Australian Journal of Taxonomy
Open-access, online, rapid taxonomy
https://doi.org/10.54102/ajt

A preliminary investigation of the diversity of *Hodophilus* (*Clavariaceae*) in Australia, with description of *Hodophilus citrinofoetens sp. nov.*

Luke J. Vaughan[1]*, Gareth D. Holmes[1], Genevieve M. Gates[2], Katrina Syme[3], Tom W. May[1]

[1] Royal Botanic Gardens Victoria, Birdwood Avenue, Melbourne, Victoria 3004, Australia
[2] 9 Winmarleigh Ave, Taroona, Tasmania 7053, Australia
[3] 24 Offer Street, Denmark, Western Australia 6003, Australia
*Corresponding author: luke.vaughan@rbg.vic.gov.au

Luke J. Vaughan https://orcid.org/0000-0003-1659-9938; Gareth D. Holmes https://orcid.org/0000-0003-1120-8731; Genevieve M. Gates https://orcid.org/0000-0002-9561-7788; Tom W. May https://orcid.org/0000-0003-2214-4972

Abstract

Hodophilus citrinofoetens sp. nov. is described from Australia using morphological characters and phylogenetic analyses of ITS and LSU rDNA sequences. New combinations are provided for *Camarophyllopsis darwinensis* from northern Australia and *C. kearneyi* from south-eastern Australia, which are confirmed as species of *Hodophilus* based on their phylogenetic placement and the presence of clavate to sphaeropedunculate terminal elements in a hymeniderm pileipellis. *Hodophilus citrinofoetens* is a rarely detected species with yellow sporing bodies and a strong naphthalene odour that is so far known from Tasmania and the South West region of Western Australia. It is macromorphologically distinct from other Australian *Hodophilus*, which are mostly shades of brown. The phylogenetic analysis revealed further unnamed species, amongst which are six putative novel species known from multiple collections, as well as additional singleton sequences. Further morphological and molecular investigations are required to confirm species delimitation among these putative phylogenetic species.

Cite this paper as: Vaughan LJ et al. (2026). A preliminary investigation of the diversity of *Hodophilus* (*Clavariaceae*) in Australia, with description of *Hodophilus citrinofoetens sp. nov.*. *Australian Journal of Taxonomy* 128: 1–15. doi: https://doi.org/10.54102/ajt.r8381

Introduction

Arnolds (1986) recognised *Camarophyllopsis* Herink with synonyms *Hodophilus* R. Heim and *Hygrotrama* Singer and accepted two subgenera: subgenus *Camarophyllopsis*, with a trichoderm pileipellis, and subgenus *Hodophilus* (R. Heim) Arnolds, with a hymeniderm pileipellis. Species of *Camarophyllopsis* form agaricoid, lamellate, stipitate sporing bodies with thick, widely spaced lamellae and a wax-textured appearance, which led to placement of the genus in the waxcap family *Hygrophoraceae* Lotsy (Arnolds 1986, Young 2005). *Camarophyllopsis* was distinguished from other waxcaps by sporing bodies with a generally dull colouration; a

This paper was submitted on 11 March 2026 and published on 29 June 2026 (2026-06-29T07:19:24.427Z). It was reviewed by Joshua Birkebak and Slavomír Adamčík, and edited by Kevin Thiele. Tom May is an Editor of the Australian Journal of Taxonomy. He did not at any stage have access to the manuscript while in peer review, and had no influence on its acceptance or handling, as is standard practice for manuscripts submitted by editors. Australian Journal of Taxonomy. ISSN: 2653-4649 (Online).

pilepellis of inflated, often clavate, terminal elements in a hymeniderm, epithelium or trichoderm; and the presence of caulocystidia (Arnolds 1990, Young 2005).

Based on a multilocus molecular phylogeny of *Agaricales*, Matheny et al. (2006) recovered *Camarophyllopsis* within *Clavariaceae* Chevall. In a single locus phylogeny of *Clavariaceae* using the large subunit (LSU) rDNA, Birkebak et al. (2013) recovered species of *Camarophyllopsis* in two separate lineages. Relationships of *Camarophyllopsis* were investigated further by Birkebak et al. (2016), who assembled a multilocus phylogeny of *Clavariaceae* and recovered three distinct clades of agaricoid fungi. One clade represented a novel genus described as *Lamelloclavaria* Birkebak & Adamčík, while the other two clades represented the morphological taxonomic concepts of *Camarophyllopsis* subgenus *Camarophyllopsis* and *Camarophyllopsis* subgenus *Hodophilus*. Consequently, Birkebak et al. (2016) recognised *Hodophilus* R. Heim at genus level, distinguished from *Camarophyllopsis* and *Lamelloclavaria* by the composition of the pileipellis, which is typically a vertically-arranged hymeniderm of inflated, globose to sphaeropedunculate terminal elements.

Twenty-eight species are currently accepted in *Hodophilus* (Species Fungorum 2026), with most diversity known so far described from Europe (Kovalenko et al. 2010, Adamčík et al. 2017, Arauzo & Iglesias 2018, Adamčík et al. 2018, 2020), North America (Adamčík et al. 2016) and Asia (Crous et al. 2017, Zhang et al. 2019, Tang et al. 2023). *Hodophilus roseolus* (G. Stev.) J.A. Cooper is known from New Zealand (Index Fungorum 2023). Three sections are recognised by Adamčík et al. (2020) based on strongly supported lineages in the phylogeny of Northern Hemisphere species. *Hodophilus* sect. *Hodophilus* contains the type species *H. foetens* (W. Phillips) Birkebak & Adamčík, and includes European and North American species with distinct naphthalene odours that are mostly shades of brown, except for *H. atropunctus* (Pers.) Birkebak & Adamčík, which does not have a distinct odour and has dark dots on the stipe (Adamčík et al. 2016, 2017, 2020). *Hodophilus* sect. *Micacei* Adamčík & Dima includes European and North American species characterised by yellow colours on the stipe and lacking strong naphthalene odours (Adamčík et al. 2018). *Hodophilus* sect. *Phaeophylli* Adamčík & Dima contains European species without naphthalene odours or yellow colours (Adamčík et al. 2020).

Two species of *Camarophyllopsis* were formally described from specimens collected in Australia by A.M. Young: *C. darwinensis* A.M. Young, a small, pale pinkish-brown mushroom from tropical Northern Territory and Queensland (Young & Wood 1997, Young 2005); and *C. kearneyi* A.M. Young, a smaller, dull pale-brown mushroom from temperate New South Wales and Tasmania (Young 1999, 2005, Young & Mills 2002). Young (2005) placed both these Australian species in *Camarophyllopsis* subgenus *Hodophilus* based on the epithelium or hymeniderm structure of the pileipellis. Based on the pileipellis structure described by Young (Young & Wood 1997, Young 1999, 2005), *C. kearneyi* and *C. darwinensis* require recombination in the genus *Hodophilus.* Indeed, Zhang et al. (2019) keyed out *C. kearneyi* and *C. darwinensis* (as *C. darminensis*) under *Hodophilus* but did not make new combinations. Gates and Ratkowsky (2014) illustrated *Camarophyllopsis darwinensis* and two undescribed species, *C.* sp. 'brown' and *C.* sp. 'yellow', that are noted to have naphthalene odours. The Australasian Virtual Herbarium (https://avh.ala.org.au/) lists various specimens of *Camarophyllopsis* from Australia.

We assembled Australian fungarium specimens identified in collections as *Camarophyllopsis* and *Hodophilus* for morphological examination and phylogenetic analyses. Based on the phylogenetic placement and the inflated terminal elements of the hymeniderm pileipellis, we provide new combinations for *C. darwinensis* and *C. kearneyi* in *Hodophilus* and describe the new species *Hodophilus citrinofoetens*. We discuss additional diversity of Australian *Hodophilus* recovered in the phylogeny.

Methods

Presentation of names.

Names of taxa at all ranks are italicised following Thines et al. (2020).

Specimen selection.

Fungarium specimens collected in Australia and identified as *Camarophyllopsis* or *Hodophilus* in collections were selected for examination from the National Herbarium of Victoria (MEL), the Queensland Herbarium (BRI), the NSW Plant Pathology & Mycology Herbarium (DAR), the Tasmanian Herbarium (HO), the Western Australian Herbarium (PERTH), the University of Tennessee Fungal Herbarium (TENN-F) and the John T. Waterhouse Herbarium (UNSW). Additional specimens from MEL that were identified in collections as *Marasmius* or indetermined Fungi were included for examination because their morphology was consistent with *Hodophilus*.

Morphological examination.

The macromorphological description for the novel species is assembled from descriptive notes and photographs of fresh collections recorded by collectors, as well as examination of dried material. Colours of fresh collections are described based on field notes made by collectors in daylight conditions and, where possible, according to Kornerup and Wanscher (1978) in the format, for example, 4A5. Key characters of existing species are a precis of descriptions from Young (2005).

The micromorphological description for the novel species is based on examination of dried fungarium specimens, from which hand cut sections were rehydrated in 5% potassium hydroxide (KOH) following Tang et al. (2023) and then stained with Congo red to easily observe cell walls. Microscopic features were observed

and photographed using an Olympus BX51 microscope (Olympus, Tokyo, Japan) with differential interference contrast and an Olympus DP73 camera attachment. Measurements were taken at ×400 or ×1000 (with oil immersion) using measurement tools in Olympus cellSens standard (v. 1.16). Basidiospore measurements were recorded from at least 10 spores per specimen examined. Basidiospore measurements are provided in descriptions as the observed range of values, then as the range of means per specimens examined with the grand mean italicised. The number of spores measured from the the number of specimens examined is provided after the measurements (e.g., n/x), where *n* indicates the number of spores measured and *x* indicates the number of specimens examined. Measurements of basidia, cystidia, terminal and subterminal elements of the pileipellis were recorded primarily from the holotype and supplemented from additional specimens examined. These are provided as the observed range of values in the description.

DNA isolation, PCR and sequencing.

DNA was isolated from selected specimens (Table 1) using a modified CTAB method summarised in Craig et al. (2023), based on that of Gardes & Bruns (1993). Polymerase chain reactions (PCR) were performed to amplify the internal transcribed spacer (ITS) rDNA and domains D1–D2 of the large subunit (LSU) rDNA in 20 µl reactions using MyTaq Red Mix (Bioline/Meridian Bioscience, London, UK), 1 µl of DNA template and the primers pairs ITS5/ITS4 or ITS1F/ITS4 (White et al. 1990, Gardes & Bruns 1993) and LR5/LROR (Vilgalys & Hester 1990, Vilgalys Lab 1992), respectively, using protocols outlined by Craig et al. (2023). Sequencing was undertaken by the Australian Genome Research Facility (AGRF, Melbourne, Australia) and chromatograms were aligned, manually checked and edited using Geneious Prime 2021.0.3 (https://www.geneious.com) to generate consensus sequences (Table 1).

Phylogenetic analyses.

The ITS and LSU sequences generated in this study were assembled with sequences from species of *Hodophilus* and the closely related genus *Clavaria* Vaill. ex L. that were downloaded from NCBI GenBank, based on the phylogeny of Birkebak et al. (2013, 2016), Adamčík et al. (2016, 2017, 2020) and Tang et al. (2023). Additional *Hodophilus* sequences were downloaded from UNITE (Abarenkov et al. 2023) by searching for sequences (search by NCBI+UNITE sequences; filter for *Hodophilus*) and using MassBLASTer through the PlutoF workbench (Abarenkov et al. 2010) to find sequences from NCBI and UNITE with high similarity to sequences generated from Australian specimens (Supplementary material 1: Table of all sequences). The ITS and LSU datasets were aligned separately using MUSCLE Alignment (Version 3.8.425) (Edgar 2004) implemented in Geneious Prime (1000 maximum iterations, 100 maximum trees, all other settings default), followed by manual editing including trimming of sequence ends. Preliminary maximum likelihood phylogenetic analyses were conducted separately for the ITS and LSU alignments to check for incongruence. We did not detect incongruence, so we concatenated the ITS and LSU alignments and then manually partitioned for ITS1–5.8S–ITS2–LSU.

Maximum-likelihood (ML) phylogenetic analyses were performed for the ITS1–5.8S–ITS2–LSU alignment using command-line IQ-TREE 2.2.2.6 (Nguyen et al. 2015, Minh et al. 2020). IQ-TREE implemented partition models (Chernomor et al. 2016) to test merging partitions and ModelFinder (Kalyaanamoorthy et al. 2017) to test for the best-fit substitution models for partitions according to Bayesian Information Criterion (BIC). Partition models merged ITS1–ITS2 and 5.8S–LSU and ModelFinder selected TPM2u+F+G4 as best-fit model for ITS1–ITS2 and TIM2+F+I+G4 for 5.8S–LSU. The consensus tree was estimated using UFBoot2 (Hoang et al. 2018) to calculate ultrafast bootstrap support (UFBS) values from 10,000 replicates (Supplementary material 4: ML consensus tree).

Bayesian analyses (BI) were performed for the ITS1–5.8S–ITS2–LSU alignment using command line MrBayes 3.2.6 (Huelsenbeck & Ronquist 2001, Ronquist et al. 2012). The GTR+G+I nucleotide substitution model was applied. Two simultaneous runs of two million MCMC iterations were performed, with four heated chains, a heated chain temperature of 0.2, a sampling frequency of 1000, and burn-in length of 25%, which resulted in stable average standard deviation of split frequencies below 0.01. Sequences of *Clavaria pullei* were included as the outgroup for ML and BI according to the phylogeny of Birkebak et al. (2013, 2016).

As the topology of ML and BI analyses were consistent, only ML UFBS values ≥ 95% and BI posterior probability (PP) ≥ 0.90 are shown at nodes. For clades with ML UFBS values ≥ 95% and BI PP < 0.90, BI PP are shown in parentheses, and vice versa.

Supplementary materials, including the complete list of sequences (Supplementary material 1: Table of all sequences), the concatenated alignment (Supplementary material 2: ITS+LSU alignment), the partition file (Supplementary material 3: ML partition file), the consensus maximum likelihood phylogeny (Supplementary material 4: ML consensus tree) and the data block used for BI analyses (Supplementary material 5: BI data block) are deposited on figshare (https://doi.org/10.6084/m9.figshare.31064017).

Results

Phylogenetic analyses.

The ITS+LSU dataset contained DNA sequences from 97 specimens of at least 44 putative species of *Hodophilus* (Supplementary material 1: Table of all sequences), including sequences from 26 specimens from Australia published in this study (Table 1). The aligned ITS+LSU

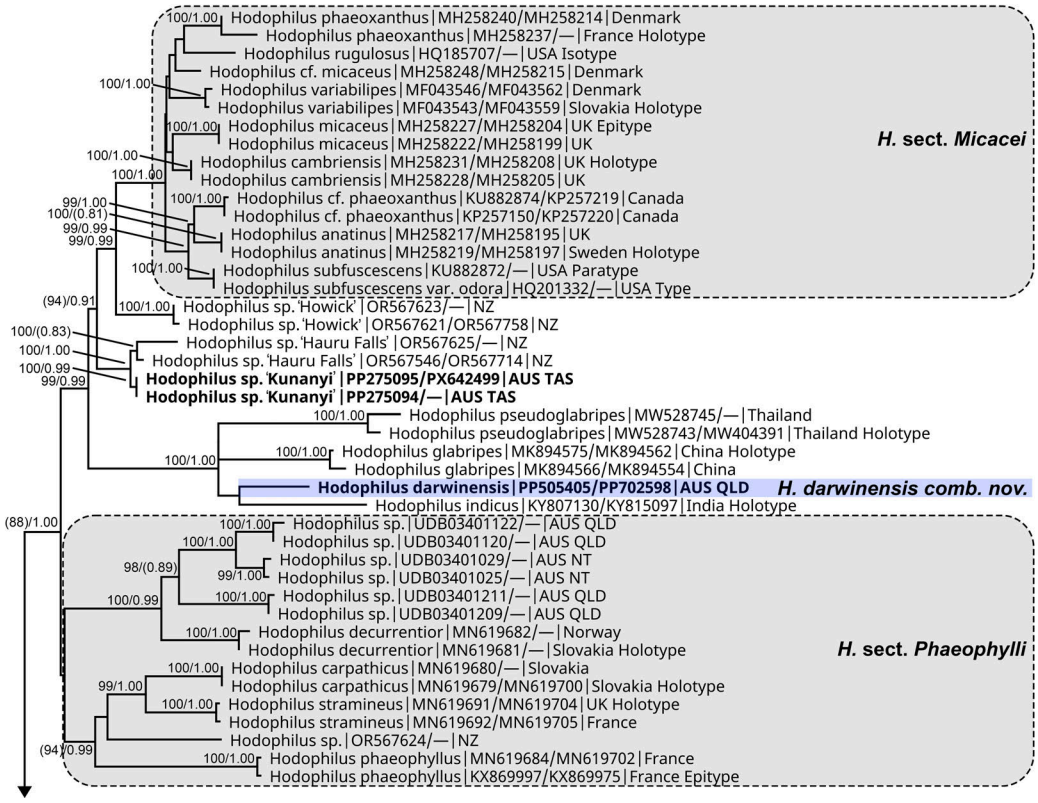

Figure 1. Maximum likelihood consensus phylogeny of *Hodophilus* based on ITS and LSU sequences, revealing the placement of *H. darwinensis comb. nov.*, *H. kearneyi comb. nov.*, *H. citrinofoetens sp. nov.* and several undescribed species from Australia within the genus. ML UFBS values ≥ 95% and BI posterior probability (PP) ≥ 0.90 are shown at nodes. For clades with ML UFBS values ≥ 95% and BI PP < 0.90, BI PP are shown in parentheses, and vice versa. Sequences of *Clavaria pullei* were included as the the outgroup following Birkebak et al. (2013, 2016). Sequences generated in this study are in bold type. New combinations are shown in blue highlight. The new species is shown in yellow highlight. Sections of *Hodophilus* defined by Adamčík et al. (2020) are shown in grey highlight. GenBank or UNITE sequence accessions, location from which specimens were collected, and type status are given after taxon names.

dataset comprised 1633 characters, of which 1116 were constant and 390 were parsimony informative.

In the ML and BI phylogenetic analyses of ITS+LSU (Fig. 1), the clade containing all the species of *Hodophilus* has high support (100% UFBS, 1.00 PP). The type species of the genus, *Hodophilus foetens*, is recovered within a well-supported (100% UFBS, 0.99 PP) clade corresponding to section *Hodophilus*, as far as the species included in this section by Adamčík et al. (2020). *Hodophilus* section *Micacei* is also recovered with high support (100% UFBS, 1.00 PP), as far as the species included in this section by Adamčík et al. (2020). There is a clade that contains all the species included in *H.* section *Phaeophylli* by Adamčík et al. (2020) and Tang et al. (2023), as well as an undetermined species from New Zealand and three separate clades of eDNA sequences from Australia. This clade has weak support that is below the significance thresholds for ML UFBS and BI PP. Within this clade there are two subclades. One clade (94% UFBS, 0.99 PP) represents *H. phaeophyllus*, *H. stramineus*, *H. carpathicus* and an undescribed species from New Zealand. The sister clade (100% UFBS, 0.99 PP) includes *H. decurrentior*, along with Australian eDNA sequences forming three distinct clades.

Sequences from Australian fungarium specimens or soil samples place in multiple separate clades, representing the two species recombined here as *Hodophilus darwinensis* and *H. kearneyi*, the novel species *H. citrinofoetens*, and at least six putative undescribed species, as well as singletons that remain unnamed. We have assigned the provisional names *H*. sp. 'Coachwood', *H*. sp. 'eastern brown', *H*. sp. 'GG0196', *H*. sp. 'Kunanyi', *H*. sp. 'light brown' and *H*. sp. 'western brown' to clades newly identified based on Australian sporing body material, alongside *H*. sp. 'Aongatete', *H*. sp. 'Hauru Falls' and *H*. sp. 'Howick' from New Zealand as identified by Cooper (2023). Four clades containing DNA sequences from Australian soil samples remain "dark taxa" because sporing bodies with DNA sequences have not yet been matched to these clades to determine the morphology of species.

Hodophilus darwinensis places in a well-differentiated, highly supported (100% UFBS, 1.00 PP) clade represented by species from Asia, including *H. glabripes* from China, *H. pseudoglabripes* from Thailand and *H. indicus* from India. Within this clade, *H*. *darwinensis* is sister to *H. indicus* in the consensus ML tree and BI tree, although support for this relationship is below significance

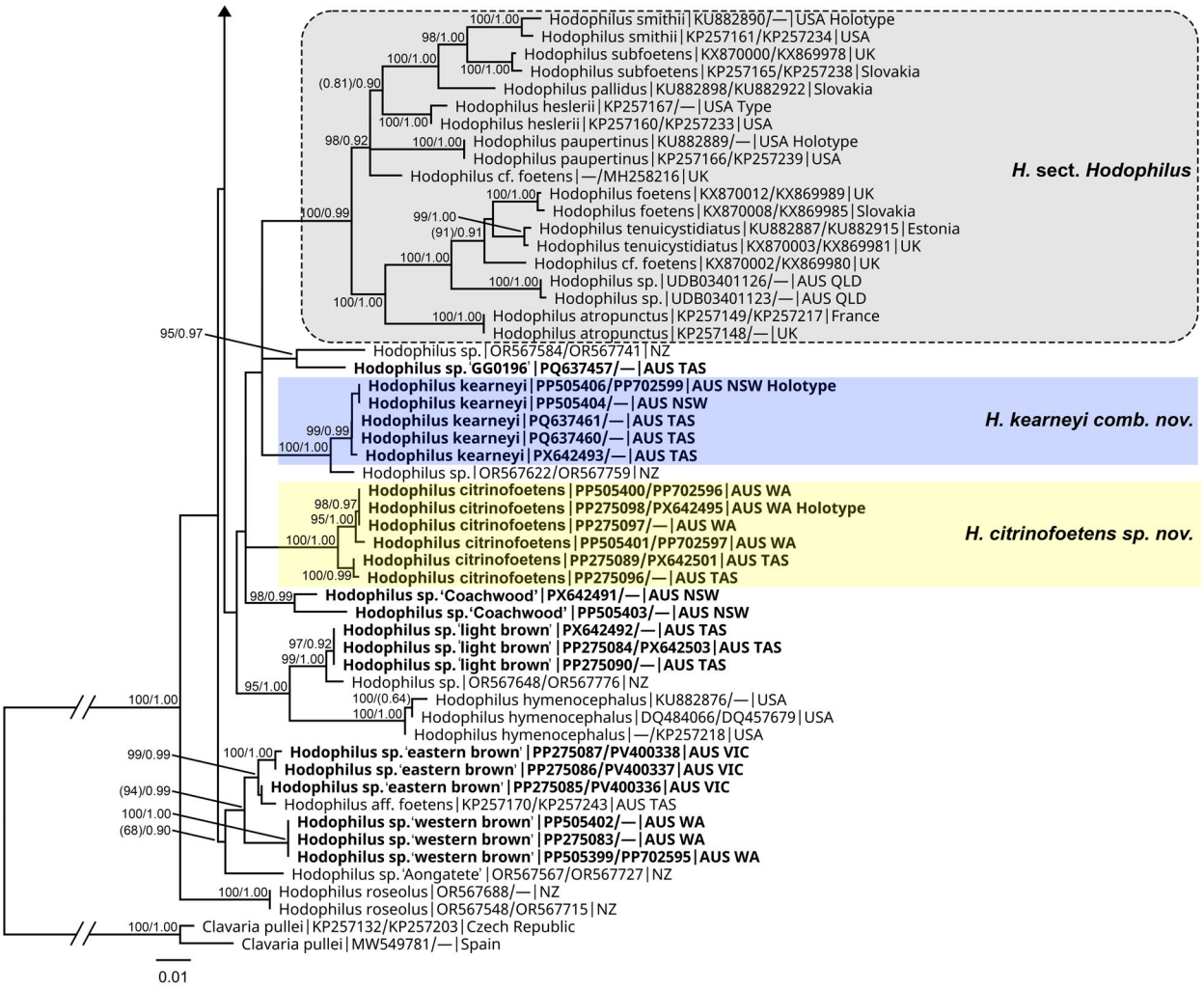

Figure 1. (Continued).

thresholds. *Hodophilus kearneyi* (99% UFBS, 0.99 PP) and *H. citrinofoetens* (100% UFBS, 1.00 PP) both form highly supported clades among a grade of several undescribed putative species from Australia and New Zealand that are phylogenetically close to *H. hymenocephalus* from the USA. The clade of *H. kearneyi* is sister to a single sequence from a specimen collected in New Zealand that has 96.40–98.56% pairwise identity to ITS sequences in the *H. kearneyi* clade. The *H. kearneyi* clade includes two sequences from specimens collected in NSW, including from the type locality in Lane Cove Bushland Park, and three sequences from specimens collected in Tasmania, which confirms the distribution of the species given by Young (2005). Two sequences from specimens collected from the type locality of *H. kearneyi* that were originally identified as *H. kearneyi* place in a separate clade that we refer to as *H.* sp. 'Coachwood' within the grade containing *H. citrinofoetens*. This clade represents at least one undescribed species and the variation between the two ITS sequences (95.28% pairwise identity) suggests the possibility of two separate lineages that require further sampling. Another putative undescribed species represented by sequences from Australia and New Zealand, *H.* sp. 'light brown', is sister to *H. hymenocephalus*.

The clade of *H. citrinofoetens* comprises two distinct, highly supported clades represented by specimens from eastern and western Australia, respectively. Although these clades are distinct, the pairwise identity of ITS sequences across both the eastern and western clades are between 97.83–100%, and consistent morphological differences between the clades were not detected. This species is formally described below based on the phylogenetic placement and morphological characters.

Morphological examination.

The morphological examination of Australian specimens focused on three species recognised in the phylogeny: *H. darwinensis*, *H. kearneyi*, and *H. citrinofoetens*. We recognise the clade containing sequences from the type specimen of *Camarophyllopsis kearneyi* in the phylogeny as *H. kearneyi*. Examination of the pileipellis tissue of *H. kearneyi* specimens was consistent with the descriptions by Young (1999, 2005), which are congruent with other species placed in *Hodophilus*. We assign the name *Hodophilus darwinensis* to the sequenced specimen (BRI

AQ0669231) in the phylogeny identified as *Camarophyllopsis darwinensis* by Young (2005). Although we were unable to obtain sequences from the holotype specimen of this species, examination of both specimens showed that the micromorphology of BRI AQ0669231 is consistent with the holotype.

We assign the name *H. citrinofoetens* to the clade of sequences from specimens with bright yellow colours and strong naphthalene odour, which was selected for description based on its unique morphological features in comparison to the other undescribed species from Australia.

Discussion

Infrageneric classification.

In the phylogeny (Fig. 1), we have indicated the membership of species within *H*. sections *Hodophilus*, *Micacei* and *Phaeophylli* based primarily on the placement of Northern Hemisphere species that have already been assigned to these sections by Adamčík et al. (2020). We place a number of additional putative Southern Hemisphere species within *H*. sect. *Phaeophylli* because these putative species are intermingled with Northern Hemisphere species in that section. We note, however, that there is low support for the clade of *H*. sect. *Phaeophylli*. We do not have morphological data for the Australian putative species that are represented by eDNA sequences from soil. The New Zealand specimen (PDD 107271; GenBank: OR567624) appears to conform morphologically with the section, without yellow colour or dark dots on the stipe, but it is noted to have an unspecified distinctive odour.

We also note there are some clades in the phylogeny that could potentially be included in other existing sections, including *H*. sect. *Micacei,* by extending the boundaries of those clades. For example, a number of putative Southern Hemisphere putative species, including *Hodophilus* sp. 'Kunanyi', and the clade of tropical species from Asia and Oceania, including *H. darwinensis*, are recovered within a strongly supported clade that includes *H*. sect. *Micacei*. However, we hesitate to include these species in *H*. sect. *Micacei* on the basis of this phylogeny and without detailed morphological examination. It can also be argued that the clade of tropical species may represent another viable section defined by its robust phylogenetic placement and the disjunct distribution of its species from those of other currently defined sections.

Some undescribed putative species from Australia and New Zealand that are phylogenetically close to *H. hymenocephalus* form an unsupported clade with *H*. sect. *Hodophilus*, and additional Southern Hemisphere species such as *H. roseolus* place outside that unsupported clade. Some of these species could potentially be included in *H*. sect. *Hodophilus* but there is no support for the backbone of the tree to justify this. It is unclear if some of these Australian and Zealand taxa may also require their own infrageneric taxa. Future studies with additional coding markers and comprehensive sampling of Southern Hemisphere diversity would assist with determining the infragenetic placement of Southern Hemisphere species, as well as effective species delimitation. Mapping of morphological characters onto a multi gene phylogeny would also be of interest.

Recombination of former Camarophyllopsis *species* H. darwinensis *and* H. kearneyi*.*

The recombination of *H. darwinensis* and *H. kearneyi* within the genus *Hodophilus* is justified by the phylogenetic placement of representative sequences and the robust support for the clades within which these sequences are recovered. The recombination is also supported morphologically by the hymeniderm pileipellis that is composed of globose, clavate or sphaeropedunculate terminal cells. With *H. darwinensis* and *H. kearneyi* recombined in *Hodophilus*, we do not have any confirmed specimen records of *Camarophyllopsis* from Australia, since all available sequences from specimens previously identified as *Camarophyllopsis* place within *Hodophilus*. However, 105 eDNA sequences on the PlutoF database that were isolated from soil samples collected in Australia are labelled as *Camarophyllopsis* (Abarenkov et al. 2010). Preliminary phylogenetic analyses (not shown) of the PlutoF eDNA sequences labelled as *Camarophyllopsis* confirms they place in a clade with *Camarophyllopsis schulzeri* (Bres.) Herink, the type species of that genus. Further collections of sporing bodies that match these sequences would be needed to confirm the presence of *Camarophyllopsis* in Australia.

Taxonomy

Hodophilus darwinensis (A.M. Young) L.J. Vaughan & T.W. May, *comb. nov.*

MB861980

Basionym: *Camarophyllopsis darwinensis* A.M. Young, in Young & Wood, *Austral. Syst. Bot*. 10: 1017 (1997).

Typification: NORTHERN TERRITORY, Darwin (12.399917° S, 130.93125° E), on soil in monsoon forest, 22 Feb 1985, *A.E. Wood & W. Kilkeary UNSW 85/127* (**holotype** UNSWDB16576!).

Fig. 2

Key characters: Sporing bodies with creamy buff-brown or pinkish fawn (5AB–5B3) pileus, drying to pale buff with pinkish tints (4A3); pale pinkish (5A2) lamellae; stipe white to very pale cream-coloured (4A2); basidiospores 5.2 x 4.8 µm, Q = 1.0–1.3; pileipellis an epithelium of globose or pyriform elements 12–26 × 6–16 µm.

For a full description based on the holotype see Young & Wood (1997) and for the description also including material from Queensland, see Young (2005).

Table 1. Australian *Hodophilus* specimens for which ITS and LSU sequences were generated for this study.

Taxon	Original determination	Specimen	Locality	Date	Collector	ITS	LSU
H. citrinofoetens	*Camarophyllopsis* sp.	MEL 2524949	AUS:TAS	30-Aug-2003	G.M. Gates, D.A. Ratkowsky 4141	PP275096	—
H. citrinofoetens	*Camarophyllopsis* sp.	PERTH 08118914	AUS:WA	23-Jun-2006	K. Syme 1543	PP505401	PP702597
H. citrinofoetens	*Camarophyllopsis* sp.	MEL 2526029	AUS:WA	23-Jun-2006	K. Syme 1543	PP275097	—
H. citrinofoetens	*Camarophyllopsis* sp.	PERTH 08166587	AUS:WA	6-Jun-2013	R.M. Robinson, P. Anderson FC 1896	PP505400	PP702596
H. citrinofoetens	*Camarophyllopsis* sp.	MEL 2392821	AUS:TAS	24-Aug-2015	G.M. Gates 3151	PP275089	PX642501
H. citrinofoetens HOLOTYPE	*Marasmius* sp.	MEL 2292260	AUS:WA	19-Jun-2004	K. Syme 1327/04	PP275098	PX642495
H. darwinensis	*Camarophyllopsis darwinensis*	BRI AQ0669231	AUS:QLD	20-May-2001	P.I. Forster, R. Booth, A.M. Young PIF27253	PP505405	PP702598
H. kearneyi	*Camarophyllopsis* sp.	HO587534	AUS:TAS	30-Aug-1995	A.K. Mills 1352	PQ637460	—
H. kearneyi	*Camarophyllopsis* sp.	HO587536	AUS:TAS	16-Apr-1996	A.K. Mills 1382	PQ637461	—
H. kearneyi	*Camarophyllopsis kearneyi*	BRI AQ0807939	AUS:NSW	28-Jun-1998	R. Kearney, E. Kearney 2158	PP505404	—
H. kearneyi	*Camarophyllopsis kearneyi*	MEL 2089735	AUS:TAS	26-May-1999	A.M. Young 2236	PX642493	—
H. kearneyi HOLOTYPE	*Camarophyllopsis kearneyi*	DAR0073919	AUS:NSW	13-Jun-1998	R. Kearney, E. Kearney s.n.	PP505406	PP702599
H. sp. 'Coachwood'	*Camarophyllopsis kearneyi*	BRI AQ0799520	AUS:NSW	16-Jun-1998	A.M. Young 2152	PP505403	—
H. sp. 'Coachwood'	*Camarophyllopsis kearneyi*	BRI AQ0799519	AUS:NSW	26-Jun-1998	A.M. Young 2159	PX642491	—
H. sp. 'eastern brown'	*Hodophilus* sp.	MEL 2533398	AUS:VIC	12-Aug-2023	L.J. Vaughan 11	PP275085	PV400336
H. sp. 'eastern brown'	*Hodophilus* sp.	MEL 2533399	AUS:VIC	12-Aug-2023	L.J. Vaughan 12	PP275086	PV400337
H. sp. 'eastern brown'	*Hodophilus* sp.	MEL 2533400	AUS:VIC	12-Aug-2023	L.J. Vaughan 13	PP275087	PV400338
H. sp. 'GG0196'	*Camarophyllopsis* sp.	HO608630	AUS:TAS	7-Nov-2000	G.M. Gates, D.A. Ratkowsky 0196	PQ637457	—
H. sp. 'Kunanyi'	*Camarophyllopsis* sp.	MEL 2300641	AUS:TAS	26-Jul-1999	S.J.M. McMullan-Fisher 403	PP275095	PX642499
H. sp. 'Kunanyi'	*Camarophyllopsis* sp.	MEL 2300665	AUS:TAS	23-Jul-2001	S.J.M. McMullan-Fisher 1500	PP275094	—
H. sp. 'light brown'	*Camarophyllopsis* sp.	HO608636	AUS:TAS	10-Jul-2001	G.M. Gates, D.A. Ratkowsky 0201	PX642492	—
H. sp. 'light brown'	*Camarophyllopsis* sp.	MEL 2524961	AUS:TAS	6-May-2003	G.M. Gates, D.A. Ratkowsky 4147	PP275090	—
H. sp. 'light brown'	*Camarophyllopsis* sp.	MEL 2524962	AUS:TAS	22-Jul-2003	G.M. Gates, D.A. Ratkowsky 4146	PP275084	PX642503
H. sp. 'western brown'	Fungi indet.	MEL 2233864	AUS:WA	16-Jul-2002	K. Syme 1205/02	PP275083	—
H. sp. 'western brown'	*Camarophyllopsis* sp.	PERTH 08118701	AUS:WA	16-Jul-2002	K. Syme 1205/02	PP505402	—
H. sp. 'western brown'	*Camarophyllopsis foetens*	TENN-F-066509	AUS:WA	18-Jul-2011	P.B. Matheny 3644	PP505399	PP702595

Sequenced specimen examined: QUEENSLAND, State Forest 185 Danbulla, Kauri Creek Rd (17.110131° S, 145.551937° E), in sandy soil under ferns beside creek, within 20 cm of water line, in open forest of *Allocasuarina torulosa*, *Syncarpia glomulifera*, *Eucalyptus tereticornis* and *E. portuensis*, damp creeklet on granite, 19 May 2001, *P.I. Forster, R. Booth, A.M. Young PIF27253* (BRI AQ0669231). GenBank: ITS = PP505405; LSU = PP702598.

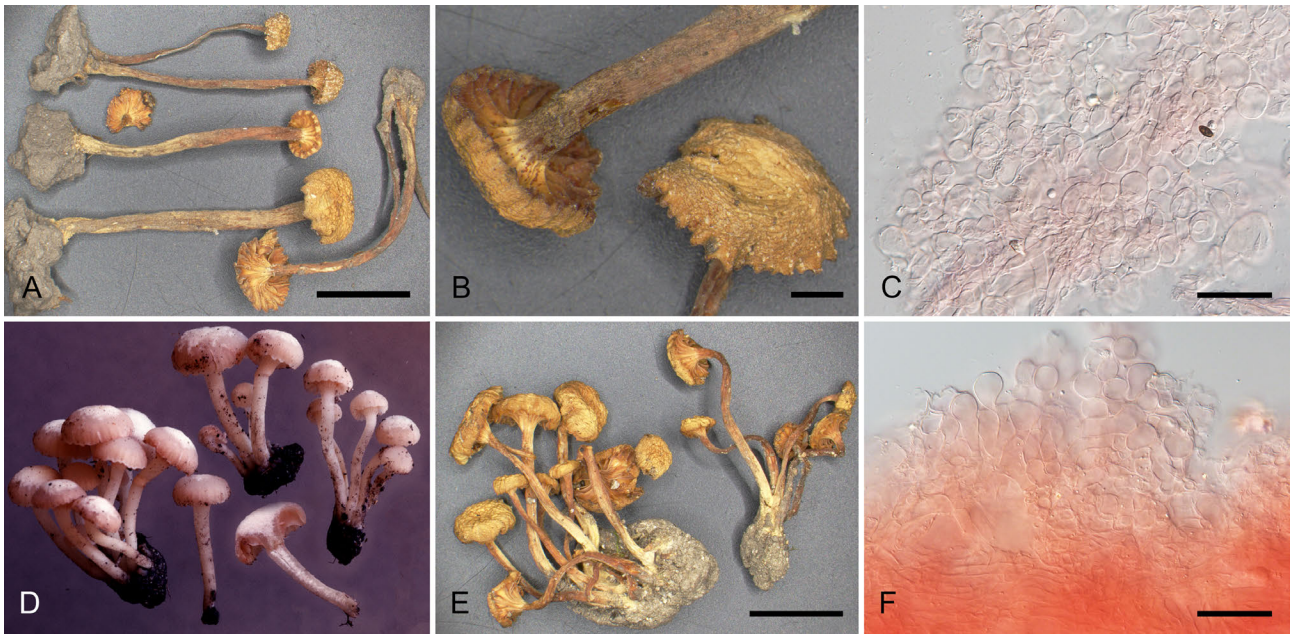

Figure 2. Morphology of *Hodophilus darwinensis comb. nov.* **A**–**C**. Holotype UNSWDB16576. **A**–**B**. Dried specimens. **D**–**F**. BRI AQ0669231. **D**. Fresh specimen, photograph by P.I. Forster (Queensland Herbarium and Biodiversity Services). **E**. Dried specimen. **C**, **F**. Pileipellis in 5% KOH and Congo Red, showing globose or pyriform terminal elements of the epithelium pileipellis. Scale: A, E = 10 mm; B = 2 mm; C, F = 40 µm.

***Notes*.** The pileipellis of *Hodophilus darwinensis* is an epithelium of globose or pyriform cells according to Young & Wood (1997) and this was confirmed from the two known specimens identified by Young (2005) that were examined for this study. This morphological character, as well as the placement of DNA sequence data from BRI AQ0669231 within the clade of *Hodophilus*, justify its recombination in this genus as also suggested by Zhang et al. (2019). We were unable to obtain DNA sequences from the holotype to confirm that the two specimens identified as this species by Young (2005) are phylogenetically conspecific, but microscopic characters are consistent between the two specimens. *Hodophilus darwinensis* is the only representative of the genus so far known from northern Australia. Additional modern collections from tropical Australia with photographs, field notes and DNA sequence data may assist in determining the morphological, phylogenetic, and ecological limits of this species and if there is additional diversity to recognise.

The report of *Hodophilus darwinesis* in *A field guide to Tasmanian Fungi* (Gates & Ratkowsky 2014) appears to be a misidentification. The sporing bodies are described as "dull pinkish brown" and the accompanying photograph shows sporing bodies that are pinkish brown, becoming browner as they expand. The colour at maturity is browner in comparison to the characters of the sequenced specimen from north Queensland (BRI AQ0669231) identified by Young (2005) and in comparison to the original description of *H. darwinensis,* which was based on the type from the Northern Territory, where the pileus is described as "creamy buff brown when young aging to pallid cream with a faint pinkish hue" (Young & Wood 1997). In addition, it is unlikely that a species such as *H. darwinensis,* originally described from tropical Northern Australia, would also be found in Tasmania. The pictured collection has a voucher (MEL 2525022) for which a sequence is yet to be generated. The collection may represent one of the four undescribed putative species in the phylogeny that are represented in Tasmania, which all have a brownish or light brownish pileus.

Seven observations from southern Australia on the citizen-science platform iNaturalist (https://www.inaturalist.org/) have been identified as *C. darwinensis*, but these are erroneous identifications that are not consistent with the original description of the species. These observations (e.g., https://www.inaturalist.org/observations/168932357) are representative of another putatively novel species that belongs in the vicinity of *Loreleia* Redhead et al. in *Hymenochaetales* Oberw., based on DNA sequences obtained from the collection MEL 2573166 (https://www.inaturalist.org/observations/299815106).

The specimen barcode of the holotype, UNSWDB16576, is from the Australasian Virtual Herbarium (https://avh.ala.org.au/). The holotype was originally cited in the protologue as UNSW 85/127 (Young & Wood 1997).

Hodophilus kearneyi (A.M. Young) L.J. Vaughan & T.W. May, *comb. nov.*

MB861981

Basionym: *Camarophyllopsis kearneyi* A.M. Young, *Austrobaileya* 5: 562 (1999).

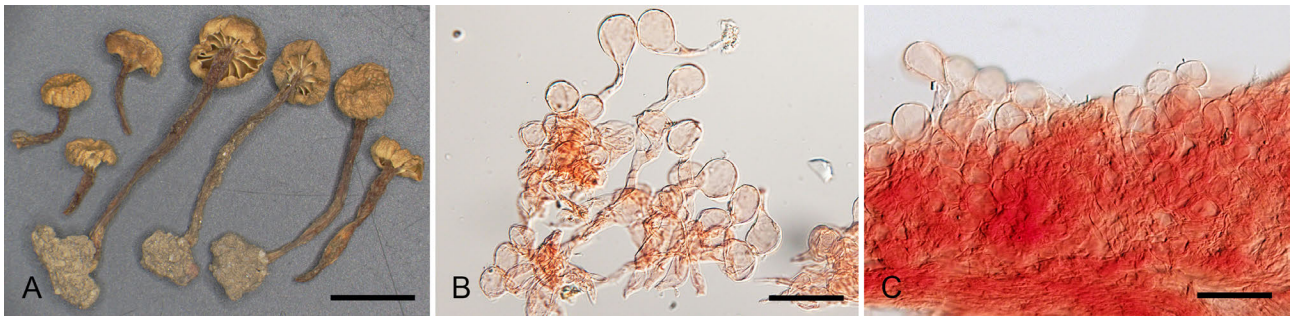

Figure 3. Morphology of *Hodophilus kearneyi comb. nov.* **A**–**C**. Holotype DAR 73919. **A**. Dried specimen. **B**–**C**. Squash of the pileipellis in 5% KOH and Congo Red, showing globose to pyriform terminal cells of the epithelium pileipellis. Scale: A = 6 mm; B, C = 40 µm.

Typification: NEW SOUTH WALES, Lane Cove Bushland Park (33.816667° S, 151.166667° E), in sandy soil under ferns beside creek in gallery warm-temperate rainforest, 13 June 1998, *R. & F. Kearney s.n.* (**holotype** DAR 73919!). GenBank: ITS = PP505406; LSU = PP702599.

Fig. 3

Key characters: Sporing bodies with pale brown (5C4) pileus with a darker centre, with smooth surface that is finely micaceous under lens; lamellae white to greyish white; stipe pale brown (5C2) with fine scattered brownish fibrils; basidiospores 4–*4.9*–6 × 4–*4.6*–5 µm, Q=1.0–1.2(–1.3); pileipellis an epithelium of globose or pyriform elements 13–23 µm diameter.

For a full description see Young (1999).

Sequenced specimens examined: AUSTRALIA. NEW SOUTH WALES: Gore Creek (33.819533° S, 151.177544° E), in rainforest gully, 28 Jun 1998, *R. Kearney, E. Kearney 2158* (BRI AQ0807939). TASMANIA: Mount Wellington, Jacksons Bend Track (42.916667° S,147.266667° E), 30 Aug 1995, *A.K. Mills 1352* (HO 587534); 16 Apr 1996, *A.K. Mills 1382* (HO 587536); Growling Swallet, near Mount Field (42.6833° S, 146.4867° E), gregarious in moss, cool temperate rainforest, 19 May 1999, *A.M. Young 2236* (MEL 2089735).

Additional specimen examined: AUSTRALIA. TASMANIA: Little Florentine River (42.7369° S, 146.4233° E), caespitose and gregarious in soil in very sheltered site amongst moss and under old tree fern, in cool temperate rainforest, 26 May 1999, *A.M. Young 2269* (MEL 2089736).

Distribution & habitat: So far known from New South Wales and Tasmania in warm-temperate and cool-temperate rainforests.

Conservation status. *Hodophilus kearneyi* (as *Camarophyllopsis kearneyi*) is listed as endangered in NSW (https://threatenedspecies.bionet.nsw.gov.au/profile?id=10141) due to the limited number of places it has been found.

***Notes*.** The placement of DNA sequences from the *Camarophyllopsis kearneyi* holotype DAR 73919 within the clade of *Hodophilus* justifies the recombination of this species in the genus *Hodophilus*. This phylogenetic placement is also supported by morphological characters, such as the epithelium pileipellis of globose to pyriform terminal elements and the scattered fibrils on the stipe surface. These morphological characters were consistent in two MEL specimens identified by Young (2005) and additional collections from HO and BRI that were examined for this study.

Hodophilus kearneyi is among the Southern Hemisphere species that place phylogenetically close to *H*. sect. *Hodophilus*, but whose placement is not currently justified within this section because of the lack of support for the backbone of tree based on current available data, as discussed above. The morphology of the species as described by Young (1999) illustrates a pale brown species with scattered brown fibrils on the stipe but without any information about odour. Most species in *H*. sect. *Hodophilus* are described as having distinct naphthalene-like odours, except for *H. atropunctus*, as noted in the introduction, which lacks a strong odour but does have dark dots on the stipe (Adamčík et al. 2016, 2017, 2020). *Hodophilus variabilipes* Jančovič., Adamčík & Looney is the only other *Hodophilus* species described as having dark dots on the stipe, for example in the key from Adamčík et al. (2020) or Tang et al. (2023), but this has been observed in *H. kearneyi* and other Australian putative species yet to be described. Although odour is not mentioned in the species description of *H. kearneyi* or in the collection notes of specimens cited here, this does not necessarily mean the species does not have an odour that was simply not detected at the time of collection. Modern collections of *H. kearneyi* with photographs and field notes, paying particular attention to the odour of fresh specimens, especially when bruised, will be informative in further characterising how this species differs from known species around the world and other putative Australian species.

Four collections (BRI AQ0799519, BRI AQ0799520, HO616959, HO616961) made by A.M. Young from under Coachwood (*Ceratopetalum apetalum* D.Don) at the type locality of *C. kearneyi* around Gore Creek in Lane Cove, New South Wales, were originally identified as *C. kearneyi*. Young (1999) was presumably referring to these

collections when he noted that "There may possibly be a second species of *Camarophyllopsis* at the Gore Creek site. Collections of material readily identified as the genus *Camarophyllopsis* have been found caespitose on sandy soils under coachwood (*Ceratopetalum apetalum*). Dried material and descriptions so far have been inconclusive and the coachwood collections may just be a variety of *C. kearneyi*". DNA sequences from the two BRI collections place in a separate clade to *H. kearneyi* that we label *H*. sp. 'Coachwood'. This clade represents at least one putative species requiring formal description. However, the variation between the two sequences in the clade (95.28% pairwise identity) indicates there might be more than one novel species requiring formal description.

Hodophilus citrinofoetens L.J. Vaughan & T.W. May, *sp. nov.*

MB862780

Typification: AUSTRALIA, WESTERN AUSTRALIA, Denmark Shire, Tingledale, Pedro Fireline Road off Dingo Flat Road (34.9167 S, 116.6833 E), in litter of *Eucalyptus diversicolor*, *Corymbia calophylla* and *E. jacksonii*, in tall forest, at side of gravel road, 19 Jun 2004, *K. Syme 1327/04* (**holotype** MEL 2292260!). GenBank: ITS = PP275098, LSU = PX642495.

Synonymy: *Camarophyllopsis* sp. 'yellow' as used in Gates & Ratkowsky (2014).

Figs. 4, 5

Diagnosis: Pileus, lamellae and stipe all with yellow colours that become slightly more intense when dry; with a strong naphthalene odour; decurrent lamellae.

Etymology: from Latin *citrinus* (lemon yellow) and *foetidus* (stinking); named for the yellow sporing bodies and the distinctive naphthalene odour that has previously been described from *Hodophilus* species of the Northern Hemisphere, including the type species, *Hodophilus foetens*. The colour is close to "citrinus" as illustrated by Saccardo (1894).

Habit sporing bodies terrestrial, occurring gregariously or sometimes in caespitose groups.

Pileus 3–14 mm wide, convex, sometimes becoming truncated at apex, circular, margin straight, crenate to crenulate, sometimes inrolled between lamellae, transluscent-striate; surface dry, dull, smooth, glabrous, or appearing sometimes slightly atomate under lens; dull light yellow near 4A5 to bright deep yellow 4A6–7, sometimes with yellow pink undersurface, sometimes drying paler 3A3 to 4A2–4, hygrophanous; pileus context firm, solid, to about 2 mm thick, yellow, almost translucent when moist. **Lamellae** up to 7 mm long, up to 5 mm deep, decurrent to subdecurrent, arcuate, moderately thick, subdistant to distant (L = 9–13 per sporing body), with lamellulae present but sometimes very short (l = 8–12 per sporing body); edge and face smooth; pastel yellow 1A4, yellow 4A5 to orange-yellow between 4A6 and 5A6, sometimes with a hint of pink. **Stipe** 18–33 mm long, 1.5–4 mm wide; central; cylindrical, often tapering downwards, and in cross section often much wider at apex between lamellae and pileus; surface smooth, glabrous, or sometimes with innately appressed fibrils or minute scales forming banded aggregations; pale yellow 3A3–5, sometimes tending greenish, or sometimes almost translucent when moist,

Figure 4. Macromorphology of *Hodophilus citrinofoetens sp. nov.* **A**–**C**. Holotype MEL 2292260. **A**. Fresh specimen, photograph by K. Syme. **B**–**C**. Dried specimens. **D**–**E**. MEL 2524950. **D**. Fresh specimen, photograph by G.M. Gates. **E**. Dried specimen. **F**. HO608631 fresh specimen, photograph by G.M. Gates. Scale: A, F = 10 mm; B, E = 6 mm; C = 2 mm.

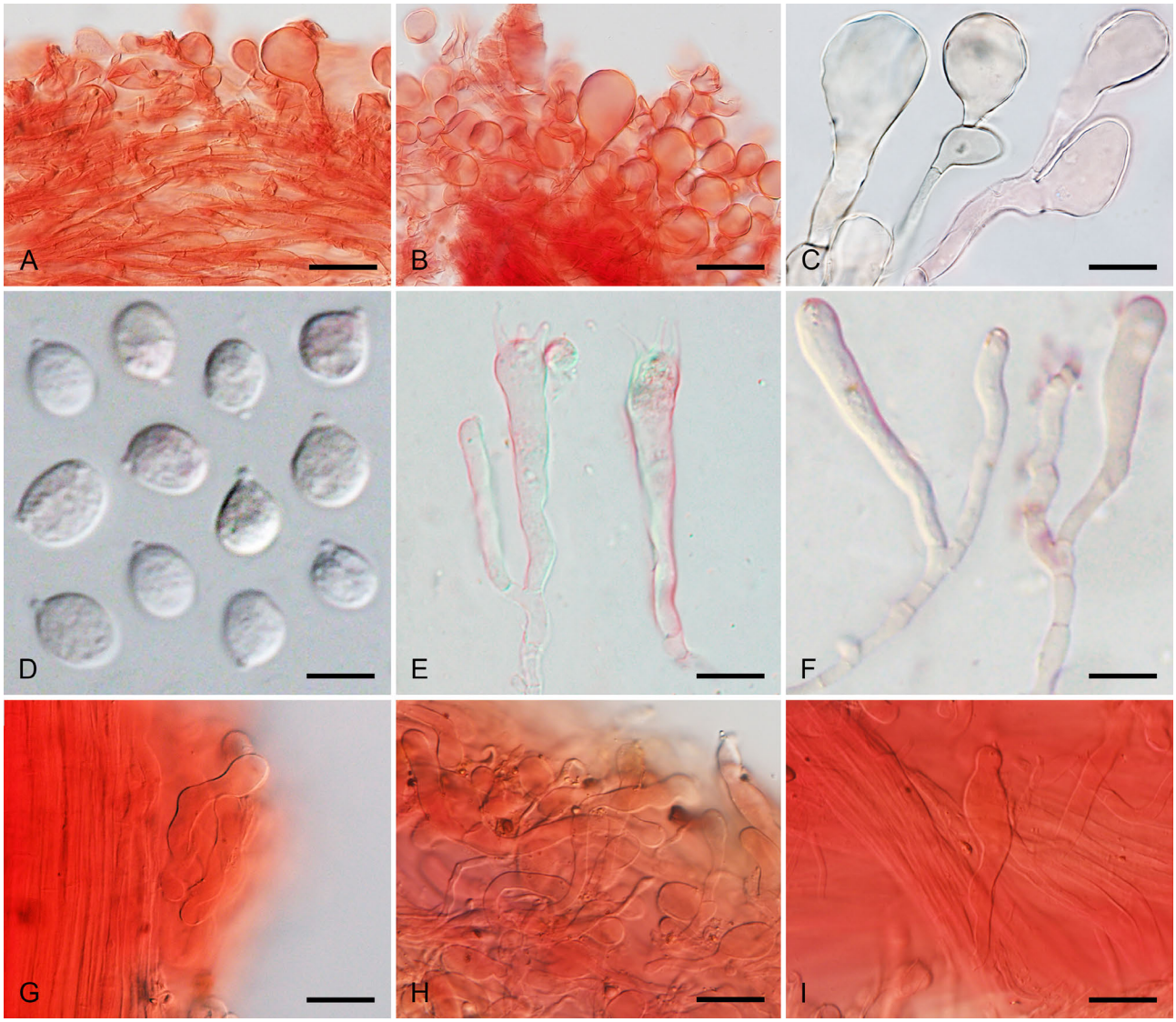

Figure 5. Micromorphology of *Hodophilus citrinofoetens sp. nov.* in 5% KOH and Congo Red. **A**–**C**. PERTH 08118914, elements of the pileipellis. **D.** PERTH 08118914, basidiospores. **E**. Holotype MEL 2292260, basidia (two right elements). **F**. Holotype MEL 2292260, cheilocystidia of the lamellae edge (two central elements). **G**–**I**. PERTH 08166587, caulocystidia of the stipe. Scale: A, B = 40 µm; C, G, H, I = 20 µm; E, F = 10 µm; D = 5 µm.

then drying opaque, yellow 3A4. Odour very strong naphthalene. Spore print creamy white.

Basidiospores 5–9.5 × 4–7 µm, 5.80–*6.402*–6.90 × 4.43–*5.297*–6.00 µm (149/10), globose to subglobose, Q = 1–1.9, 1.068–*1.224*–1.407, hyaline, hilar appendage up to 1 µm, subdermal oil vessels often present. **Basidia** 40–45 × 7–8 µm, 4-spored, occasionally 2-spored, narrowly clavate, with sterigmata 4–7 × 2–2.5 µm. **Cheilocystidia** present on lamellae edge, thin-walled, usually narrowly clavate to cylindrical with wavy outline, apex rounded, up to 35 × 2.5–6 µm. **Pleurocystidia** present on lamellae face, like cheilocystidia. **Hymenophoral trama** regular, consisting of cylindrical hyphae 2–5 µm diameter, thin-walled, hyaline, as well as larger inflated elements up to 10 µm diameter. **Pileipellis** a hymeniderm of vertically arranged elements; terminal cells of pileus margin 27–91 × 15–35 µm (15–35 µm wide at widest point, often 5–7 µm at base), sphaeropedunculate to broadly clavate to subglobose, occasionally branching near base; subterminal cells of pileus margin often septate, often arranged in chains of cylindrical segments 5–7 µm wide, sometimes of similar shape to terminal elements, up to 77 µm long and 37 µm wide; terminal cells of pileus centre 23–160 × 14–49 µm, subglobose to broadly clavate, sphaeropedunculate, or ballon-shaped; subterminal cells of pileus centre similar to those at margin; emerging from regularly arranged pileus trama. **Stipitipellis** a cutis of cylindrical hyphae 1.5–6 µm wide, occasionally inflated up to 11 µm wide, thin-walled, hyaline. **Caulocystidia** scattered, 35–90 × 6–11.5 µm, clavate to cylindrical, outline often wavy, apex rounded and often slightly capitate. **Clamp connections** absent.

Sequenced specimens examined: AUSTRALIA. WESTERN AUSTRALIA: West Cape Howe NP, Bibbulmun Track, west of road (35.099861° S, 117.628306° E), in grey sand

with species of *Melaleuca* (long-leaved paperbark), *Agonis*/*Taxandria* and *Acacia,* 23 Jun 2006, *K. Syme 1543* (PERTH 08118914, dupl. MEL 2526029); Grid FC 56, Barlee forest block, access from the N via track from Graphite Road (34.162653° S, 116.503883° E), on ground in tall open forest associated with vegetation of *Corymbia calophylla* and *Eucalyptus marginata* subsp. *marginata*, 6 Jun 2013, *R.M. Robinson, P. Anderson FC 1896* (PERTH 08166587); TASMANIA: Kunanyi/Mt Wellington, track to Silver Falls (42.916667° S, 147.25° E) on soil in wet sclerophyll, 30 Aug 2003, *G.M. Gates, D.A. Ratkowsky 4141* (MEL 2524949); Mt Wellington, Middle Island Fire Trail (42.916667° S, 147.25° E), on soil in wet sclerophyll, 25 Aug 2015, *G.M. Gates 3151* (MEL 2392821).

Additional specimens examined: AUSTRALIA. WESTERN AUSTRALIA: South Coast Highway, Loc 406, N of stream, adjoining Mt Shadforth Reserve (34.979722° S, 117.284444° E), gregarious in loam with *Corymbia calophylla* and *Allocasuarina decussata,* 6 Jul 1995, *K. Syme 840/95* (PERTH 08969930); West Bay Bushland, Leeuwin-Naturaliste National Park, Augusta (34.288778° S, 115.147972° E), within litter, in open woodland of *Corymbia calophylla* and *Agonis flexuosa,* 29 Jun 2008, *M. Brundrett, A. Dyson E 9157* (PERTH 08095213). TASMANIA: Mt Wellington, Jackson's Bend (42.916667° S, 147.25° E), wet sclerophyll, 7 Nov 2000, *G.M. Gates 0193* (HO608631); Bermuda Road (a.k.a. Bermuda Hill) (43.066667° S, 146.9° E), on soil in wet sclerophyll, 16 August 2003, *G.M. Gates, D.A. Ratkowsky 4139* (MEL 2524950); Kunanyi/Mt Wellington, Old Farm Trail (42.9° S, 147.25° E), 19 Aug 2003, *G.M. Gates, D.A. Ratkowsky 4140* (MEL 2525012).

Distribution & habitat: Known from Tasmania, in wet sclerophyll forests, and the South West region of Western Australia, where it has been found associated with *Eucalyptus diversicolor*, *E. jacksonii*, *Corymbia calophylla*, and species of *Acacia*, *Allocasuarina*, *Melaleuca*, *Agonis* and *Taxandria*. Emerging from leaf litter or sometimes from soil, sometimes attached to leaf litter.

Notes. This species was included by Gates & Ratkowsky (2014) as *Camarophyllopsis* sp. 'yellow'. We examined the specimen (HO608631) pictured in Gates and Ratkowsky (2014) and confirm this as *H. citrinofoetens* based on morphology. Some fungarium collections have been labelled as *Camarophyllopsis* sp. 'yellow with mothball odour'. This is a rarely detected species that has only been found in a small number of localities in Tasmania and the South West region of Western Australia. Two iNaturalist observations (iNaturalist: 52915949, WA; 4300939, TAS) may be referable to this species.

Structures in the hymenium described as cheilocystidia did not project beyond the basidia but nevertheless were differentiated from basidioles because the cheilocystidia were wavy in outline and narrower than basidioles.

Phylogenetic and morphological comparison of H. citrinofoetens *to similar species.*

The bright yellow colours in the pileus, stipe and lamellae of *H. citrinofoetens* in combination with a strong naphthalene odour are unique among previously described *Hodophilus* species. Species of *H.* sect. *Hodophilus,* such as *H. foetens*, are noted for having distinct naphthalene odours (except for *H. atropunctus*) but sporing bodies of this section are mostly shades of brown and not typically yellow (Adamčík et al. 2016, 2017, 2020). Sporing bodies of *H*. sect. *Micacei* have yellow colours on the stipe, and sometimes on the pileus, but are not typically noted for having strong naphthalene odours, even though some species are noted to have weak odours (Adamčík et al. 2018). Species of *H*. sect. *Phaeophylli* usually have pale to dark brown sporing bodies without naphthalene odours or yellow colours (Adamčík et al. 2020). *Hodophilus citrinofoetens* places outside all three sections, as they are currently defined, and is readily phylogenetically distinguishable.

Some morphologically similar species in Australasia include *H. roseolus* (G. Stev.) J.A. Cooper from New Zealand, and *H. kearneyi* and *H. darwinensis* in Australia. When fresh, *H. citrinofoetens* can be easily distinguished from these species by the brighter, yellow colours of the pileus, lamellae and stipe, and also by having larger spores than *H. darwinensis* and *H. kearneyi*. However, it is noted that each of these species are pale-coloured and dried material of *H. citrinofoetens* is very similar in colour to dried specimens of *H. kearneyi* and *H. darwinensis* examined for this study (Fig. 2, 3, 4). Sporing body colours become less reliable for distinguishing species in the examination of preserved collections of these species, even though *H. darwinensis* is a phylogenetically distant species from northern Australia with non-overlapping distribution. Therefore, thorough field notes are important for recording characters that are not preserved in dried material, such as colours, shape, odour and size when fresh. Photographs capturing these morphological features when fresh, especially across a range of sporing body ages, will greatly assist in recognising the distinctive morphological features of the other undescribed Australian *Hodophilus* species.

Comparison of H. citrinofoetens *to undescribed Australasian species.*

The closest known phylogenetic relatives of the novel species *H. citrinofoetens* include *H*. sp. 'Coachwood' from Lane Cove, NSW, previously misidentified as *Camarophyllopsis kearneyi*, as well as a specimen from New Zealand (PDD 107269: GenBank ITS = OR567622) and the clade of *H. kearneyi*. Specimens from these clades have rather dull-coloured, waxy sporing bodies with decurrent lamellae that are various shades of pale brown. *Hodophilus citrinofoetens* is macromorphologically well differentiated from these putative phylogenetic species and most of the other remaining Australian putative phylogenetic species of *Hodophilus*, which are

also typically shades of brown. *Hodophilus* sp. 'eastern brown' and *H*. sp. 'western brown' are both brown to dark brown species that have been collected from similar localities to *H. citrinofoetens* in Tasmania and the South West region of Western Australia. They share the strong naphthalene odour character with *H. citrinofoetens*, but are easily distinguished from *H. citrinofoetens* by sporing body colour. Each of the undescribed putative phylogenetic species from Australia require further investigation to phylogenetically delimit species and establish the most appropriately informative taxonomic characters to differentiate them.

Disclosures

No conflicts to declare.

Acknowledgments

The authors acknowledge the traditional owners of the land where this research took place, the Wurundjeri Woi Wurrung and Bunurong Boon Wurrung of the Kulin nation. We pay respects to elders past and present and acknowledge the enduring connection of first peoples to country. We thank the curation staff and volunteers at the National Herbarium of Victoria (MEL), especially Eugenia Pacitti, Rebecca Le Get, Catherine Gallagher and Alison Vaughan, for assistance with access to MEL specimens and for handling loans from external institutions. Staff from the following institutions are thanked for the loan of specimens to MEL: Queensland Herbarium (BRI), the NSW Plant Pathology & Mycology Herbarium (DAR), the Tasmanian Herbarium (HO), the Western Australian Herbarium (PERTH), the University of Tennessee Fungal Herbarium (TENN-F) and the John T. Waterhouse Herbarium (UNSW). We thank editor Kevin Thiele and reviewers Slavomír Adamčík and Joshua Birkebak for constructive comments and suggestions that improved the manuscript. A generous donation from the late Wendy Dodd (Canberra, 1946–2023) funded the establishment of Luke Vaughan's position at Royal Botanic Gardens Victoria.

References

Abarenkov K, Nilsson H, Larsson K-H, Taylor AFS, May TW, Frøslev T, Pawlowska J, et al. (2023) The UNITE database for molecular identification and taxonomic communication of fungi and other eukaryotes: sequences, taxa, and classifications reconsidered. *Nucleic Acids Research* 52: D791–D797. <https://doi.org/10.1093/nar/gkad1039>

Abarenkov K, Tedersoo L, Nilsson RH, Vellak K, Saar I, Veldre V, Parmasto E, et al. (2010) PlutoF - a Web based workbench for ecological and taxonomic research, with an online implementation for fungal ITS sequences. *Evolutionary Bioinformatics* 6: 189–196. <https://doi.org/10.4137/EBO.S6271>

Adamčík S, Looney BP, Birkebak JM, Jančovičová S, Adamčíková K, Marhold K, Matheny PB (2016) Circumscription of species of *Hodophilus* (*Clavariaceae*, *Agaricales*) in North America with naphthalene odours. *Botany* 94: 941–956. <https://doi.org/10.1139/cjb-2016-0091>

Adamčík S, Jančovičová S, Looney BP, Adamčíková K, Birkebak JM, Moreau PA, Vizzini A, Matheny PB (2017) Circumscription of species in the *Hodophilus foetens* complex (*Clavariaceae*, *Agaricales*) in Europe. *Mycological Progress* 16: 47–62. <https://doi.org/10.1007/s11557-016-1249-x>

Adamčík S, Dima B, Adamčíková K, Harries D, Læssøe T, Moreau PA, Jančovičová S (2018) European *Hodophilus* (*Clavariaceae*, *Agaricales*) species with yellow stipe. *Mycological Progress* 17: 1097–1111. <https://doi.org/10.1007/s11557-018-1418-1>

Adamčík S, Dima B, Adamčíková K, Corriol G, Læssøe T, Moreau PA, Caboň M, Jančovičová S (2020) *Hodophilus phaeophyllus* complex (*Clavariaceae*, *Agaricales*) is defined as new phylogenetic lineage in Europe. *Mycological Progress* 19: 111–125. <https://doi.org/10.1007/s11557-019-01544-9>

Arnolds, EJM (1986) Notes on *Hygrophoraceae*. IX. *Camarophyllopsis* Herink, an older name for *Hygrotrama* Sing. *Mycotaxon* 25: 639–644. <https://doi.org/10.5962/p.417102>

Arnolds E (1990) *Camarophyllopsis*. In: Bas C, Kuyper TW, Noordeloos ME, Velinga EC (eds) Flora Agaricina Neerlandica, vol. 2. A.A. Balkema, Rotterdam, pp. 111–115.

Birkebak JM, Mayor JR, Ryberg M, Matheny PB (2013) A systematic, morphological, and ecological overview of the *Clavariaceae* (*Agaricales*). *Mycologia* 105: 896–911. <https://doi.org/10.3852/12-070>

Birkebak JM, Adamčík S, Looney BP, Matheny PB (2016) Multilocus phylogenetic re- construction of the *Clavariaceae* (*Agaricales*) reveals polyphyly of the agaricoid members. *Mycologia* 108(5): 860–868. <https://doi.org/10.3852/15-370>

Chernomor O, von Haeseler A, Minh BQ (2016) Terrace aware data structure for phylogenomic inference from supermatrices. *Systematic Biology* 65(6): 997–1008. <https://doi.org/10.1093/sysbio/syw037>

Cooper JA (2023) *Mycological Notes 43: New Zealand Clavariaceae*. Fungal Network of New Zealand. <https://www.funnz.org.nz/node/170>

Craig S, Vaughan LJ, Holmes GD, May TW (2023) *Pseudobaeospora taluna* (*Fungi*: *Agaricales*) newly described from southern Australia. *Australian Journal of Taxonomy* 24: 1–16. <https://doi.org/10.54102/ajt.yuij6>

Crous PW et al. (2017) Fungal Planet description sheets: 558–624. *Persoonia* 38: 330–331. <https://doi.org/10.3767/003158517X698941>

Edgar RC (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids*

Research 32(5): 1792–1797. <https://doi.org/10.1093/nar/gkh340>

Gardes M, Bruns TD (1993) ITS primers with enhanced specificity for basidiomycetes - application to the identification of mycorrhizae and rusts. *Molecular Ecology* 2: 113–118. <https://doi.org/10.1111/j.1365-294X.1993.tb00005.x>

Gates GM, Ratkowsky DA (2014) *A field guide to Tasmanian Fungi*, Tasmanian Field Naturalists Club, pp. 36–37.

Hoang DT, Chernomor O, von Haeseler A, Minh BQ, Vinh LS (2018) UFBoot2: Improving the ultrafast bootstrap approximation. *Molecular Biology and Evolution* 35: 518–522. <https://doi.org/10.1093/molbev/msx281>

Huelsenbeck JP, Ronquist F (2001) MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics* 17(8): 754–755. <https://doi.org/10.1093/bioinformatics/17.8.754>

Index Fungorum (2023) Nomenclatural Novelties: Jerry A. Cooper. 531: 3 <https://www.indexfungorum.org/Publications/Index%20Fungorum%20no.531.pdf>

Kalyaanamoorthy S, Minh BQ, Wong TKF, von Haeseler A, Jermiin LS (2017) ModelFinder: fast model selection for accurate phylogenetic estimates. *Nature Methods* 14: 587–589. <https://doi.org/10.1038/nmeth.4285>

Kornerup A, Wanscher JH (1978) *Methuen Handbook of Colour.* 3rd edn. E. Methuen: London.

Kovalenko AE, Malysheva EF, Morozova OV (2012) The genus *Camarophyllopsis* in Russia: new records and new species *C. alboffloccipes*. *Mikologia i Fitopatologia* 46: 54–66.

Matheny PB, Curtis JM, Hofstetter V, Aime MC, Moncalvo JM, Ge ZW, Yang ZL, et al. (2006) Major clades of *Agaricales*: a multilocus phylogenetic overview. *Mycologia* 98: 982–995. <https://doi.org/10.3852/mycologia.98.6.982>

Minh BQ, Schmidt HA, Chernomor O, Schrempf D, Woodhams MD, von Haeseler A, Lanfear R (2020) IQ-TREE 2: New models and efficient methods for phylogenetic inference in the genomic era. *Molecular Biology and Evolution* 37(5): 1530–1534. <https://doi.org/10.1093/molbev/msaa015>

Nguyen L-T, Schmidt HA, von Haeseler A, Minh BQ (2015) IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution* 32(1): 268–274. <https://doi.org/10.1093/molbev/msu300>

Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61(3): 539–542. <https://doi.org/10.1093/sysbio/sys029>

Saccardo PA (1894) *Chromotaxia seu Nomenclator Colorum*... Typis Seminarii: Patavii.

Species Fungorum (2026) Published on the Internet http://www.speciesfungorum.org, The Royal Botanic Gardens, Kew. [Retrieved 22 June 2026].

Tang S, Lv T, He J, Yu F, Luo H, Li S (2023) *Hodophilus pseudoglabripes* (*Clavariaceae*, *Agaricales*), a new species from Thailand. *Phytotaxa* 597(3): 219–230. <https://doi.org/10.11646/phytotaxa.597.3.3>

Thines M, Aoki T, Crous PW, Hyde KD, Lücking R, Malosso E, May TW, *et al.* (2020) Setting scientific names at all taxonomic ranks in italics facilitates their quick recognition in scientific papers. *IMA Fungus* 11: 25. <https://doi.org/10.1186/s43008-020-00048-6>

Vilgalys R, Hester M (1990) Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. *Journal of Bacteriology* 172(8): 4238–4246. <https://doi.org/10.1128/jb.172.8.4238-4246.1990>

Vilgalys Lab (1992-) Conserved primer sequences for PCR amplification of fungal rDNA. Duke University, updated 3 Feb 1992, 1–5. <https://sites.duke.edu/vilgalyslab/files/2017/08/rDNA-primers-for-fungi.pdf>

White TJ, Bruns TD, Lee S, Taylor J (1990) 38 - Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics, In PCR Protocols. (Eds MA Innis, DH Gelfand, JJ Sninsky, TJ White) pp. 315–322. Academic Press: San Diego. <http://dx.doi.org/10.1016/B978-0-12-372180-8.50042-1>

Young AM, Wood AE (1997) Studies on the *Hygrophoraceae* (*Fungi*, *Homobasidiomycetes*, *Agaricales*) of Australia. *Australian Systematic Botany* 10: 911–1030. <https://doi.org/10.1071/SB96005>

Young AM (1999) The *Hygrocybeae* (*Fungi*, *Basidiomycota*, *Agaricales*, *Hygrophoraceae*) of Lane Cove Bushland Park, New South Wales. *Austrobaileya* 5(3): 535–564. <https://doi.org/10.5962/p.299626>

Young AM, Mills AK (2002) The *Hygrophoraceae* of Tasmania. *Muelleria* 16: 3–28. <https://doi.org/10.5962/p.254654>

Young AM (2005) Fungi of Australia: *Hygrophoraceae*. CSIRO Publishing, Australian Biological Resources Study, Canberra.

Zhang M, Wang C-Q, Li T-H (2019) Two new agaricoid species of the family *Clavariaceae* (*Agaricales*, *Basidiomycota*) from China, representing two newly recorded genera to the country. *MycoKeys* 57: 85-100. <https://doi.org/10.3897/mycokeys.57.36416>