora,* which he considered the correct generic name for the asexual morph of the fungus now known as *Erythricium salmonicolor* (*Corticiales*). McNabb did not propose a synonymy of *H. fragiformis* with *H. aurantiacus,* and the former name has often been used for specimens collected in North America (MyCoPortal 2019), irrespective of sporodochial colour. Tubaki (1976) accepted only *H. aurantiacus* in the genus, although he did not critically revise the other named species.

In their compilation of hyphomycete genera, Seifert *et al.* (2011) listed two other genera as synonyms of *Hormomyces*: *Sphaerocolla* (following the opinions of von Höhnel 1917; Donk 1962) and *Hormisciopsis*. *Sphaerocolla* Karsten (1892) comprises *S. aurantiaca* from Finland from living *Betula* bark, reported as producing large, effuse, orange sporodochia up to 10 cm long, with branched chains of globose conidia 3–9 µm diam, reminiscent of *H. fragiformis* or *H. aurantiacus*. *Hormisciopsis* Sumstine (1914) was proposed for *Ho. gelatinosa,* producing red, gelatinous sporodochia on wood collected in Pennsylvania, with branching chains of globose to ellipsoidal conidia 6–10 × 5–6 µm. The description corresponds well with *H. fragiformis* and *H. aurantiacus,* and the illustration is very similar to those of *H. aurantiacus* provided by Lloyd (1916) and *H. fragiformis* by Patouillard (1900). Although Sumstine (1914) compared *Hormisciopsis gelatinosa* to *Hormiscium,* he was apparently unaware of *Hormomyces*.

The taxonomic relationships of *Hormomyces* were a matter of debate, although it has usually been regarded as a basidiomycete. Patouillard (1900) suggested that *Hormomyces* is the budding state of a *Dacrymyces*. Lloyd (1916) disagreed but did not provide an alternative classification. That same year, Saccardo suggested that *H. aurantiacus* might be the asexual morph of *Tremella mesenterica* (Saccardo 1916). Bresadola (1932) reiterated this putative connection in a short note, reporting that the fungus he examined had conidia up to 3 µm long but he did not illustrate it; unfortunately, no specimens were mentioned. Donk (1962) also suggested a relationship between *Tr. mesenterica* and *H. aurantiacus*, noting that immature *Tr. mesenterica* also produced conidia. McNabb (1969) suggested that this connection was "currently accepted in Europe." Later, however, Pippola & Kotiranta (2008) described the asexual morph of *Tr. mesenterica* as producing chains of ellipsoidal conidia (1.8–)2.2–4.5(–5.9) × (1.6–)1.8–3.8(–4.2) µm, originating from clamped conidiogenous cells, which matches the dimensions given by Bresadola (1932). The characters diverge significantly from *H. aurantiacus* as described by Bonorden (1851), *i.e.* with globose conidia and no clamp connections. Tubaki (1976) also disagreed with this supposed connection, remarking that many asexual morphs of *Tremella* species are yeasts, while his culture of *H. aurantiacus* was filamentous. Thus, the purported asexual-sexual morph connection was a speculation that was never established experimentally and was contradicted by subsequent observations. Given their different ecological niches, *H. aurantiacus* on rotten wood and *Tr. mesenterica* as a mycoparasite usually on rather solid wood, it is unlikely that the two were seen in close proximity.

In 2015, we isolated a culture from a freshly collected specimen of *H. aurantiacus* and our initial 18S nrDNA sequences obtained from that culture suggested an affinity of *Hormomyces* with *Tulasnella* rather than *Tremella* or *Dacrymcyes*. The genus *Tulasnella* contains about one hundred sexual species, most of which occur on wood, and most known asexual species are usually isolated from orchid roots or liverworts. The basidiomes are usually thin and waxy and the basidia have four basally swollen sterigmata delimitated from the probasidium by a septum. So far, no asexual species of *Tulasnella* have been recorded from wood. The morphology and ontogeny of the conidial chains of *H. aurantiacus* are similar to the monilioid hyphae of the orchid mycorrhizal *Tulasnella* asexual morphs formerly attributed to *Epulorhiza* (Roberts 1994), and together with its dikaryotic hyphae, support a relationship with *Tulasnellaceae.* In this paper, our goal is to clarify the family and genus level classifications of this fungus using Bayesian Inference (BI) and Maximum Likelihood (ML) analyses of nuc rDNA regions and genes, and to evaluate the morphological characters of *H. aurantiacus* and the other described species of the genus based on studies of types and supplementary specimens and cultures. Should *Hormomyces* be considered distinct from or a synonym of *Tulasnella*? And if *H. aurantiacus* is classified in *Tulasnella*, might it be the asexual morph of a known sexual species, or identical with one of the other asexual species previously attributed to *Epulorhiza*? Because *H. aurantiacus* is apparently lignicolous, understanding its relationship with other *Tulasnella* species and mycorrhizal species formerly classified in *Epulorhiza* may provide insight into ecological patterns in this family.

MATERIALS AND METHODS

Cultures, specimens and morphological examination

Fresh specimens of *H. aurantiacus* were collected in 2014 and 2015 near Ottawa, Ontario, Canada, with additional specimens and one culture provided by colleagues; all material studied is listed in the Specimens Examined paragraphs of the Taxonomy section. Cultures were obtained by squashing a small fragment of a sporodochium and making a slurry that was further diluted with sterile dH_2O. Ten 20 µL drops of the dilution were pipetted onto malt extract agar (MEA, recipe from Raper and Thom 1949), using BD Bacto Malt Extract, and 15 g/L BD Bacto Agar, with the addition of 0.1 g/L $ZnSO_4.7H_2O$ and 0.005 g/L $CuSO_4.5H_2O$, and examined 24 h later for germinating conidia, which were then transferred individually to new MEA plates to reduce the risk of contamination. Thereafter, we did not attempt to make single spore isolations because the conidia produced *in vivo* remain in strongly coherent chains and can be separated only with difficulty. No evidence of contamination of the cultures by other fungi or bacteria was evident under the dissecting microscope or by light microscopy of mounts from the original isolates.

Culture characters were observed by growing all strains on MEA and oatmeal agar (OA; Gams *et al.* 1987).

For each strain and medium, one plate was incubated under nrUV light for 16 h and in darkness for 8 h per day at ambient RT (varying between 20–25 °C), and another in darkness in a 25 °C incubator. Specimens were inoculated at a single, central point in a 90 mm polystyrene Petri dish. All cultures were then examined and measured every 7 d for 4 wk, with coloration noted on days 14 and 28. To determine cardinal temperatures, two strains were grown in darkness at temperatures ranging from 5–40 °C, at increments of 5 °C (except 37 °C was used instead of 35 °C), and measured every 7 d for 4 wk. Culture photographs were taken with an Olympus Tough TG-5 camera (Olympus, Tokyo) with black velvet as a background.

Herbarium specimens, including available types, were borrowed from BPI (26 specimens), DAOM (7), K(M) (5) and HKAS (1) (herbarium acronyms follow Thiers 2019).

Microscopic observations of living specimens were made using tissue mounted in water. Herbarium specimens were rehydrated with a small drop of dH_2O for 10 min, then small fragments of sporodochia were removed using jewellers' forceps and heated in 85 % lactic acid for five minutes on an electric hot plate. Herbarium specimens and cultures were examined using an Olympus SZX12 dissecting microscope and BX50 compound microscope (Olympus, Tokyo), and photographed using Infinity 2 or Infinity X USB microscope cameras, using Infinity Capture software (Lumenera, Ottawa). Specimen and colony colours were described using the alphanumeric codes and names (with initial capitals) used by Kornerup & Wanscher (1976). Photographic plates were assembled using Photoshop v. 5.5 (Adobe Systems, San Jose, CA).

To demonstrate dikaryotic nuclei, hyphae from a 9-d-old culture of DAOMC 251988 grown on MEA were mounted in 10 µL of SYTO 13 green fluorescent nucleic acid stain (Invitrogen, Carlsbad, California) on a microscope slide. After the placement of the cover glass, the sample was left in darkness for 30 min at 37 °C, then examined with a Nikon ECLIPSE E800 fluorescence microscope (Nikon, Tokyo) using the UV2 setting. Pictures were taken with a Nikon DS-Ri2 camera (Nikon, Tokyo).

For each specimen, 50 conidia were measured, and mean and standard errors are provided. Q values for conidia were calculated as length divided by width. To assess the possible significance of conidial dimensions as a diagnostic character for species identification, means (with upper and lower limits represented by standard error, and outliers in brackets) were compared for all specimens. All calculations were made with Excel 2016 (Microsoft, Redmond).

DNA extraction, sequencing and phylogenetic analysis

Genomic DNA was extracted from pure cultures of *H. aurantiacus* using the DNeasy UltraClean Microbial Kit (Qiagen, Hilden), following the manufacturer's protocol. Permission was not obtained to attempt extraction of genomic DNA from specimens loaned by fungaria. For preliminary phylogenetic placement of an early isolate of *H. aurantiacus* (DAOMC 252084), a partial sequence of the 18S nrRNA gene was generated using primers NS1 and NS4, and an amplification profile of 95 °C for 10 min for the initial denaturing of the DNA template, then 40 cycles with denaturation at 95 °C for 60 s, annealing at 56 °C for 45 s and extension at 72 °C for 90 s, with a final extension at 72 °C for 10 min. Because of the relationship with *Tulasnellaceae* (*Cantherellales*) suggested by these results, we tried a *Tulasnella*-specific ITS4 primer designed by Taylor & McCormick (2008) in combination with ITS5; this resulted in sporadic and low yield amplification for our strains of *H. aurantiacus*. Amplification of the 28S nrRNA gene with LROR and either LR8 or LR5 invariably failed or yielded multiple PCR bands. Amplification was eventually achieved using V9G as the forward primer and LR3 as the reverse primer. See Results for primer references. The PCR profile had an initial denaturation at 94 °C for 90 s, five cycles of denaturation at 94 °C for 45 s, annealing at 56 °C for 45 s and extension at 72 °C for 60 s. Annealing temperatures were then decreased by 1 °C every five cycles until reaching 51 °C, which was used for another 30 cycles, with a final extension of 10 min, for a total of 55 cycles.

Our sequences of *H. aurantiacus* were edited and trimmed using Geneious v. 11.1.5 (Biomatter, Auckland). BLAST analyses of all three nrDNA markers indicated a relationship to reference sequences in *Tulasnellaceae*, which guided our sampling for subsequent phylogenetic analyses. Our sequences were aligned using MUSCLE v. 3.8.425 (Edgar 2004) in datasets containing sequences of *Cantharellales* downloaded from GenBank (Table 1 for ITS, Table 2 for 28S), sampled to include all available taxa of *Tulasnellaceae* and a few similar, mostly ITS, environmental sequences and unidentified species uncovered during BLAST searches, along with selected representatives of other genera in the order. We also used an ITS and partial 28S sequence of *H. aurantiacus* (NBRC 30400, the culture referred to by Tubaki 1976) published in the NBRC culture collection database (NITE Biological Resource Center 2019), which were not deposited in GenBank. Reference sequences of *Craterellus tubaeformis* were used as the outgroup for the ITS analysis, which examined relationships among species of *Tulasnella, Epulorhiza* and *H. aurantiacus*. A reference sequence of *Ustilago maydis* was used as the outgroup for the LSU analysis, which focused on the relationship between *Hormomyces* and *Tulasnella* in the *Cantharellales*, and tested prior hypotheses of relationships between *Hormomyces* and *Tremella* or *Dacrymyces*.

Independent phylogenetic analyses were conducted using the Maximum Likelihood (ML) and the Bayesian Inference (BI) algorithms for both markers. The ML analysis was done with PHYML v. 3.0 using the GTR + G + I model as the most suitable model for both 28S and ITS (Guindon *et al*. 2010). For BI, JModelTest v. 0.1.1 (Darriba *et al.* 2012) was used to determine the most suitable model, GTR + G for both ITS and 28S. The BI analyses were run using MrBayes v. 3.2 (Ronquist *et al.* 2012), with four simultaneous Markov chains run until the average standard deviation of split frequency reached < 0.01. Convergence was assessed when the standard deviation of split frequency reached < 0.01. Sampling frequency was 1 in 500 generations with the first 25 % of the trees discarded as burnin. Trees were visualized using FigTree v. 1.4.3 (Rambaut 2016) and modified using Adobe Illustrator 10 (Adobe, San Jose) and PowerPoint 2016 (Microsoft, Redmond). The alignments and phylogenetic trees were deposited in TreeBASE (Treebase.org Study ID: 25624 and 27256). Proposed new names and typifications were deposited in MycoBank (MB) and the MycoBank typification (MBT) database (Westerdijk Fungal Biodiversity Institute, Utrecht).

RESULTS

Phylogenetic analysis

An initial 1 045 bp sequence of the 5' end of the 18S nrRNA gene of DAOMC 252084 (deposited as GenBank MN719097) indicated a relationship of *H. aurantiacus* with *Tulasnella*, with a 99.2 % similarity to an AFTOL generated sequence of *Tulasnella violea* (AY707097), based on a query coverage of 99 %, with sequence similarities of about 80–99 % with other *Tulasnellaceae*, mostly with query coverages of about 55 %. The distance tree accompanying the BLAST search was consistent with the close placement of our sequence in this family. Because the taxon sampling for 18S sequences of *Tulasnellaceae* is so sparse in GenBank, with only three named species among the 32 reference sequences available, we did not pursue further 18S analyses.

Table 1. ITS sequences retrieved from GenBank or newly generated during this study.

Species	Strain no.	Origin	Host	GenBank accession no.	Reference
Ceratobasidium albasitensis	EaB-T2	–	–	AJ427398	Gonzalez, unpublished
C. angustisporum	CBS 568.83	Eyre Peninsula, SA, Australia	*Pterostylis mutica* endophyte	AJ427403	Gonzalez, unpublished
C. cereale	C13	–	*Triticum aestivum*	AJ302009	Gonzalez *et al.* (2002)
C. cornigerum	C6	–	*Erigeron canadensis*	AJ301902	Gonzalez *et al.* (2002)
C. ramicola	CBS 758.79^{T}	Florida, USA	*Pittosporum*, leaf	AJ427404	Gonzalez, unpublished
C. stevensii	CBS 477.82	Kentucky, USA	*Malus domestica,* twig	AJ427405	Gonzalez, unpublished
Craterellus tubaeformis	S9	–	–	MH394713	Jensen-Vargas & Marizzi (2018)
	1D3	Kunigami, Okinawa, Japan	–	AB973729	Matsuoka, unpublished
Tulasnella albida	KC 110	–	–	AY373294	McCormick *et al*. (2004)
T. amonilioides	–	–	–	JF907600	Almeida *et al.* (2014)
T. anaticula	13o004	Mt. Hambeak, South Korea	*Platanthera chlorantha*	KT164598	Direct submission
T. asymetrica	MA FF305808 Clone C002	Australia	*Thelymitra epipactoides*	KC152347	Cruz *et al*. (2014)
	MAFF 305808 Clone C005	Australia	*Thelymitra epipactoides*	KC152348	Cruz *et al*. (2014)
	MAFF305808 Clone C009	Australia	*Thelymitra epipactoides*	KC152349	Cruz *et al*. (2014)
T. aurantiaca	DAOMC 251988 DAOM 970795	Pennsylvania, USA	Rotten wood	MK626686	This study
	DAOMC 251989 PBM4158	Tennessee, USA	Rotten wood and *Crepidotus* spp.	MK626533	This study
	DAOMC 252083 DAOM 970821	Victoriaville, Quebec, Canada	*Fomitopsis betulina*	MK626687	This study
	DAOMC 252084 DAOM 970822	Ottawa, Ontario, Canada	Rotten *Populus* wood	MK626567	This study
	DAOMC 252086 DAOM 970819	Montreal, Quebec, Canada	Rotten wood	MK593626	This study
	DAOMC 252085 DAOM 970820	Ottawa, Ontario, Canada	Rotten wood	MK626568	This study
	NBRC 30400	New York, USA	Twig of *Tsuga canadensis*	Sequence not in Genbank	NITE Biological Resource Center, 2019
T. australiensis	CLM 031	New York, USA	*Arthrochilus oreophilus*	KF476602	Arifin *et al.* (2020)
	CLM 1945^{T}	Nowra, NSW, Australia	*Cryptostylis erecta* root	MT003730	Arifin *et al.* (2020)
	CLM 2004	Northern Sydney NSW, Australia	*Cryptostylis erecta* root	MT003715	Arifin *et al.* (2020)
T. calospora	CBS 326.47	–	–	AY373298	McCormick *et al*. (2004)
	Ch5-3	–	–	HM450045	Idris (2010)
T. concentrica	CLM 2071	Morton NP, NSW, Australia	*Cryptostylis leptochila* root	MT036547	Arifin *et al.* (2020)
	CLM 2098^{T}	Nowra, NSW, Australia	*Cryptostylis erecta* root	MT003744	Arifin *et al.* (2020)
	CLM2198	Bunyip SP, Vic, Australia	*Cryptostylis leptochila* root	MT036533	Arifin *et al.* (2020)
T. cumulopuntioides	MAFF 245682	Tsukuba City, Ibaraki, Japan	*Spiranthes sinensis*	LC175323	Fujimori *et al*. (2019)

Table 1. (Continued).

Species	Strain no.	Origin	Host	GenBank accession no.	Reference
T. danica	KC 388	–	–	AY373297	McCormick *et al*. (2004)
T. deliquescens	MAFF 244717	–	*Spiranthes sinensis*	LC175329	Fujimori *et al.* (2019)
T. densa	CLM 2110	Bulahdelah, NSW, Australia	*Cryptostylis hunteriana*	MT036526	Arifin *et al.* (2020)
	CLM 2111	Bulahdelah, NSW, Australia	*Cryptostylis hunteriana*	MT036525	Arifin *et al.* (2020)
	CLM 2117^{T}	Bulahdelah, NSW, Australia	*Cryptostylis hunteriana*	MT036520	Arifin *et al.* (2020)
T. dentritica	MAFF 244709^{T}	–	*Spiranthes sinenis*	LC175308	Fujimori *et al*. (2019)
T. eichleriana	KC 852	–	–	AY373292	McCormick *et al*. (2004)
	K(M) 143600	England, UK	Wood of decorticated sapling	KC152381	Cruz *et al*. (2014)
T. ellipsoidea	MAFF 245686	Tsukuba City, Ibaraki, Japan	*Spiranthes sinensis*	LC175315	Fujimori *et al.* (2019)
T. epiphytica	AERO_3.2	–	–	JF907598	Almeida *et al*. (2014)
T. irregularis	CBS 574.83^{T}	NT, Australia	*Dendrobium dicupum* root	MH861654	Vu *et al.* (2019)
T. occidentalis	CLM 1938^{T}	Boyanup, WA, Australia	*Cryptostylis ovata* root	MT008096	Arifin *et al*. (2020)
	CLM 1942	Boyanup, WA, Australia	*Cryptostylis ovata* root	MT008092	Arifin *et al*. (2020)
	CLM 1943	Boyanup, WA, Australia	*Cryptostylis ovata* root	MT008091	Arifin *et al*. (2020)
T. prima	CLM 159^{T}	Blue Mountains, NSW, Australia	*Chiloglottis trilabra*	KF476556	Linde *et al.* (2013)
	CLM 377	Kanangra Boyd NP, NSW, Australia	*Chiloglottis* aff. *jeanesii*	KF476544	Linde *et al.* (2013)
	5O5.III.3	–	*Chiloglotis dyphilla*	HM196792	Roche *et al.* (2010)
	SRBG01.II.3	Australian National Botanical Garden, Acton, ACT, Australia	*Chiloglottis trapeziformis*	HM196793	Roche *et al.* (2010)
T. pruinosa	DAOM 17641	Ontario, Canada	Sporophore on *Populus* sp.	AY373295	McCormick *et al.* (2004)
T. punctata	CLM 2012	Northern Sydney, NSW, Australia	*Cryptostylis subulata* root	MT008124	Arifin *et al.* (2020)
	CLM 2017^{T}	Northern Sydney, NSW, Australia	*Cryptostylis subulata* root	MT008122	Arifin *et al.* (2020)
	CLM 2018	Northern Sydney, NSW, Australia	*Cryptostylis subulata* root	MT008121	Arifin *et al.* (2020)
T. rosea	CLM 1770	WA, Australia	*Spiculaea ciliata* root	MN947568	Arifin *et al.* (2020)
	CLM 1773^{T}	WA, Australia	*Spiculaea ciliata* root	MN947569	Arifin *et al.* (2020)
	CLM 1774	WA, Australia	*Spiculaea ciliata* root	MN947570	Arifin *et al.* (2020)
T. secunda	CLM 274	Talbot, WA, Australia	*Paracaleana triens*	KF476580	Linde *et al*. (2013)
	CLM 222	Talbot, WA, Australia	*Paracaleana minor*	KF476568	Linde *et al*. (2013)
	CLM 009^{T}	Talbot, WA, Australia	*Drakaea elastica*	KF476575	Linde *et al*. (2013)
Tulasnella sp. ECU 5	DC 225	Ecuador	Branch	KC152397	Cruz *et al.* (2014)
	DC 225	Ecuador	Branch	KC152398	Cruz *et al.* (2014)
Tulasnella sp. ECU 6	DC 185	Ecuador	Branch	KC152401	Cruz *et al.* (2014)

Table 1. (Continued).

Species	Strain no.	Origin	Host	GenBank accession no.	Reference
	DC 262	Ecuador	Branch	KC152409	Cruz *et al.* (2014)
Tulasnella sp.	DC 294 C009	Germany	Rotten wood	KC152387	Cruz *et al.* (2014)
	DC 294 C016	Germany	Rotten wood	KC152394	Cruz *et al.* (2014)
	CLM 084	Australia	*Arthrochilus oreophilus*	KF476594	Linde *et al.* (2013)
	CLM 085	Australia	*Arthrochilus oreophilus*	KF476595	Linde *et al.* (2013)
T. sphagneti	12033.1[T]	Kosciuszko NP" NSW, Australia	*Chiloglottis* aff. *valida*	KY095117	Linde *et al.* (2017)
	13102.1	Kosciuszko NP" NSW, Australia	*Chiloglottis turfosa*	KY445924	Linde *et al.* (2017)
	13065.2	Kosciuszko NP" NSW, Australia	*Chiloglottis* sp.	KY445925	Linde *et al.* (2017)
T. tomaculum	KC 429	–	–	AY373292	McCormick *et al.* (2004)
	K(M)123675	England, UK	–	KC152380	Cruz *et al.* (2014)
T. violea	DC 177	Ecuador	Decaying wood	KC152414	Cruz *et al.* (2014)
	DC 292	Germany	Decaying wood	KC152412	Cruz *et al.* (2014)
	DC 292	Germany	Decaying wood	KC152435	Cruz *et al.* (2014)
	DC 293	Germany	Decaying wood	KC152437	Cruz *et al.* (2014)
	KC 851	–	–	AY373293	McCormick *et al.* (2004)
	K(M) 164256	England, UK	Underside of *Fagus sylvatica* log	KC152411	Cruz *et al.* (2014)
T. warcupii	CLM 007	Atherton, Tablelands, QLD, Australia	*Arthrochilus oreophilus*	KF476600	Linde *et al.* (2013)
	CLM 022	Australia	*Arthrochilus oreophilus*	KF476601	Linde *et al.* (2013)
	CLM 028	Australia	*Arthrochilus oreophilus*	KF476599	Linde *et al.* (2013)

[T]Indicates type specimens.

Table 2. Gene sequences (28S) retrieved from GenBank, and newly generated in this study.

Species	Strain no.	Origin	Host	GenBank accession no.	Reference
Agaricus bisporus	CBS 151.46	–	–	MH867670	Vu *et al.* (2019)
Botryobasidium botryosum	AFTOL-ID 604	–	–	DQ089013	Nilsson, unpublished
Bo. isabellinum	GEL2109	–	–	AF393047	Nilsson, unpublished
Bo. subcoronatum	GEL 1286	–	–	AF287850	Binder & Hibbett (2002)
Burgella lutea	Etayo 27623[T]	Bolivia	Corticolous lichens	KC336075	Diederich *et al.* (2014)
Bu. flavoparmeliae	JL192-01	Oklahoma, USA	*Flavoparmelia baltimorensis*	DQ915469	Lawrey *et al.* (2007)
Burgoa moriformis	VCH 33[T]	Inisherk, Crom, Fermanagh, Ireland	*Salix* bark	DQ915477	Lawrey *et al.* (2007)
Cantharellus addaiensis	BB 96.010	Zambia	–	KM484680	Shao *et al.* (2014)
Ca. altipes	BB 07.019[T]	USA	–	KF294627	Buyck *et al.* (2014)
Ca. amethysteus	993/estades	–	–	MG450679	Buyck *et al.* (2018)
Ca. cibarius	CC15SWE	Sweden	*Betula*	JX030441	Foltz *et al.* (2013)
Ca. ferruginasecens	GE sn	France	–	KM484681	Shao *et al.* (2014)
Ca. formosus	BB 13.163	USA	–	KM484683	Shao *et al.* (2014)
Ca. lateritius	JJ NC-Canth 2	USA	–	KM484686	Shao *et al.* (2014)
Ca. longisporus	ER 107	Madagascar	–	KM484688	Shao *et al.* (2014)
Ca. minor	BB 07.057	USA	–	KF294632	Buyck *et al.* (2014)
Ca. texensis	BB O7.018[T]	USA	–	KF294626	Buyck *et al.* (2014)

Table 2. (Continued).

Species	Strain no.	Origin	Host	GenBank accession no.	Reference
Ceratobasidium bulbillifaciens	Eichler-Cezanne 8193	Germany	Bark of *Acer platanoides*	KC336073	Diederich *et al.* (2014)
C. bulbilllifaciens	Eichler-Cezanne 8067	–	Bark of *Fraxinus*	KC336071	Diederich *et al.* (2014)
C. globisporum	CBS 569.83^{T}	Queensland Australia	–	MH873365	Vu *et al.* (2019)
C. pseudocornigerum	CBS 568.83^{T}	Australia	–	MH873364	Vu *et al.* (2019)
C. ramicola	Java 11	Java	*Theobroma cacao*	HQ424243	Samuels *et al*. (2012)
C. theobromae	South Sulawesi 1	South Sulawesi	Petiole of *Theobroma cacao*	KU319575	Samuels *et al*. (2012)
	South Sulawesi 6	South Sulawesi	Petiole of *Theobroma cacao*	KU319577	Samuels *et al*. (2012)
	South Sulawesi 11	South Sulawesi	*Theobroma cacao*	HQ424241	Samuels *et al*. (2012)
	South Sulawesi 10	South Sulawesi	*Theobroma cacao*	HQ424242	Samuels *et al*. (2012)
Ceratorhiza oryzae-sativae	CBS 439.80	Japan	*Oryza sativa*	MH873047	Vu *et al.* (2019)
Clavulina amazonensis	AMV1973	Colombia	*Pseudomonotes tropenbosii*	KT724123	Vasco-Palacios (2016)
Cl. cinerea	KHL 11694	Lammi, Finland	–	AM259211	Nilson *et al.* (2006)
Cl. cf. cristata	BB 12.083	Italy	–	KM484694	Shao *et al*. (2014)
Cl. purpurascens	ZP-3065	China	Soil	MK564124	Wu *et al.* (2019)
Clavucilium delectabile	KHL 11147	Norway	–	AY586688	Larsson *et al.* (2004)
Craterellus cinereofimbratus	JOH4	Columbia	*Pseudomonotes tropenbosii*	KT724159	Vasco-palacios (2016)
Cr. lutescens	BB 13.048	Canada		KM484696	Shao *et al.* (2014)
Cr. tubaeformis	BB 1324	USA	–	KM484697	Shao *et al.* (2014)
	BB 07.293	Slovakia	–	KF294640	Buyck *et al.* (2014)
Dacrymyces chrysospermus	FPL11353	–	–	AF287855	Hibbett *et al*. (2000)
D. stillatus	CBS 195.48	France	–	MH867857	Vu *et al.* (2019)
Gloeotulasnella cystidiophora	KW 2871	–	–	AY585831	Shefferson *et al*. (2005)
Haplotrichum conspersum	AFTOL ID 1766	–	–	DQ521414	Matheny *et al*. unpublished
Hydnum elatum	FRI62309	Kampung Jelawat-Tasik Bera Pahang Malaysia	–	KU612691	Feng *et al.* (2016)
H. ellipsosporum	FD3281	Switzerland	–	KX086217	Beenken, unpublished
H. magnorufescens	161209	Slovenia	–	KU612669	Feng *et al.* (2106)
H. rufescens	BB 07.340	Slovakia	–	KM484698	Shao *et al.* (2014)
H. versterholtii	HKAS92342	Yulong snow mountain, Yunnan, China	–	KU612646	Feng *et al.* (2016)
Minimedusa obcoronata	CBS 120605	Thailand	*Eucalyptus camaldulensis*	GQ303309	Cheewangkoon *et al.* (2009)
Multiclavula mucida	DSH96-056	–	–	AF287875	Hibbett *et al*. (2000)
M. mucida	TUB 011734	–	–	EU909345	Krause *et al.* (2011)
M. vernalis	GB-BN-1	Sweden	–	AM259214	Nilsson *et al*. (2006)
Rhizoctonia floccosa	CBS 337.36^{T}	Indonesia	–	MH867319	Vu *et al.* (2019)
R. quercus	CBS 313.35^{T}	Italy	Root of *quercus pedunculata*	MH867202	Vu *et al.* (2019)
R. repens	CBS 298.32	Netherlands	*Orchis morio*	MH866781	Vu *et al.* (2019)
Schizophyllum commune	MUT 4875	Mediterranean Sea	*Flabellia petiolata*	MF115832	Poli *et al.* (2018)
Sistotrema adnatum	FCUG 700	–	–	DQ898699	Moncalvo *et al*. (2006)
S. biggisae	FCUG 782	–	–	DQ898697	Moncalvo *et al*. (2006)
S. coronilla	AFTOL-ID 618	–	–	DQ457641	Moncalvo *et al*. (2006)

Table 2. (Continued).

Species	Strain no.	Origin	Host	GenBank accession no.	Reference
S. hypogaeum	CBS 394.63[T]	Australia	Soil	MH869926	Vu *et al.* (2019)
S. oblongisporum	FCUG 2117	–	–	DQ898703	Moncalvo *et al*. (2006)
S. sernanderi	CBS 926.70	–	–	AF518650	Hibbett & Binder (2002)
Sistotremella brinkmanii	CBS 186.39	Michigan, USA	–	MH867474	Vu *et al*. (2019)
Sistotremella perpusilla	CBS 126048	North Carolina, USA	*Abies*	MH875516	Vu *et al*. (2019)
Thanatephorus cucumeris	AFTOL-ID 2022	–	–	DQ917658	Matheny *et al*. unpubl.
	CBS 340.51	England, UK	–	MH868410	Vu *et al.* (2019)
Tremella macrobasidiata	AM453	Portugal	*Lecanora chlorotera*	KT334595	Zamora *et al*. (2016)
Tr. mesenterica	AM30	Wedin, Sweden	–	JN043569	Millanes *et al.* (2011)
	CBS:6973[T]	Vancouver, British-columbia, Canada	*Alnus rubra*	KY109900	Vu *et al.* (2016)
T. anaticula	UAMH 5428	Alberta, Canada	Roots of *Calypso bulbosa*	AY243520	Taylor *et al*. (2003)
T. asymmetrica	MAFF P305806		*Thelymitra luteocilium*	DQ388046	Suarez *et al.* (2006)
T. aurantiaca	DAOMC 251988	Pennsylvania, USA	Rotten wood	MK627511	This study
	DAOM 970795				
	DAOMC 251989	Tennessee, USA	Rotten wood and *Crepidotus* spp.	MK627512	This study
	PBM 4158				
	DAOMC 252083	Victoriaville, Quebec, Canada	*Fomitopsis betulina*	MK627513	This study
	DAOM 970821				
	DAOMC 252084	Ottawa, Ontario, Canada	Rotten *Populus* wood	MK627514	This study
	DAOM 970822				
	DAOMC 252086	Montreal, Quebec, Canada	Rotten wood	MK627515	This study
	DAOM 970819				
	DAOMC 252085	Ottawa, Ontario, Canada	Rotten wood	MK627516	This study
	DAOM 970820				
T. calospora	SPRR.R2	India	*Paphiopedilum druryi*	MN271391	Parthibhan & Rammasubu (2020)
T. eremophila	13062 MD	–	*Euphorbia officinarum*	KJ701189	Crous *et al.* (2015)
T. irregularis	CBS 574.83	NT, Australia	*Dendrobium dicuphum*	AY243519	Taylor *et al*. (2003)
T. phuhinrongklaensis	SDBR-CMU-CR41[T]	–	–	MF427703	Rachanarin *et al.* (2018)
	SDBR-CMU-CR42	–	–	MF427704	Rachanarin *et al.* (2018)
	SDBR-CMU-CR43	–	–	MF427705	Rachanarin *et al.* (2018)
	SDBR-CMU-CR44	–	–	MF427706	Rachanarin *et al.* (2018)
T. pruinosa	DAOM 17641	Richmond Hill, Ontario, Canada	*Populus* sp.	AF518662	Hibbett & Binder (2002)
Tulasnella sp.	GEL 4461	–	–	AJ406436	Langer (2001)
	GEL 4745	–	–	AJ406436	Langer (2001)
	GEL 5130	–	–	DQ898731	Moncalvo *et al*. (2006)
T. violea	DAOM 222001	–	–	AY293216	Binder *et al*. (2005)
	AFTOL-ID 1879	–	–	DQ520097	Garnica & Weiß, unpublished
Ustilago maydis	CBS 358.32	–	–	MH866814	Vu *et al.* (2019)

[T]Indicates type specimens or ex-type strains.

Table 3. Primer names and sequences used for this study, including the new primers ITS5_hormo, ITS4_hormo and LROR_hormo and the *Tulasnella*-specific ITS4 primer, ITS4_tul, with melting temperature (T_m) in degrees Celsius. Point mutations are in bold, nucleotide additions are in bold and underlined and nucleotide deletions are shown as a blank space with a bold underline.

	Sequence (5' to 3')	T_m (°C)	Reference
V9G	TTACGTCCCTGCCCTTTGTA	56	de Hoog & Gerrits van den Ende (1998)
ITS5	GGAAGTAAAAGTCGTAACAAGG	51	White *et al.* (1991)
ITS5_hormo	GGAAGTA**C**AAGTCGTAACAAGG	53	This study
ITS4	TCCTCCGCTTATTGATATGC	52	White *et al*. (1991)
ITS4_tul	CCGCCAGATTCACACATTGA	55	Taylor & McCormick (2008)
ITS4_hormo	TCCTCCGCT**G**A**A**T**A**ATATGC	52.1	This study
LROR	ACCCGCTGAACTTAAGC	52	Moncalvo *et al*. (2000)
LROR_hormo	ACCCGCT**T**GA_**T**TTAAGC	50	This study
LR3	CCGTGTTTCAAGACGGG	53	Moncalvo *et al.* (2000)
LR3R	GTCTTGAAACACGGACC	50	Moncalvo *et al.* (2000)
LR5	TCCTGAGGGAAACTTCG	51	Moncalvo *et al.* (2000)
LR8	CACCTTGGAGACCTGCT	54	Hopple & Vilgalys (1999)

Our initial attempts to amplify ITS and 28S separately from cultures of *H. aurantiaca* using universal primers, or a putative *Tulasnella*-specific ITS primer (Taylor & McCormick 2008), were unsuccessful, with only faint or multiple bands visualized. Diverse techniques such as annealing point gradients from 60–55 °C, a touchdown PCR of 40 cycles each at 57 and 55 °C, and altering primer and DNA concentrations were all unsuccessful in amplifying the DNA. This was solved using the forward primer V9G, slightly upstream from the ITS locus at the end of the 18S (de Hoog & Gerrits van den Ende 1998) along with the reverse primer LR3, slightly downstream from the LROR primer on the 28S (Raja *et al.* 2017). Sequences of this fragment showed that *H. aurantiacus* DAOMC 251989 has mismatched binding sites in the ITS4, ITS5, ITS1F and LROR priming regions. For subsequent amplification and sequencing, we designed the new primers ITS4_hormo, ITS5_hormo and LROR_hormo (Table 3), correcting the mismatches identified by our first sequence. This enabled the routine amplification and sequencing of both markers.

The sequences of our six strains of *Hormomyces* were very similar. For the ITS (Fig. 2), four of the strains had identical sequences; DAOMC 251989 had a single nucleotide insertion, and DAOMC 252084 differed from the other strains by 3−4 nucleotides. For the 28S (Fig. 3), the differences between each strain were no more than two nucleotides, resulting in similarities > 99.5 %.

All analyses of both genes confirmed the phylogenetic relationship with *Tulasnellaceae*, *Cantharellales*, suggested by the initial 18S sequence, remote from the previously proposed relatives of *H. aurantiacus* in *Tremellales* or *Dacrymycetales*. This directed our sampling of taxa to test whether *Hormomyces* was nested within or distinct from existing genera of *Tulasnellaceae*. All BI and ML analyses resulted in all strains of *H. aurantiacus* forming a monophyletic clade nested within *Tulasnella* and separate from other genera of *Cantherellales*. In the ITS analysis, *H. aurantiacus* belongs with high support to a clade including various *Tulasnella* species including *T. violea*, *T. eichleriana* and several orchid root endophytes. Unfortunately our BI analysis of the ITS loci tends to result in polytomy for this clade, although each species remains phylogenetically coherent and distinct. The exact sister group of *T. aurantiaca* in this clade is unclear. A phylogenetic analyses of the ITS locus by Arifin *et al.* (2020), which used sequences of *H. aurantiacus* obtained during our study, also suggested the placement *of H. aurantiaca* in the same clade within *Tulasnella*, but sister to two unidentified *Tulasnella* species from Ecuador.

Our 28S analysis also nests *H. aurantiacus* within *Tulasnella,* suggesting it is sister to *Tulasnella* sp. GEL4461, with a difference of 47 bp (94.6 % similarity). Based on a MegaBLAST search of GenBank, the closest identified match for the LSU locus was *Tulasnella obscura* (AJ406435, identities = 485/517(94 %), 7 gaps (1 %) with a 57 % query cover). Other matches were less than 85 % similar and with an E value below 1e-100.

Based on our analyses, *Tulasnella* appears to be monophyletic (with the exception of *Tulasnella eremophila*), forming two distinct clades with high statistical support in the ITS phylogeny, and possibly four distinct clades in the 28S phylogeny. Because only six species of *Tulasnellaceae*, including our own, have sequences for both ITS and 28S, a concatenated analysis was not attempted. All of the asexual species previously referred as *Epulorhiza* currently sequenced using the ITS and LSU loci are easily separated from *H. aurantiacus,* suggesting that *H. aurantiacus* is a distinct species of *Tulasnella*.

Comparison of herbarium specimens of *H. aurantiacus, H. fragiformis* and *H. callorioides*

All of the examined specimens identified as *H. aurantiacus, H. fragiformis* or *H. callorioides* had similar micromorphology and no distinct separation was detected based on an extensive analysis of conidial sizes (Supplementary Fig. S1). Measurements overlapped with the lectotype specimen of *H. fragiformis* [(7–)7.5–9.5(–11) × 6–7.5(–8.5) µm (mean 8.66 ± 0.1 × 6.75 ± 0.1, Q 1.29, n = 50)] and the holotype of *H. callorioides* [(7–)7.5–9.5(–11) × (5–)5.5–6.5(–7) µm (mean 8.45 ± 0.1 × 6.21 ± 0.1, Q 1.37, n = 50)], with the average conidial size for all examined specimens being 8.43 ± 0.1 × 6.37 µm ± 0.1 (Supplementary Fig. S2).

Although the protologue of *H. callorioides* described its sporodochia as pink (Kalchbrenner & Cooke 1880), our examination of the holotype showed dried sporodochia that were terracotta to dark brown. The original pigments may have degraded over the years or darkened with preservation. The colours observed on the lectotype of *H. fragiformis* designed by McNabb (1969)

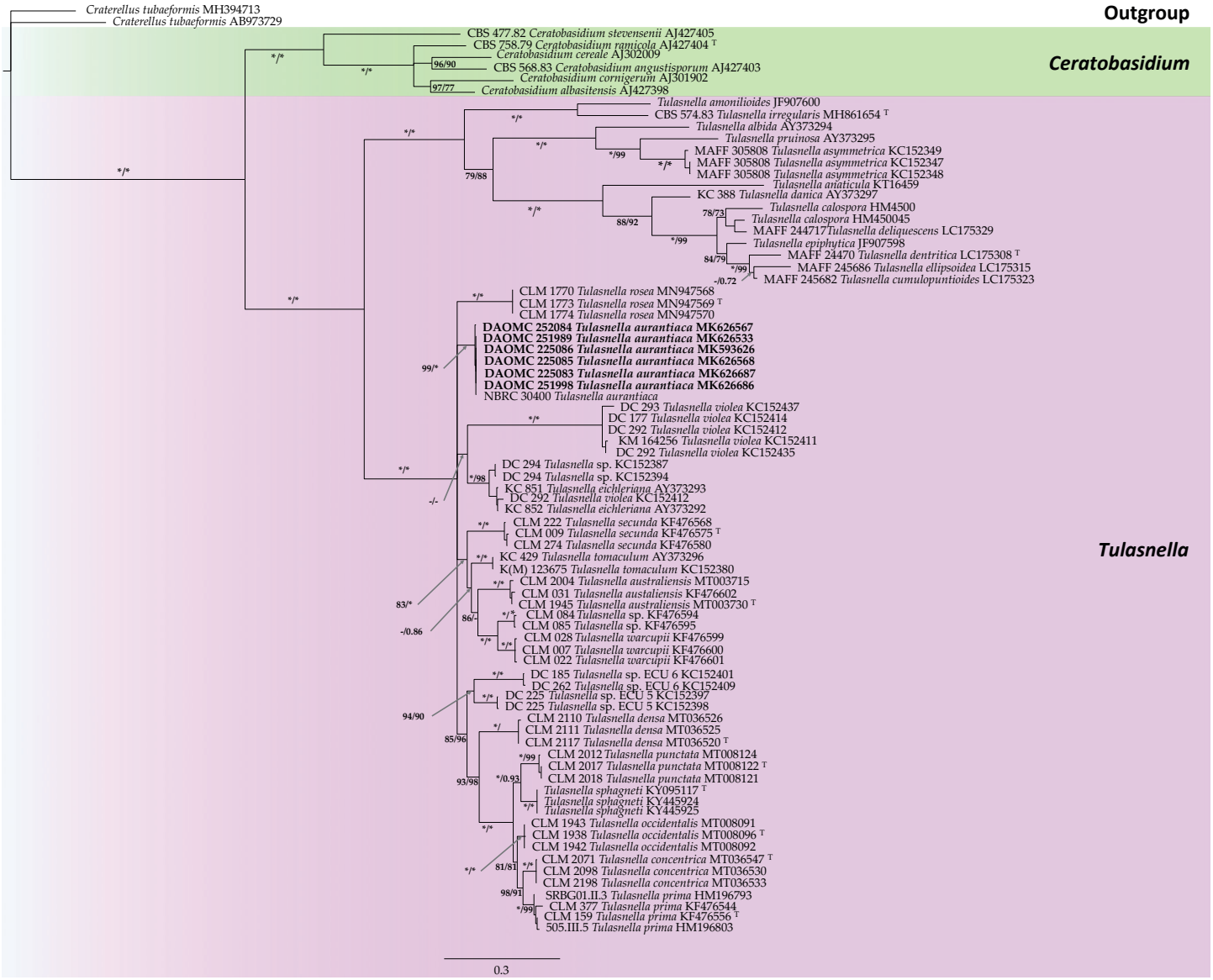

Fig. 2. Phylogenetic tree for species of *Tulasnella* and *Ceratobasidium* for the ITS region, based on Bayesian inference analysis using MrBayes. The values above the branches are Bayesian posterior probabilities/maximum likelihood bootstrap values. Bootstrap values of ≥ 70 % and Bayesian posterior probabilities of ≥ 0.70 are shown with bootstrap values of 100 % and Bayesian posterior probability of 1.00 replaced by an asterisk (*). ^{T} indicates type specimens.

and holotype of *H. callorioides*, both in dry specimens and after rehydration, were within the same range as that we saw in our own specimens and those preserved in BPI and DAOM. We found no evidence to support a hypothesis that sporodochial colour can be used to distinguish these three putative species when the specimens were examined side by side. Similarly, there were no other morphological or microscopic characters that allowed the distinction of the several specimens identified as *H. fragiformis* or *H. aurantiacus,* or the holotype of *H. callorioides*, despite the disjunct geographical locations among the three species.

Taxonomy

The genus *Tulasnella* was proposed for protection against *Epulorhiza* and *Hormomyces* by Stalpers *et al.* (2021), in accordance of the Shenzhen code (Turland *et al.* 2018). The remaining names in *Epulorhiza* were transferred to *Tulasnella* there. Here, the generic description of *Tulasnella* is emended to include the asexual morph characters for taxa described in *Hormomyces* and *Epulorhiza*.

Tulasnella J. Schröt., *Kryptogamen-Flora von Schlesien* **3.1**(25–32): 397. 1888. ***nom. cons. prop.***

Synonyms: *Hormomyces* Bonord., *Handb. Allgem. mykol.* (Stuttgart): 150. 1851 (asexual synonym).

Prototremella Pat., *J. Bot.,* Paris **2**: 269. 1888, *fide* Donk 1966.

Pachysterigma Johan-Olsen ex Bref., *Unters. Gesammtgeb. Mykol*. (Liepzig) **8**: 5. 1888, *fide* Donk 1966.

Muciporus Juel, *Bih. K. svenska VetenskAkad. Handl., Afd.*: 23. 1897, *fide* Donk 1966.

Gloeotulasnella Höhn. & Litsch., *Wiesner Festschrift* (Wien): 57. 1908, *fide* Donk 1966.

Hormisciopsis Sumst., *Mycologia* **6**: 32. 1914 (asexual synonym).

Epulorhiza R.T. Moore, *Mycotaxon* **29**: 94. 1987 (asexual synonym).

Typification: *Tulasnella lilacina* J. Schröt. 1888.

Basidiomes (when present) crust-like, often on rotten wood, leaves or litter, often pinkish or purple. *Hymenium* composed

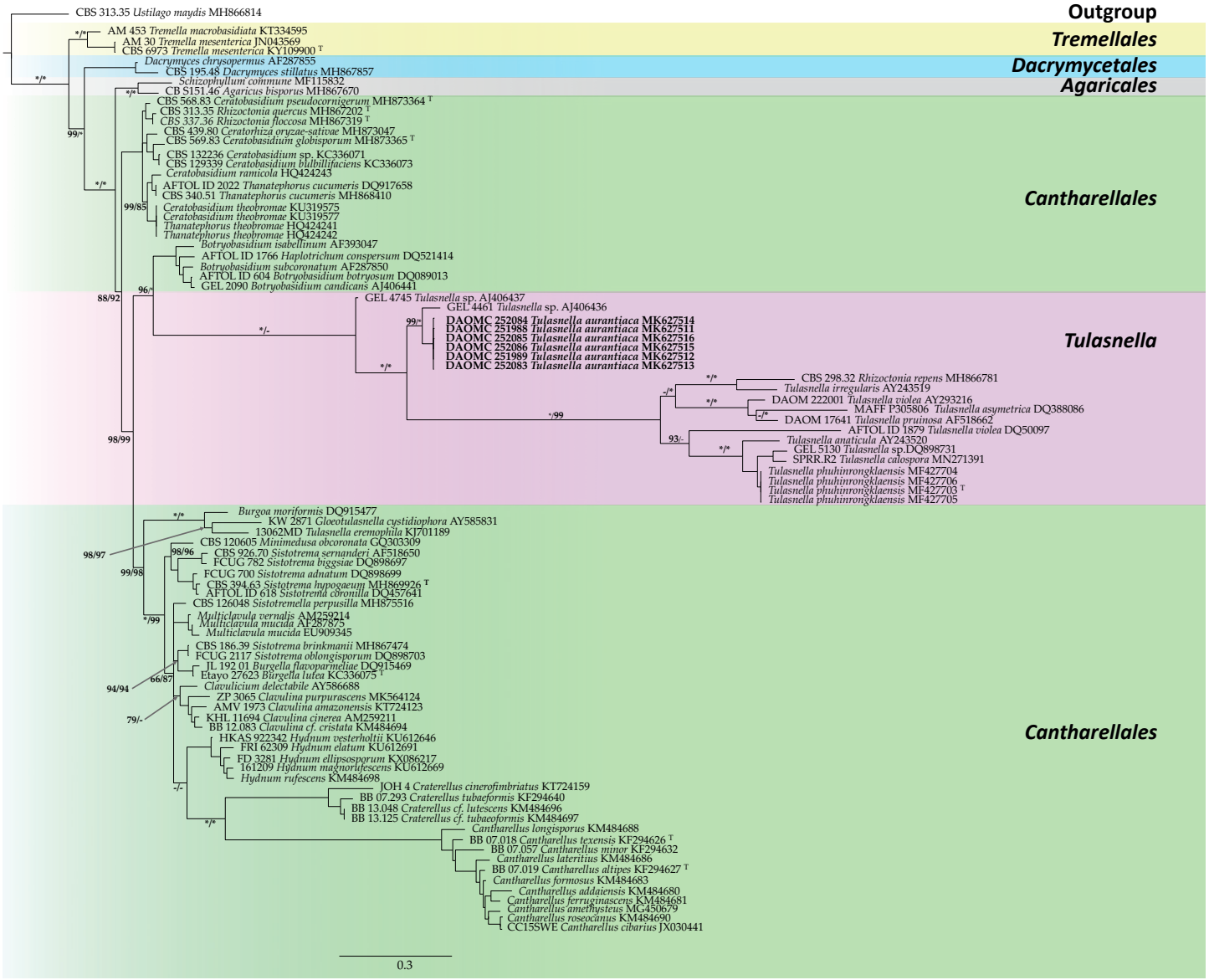

Fig. 3. Phylogenetic tree for species of *Cantharellales* including species of *Tulasnella* for the 28S gene, based on Bayesian inference analysis using MrBayes. The values above the branches are Bayesian posterior probabilities/maximum likelihood bootstrap values. Bootstrap values of ≥ 70 % and Bayesian posterior probabilities of ≥ 0.70 are shown with bootstrap values of 100 % and Bayesian posterior probability of 1.00 replaced by an asterisk (*).[T] indicates type specimens.

of hyphae with or without clamps depending on the species, subhymenial structures often absent. *Basidia* with four sterigmata that are strongly swollen at the base, each separated by a septum from the clavate basal cell, which often collapses. *Basidiospores* variably shaped, from globose to helicoid; secondary conidia occasionally produced on germinating primary spores (Ingold 1984). Septa with central dolipores with continuous parenthesomes. *Asexual morphs* (when present) forming mycorrhizae with orchid roots or liverworts, or conspicuous orange to red pustulate, gelatinous, sporodochia on rotten wood. *Stroma* absent. *Conidia* in blastic, acropetal chains, which are dichotomously branched in some species, and arise directly from submerged hyphae or in sporodochia. Conidia aseptate, smooth or with minute pits, globose, subglobose, ellipsoidal to barrel-shaped, aseptate, hyaline, sometime with orange droplets. Somatic hyphae dikaryotic (Currah *et al.* 1990), lacking clamp connections when associated with asexual structures. Sclerotia occasionally produced.

Notes: The sexual morphs of *Tulasnella* are well-characterized by the production of thin, resupinate basidiomes on decaying substrates. They have unique "tulasnelloid" basidia with a basally swollen sterigma separated by a septum from the club-shaped basal cell, which usually collapses (Roberts 1994). Ultrastructure of dolipore septa is often used as a character to support class-level classification of *Basidiomycota* (Celio *et al.* 2006). Comparatively few exemplars are studied for each class and the character is rarely used for genus or species level classifications, which tend to be supported by DNA sequencing (*e.g.* Almeida *et al*. 2014, Linde *et al*. 2017, Arifin *et al*. 2020). We did not examine septal ultrastructure in this study. Most known asexual morphs of *Tulasnella* are characterized by the production of acropetal chains of conidia, and for most of the known asexual species, a relationship with orchids. *Tulasnella aurantiaca* is the exception because it grows on wood.

Apart from the species formerly included in *Epulorhiza*, a few other asexual states are described for other species of *Tulasnellaceae* but lack the characteristic monilioid conidial

chains of *T. aurantiaca. Tulasnella valentini*, which grows on rotten wood, is reported to produce single apiculate, obclavate or fusiform conidia terminating irregularly lanceolate conidiogenous cells (Van de Put & Antonissen 1996). This is an unusual character state for a member of *Tulasnellaceae* and this asexual-sexual connection needs to be confirmed experimentally to eliminate the possibility that the observed conidia might have been those of a mycoparasite; for that reason, we did not include these deviating character states in the generic diagnosis above. *Stilbotulasnella conidiophora*, described from palm fronds but to date unsequenced, can be distinguished by its synnematous conidiomata and ellipsoidal ameroconidia produced in slimy masses from percurrently proliferating conidiogenous cells (Bandoni & Oberwinkler 1982).

Seifert *et al*. (2011) synonymized the monotypic *Hormisciopsis* with *Hormomyces* based on the protologue, and we include it as a synonym of *Tulasnella* above. We did not examine specimens of *Hormisciopsis gelatinosa,* but the protologue (Sumstine 1914) provides observations that are identical to what we have seen in specimens of *T. aurantiaca*. Seifert *et al*. (2011) followed von Höhnel (1917) and Donk (1962) in synonymizing *Sphaerocolla* with *Hormomyces*. However, re-examination of the protologue and slides from the holotype of *S. aurantiaca* (on *Betula,* Mustiala, June; H herb. Karsten PAK 3341; Supplementary Fig. S3), the type species of *Sphaerocolla*, suggests this was an error. Although the micromorphology is similar, the conidia of *S. aurantiaca* are slightly oblate rather than slightly ellipsoidal, and the fungus is reminiscent of the poorly-documented yeast *O. margaritiferum*, which occurs on slime fluxes on trees (Kurtzman 2011), a similar ecological niche to that reported for *S. aurantiaca* on living *Betula* trees. A notable difference is that *O. margaritiferum* produces endospores, which we did not observe in the material of *S. aurantiaca,* but these are apparently produced only in culture (Smith 1997) and no cultures of *S. aurantiaca* were isolated. Therefore, *S. aurantiaca* should be considered distinct from *T. aurantiaca* and may be conspecific with *O. margaritiferum*.

Based on our nuc rDNA phylogenies, *Hormomyces* is congeneric with *Tulasnella*, but appears to be distinct from all sequenced species of the latter genus. Therefore, a new combination is proposed:

Tulasnella aurantiaca (Bonord.) J. Mack & Seifert, ***comb. nov.*** MycoBank MB832426. Fig. 4.
Synonyms: *Hormomyces aurantiacus* Bonord., *Handb. Allgem. mykol*. (Stuttgart): 150. 1851.

Typification: fig. 234, taf. XI, in Bonorden 1851, Handb. Allgem. mykol. (Stuttgart): (**lectotype***,* proposed here MBT388543, reproduced here as Fig. 1).
Hypsilophora callorioides Kalchbr. & Cooke, *Grevillea* **9**: 18. 1880.
Hormomyces callorioides (Kalchbr. & Cooke) Sacc., *Syll. fung.* (Abellini) **6**: 813. 1888.
Hypsilophora fragiformis Cooke, in Farlow, *Appalachia* **3**: 247. 1884
Hormomyces fragiformis (Cooke) Sacc., *Syll. fung*. (Abellini) **6**: 182. 1888.
Hormisciopsis gelatinosa Sumst., *Mycologia* **6**: 32. 1914.

Basidiomes unknown. *Sporodochia* effuse, often pustulate, confluent in masses up to 5 cm long, occasionally more, or rarely solitary and <1 cm long, gelatinous or cartilaginous when fresh, waxy when dried, colours variable, from deep orange to garnet red when fresh, ranging from blonde to brown with various shades of orange and red when dry. *Hyphae* immersed, septate, branched, 2–4 µm wide, dikaryotic, binucleate (Supplementary Fig. S4), clamp connections absent, no stroma formed. *Conidiophores* arising from hyphal cells, clamp connection absent. *Conidia* blastic, in monilioid, branched acropetal chains, branching bifurcate, pattern variable, occurring mainly near the base of the chains, with usually fewer than five conidia between bifurcations, the terminal chains typically longer, often with up to 15 conidia and occasionally more, chains not readily separating into individual conidia. Conidia hyaline, often with conspicuous orange guttules when fresh, aseptate, smooth, subglobose to ellipsoidal or occasionally globose, often truncate, variable in length and width, (4.5–)7.5–9.5(–13) × (4–)5.5–7(–8.5) µm (mean 8.4 ± 0.1 × 6.4 ± 0.1, Q 1.31), thick-walled with walls ~1 µm thick.

Colony diam after 14 d, on MEA with near-UV (spectral range 300–400 nm) 30−50 mm on MEA in darkness 30−50 mm on CMA with near-UV 25−45 mm, on CMA in darkness 30−50 mm, on OA with near-UV 55−65 mm, on OA in darkness 40−55 mm. *Colonies* flat, often immersed, filamentous, often circular or irregular with undulate margins. *Hyphae* 2–5 µm wide. Sporodochia produced after 1−2 wk abundantly on OA, and in some strains on MEA, sterile on CMA, concolorous with mycelium, or more vibrantly coloured, especially when exposed to light: on CMA with near-UV after one month Salmon (6A4) to Pinkish White (9A2) in four strains and Cognac (6E7) in one; on CMA in darkness white, Blonde (5C4), Pinkish White (9A2) or Cognac (6E7); on MEA with near-UV white in four strains and Tangerine (6B7) in one; on MEA in darkness white in four strains and Yellowish White (4A2) in one; on OA under near-UV Greyish Red (7B4) to Pastel Red (8−9A5); on OA in darkness Pale Yellow (3A3) to Orange White (5A2) or Pale Orange (6A3). Conidia similar to those *in vivo* but slightly longer and narrower, (6.5–)7.5–10(–12.5) × (4–)5–6.5(–8) µm (mean 9 ± 0.5 × 5.8 ± 0.3, Q 1.57± 0.1).

Cardinal temperatures: Optimum 25 °C, minimum <5 °C, maximum 30−37 °C. Growth does not resume in cultures left for 1 mo at 37 °C, when moved to an incubator at 20 °C.

Distribution: Widely distributed in eastern North America, known from Ontario and Québec south to North Carolina and Tennessee and westward to Ohio. *Tulasnella aurantiaca* is known from western North America (one specimen collected in Arizona), Europe (Austria, Germany) and South Africa (Western Cape).

Habitat: Lignicolous and apparently saprobic, reported on rotten wood of conifers (*Thuja*) and angiosperms such as species of *Populus*, *Platanus*, *Liquidambar* and *Vaccinum*. It sometimes overgrows other fungi such as *Fomitopsis betulina* and *Crepidotus* spp.

Specimens examined (*indicates specimens that were cultured): As *Hormomyces aurantiacus*: **Austria**, Salzburg, Salzburg, on bark of rotten wood, 1880, *E.A. Rau* (BPI 726623). **Canada**, Ontario, Ottawa, Portobello Park, on rotten wood, probably *Populus* sp., Aug. 2014, *J. Mack* (DAOM 970822); *ibid*., Jul. 2015 (*DAOMC 252084); Ottawa, on rotten wood, probably *Populus* sp., 15 Jul. 2017, *J. Mack* (DAOM 970820, *DAOMC 252085); Quebec, Montreal, on rotten wood, 25 Oct. 2018, *G. Cartier*, isol. *J. Mack* (DAOM 970818, *DAOMC 252086); Victoriaville, on *Piptoporus*

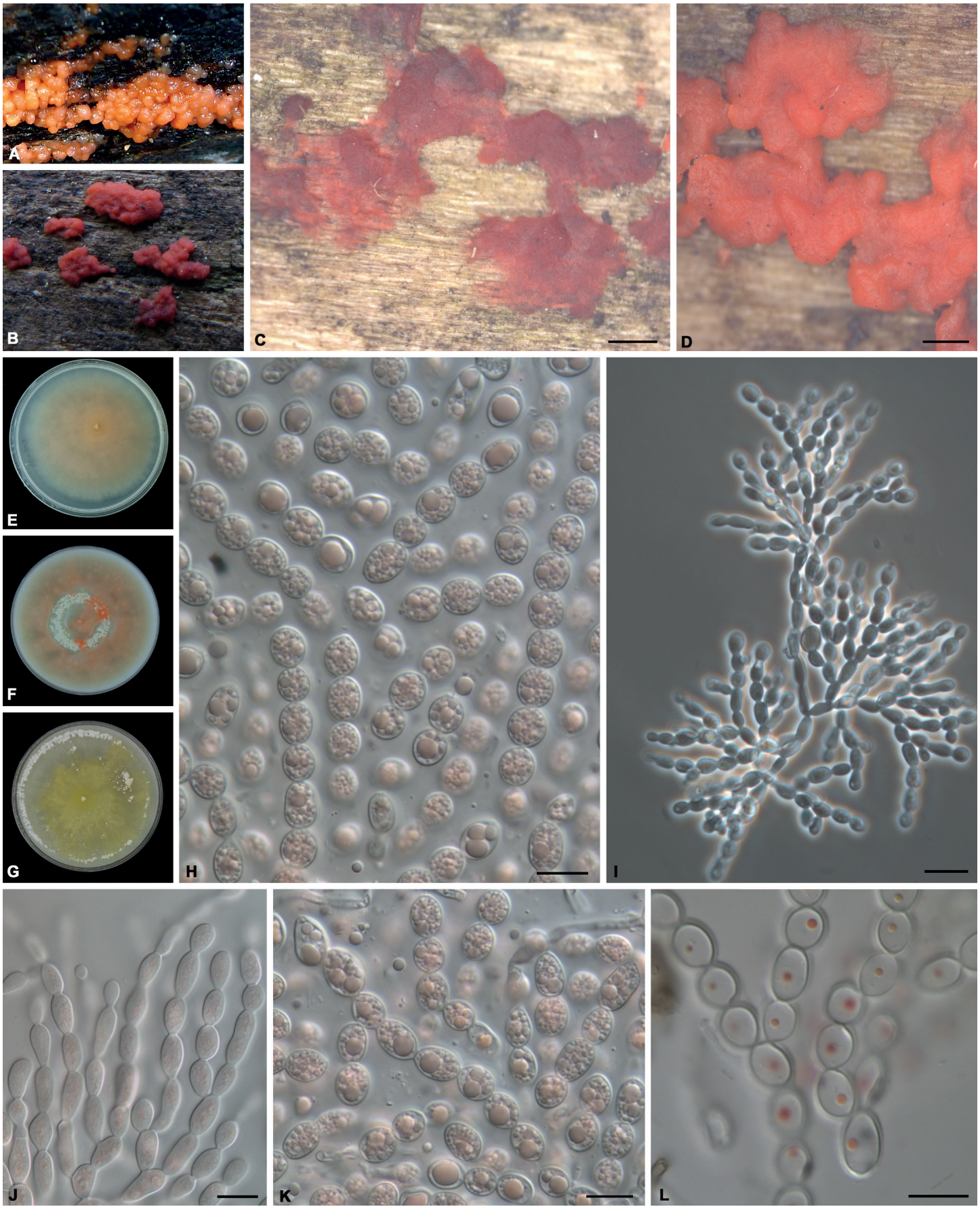

Fig. 4. *Tulasnella aurantiaca*. **A, B.** Appearance of fresh sporodochia on rotten wood. **C.** Detail of dried sporodochia. **D.** Detail of rehydrated sporodochia. **E–G**: 28-d-old culture, E on CMA with near-UV, F on OA with near-UV, G on OA in darkness. **H, K**. Living conidial chains in water. **I, J.** Conidial chains from culture on OA for 27 d under near-UV. **L.** Conidial chains in lactic acid. Scale bars: C–D = 500 µm, H, K–L = 10 µm, I, J = 20 µm.

betulinus, 13 Jun. 2016, *B. Fortier*, isol. *J. Mack* (DAOM 970821, *DAOMC 252083). **South Africa**, on bark of unidentified tree, undated, *V. Duthie Augusta* (BPI 702911). **USA**, Arizona: Portal, Greenhouse Canyon, on rotten wood of *Platanus* sp., 26 Aug. 1956, *J.L. Lowe & R.L. Gilbertson* (BPI 726600); Kentucky, Crittenden, on rotten wood, 11 Jul. 1910, *C.G. Lloyd* (BPI 702908); Maryland, Great Falls, on rotten wood, 10 Oct. 1936, *J.A. Stevenson* (BPI 726621); Great Falls, on rotten log, 17 Oct. 1936, *J.A. Stevenson* (BPI 726619); Patuxent Wildlife Refuge, on wood of *Liquidambar styraciflua,* Jul. 1952, *F. Berry* (BPI 726599); Sligo, on rotten wood and polypores, 16 Oct. 1936, *V.K. Charles & E.E. Dick* (BPI 726619); New York, Adirondack Mountains, Paul Smiths, on rotten wood, 21 Sep. 1927, *H.M. Fitzpatrick* (BPI 702905); Greenport, on bark of *Vaccinium* sp., 3 May 1921, *L. Roy* (BPI 702904); North Carolina, Macon County, Highland, Mirror Lake Rd, on a fallen branch, 27 Aug. 1989, *R.J. Bandoni* no. 8495 (DAOM 970797, as *Hormomyces* sp.). Pennsylvania, Meadville, on rotten wood, 1922, *E.C. Smith* (BPI 702909); no location, on rotten wood, 2018, *D. Newman*, isol. *J. Mack* (*DAOMC 251988); Tennessee, Great Smoky Mountains National Park, Cosby, on rotten wood and *Crepidotus* spp., 27 May 2018, *B.P Matheny*, isol. *B.P. Matheny* (received as a culture, *DAOMC 251989); West Virginia, Fairmont, on rotten wood, no date, *A. Boutlou* (BPI 702903). As *Hormomyces fragiformis*: **Canada**, Ontario, Coopers Falls, on rotten log, 16 Sep. 1952, *R.F. Cain* (DAOM 82339); South of Pottageville, on hardwood plank, 6 Jul. 1954, *R.F. Cain* (DAOM 52048); New Durham, on decaying log, 11 Nov. 1930, *R.F. Cain* (DAOM 81729). **USA**, New Hampshire, Shelburne, on dead wood and polypore, Jun. 1883, *M.C. Cooke* K(M) 257483 (holotype); Maryland, Grand Falls, on rotten wood, 11 Oct. 1936, *J.A. Stevenson* (BPI 726622); Missouri, Perryville, Jun. 1883, *C.H. Demetrio* (BPI 726620); North Carolina: Asheville, on rotten wood, 1918, *C.G. Lloyd* (BPI 726625), Winston-Salem, on bark of rotten wood, 4 Jul. 1936, *P.O. Schallert* (BPI 726626); Ohio, Cincinnati, on bark, 3 Oct. 1920, *C.G. Lloyd* (BPI 702914); Chapel Hill, 14 Jan. 1924, on rotting deciduous wood, *J.N. Couch* (UNC 7236, in DAOM); Vermont, Middlebury, on dead wood, 20 Aug. 1896, *E.A. Burt* (BPI 702913); Virginia, W slope of Mt. Elliot, Augusta Co., on rotten wood, 17–21 Jul. 1936, *J.A. Stevenson* (BPI 726617); Rapidan River, Shenandoah National Park, rotten wood, 24 Sep. 1936, *J.A. Stevenson* (BPI 726616); West Virginia, Fairmont, on bark of rotten wood, no date, *A. Boutlou* (BPI 626624). As *Hormomyces callorioides*: **South Africa**, Somerset West, on rotting wood, no date, *MacOwan* (holotype K(M) 257481).

Notes: *Tulasnella aurantiaca* is characterized by orange to red sporodochia growing on wood or rarely, on other fungi, and the production of ellipsoidal conidia generally shorter than 10 µm. No sexual morph is known. While most species of *Tulasnella* occur on rotten wood (Roberts 1994), until now their asexual morphs have only been reported as symbionts of orchids or liverworts. Most of these symbiotic *Tulasnella* spp. have conidia > 10 µm long. The conidia of *T. aurantiaca* are most similar to those of *T. epiphytica,* which are also < 10 µm long and occur in branched, monilioid chains; those of *T. epiphytica,* however, have pitted walls (Pereira *et al.* 2003). Like *T. aurantiaca, T. calendulina* also produces orange colonies in culture, but its monilioid cells are larger (Zelmer & Currah 1995). Monilioid chains have been reported from basidiomes of *T. violea*, but the component cells are also >10 µm long (Roberts 1994). Sporodochial asexual morphs resembling *T. aurantiaca* include *Oosporidium margaritiferum* (*Eurotiomycetes*, *Ascomycota*), which also produces gelatinous sporodochia with long, branched chains of globose conidia, but differs by yeast-like growth in culture and its habit on living woody plants (Kurtzman 2011). *Calloria fusarioides* (*Dermateaceae*, *Helotiales*, Ascomycota; asexual morph formerly known as *Cylindrocolla urticae*), also produces gelatinous, orange sporodochia with long, branched acropetal chains but its conidia are cylindrical (Seifert *et al.* 2011). *Heteromycophaga glandulosa* (tentatively *Tremellomycetes*, *cf.* Weiß *et al.* 2014), a parasite of basidiomes of *Exidia glandulosa*, produces clavate conidia attached to conidiogenous cells by a clamp connection (Roberts 1997); it is unclear from the protologue whether the conidia are single or formed in chains.

Tulasnella aurantiaca grows easily on standard mycological media and grows *in vitro* between 5 and 30 °C, suggesting that it may be well-adapted to grow in different biomes. Most of the specimens examined were collected between May to October, suggesting that *T. aurantiaca* has a long sporulating season, which generally correlates with its optimum growth temperature of 25 °C in temperate climates. However, this species can also occur during the winter, as an examined specimen was collected in January.

After studying the available types of all described *Hormomyces* species and many other specimens, only *H. fragiformis* and *H. callorioides* were appropriately placed in Tubaki's (1976) concept of *Hormomyces.* After careful studies of sporodochial coloration and conidial dimensions (Supplementary Fig. S1), we tentatively consider these two taxa to be conspecific with *H. aurantiacus* in agreement with Lloyd (1916). As far as we have been able to determine by microscopy, the herbarium specimens from Europe and South Africa are identical to the North America material. The colour variations we observed by growing cultures on different media in darkness or light, rewetting of sporodochia on *ca*. 30 herbarium specimens, and evaluation of approximately 35–40 photographs of both dried and fresh specimens on Mushroom Observer (Wilson *et al.* 2020), suggests that the colour distinctions used by previous authors, who examined only a few specimens, may not be diagnostic. However, the taxonomic significance of colour differences should be re-evaluated if additional evidence suggests the existence of cryptic, phylogenetic species within *T. aurantiaca.*

The cultures we examined and sequenced were all from North America and form a phylogenetically coherent clade. Bonorden's *H. aurantiacus* was described from Europe. Unfortunately, despite the many collecting excursions by the senior author in the Netherlands in the mid-1980s, two visits to South Africa in 1996 and 2006, and requests to both professional and amateur colleagues to watch for this fungus over the past five years, we were unable to obtain fresh specimens or cultures of *T. aurantiaca*-like asexual morphs from Europe or Africa. Whether phylogenetically distinct species might occur in other parts of the world remains unknown, and we chose to exercise caution and not to propose any of the currently available material to epitypify *T. aurantiaca.* In any case, Bonorden's illustration (reproduced here as Fig. 1), must serve as the lectotype (Art. 9.12, Turland *et al.* 2018) as proposed in the nomenclator above. If future studies of cryptic species support geographic separation, then *H. fragiformis* may be the appropriate name for material from North America, and *H. callorioides* for specimens from South Africa.

As reviewed in the Introduction, *T. aurantiaca* often was considered the asexual morph of *Tremella mesenterica* (McNabb 1969). Based on our phylogenetic results, the description of the asexual morph of *Tr. mesenterica* by Pipolla & Kotiranta (2008) and the yeast-like rather than filamentous growth of the latter in cultures (Fenwick 1995), this speculative connection is clearly untrue. The sexual morph of *T. aurantiaca,* if extant, remains unknown, but would be expected to have typical *Tulasnella* basidiomes and basidia.

Excluded species

Only *H. aurantiacus, H. fragiformis* and *H. callorioides,* discussed above, conform with the Tubaki (1976) concept of *Hormomyces,* now merged with *Tulasnella.* The remaining described species are discussed here.

Hormomyces abietinus P. Karst., Hedwigia 29: 271. 1890.
Synonym: ? *Dacrymyces deliquescens* Nees, 1816, *fide* Kennedy 1958.

We did not examine the type specimen. Kennedy (1958) considered *H. abietinus* a synonym of *Dacrymyces deliquescens*. McNabb (1973) synonymized *D. deliquescens* with *D. stillatus* and described the asexual morph of *D. stillatus*, which produces gelatinous, orange sporodochia with chains of arthroconidia 8–16 × 2.5–5.5 µm, similar to the conidial dimensions of *H. abietinus* reported by Karsten (1890). Neither Kennedy (1958) nor McNabb (1973) examined the holotype of *H. abietinus* and our request to examine the specimen in H remained unanswered; the synonymy remains tentative for this reason.

Hormomyces paridiphilus M. Zang & S.L. Wang, *Acta bot. Yunn*. **19**: 324. 1997.

This species was reported as a inhabitant of tubers of *Paris polyphylla* var. *yunnanensis* (*Melanthiaceae*) in China (Zang & Wang 1997). The holotype consists of fragments of uncertain composition overgrown by a dry, greyish oidiodendron-like hyphomycete with chains of light brown, subglobose, finely ornamented conidia (2–)2.5–3(–3.5) × (1.5–)2–2.5 µm (mean 2.78 ± 0.4 × 2.35 ± 0.1, Q 1.18, n = 50). Globose chlamydospores-like structures (7–)9–13(–15) × (5–)6–10 µm (mean 10.1 ± 0.6 × 7.89 ± 0.4, Q 1.3, n = 15) composed of oblong, pale brown cells, 2–4(–6.5) × (1–)1.5–3.5 µm (mean 3.03 ± 0.1 × 2.13 ± 0.1, Q 1.45) were also observed, growing singly and terminally on hyphae. It seems unlikely that the authors would have misinterpreted the *Oidiodendron* as a *Hormomyces*, and dimensions of the observed conidia do not match the protologue; it seems more likely that the original specimen was overgrown by this mould later on. The species will have to be re-collected to re-evaluate its taxonomy. Until then, the taxon should be considered a *nomen dubium*.

Specimen examined: **China**, Yunnan, on tubers of *Paris polyphylla* var. *yunnanensis*, 10 Sep. 1995, *S.L. Wang* (**holotype** HKAS 30237).

Hormomyces peniophorae P. Roberts, *Mycotaxon* **63**: 214, 1997.

The holotype consisted of twigs covered with basidiomes of *Peniophora lycii*, with inconspicuous gelatinous sporodochia ~1 mm diam forming pale spots on the hymenium. Conidia, conidiophores and haustoria consistent with those described by Roberts (1997) were observed. However, because the conidia are not formed in chains, there is no morphological reason to include this fungus in *Hormomyces,* and the presence of "tremellaceous" haustoria described and mycoparasitic ecology are more suggestive of *Tremellales* than *Cantharellales*. Because the haustoria are terminal, Roberts (1997) suggested a possible relationship of his species with the genus *Sirotrema*. However, the species of *Sirotrema* parasitize hosts in *Rhytismataceae*, and its species have clamp connections and yeast-like asexual morphs (Bandoni 1986). *Hormomyces peniophorae* should be recollected, cultured and sequenced before changes are proposed to its classification.

Specimens examined: **UK, England**, Devon, Scadson woods, Torquay, as a mycoparasite of *Peniophora lycii* growing on *Rubus idaeus*, 21 Jan. 1996, *P. Roberts* (**holotype** K(M):337706); Slapton woods, mycoparasite of *Peniophora lycii* growing on *Ulmus*, 10 Dec. 1994, *P. Roberts* (K(M):33198).

Hormomyces pezizoideus Speg., *Boln Acad. nac. Cienc. Córdoba* **2**: 467. 1889.

The holotype specimen (LPS 28379) could not be provided on loan, but with the kindness of the curators, we were able to examine Spegazzini's pencil drawing and a macro photograph of the specimen. These suggest a fungus with reddish sporodochia and branched chains of cuboidal or globose conidia ~1.5–2 µm diam, growing on a bamboo. These limited observations do not allow accurate identification of the species, but the small conidial size and bamboo habitat suggest it is not congeneric with *T. aurantiaca*.

DISCUSSION

Our taxonomic and phylogenetic revision of the hyphomycete genus *Hormomyces* provides the evidence for the formal synonymy with *Tulasnella* (*Cantharellales*) proposed by Stalpers *et al.* (2021), and the transfer of the type species *H. aurantiacus* to the latter genus. We consider two described species to be synonyms of *T. aurantiacus* based on type studies, and one species described in *Hormisciopis* is considered a synonym based on its protologue. *Tulasnella aurantiaca* is a relatively common fungus in temperate North America, conspicuous because of its gelatinous orange to reddish sporodochia and abundant globose to ellipsoidal conidia in branched, acropetal chains. While this combination of characters is diagnostic for *T. aurantiaca*, other sporodochial fungi with either Basidiomycetous or Ascomycetous affinities could be confused with *T. aurantiaca.* A key to similar genera is provided below. The species grows on rotten wood and occasionally overgrows wood-decaying fungi such as *Fomitopsis betulina* and *Crepidotus* sp. We did not observe microscopic structures that might indicate mycoparasitism, such as haustoria, in any specimens, suggesting that *T. aurantiaca* sometimes opportunistically overgrows fleshy basidiomes without parasitizing them. *Hormomyces* species are sometimes recorded from unusual substrates. One specimen of a *Hormomyces* sp. was reported from the palm *Rhopalostylis sapida* (McKenzie *et al.* 2004). A single strain identified as *H. aurantiacus* was isolated from the surface of a hibernating bat (*Myotis septentrionalis*) collected in a cave in New Brunswick, Canada (Vanderwolf *et al*. 2013). We did not examine either of these collections.

As described above, sporodochial colour is variable in this species. Our interpretation is that differences in colours of sporodochia constitute infraspecific variation related to age or environmental factors, and there are presently no correlations noted with other characters. In several other fungi, pigmentation is influenced by abiotic factors such as light, (*e.g.* Yu & Fischer 2018). Other sporodochial hyphomycetes, such as *Clonostachys rosea*, are well-known to produce conidiomata with variable colouration, ranging from yellow to orange, pink to red (Schroers

et al. 1999), with a striking bluish green colour defining *C. rosea f. catenulata* (Schroers 2001). Variation and overlapping characters in basidiome colour or micromorphology are also problems for the identification of basidiomes of *Tulasnella* species in the absence of DNA sequencing (Cruz *et al.* 2014).

When this species was known as *H. aurantiacus*, it was frequently considered the asexual morph of *Tremella mesenterica*. However, all nuc rDNA analyses confidently place this species in *Tulasnella* among sequences identified as *T. violea*. The latter species is often considered a synonym of *T. lilacina,* the type species of *Tulasnella,* but this synonymy has not yet been evaluated by DNA sequencing. Sequences attributed to *T. violea* appear to be monophyletic in the ITS phylogenetic tree, with the exception of a single strain that may be a misidentified strain of *T. eichleiriana*. In the 28S tree, the two GenBank sequences labelled as *T. violea* are polyphyletic but the strains sampled are different from those in the ITS trees and it is unclear whether one or both are misidentified. Based on our ITS phylogenetic analysis, *Tulasnella* appears to be divided into two clades with *T. aurantiaca* in the same clade, with high support, as all the sequences labelled as *T. violea*. If the synonymy of *T. violea* and *T. lilacina* is eventually confirmed, and the concept of the species is clarified, it is probable that *Hormomyces* would remain a synonym of *Tulasnella.*

Until very recently, only nuc rDNA sequences were available for *Tulasnella* species. Sequences for the nuc glutamate synthase gene (*C4102*), and mito ATP synthase (*C14436*) were introduced by Arifin *et al.* (2020) for species from Australia belonging to a clade within *Tulasnella* that includes orchid root endophytes and possibly *T. aurantiaca*. Only a few RNA polymerase subunit I (*RPB1*) and RNA polymerase subunit II (*RPB2*) sequences are available (Matheny *et al.* 2006, Moncalvo *et al.* 2006). A phylogenetically robust generic concept and any subdivision of *Tulasnella* into segregate genera will require the generation of addition sequences covering the entire family, possibly using *C4102* and *C14436*. Even if such studies justify splitting *Tulasnella* into segregate genera, it is probable that *Hormomyces* would stay nested within any narrower concept of the genus. Understanding the phylogenetic structure and species concepts in the core clade of *Tulasnella* around the type species clearly requires increased sampling and critical study. The inclusion of strictly asexual species in such analyses should provide additional phylogenetic and morphological characters and perhaps some clarity as future revisions proceed. The eventual taxonomic fate of *Epulorhiza* is less certain. The type species, *E. repens* (= *Tulasnella calospora*), and the other sequenced species of *Epulorhiza* are in the second ITS clade within *Tulasnella,* but this grouping is less evident in the 28S phylogeny. Therefore, it is possible that *Epulorhiza* could be re-instated if *Tulasnella* were divided.

Tulasnella species form mycorrhizae with several types of plants, especially several genera of orchids (Currah *et al*. 1997, Dearnaley *et al*. 2012, Almeida *et al.* 2014, Linde *et al.* 2017, Oberwinkler *et al*. 2017, Fujimori *et al*. 2019, Arifin *et al.* 2020), and liverworts (Preußing *et al*. 2009). Using mito 28S, Almeida *et al.* (2014) showed that the species formerly included in the asexual genus *Epulorhiza,* namely *T. amonilioides*, *T. epiphytica*, *T. albertaensis* and *T. anaticula,* do not form their own distinct clade, but are distributed across *Tulasnella*. In their phylogenetic analysis, strains identified as the type species of *Epulorhiza*, *E. repens* or its sexual morph *T. calospora,* are polyphyletic, and most of the clades represent unnamed endophytes isolated from orchid roots. We wonder whether *T. aurantiacus* may also be able to infect orchid roots because closely related species such as *T. prima*, *T. secunda, T. warcupii*, *T. australiensis, T. rosea* and several others occur in that niche (Linde *et al*. 2017, Arifin *et al*. 2020). *Cantharellales* are known for accelerated evolution of their nuc rDNA loci (Moncalvo *et al.* 2006) and the mutations in *T. aurantiaca* at the binding sites for the universal nuc rDNA primers, ITS4, ITS5 and LROR, may explain why it has not been detected in environmental samples. Different mutations in ITS primer binding sites of *Tulasnella* species were reported by Cruz *et al.* (2011), who designed specific primers different than those we designed for our study. Our modified primers for *T. aurantiacus* (Table 3) may be interesting to try for DNA surveys of orchid mycorrhizae or for the detection of related cryptic species.

Key to genera of hyphomycetes similar to *Tulasnella aurantiaca* (A = *Ascomycota*, B = *Basidiomycota*, U = unknown).

1. Clamp connections present on hyphae ..... *Heteromycophaga* (B)
1'. Clamp connections absent on hyphae 2

2. No sporodochia produced 3
2'. Sporodochia produced 5

3. Stipe dematiaceous ..... *Phaeomonilia* (A)
3'. Stipe hyaline 4

4. Producing large, inflated conidiogenous cells, often on *Eucalyptus* ..... *Quambalaria* (B)
4'. Conidia arising from simple hyphae conidia in long branched chains, only known from cultures derived from ascospores ..... *Chaenothecopsis haematopus* (A)

5. Conidia not in chains 6
5'. Conidia in chains that may be branched 8

6. Sporodochia cup-shaped, conidiogenous cells not in chains ..... *Ditangium* (B)
6'. Sporodochia not cup-shaped, conidiogenous cells in chains 7

7. Conidiogenous cells clavate ..... *Algonquinia* (U)
7'. Conidiogenous cells cuneiform ..... *Catenocuneiphora* (U)

8. Sporodochia gelatinous or slimy 9
8'. Sporodochia dry 14

9. Conidia 1-septate ..... *Dacrymyces stillatus* (B)
9'. Conidia aseptate 10

10. On orchid roots, liverworts or slime fluxes on trees 11
10'. In beetle galleries, or on rotten wood or mushrooms 12

11. Endophytic on orchid roots, or liverworts ..... *Tulasnella* (excluding *T. aurantiaca*)(B)
11'. On slime fluxes on living trees ..... *Oosporidium* (A)

12. In beetle galleries ..... *Raffaelea* (A)
12'. On rotten wood, litter or rotten mushrooms 13

13. Conidia cylindrical ..... *Calloria* (A)
13'. Conidia mostly ellipsoidal ..... *Tulasnella aurantiaca* (B)

14. Conidia yellow and with a very thick cell wall ..... *Sphaerosporium* (A)
14'. Conidia not as above 15

15. Parasitic on fresh fruits ..... *Monilia* (A)
15'. Not parasitic of fresh fruits 16

16. Conidia cuneiform ..... *Hyaloscypha* (asexual morphs formerly included in *Pseudaegerita*)(A)
16'. Conidia ellipsoidal to fusiform, not cuneiform 17

17. Conidia hyaline ..... *Cylindrium* (A)
17'. Conidia pigmented ..... *Hoornsmania* (U)

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Conflict of interest: The authors declare that there is no conflict of interest.

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Supplementary Material: http://fuse-journal.org/

Figure S1. Mean conidial dimensions (with error bars representing standard error) for all herbarium specimens and cultures examined, with the holotype of *H. fragiforme* represented by orange bars and the holotype of *H. callorioides* represented by green bars.

Figure S2. Lectotype of *H. fragiformis* (A, C, E) and holotype of *H. callorioides* (B, D, F). **A, B.** Rehydrated sporodochia. **C–F.** Conidial chains. Scale bars: A, B = 500 µm. C–F = 10 µm.

Figure S3. Conidia and conidial chains. **A.** *Oosporidium* sp. (DAOM 970823) identified using DNA sequencing. **B.** Holotype of *Sphaerocolla aurantiaca* (H). Both have similar conidial morphology and dimensions, suggesting that *S. aurantiaca* may be conspecific with *Oosporidium margaritiferum*. Scale bar = 10 µm.

Figure S4. Nuclear staining of hyphae of DAOMC 251988, showing dikaryotic, binucleate hyphae, A, using near-UV light showing the stained nuclei and B with regular light. Scale bar = 20 µm.

Table S1. Species, geographical location, host and herbaria for known type specimens of *Hormomyces* species.