MYCOLOGY
2025, VOL. 16, NO. 1, 210–237
https://doi.org/10.1080/21501203.2024.2309898

Taylor & Francis
Taylor & Francis Group

RESEARCH ARTICLE

OPEN ACCESS

Metacampanella gen. nov.: The *Campanella dendrophora* complex

Ronald H. Petersen and Karen W. Hughes

Department of Ecology and Evolutionary Biology, University of Tennessee Knoxville, Knoxville, TN, USA

ABSTRACT

Metacampanella is proposed as a new genus in Family Marasmiaceae to accommodate a small group of six species morphologically resembling *Tetrapyrgos* or *Campanella* but molecularly distinct from both genera. Newly described taxa include *M. costaricensis*, *M. sinecystidia*, and *M. dendrophora* f. *washingtonensis*; species epithets transferred are *M. caesia*, *M. dendrophora*, *M. olivaceonigra*, and *M. subdendrophora*. Members of this complex habitually fruit on dead monocot stems and in one case, dead dicot wood. A comparison of nrITS sequences deposited in GenBank indicates that some members of *Metacampanella* include or are related to grass endophytes. *Metacampanella* appears to be global in distribution.

ARTICLE HISTORY
Received 21 August 2023
Accepted 20 January 2024

KEYWORDS
Basidiomycota; Marasmiaceae; new species; new genus; taxonomy

1. Introduction

For some time, the boundaries delineating the Omphalotaceae and the Marasmiaceae have been uncertain, with some workers suggesting that the two families were synonymous (Kirk et al. 2008). With the development of molecular techniques, some of the uncertainty was resolved with phylogenies showing the Omphalotaceae and Marasmiaceae as distinct (Moncalvo et al. 2000; Wilson and Desjardin 2005; Matheny et al. 2006; Nakasone et al. 2009). Subsequent molecular analyses began the process of determining the placement of taxa in these families at finer (generic) phylogenetic ranks (Nakasone et al. 2009).

With the subdivision of *Marasmiellus* [i.e. *Collybiopsis* (Petersen and Hughes 2021); Marasmiaceae], some subgeneric taxa (including type species *M. juniperinus* and *Co. ramealis*) remained in the Omphalotaceae, while others (i.e. *Marasmiellus* sects. *Candidi* and *Stenophylloides*) were placed in the Marasmiaceae. Over the last decade, significant papers on *Crinipellis* (Kerekes and Desjardin 2009), *Tetrapyrgos* (Honan et al. 2015; Komura et al. 2020), *Marasmiellus* (Oliveira et al. 2019; Petersen and Hughes 2021) and *Neocampanella* (Nakasone et al. 2009) have appeared, reinforcing this separation. Several of these papers included phylogenies in which the genus name *Campanella* appeared interspersed among collections of *Tetrapyrgos* (Nakasone et al. 2009; Honan et al. 2015; Komura et al. 2020). While *Tetrapyrgos* was treated in depth by Honan et al. (2015), *Campanella* remained without a summary except that by Singer (1975b). Based on this, a survey of specimens labelled as *Campanella* in herbarium TENN was undertaken. The primary literature on *Campanella* was contributed by Singer, and his floristic monograph of neotropical taxa (Singer 1975b) was a constant reference; but there were problems with Singer's monograph: (1) Singer's terminology was unfamiliar and his illustrations were scanty; (2) Although several TENN collections were from Central and South America, they did not seem to match Singer's descriptions; (3) Singer's work pre-dated molecular data.

Early in the development of molecular phylogenetics, few appropriate sequences from *Campanella* and *Tetrapyrgos* were available. Beginning in 2015, however, three sources provided additional sequence information, Honan et al. (2015), Cooper (pers. comm.), and Komura et al. (2020). In all of these phylogenies, *C. subdendrophora* (as *T. subdendrophora*) was placed in a small clade separated from *Campanella* and *Tetrapyrgos* (although closer to the latter). These taxa have not previously been recognised at genus rank or assigned a generic name. This paper intends to do this

CONTACT Karen W. Hughes khughes@utk.edu Department of Ecology and Evolutionary Biology, University of Tennessee Knoxville, Knoxville, TN 3799, USA

This article has been corrected with minor changes. These changes do not impact the academic content of the article.
This article has been republished with minor changes. These changes do not impact the academic content of the article.
Supplemental data for this article can be accessed online at https://doi.org/10.1080/21501203.2024.2309898.

by recognising the clade as *Metacampanella* gen. nov. (see below), with a summary of its taxa.

We present an expanded phylogeny of *Tetrapyrgos*, *Campanella*, and the proposed *Metacampanella* clades based on the nuclear ribosomal ITS (nrITS) and LSU (nrLSU) gene regions. Additionally, the organisation of descriptions has been made uniform, with characters numbered in the order in which they were described by Singer (1975b).

2. Materials and methods

2.1. Morphology

Colours within quotation marks ("") are from Ridgway (1912); matching colours from Kornerup and Wanscher (1967) are cited alphanumerically by plate, column, and row (i.e. "28E5").

Microscopic observations were made with an Olympus B×60 research microscope, fitted with phase contrast microscopy (PhC) and photos were produced using an Olympus Q-colour 5 camera/computer attachment. All micromorphology was accomplished with squash mounts of minute amounts of basidioma tissue in 3% aqueous KOH; in a few cases, enough material existed to make a second mount in Melzer's reagent (cited as IKI) to test for amyloidity.

Global Positioning System (GPS) latitude/longitude metrics were often not part of collection label data, but added throughout using Google Earth with actual position estimated from reference to nearby locations.

Singer (1975b) adopted a description outline through which characters were presented in a consistent order. Generally, this order has been followed below, with characters numbered for ease of reference as follows: Macromorphology: 1) basidiomata; 2) pileus; 3) hymenophore; 4) stipe; 5) odour and taste; Micromorphology: 6) basidiospores; 7) pleurocystidia; 8) basidioles and basidia; 9) cheilocystidia; 10) pileipellis; 11) substratum and phenology.

Singer's (Singer 1975b) terminology describing macro- and micromorphological characters was not explained or well-illustrated. An attempt to clarify Singer's terminology is given below. "Tetrapyrgoid:" Part of the generic diagnosis of *Tetrapyrgos* is a unique type of cystidial structure commonly found in *Campanella* as dermato-, cheilo- and/or caulocystidia (see Figures S13, S19, S26, S32). The structure consists of an axis beset with numerous diverticula, usually awl- or talon-shaped and often curved, and a swollen obovate apex, smooth and usually refringent (PhC).

Spore shape: Singer placed importance on spore shape, especially ellipsoid to broadly or subovate spores with one or two prominent "bulges" (see Singer 1975b: his Figure 4). Numerous species, however, produce spores that are truly triangular in profile, not tetrahedral [Figures 1, 2 (both drawings), S7, S10, S17, S18, S28], but the quality of microscopy may have caused misinterpretation by Singer (his observations made before 1975). Spore measurements used in this manuscript include L^m = Mean of the length of 20 measured spores, E = Spore length/spore width, and E^m = the mean of spore length/spore width for 20 measured spores.

Hymenophore configuration: Hymenophore in *Campanella* is usually considered to be "merulioid" (roughly similar to the hymenophore in the genus *Merulius*). In actuality, it is composed of a few radial lamellar and lamellular folds interconnected (anastomosed) by usually curved cross-veins. The difference between this and a meandering reticulum without any radial orientation may reflect a genetic trait rather than a collection-specific feature.

Necropigment: In *Campanella* basidiomata, there is often a rather sensational colour change from the fresh condition to the dried and herbarium-

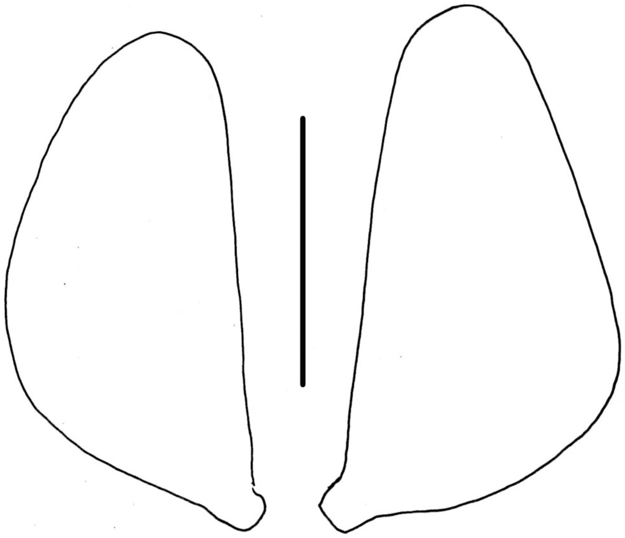


Figure 1. *Metacampanella caesia*. Basidiospores. Standard bar = 5 µm. F1070576.

stored state. In *Metacampanella*, fresh basidiomata are white or nearly so but more often with greenish suffusion or staining, with a common colour change to pastel pinkish orange ("orange buff" 5A5, "salmon orange", "apricot buff" 6A5, here often termed "cantaloupe"), but occasionally to a dark brown, opaque, "muddy" colouration (i.e. *M. subdendrophora*, *M. costaricensis*, and *M. washingtonensis*). This may prove valuable in infrageneric taxonomy, and it is described below whenever possible.

> "Ten pin-shaped cystidia:" (Figures S20, S34) In several taxa, cystidia (usually cheilocystidia but sometimes also as pleurocystidia) shaped generally like a ten pin [i.e. somewhat inflated proximal portion, a slender mesial portion ("neck") and a swollen, capitulate distal portion]. All intermediate forms may be found from this restricted characterization to similar structures with scattered thorn-like diverticula or setulae over the proximal portion (Figures S21A–C, S34B–E), especially as cheilocystidia to individuals with thickly scattered setulae resembling "tetrapyrgoid cystidia". (see above)

Metuloid: A close reading of Singer's writings on *Campanella* leaves the impression that the term "metuloid" is reserved for ventricose-rostrate to ampulliform thick-walled, smooth structures, often with apical crystalline deposits (Figure S14). This term has been a leading character for *Hohenbuehelia* taxa and is continued below.

Cystidia: In most *Campanella* taxa, Singer did not observe pleurocystidia, which he termed simply as "cystidia." But "cystidia absent" was often followed by a description of cheilocystidia. When pleurocystidia are present, they are usually elongate-fusiform, compared with clavate basidioles, but are otherwise nondescript.

Pileipellis architecture: For the most part, Singer used the term "epicutis" to refer to the outermost layer of the pileipellis and "cutis" for the entire pileipellis. "Subcutis" by Singer is here termed subpellis, the innermost layer of the pileipellis juxtaposed to and usually hardly separated from the pileus trama. Subpellis hyphae are often repented and sculptured (Figures S4A,B; S16A,B; S24E,F). For the pileipellis structure, Singer used the terms "*Rameales*-structure" and "asterostromelloid-structure" to represent the hyphal arrangements of the pileipellis. *Rameales*-structure: a tangle of repent hyphae and hyphal termini beset with short (usually less than 4 µm long), peg-like protuberances exemplified by *Collybiopsis ramealis* [typus generis (Figure S1); see also Figures S9, S23]. Asterostromelloid-structure: a reference to the subiculum structure in *Asterostromella*, a genus of corticioid fungi in the family Lachnocladiaceae. Again, a tangle of repent hyphae and hyphal termini beset by numerous side branches, digitate, awl-shaped or spine-shaped (tapering), often up to 7–8 µm. Occasionally, resinous deposits reminiscent of metuloid decoration are found in pileipellis hyphae (Figure S5).

2.2. Cultures, single-spore (monokaryon) isolates and mating studies

Isolation of single-spore isolates, culture of both monokaryon and dikaryon cultures, and procedures for crossing single-spore isolates and determining mating types are given in Petersen et al. (1999).

2.3. Molecular analyses

Sequence data from collections labelled as *Campanella* or *Tetrapyrgos* (Table 1) or *Brunneocorticium* were retrieved from GenBank and combined with sequence data from TENN specimens, from PDD (Dr. Jerry Cooper), from the University of British Columbia Herbarium (UBC-F) and the Canadian Center for the Culture of Microorganisms (CCCM). *Marasmiellus candidus* was selected as the most closely related outgroup based on sequence homology. Environmental sequences with sequence homology to *Campanella* or *Tetrapyrgos* (90% or greater) were also included.

For materials sequenced at the University of Tennessee, DNA was extracted from either dried herbarium specimens or from cultures grown on PD Broth (24 g/L Difco Potato Dextrose: Thermo Fisher Scientific, Waltham, MA, USA) using an E.N.Z.A HP Fungal DNA kit (Omega Bio-Tek: Norcross, GA, USA). The nrITS (Schoch et al. 2012) and nrLSU regions were PCR-amplified using procedures outlined in Hughes et al. (2020). Primers ITS1F, ITS4, ITS2, and ITS3 were used in various combinations to amplify the whole nrITS region or fragments of the region (White et al. 1989; Gardes and Bruns 1996). Primers LR0R and LR5 were used to amplify the 5′ end of the nrLSU region (Cubeta et al. 1991). PCR products were confirmed by gel electrophoresis. NrITS and nrLSU sequences were concatenated where available. The final data set consisted of

Table 1. NrITS and nrLSU sequences used in this study.

Name	Location*	Voucher	Collector's number	ITS GenBank identifier	LSU GenBank identifier
Campanella					
Campanella alba	Unknown	ZMXR3	None listed	MT446108	No
Campanella alba	USA: Hawaii, Lava Tree State Park	TENN-F-060782	TFB12565	DQ449943	MK277678
Campanella buettneri	China	SWFU 001873	None listed	MK809426	No
Campanella buettneri	China: Taiwan	WEI17–513	None listed	MW527101	No
Campanella buettneri (epitype)	San Tome and Principe	DED 8276 (SFSU) epitype	None listed	MF075136	MF075138
Campanella aff. *buettneri*	China: Guizhou	TENN-F-050841ss3	TFB4133ss3	OQ171234	OQ171234
Campanella burkei	Africa: Principe	BAP 632 (SFSU)	None listed	MF100970	No
Campanella candida	Cook Islands	PDD:102184	None listed	OQ282823	No
Campanella keralensis	India	AF 342	None listed	MW462889	No
Campanella nivea	China	TENN-F-051974	TFB3075	OQ171237	No
Campanella pustulata	Australia: Queensland	AQ793972	None listed	JX444168	No
Campanella aff. *pustulata*	Australia	SMF2382	None listed	JX444164	No
Campanella aff. *pustulata*	Australia	QMS0008	None listed	JX444165	No
Campanella sp.	Unknown	SFSU:AHH85	DK2015g	KT270852	No
Campanella sp.	Australia: Stanthorpe, Queensland	Clone Gs2A	None listed	FJ857922	No
Campanella sp.	USA: Puerto Rico	TENN-F-050996h1	TFB4509h1	OQ171235	No
Campanella sp.	USA: Puerto Rico	TENN-F-050996h2	TFB4509h2	OQ171236	No
Campanella sp.	Australia	EP57 (culture from *Epacris pulchella* root)		AY627833	No
Campanella sp.	Unknown	SFSU:AHH83	None listed	EF175518	No
Campanella sp.	Thailand	SFSU:AHH42	None listed	EF175519	No
Campanella sp.	Unknown	SFSU:AHH72	None listed	EF175520	No
Campanella sp.	Australia: Stanthorpe, Queensland	Clone Gs	None listed	FJ857924	No
Campanella sp.	Unknown	SFSU:AHH14	None listed	KT270850	No
Campanella sp.	India	Strain JZ31	None listed	MG719288	No
Campanella sp.	India	JZ44	None listed	MG719301	No
Campanella sp.	Polynesia	biocode 09–475	None listed	MZ997207	No
***Campanella* sp.**					
Campanella sp.	Australia: Stanthorpe, Queensland	Clone GS4A	None listed	FJ857925	No
Campanella sp.	Thailand	SFSU:AHH74	None listed	KT270851	No
Campanella sp.	Australia	FBT2220	None listed	MW192636	No
Campanella sp.	New Zealand	PDD:106952	JAC14432	OQ282805	OQ282758
Campanella sp. "Pureora"	New Zealand	PDD:111968	None listed	OQ282827	OQ282774
Campanella sp. "Pureora"	New Zealand	PDD:112459	JAC15309	OQ282810	No
Campanella sp. "Pureora"	New Zealand	PDD:96255	JAC12001	OQ282788	OQ282744
Campanella sp. "Pureora"	New Zealand	PDD:96318	JAC12078	OQ282789	OQ282745
Campanella sp. "Pureora"	Australia: Tasmania	HO:570075	JAC13104	OQ282798	OQ282753
Campanella sp. "Pureora"	Cook Islands	PDD:106889	JAC14751	OQ282807	OQ282760
Campanella sp. as *Tetrapyrgos simulans*	India	AF129	None listed	MW506836	No
Campanella sp. MCA1689	Guyana	MCA1689	MCA1689	AY916670	AY916668
Campanella sp. MCA2235	Guyana	MCA2235	MCA2235	AY916676	AY916674
Campanella sp. MCA3234	USA: Florida	MCA3234	None listed	MG717365	MG717352
Campanella sp.	Costa Rica: Coto Brus, vic. San Vito	TENN-F-053828	TFB7849	OQ171240	OQ171240
Campanella tristis	New Zealand	TENN-F-054059	TFB7177	OQ717241	OQ717241
Campanella tristis	New Zealand	PDD:87081	JAC9980	OQ282781	OQ282741
Campanella tristis	New Zealand	PDD:96329	JAC12089	OQ282790	OQ282746
Campanella tristis	New Zealand	PDD:104678	None listed	OQ282826	OQ282773
Campanella sp. "Ashurst"		PDD:106900	JAC14826	OQ282809	No
Heliomyces decolorans as *Marasmiellus* sp.	USA: Florida	FLAS:F-61167	None listed	MH211782	No
Heliomyces decolorans as *Marasmiellus* sp.	USA: Florida	FLAS-F-61223	None listed	MH211825	No
Heliomyces decolorans as *Marasmiellus* sp.	USA: Tennessee, GSMNP	TENN-F-065962	TFB14017	OR852424	OR852424
Heliomyces decolorans as *Marasmiellus* sp.	USA: Tennessee, Jackson Co	TENN-F-068115	TFB14257	OR852425	OR852425
Environmental sample	Unknown (China?)	OTU26	None listed	MH005865	No
Marasmiellus					
Marasmiellus candidus	Russia: Kedrovaya Nature Preserve	TENN-F-060723	TFB11838	OR852426	No
Marasmiellus candidus	USA: California	AHH157 (SFSU)	None listed	EF175513	No
Marasmiellus candidus	Canada: British Columbia	UBC:F19683	None listed	HM240532	HM240532
Marasmiellus candidus	USA: Massachusetts, Boston Harbor Islands	BHI-F446d	None listed	MF161268	No

(*Continued*)

Table 1. (Continued).

Name	Location*	Voucher	Collector's number	ITS GenBank identifier	LSU GenBank identifier
Marasmiellus candidus	Canada: British Columbia	UBC:F33072	None listed	MF908473	No
Marasmiellus candidus	Unknown	CBS252.39	None listed	MH856003	No
Marasmiellus candidus	France: Forêt de Carnelle	MICH175508	RLShaffer4670	MN173348	No
Marasmiellus candidus	India	KUBOT-KRMK-2020-72	None listed	MW485122	MW485123
Marasmiellus candidus	Russia: Primorsky	LE-BIN4638	None listed	OL764882	No
Marasmiellus candidus	Russia: Primorsky	LE-BIN64885	None listed	OL764885	No
Marasmiellus candidus	Canada: British Columbia	TENN-F-052592	TFB5761 (culture)	OQ171238	OQ171238
Marasmiellus candidus	USA: Connecticut	TENN-F-068189	TFB14338	OQ171253	OQ171253
Marasmiellus candidus	USA: Mississippi, Pascagoula	TENN-F-069193	TFB14502	OQ171256	OQ171256
Marasmiellus candidus	New Zealand	PDD:86918	JAC9808	OQ282779	No
Marasmiellus candidus	New Zealand	PDD:86983	JAC9874	OQ282780	OQ282740
Metacampanella					
Metacampanella subdendrophora	USA: California, Humbolt Co.	MushroomObserver.org/443698	None listed	MW433846	No
Metacampanella subdendrophora Holotype	Canada	ATCC42449 (UBC 5060/DAOM 175,393)	None listed	NR_171206/AY445121	NG_075153/AY445115
Metacampanella subdendrophora f. *washingtonensis*	USA: Washington, King Co.	TENN-F-059502	TFB9877	OQ171251	No
Metacampanella aff. caesia as Agaricales sp.	Kenya	isolate_F41	None listed	MW995635	No
Metacampanella aff. caesia as Agaricales sp.	Kenya	CSB_F175	None listed	KU680416	No
Metacampanella as *Agaricales* sp.	Mexico: Ojuelos, Jalisco	Clone O7c81H	None listed	GQ924042	No
Metacampanella as *Agaricales* sp.	USA: South Dakota	Clone 8WE1cd05	None listed	GU910299	No
Metacampanella as *Agaricales* sp.	USA: South Dakota	Clone 8WE1cf02	None listed	GU910308	No
Metacampanella as *Agaricales* sp.	USA: South Dakota	Clone 8WE1cf06	None listed	GU910311	No
Metacampanella as *Agaricales* sp.	USA: South Dakota	Clone 8WE1cf11	None listed	GU910315	No
Metacampanella as *Agaricales* sp.	USA: South Dakota	Clone 8WE1cg01	None listed	GU910317	No
Metacampanella as *Agaricales* sp.	USA: South Dakota	Clone 8WE1cg12	None listed	GU910324	No
Metacampanella as *Agaricales* sp.	USA: South Dakota	Clone 8WE3ch07	None listed	GU910438	No
Metacampanella as *Agaricales* sp.	USA: South Dakota	Clone 8WE6ca04	None listed	GU910532	No
Metacampanella as *Agaricales* sp.	USA: South Dakota	Clone 8WE6cc07	None listed	GU910546	No
Metacampanella as *Agaricales* sp.	USA: South Dakota	Clone 8WE6cg02	None listed	GU910572	No
Metacampanella as *Agaricales* sp.	Spain	T24	None listed	MH633918	No
Metacampanella caesia	Italy	BROP8 (Fruitbody)	None listed	KU168340	No
Metacampanella caesia	India: Karnataka	KUBOT-KRMK-2020-36	None listed	MW547409	No
Metacampanella costaricensis	Costa Rica: Puntaranas	TENN-F-056536 Isotype	TFB9908	OQ171247	OQ171247
Metacampanella costaricensis	Costa Rica: Puntaranas	TENN-F-056536ss1	TFB9908ss1	OQ171248	OQ171248
Metacampanella costaricensis	Costa Rica: Puntaranas	TENN-F-056538ss13	TFB9908ss13	OQ171249	OQ171249
Metacampanella dendrophora	Argentina; Chubut	TENN-F-055002ss11	TFB8328ss11	OQ171242	OQ171242
Metacampanella dendrophora	Argentina; Chubut	TENN-F-055003ss4	TFB8328ss12	OQ171243	OQ171243
Metacampanella olivaceonigra	New Zealand	PDD:112550	JAC15400	OQ282811	OQ282761
Metacampanella olivaceonigra	New Zealand	PDD:112971	JAC15824	OQ282815	OQ282765
Metacampanella olivaceonigra	New Zealand	PDD:87486	JAC10398	OQ282784	No
Metacampanella olivaceonigra as *Tetrapyrgos olivaceonigra*	Australia	MEL2220682	None listed	EF175541	No
Metacampanella sinecystidia	USA: Pacific NW	C402M (Endophyte of *Elymus mollis*)	None listed	KT203169	No
Metacampanella sinecystidia as *T. subdendrophora*	USA: California	AHH120 (SFSU)	None listed	EF175521	No
Metacampanella subdendrophora	USA: Washington, Kirkland	TENN-F-078187	TFB14727 (RHP-1)	OQ171257	No
Metacampanella subdendrophora	Mexico: Est Mexico	TENN-F-055280	TFB8451	OQ171244	OQ171244
Metacampanella subdendrophora	USA: California	AHH148 (SFSU)	None listed	EF175522	No
Metacampanella subdendrophora	USA: California	AHH79 (SFSU)	None listed	EF175523	No
Metacampanella subdendrophora	USA: California, Humbolt Co.	DED7338 (SFSU)	None listed	EF175529	No
Metacampanella subdendrophora	USA: Washington, Lummi Island	iNAT-99991981	None listed	ON979424	No
Metacampanella subdendrophora	Canada	CCCM:UBC 5060-extype	None listed	OQ171258	OQ171258
Metacampanella subdendrophora	Canada: British Columbia	UBCF33841b	None listed	OQ171259	No
Metacampanella dendrophora f. *washingtonensis*	USA: Washington	UBC-F-33841b	None listed	OQ171259	No
Tetrapyrgos					
Tetrapyrgos crassicystidiata	Brazil	INPA259607	None listed	KT287091	No
Tetrapyrgos "alboviridis" Isotype	Costa Rica: Paloverde, Cartago	TENN-F-056741	TFB10029	OQ171250	OQ171250
Tetrapyrgos aff. *nigripes*	Australia: NT, Palmerston	MEL:2382866	GMB-2014	KP012740	No
Tetrapyrgos aff. *nigripes*	Australia: NT, Palmerston	MEL:2382974	None listed	KP012833	No
Tetrapyrgos atrocyanea	Brazil	INPA259596	None listed	KT287093	No

(*Continued*)

Table 1. (Continued).

Name	Location*	Voucher	Collector's number	ITS GenBank identifier	LSU GenBank identifier
Tetrapyrgos atrocyanea	Brazil	INPA259598	None listed	KT287094	No
Tetrapyrgos atrocyanea	Brazil	INPA259611	None listed	KT287095	No
Tetrapyrgos atrocyanea	Brazil	INPA259597	None listed	KT287096	No
Tetrapyrgos atrocyanea	India	KUBOT-KRMK-2020-80	None listed	MW555782	No
Tetrapyrgos atrocyanea as *T.* sp.	USA: Florida	FLAS-F-61224	None listed	MH211826	No
Tetrapyrgos atrocyanea Type	Madagascar	JES 216 (SFSU)	None listed	NR_169666	NG_075230
Tetrapyrgos brevicystidiata	Brazil	DLK1065	None listed	KT287087	No
Tetrapyrgos brevicystidiata Holotype	Brazil	INPA259604	None listed	KT287088	No
Tetrapyrgos cerebrata	Brazil	INPA259601	None listed	KT287089	No
Tetrapyrgos cerebrata	Brazil	DLK1970	None listed	KT287101	No
Tetrapyrgos cerebrata Holotype	Brazil	INPA259594	None listed	KT287090	No
Tetrapyrgos crassicystidiata Holotype	Brazil	INPA259606	None listed	KT287092	No
Tetrapyrgos griseibrunnea	Brazil	INPA259610	None listed	KT287098	No
Tetrapyrgos griseibrunnea	Brazil	INPA259609	None listed	KT287099	No
Tetrapyrgos griseibrunnea Holotype	Brazil	INPA259608	None listed	KT287097	No
Tetrapyrgos longicystidiata	Costa Rica	REHalling7542 (SFSU)	None listed	EF175531	No
Tetrapyrgos nigripes	USA	MCA6925	MCA6925	MG717370	MG717355
Tetrapyrgos nigripes	USA: North Carolina, GSMNP	TENN-F-060065	TFB12137	DQ449941, KT270853	No
Tetrapyrgos nigripes	USA: Tennessee, GSMNP	TENN-F-060781	TFB12583	DQ449942	No
Tetrapyrgos nigripes	USA: Tennessee GSMNP	TENN-F-065074	TFB13720	OR852427	OR852427
Tetrapyrgos nigripes	Not indicated	Wong888 (SFSU)	None listed	EF175535	No
Tetrapyrgos nigripes	Not indicated	TOR89 (SFSU)	None listed	EF175540	No
Tetrapyrgos novinigripes	Brazil	INPA259605	None listed	KT287082	No
Tetrapyrgos novinigripes	Brazil	INPA259603	None listed	KT287083	No
Tetrapyrgos parvispora	Thailand	AHH66 (SFSU)	None listed	EF175536	No
Tetrapyrgos parvispora	Thailand	AHH122 (SFSU)	None listed	EF175551	No
Tetrapyrgos parvispora	Not indicated	DED7603 (SFSU)	None listed	KT270855	No
Tetrapyrgos similinigripes	Brazil	INPA25960	None listed	KT287084	No
Tetrapyrgos similinigripes	Brazil	INPA265162	None listed	KT287085	No
Tetrapyrgos similinigripes	Brazil	INPA265320	None listed	KT287086	No
Tetrapyrgos sp.	USA: Connecticut	TENN-F-068191	TFB14341	OQ171254	OQ171254
Tetrapyrgos sp.	USA: New York, Cortland Co.	TENN-F-068199	TFB14349	OQ171255	OQ171255
Tetrapyrgos sp.	Australia: Victoria	TENN-F-053779	TFB7696	OQ171239	No
Tetrapyrgos sp.	USA: Louisiana, Tammany Parish	TENN-F-055739	TFB9110	OQ171245	No
Tetrapyrgos sp.	Costa Rica: Prov. Cartago	TENN-F-056390	TFB9416	OQ171246	No
Tetrapyrgos sp.	Thailand	AHH27 (SFSU)	None listed	EF175547	No
Tetrapyrgos sp.	Brazil	INPA265272	None listed	KT287100	No
Tetrapyrgos sp. "AHH-2007long"	Bolivia	REHalling6376 (SFSU)	None listed	EF175533	No
Tetrapyrgos sp. "AHH-2007long"	Puerto Rico	TJB7902 (SFSU)	None listed	EF175542	No
Tetrapyrgos sp. "AHH-2007long"	Costa Rica	ZT12386 (SFSU)	None listed	EF175543	No
Tetrapyrgos sp. "AHH-2007long"	Puerto Rico	TJB7935 (SFSU)	None listed	EF175544	No
Tetrapyrgos sp. "AHH-2007long"	Costa Rica	REHalling8396 (SFSU)	None listed	EF175545	No
Tetrapyrgos sp. "AHH-2007parv"	Thailand	AHH26 (SFSU)	None listed	EF175546	No
Tetrapyrgos subcinerea	Malaysia: Negeri Sembilan	AHH84 (SFSU)	None listed	EF175524	No
Tetrapyrgos subcinerea	Malaysia	KUM60051 (SFSU)	None listed	EF175527	No
Tetrapyrgos subcinerea	USA: Hawaii	DED 6178 (SFSU)	None listed	EF175528	No
Tetrapyrgos subcinerea	Indonesia	AR 505 (SFSU)	None listed	EF175530	No
Tetrapyrgos subcinerea	Malaysia	DED 7517 (SFSU)	None listed	EF175532	No
Tetrapyrgos subcinerea	Thailand	AHH71 (SFSU)	None listed	EF175534	No
Tetrapyrgos subcinerea	Malaysia	AHH86 (SFSU)	None listed	EF175537	No
Tetrapyrgos subcinerea	Malaysia	RW832 (SFSU)	None listed	EF175539	No
Tetrapyrgos subcinerea	Indonesia	AR 019 (SFSU)	None listed	EF175548	No
Tetrapyrgos subcinerea	Malaysia	KUM60047 (SFSU)	None listed	EF175549	No
Tetrapyrgos subcinerea	Indonesia	AHH115 (SFSU)	None listed	EF175550	No
Tetrapyrgos subcinerea	Malaysia	AHH90 (SFSU)	None listed	EF175552	No
Tetrapyrgos subcinerea	Thailand	DED 7448 (SFSU)	None listed	EF175553	No
Tetrapyrgos subcinerea	Indonesia	AR 138 (SFSU)	None listed	EF175554	No
Tetrapyrgos subcinerea	Indonesia	AHH109 (SFSU)	None listed	EF175555	No

*GSMNP=Great Smoky Mountains National Park.

156 nrITS sequences and 25 nrLSU sequences. Five microlitres of the PCR product were treated with 2 µL ExoSAP-IT (Thermo-Fisher Scientific) using the manufacturer's directions. Sanger dideoxy sequencing reactions were performed using BigDye Terminator 3.1 (Thermo-Fisher Scientific) following manufacturers' directions but with cycles increased to 35. Sanger sequencing was performed by the

University of Tennessee UT Genomics Core, College of Arts and Sciences.

Sequences were corrected and manually aligned in Geneious 11.1.5 (Geneious 2017). NrITS and nrLSU sequences were concatenated. Ambiguous bases at the point of overlap were indicated with an "N". Sequences were deposited in GenBank (OQ171233–OQ171259 and OR852424–27).

The Akaike model of evolution was estimated in W-IQ-Tree (Nguyen et al. 2014; Trifinopoulos et al. 2016) as TPM2+F+I+G4 (AC = AT, AG = CT, CG = GT; +F = Empirical base frequencies; +I = a proportion of invariable sites; and G4 = a Gamma distribution with 4 rate categories). A Maximum Likelihood (ML) analysis was performed using this model of evolution in W-IQ-TREE (Nguyen et al. 2015; Trifinopoulos et al. 2016) with 1,000 bootstrap replicates (Figure 3a–c). Bayesian analysis was performed using MrBayes (Huelsenbeck and Ronquist 2001) as implemented in Geneious 11.1.5 using a GTR model of evolution with 4 Gamma Categories and with the following settings; nst = 6, basefreq = estimate. The MCMC search was carried out with 4 chains for 1,100,000 generations and with sampling every 1,000 generations. The first 100,000 trees were discarded when likelihood values had reached convergence. Convergence was assessed by ensuring that the average standard deviation of split frequencies was below 0.01. Posterior probabilities were estimated by sampling trees generated after likelihood values had reached equilibrium (8,252 trees).

Percent base pair similarity between major clades was calculated in Geneious 11.1.5 based on a Neighbor-Joining tree (Saitou and Nei 1987) which creates a matrix of all paired individuals. Within and between genera estimates were the average of all individuals within and between genera pairs.

3. Results

3.1. Molecular analyses

Initial phylogenetic analyses indicated that *Brunneocorticium* and some environmental sequences were too distant from the core *Tetrapyrgos-Campanella* group, and they were excluded from further analyses.

The results of maximum likelihood and Bayesian analyses are summarised in Figure 3a–c. In both Bayesian and Maximum likelihood analyses, three major clades were well supported and the topology was the same, i.e. *Tetrapyrgos*, *Campanella s.s.*, and *Metacampanella* comprised a well-supported clade with *Metacampanella* and *Tetrapyrgos* as sister taxa. *Campanella s.s.* is defined by the generic epitype of *Campanella buettneri*, DED8276 SFSU (MF075136 and MF075138; Desjardin et al. 2017). An additional small clade deposited in GenBank under the generic name *Campanella* (OQ282805, OQ282808–9) falls outside *Campanella s.s.* as did *Heliomyces decolorans* and a clade of three collections from far eastern Russia (OR852426, OL764882, and OL764885). The outgroup, *Marasmiellus candidus*, is polyphyletic and two clades labelled as *Campanella* fall within it. One of these may represent an undescribed tropical taxon (Florida, Puerto Rico, and Guyana). The second is from New Zealand.

An unusual finding occurred with sequences attributed to *M. subdendrophora*. Two cultures were obtained from the type specimen collected by Redhead (Redhead 1974), one deposited with the American Type Culture Collection (ATCC42449: GenBank AY445121) and one with the Canadian Center for the Culture of Microorganisms (CCCM). The ATCC42449 sequence is missing 74 bp in the ITS2 region compared with the CCCM culture and all other *M. subdendrophora* collections. The author of the sequence was contacted but no longer has the original files used for the GenBank submission. ATCC was unwilling to send a culture for validation. We conclude that the GenBank sequence deposited for ATCC42449 is either incorrect or the culture has acquired a deletion during the culture process. We accept the nrITS sequence for the CCCM culture as the authentic ITS sequence for the type.

Comparisons of average sequence similarity within and between the four major generic clades (*Marasmiellus candidus*, *Campanella*, *Tetrapyrgos*, and *Metacampanella*: Figure 3a–c) are given in Table 2. Within taxa, similarity varies from 91.33% to 95.88% with *Metacampanella* species being most divergent from each other overall (94.33%). Between-group values ranged from a high of 90.00% similarity between the outgroup (polyphyletic) and *Campanella*. The percent similarity of *Metacampanella* to other taxa in this study was between 86.64% and 88.54%.

3.2. Morphological key to the taxa of the Metacampanella *complex*

(1) Pileus white, hardly changing in age, not blue-grey, green or olive; on grass or sedge; metuloids absent 2
(1) Pileus some shade of blue-grey, bluish green or olive; substrate various; metuloids present or absent 3
(2) Central California; ten pin-shaped cystidia absent; basidiomata conchate, white when young, often suffused with weak greyish tan in maturity; on sedge . . . . . . 5. *M. sinecystidia*
(2) Southern California to British Columbia; ten pin-shaped cystidia present; metuloids absent . . . . 6. *M. subdendrophora*
(3) Metuloids present 4
(3) Metuloids absent 5
(4) Argentine and Chilean Andes 3. *M. dendrophora*
(4) Central Mexico . . . . "Mexicano" (see under *M. dendrophora* f. *washingtonensis*)
(5) West coast of North America; hymenophore complex; basidiomata sessile, blue-green to blue-grey; dicot wood (rarely grass) . . . . *M. dendrophora* f. *washingtonensis*
(5) Not North America 6
(6) Continental Europe; on grass; ten pin-shaped cystidia absent . . . . 1. *M. caesia*
(6) Not continental Europe; Central America, Antipodes 7
(7) Antipodes; ten pin-shaped cystidia present . . . . 4. *M. olivaceonigra*
(7) Central America; ten pin-shaped cystidia absent . . . . 2. *M. costaricensis*

3.3. Taxonomy

METACAMPANELLA R.H. Petersen, gen. nov. IF 901403

Type species: *M. dendrophora* (Singer) R.H. PetersenIF 901404.

≡ *Campanella dendrophora* Singer 1955 Mycologia 47: 763. IF 293994.

Etymology: Morphology and molecular biology close to *Campanella*, but distinct.

Genus diagnosis: Basidiomata conchate, obcupulate to obsaucer-shaped, up to 20 mm broad, sessile, pseudostipitate or laterally stipitate, flexible and rubbery when young, becoming gelatinous in maturity; pileus surface matt, white to suffused greenish or blue-greenish (rarely pale pink); hymenophore usually of some radial rounded veins, usually developing few to numerous interveins, meandering or joining the major veins. Pileipellis a thatch of slender hyphae, often encrusted with annular thickenings and sometimes mixed with tetrapyrgoid pileocystidia; pleurocystidia fusiform; basidia (2-)4-spored; spores hyaline, thin-walled, generally triangular in shape, sometimes with abaxial bulge; cheilocystidia missing, tetrapyrgoid or metuloid, with or without crystalline deposit. Fruiting on dead woody substrates, monocot including bamboo, grass, sedge or rush, or uncommonly on dicot rotting wood. Clamp connections are apparently ubiquitous. ITS sequence analysis indicates inclusion with *Tetrapyrgos* and *Campanella*, but separate from both.

Metacampanella caesia (Romagnesi) R.H. Petersen, comb. nov**.** Figures 1, 4, S2–S5, IF901405

Basionym: *Campanella caesia* Romagnesi 1980 (1981) Bull. Trim. Soc. Mycol. France 96(4): 427. IF 112153.

Type specimen: France, Dordogne, Saint-Jean-d'Eyraud, 44° 57′ 20.02″ N, 0° 27′ 12.11″ E, 20.X.1977, Romagnesi no. 77.355 (PC).

= *Campanella inquilina* Romagnesi in Redhead 1984 Canad. J. Bot. 62(5): 881. IF 106655.

Type specimen: In herb. Romagnesi, no. 71 41 (PC). Implicit (B. Buyck, pers. comm.), France, Dpte. Oise, La Chapelle en Serval, 49° 07′ 41.29″ N, 2° 32′ 04.09″ E, 19. VI.1971, coll. Mme. Mesplade, Romagnesi no. 71–41, FUSION102035 (PC).

a? = *Campanella europaea* Singer 1975a Nova Hedwigia 26(4) 873. (nom. inval). IF 106654.

Type specimen: The Netherlands, Zeeland, Onrustpolder, 51° 34′ 56.63″ N, 3° 39′ 58.62″ E, 7. X.1958, W.G. Beeltink, no. 59529/44c (L).

A diagnosis extracted from Redhead's (1981) protologue for *C. caesia* follows. 1) basidiomata (his Figure 1) 4–5 mm broad, pellicular and translucent, sessile, originating on the central reverse (= pseudostipitate) and regularly orbicular, expanding to

Table 2. Percent ITS similarity between outgroup taxa (*Marasmius candidus* and affiliated *Campanella* taxa), *Campanella*, *tetrapyrgos*, and *Metacampanella* sequences.

	Outgroup	*Campanella*	*Tetrapyrgos*	*Metacampanella*
Outgroup	**91.33%**	89.58%	88.00%	86.64%
Campanella	89.58%	**95.88%**	90.00%	88.52%
Tetrapyrgos	88.00%	90.00%	**94.70%**	88.54%
Metacampanella	86.64%	88.52%	88.54%	**94.33%**

Numbers in bold represent within-group percent ITS similarity.

become more or less dimidiate; 2) pileus glabrous, shiny, very light bluish green, paler and even whitish at margin, becoming brownish with drying; marginal hairs (his Figure 3) lageniform (= ten pin-shaped), with a base more or less bulged with a thick collar, flexuous, obtuse or a little dilated at the end, 30–40 (−80) × 4.5–9.5 µm in the middle; pileus trama strongly gelatinised, generally 150–180 µm thick; tramal hyphae very scattered, flexuous, about 3–4 µm diam., non-dextrinoid but somewhat congophilic; subhymenium strictly filamentous; 3) hymenophore composed at first of 3–5 well-formed very narrow principal radial folds bifurcating towards the margin, between which are formed fold-like lamellulae, finally more or less alveolate, whitish, with distinctly greenish tint becoming brownish with drying; 4) stipe absent; 5) odour and taste not recorded; 6) basidiospores (his Figure 2) 7.5–9 × 4.2–5.5 µm, amygdaliform, with large hilar appendage, with thin and fragile wall, agglomerated and deformed, non-amyloid; 7) pleurocystidia slender, clavate or irregularly cylindrical, very rarely with rounded head; 8) basidia clavate, 32–40 × 6–9 µm, 4-spored; contents multiguttulate or (dried) glittering refringent and yellow-brownish when observed in NH_4OH (probably bluish green in Melzer's); 9) cheilocystidia not observed; 10) cuticle around 15–20 µm thick, composed of extremely tightly interwoven hyphae, contiguous, tangled with rigid walls in NH_4OH (from exsiccata) by a very refringent, yellow-brown crystalline substance contrasting with the gelatinised, colourless, hyphae 3–3.5 µm diam.; epicutis (his Figure 4) a compact interwoven layer of diverticulate hyphae and "brushes" so tight "that we wonder if it is not about the miniscule crystals (but they resist crushing), which we see jutting out of the claviform extremities (visible portion 15–35 µm, sometimes up to 5–9 µm in width), sometimes and most often at the base although in general with downward coralloid diverticula laterally thick) sometimes terminating in a tuft of 'brushes' series of diverticula spacing out lower;" 11) on the dry stem of an herbaceous plant; France, Austria; Autumn.

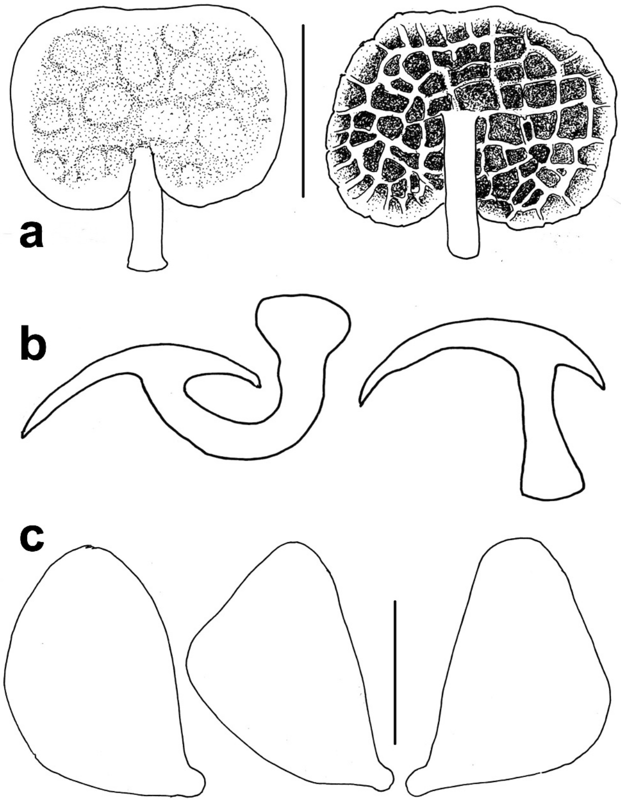
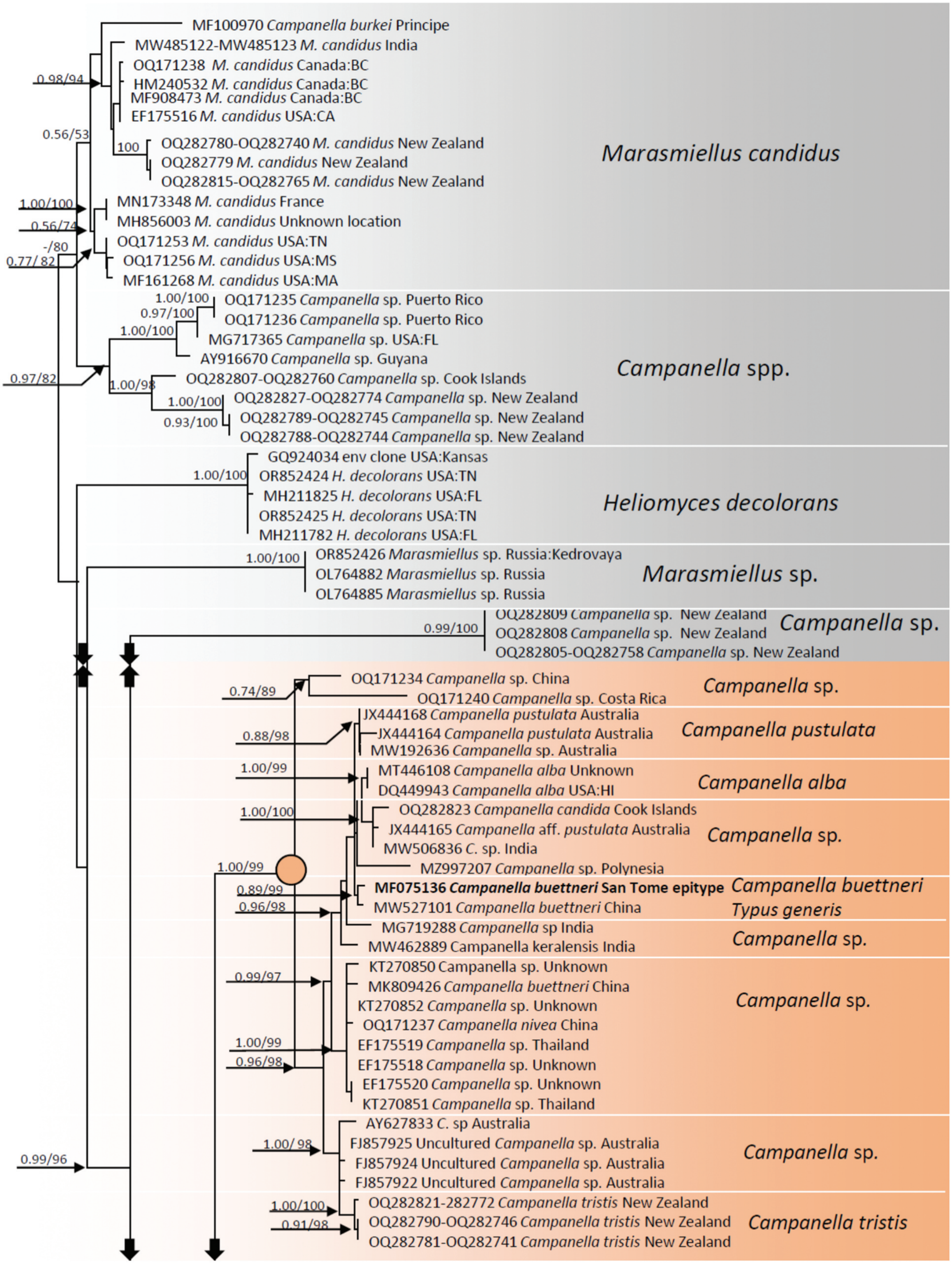


Figure 2. *Metacampanella costaricensis*. (a) Basidiomata from dorsal and ventral views. (b) Longitudinal section through basidiomata in various shapes. (c) Basidiospores. Standard bars: a = 10 mm; B = Not to scale; C = 5 µm. TFB 9908 (TENN-F-056536).

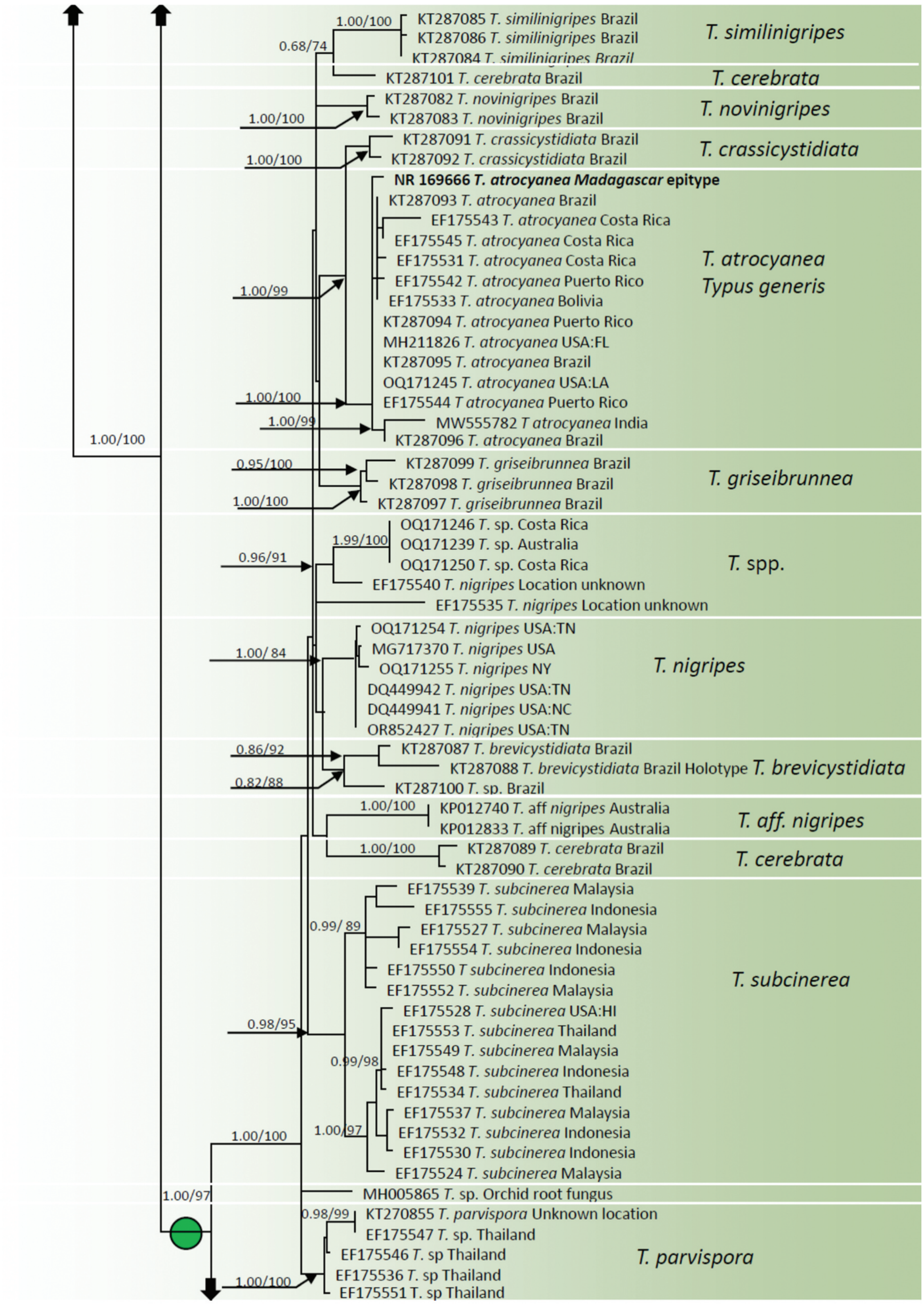
Additional habit photos appear in Læssoe and Petersen (2019), Moser and Peintner (2007); photo by Hausknecht) and as part of label material on F1075912.

At the Field Museum, there are two specimens labelled as *C. caesia*, collected by A. Hausknecht and both from Austria (see below). F075911 consists of: 1) 5–6 basidiomata on a slender portion of dicot twig. Significant characters include: 2) basidiospores (Figure 1) (8–)9–10(−12) × 4.5–5.5(−6) µm ($E = 1.78$–2.11; $E^m = 1.90$; $L^m = 10.05$ µm), ovate to ellipsoid, tapering somewhat adaxially to approximately triangular, without bulge; 3) common tetrapyrgoid



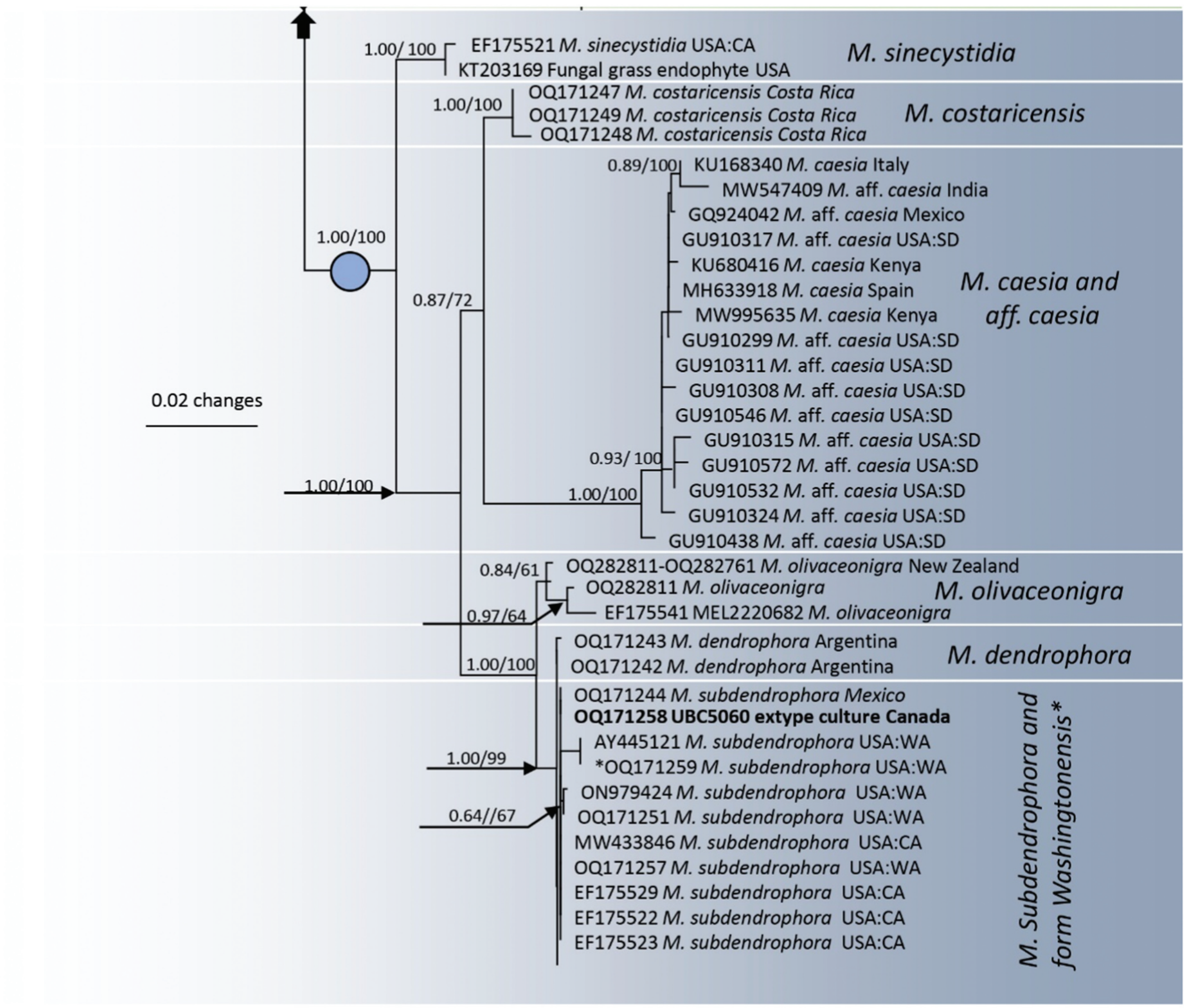
(a)

Figure 3a. Maximum likelihood analysis of *Tetrapyrgos*, *Campanella*, and *Metacampanella* based on nrITS plus LSU sequences. Node support values for maximum likelihood and Bayesian analyses are given to the left of the supported node. (a) Grey-closest genetic outgroup based on ITS sequences. (b) Orange-*Campanella* clade. (c) Green-*Tetrapyrgos* clade. USA state abbreviations are: CA = California, hi = Hawaii, MA = Maine, MS = Mississippi, NC = North Carolina, NY = New York, SD = South Dakota, TN = Tennessee, WA = Washington. Canadian province abbreviations: BC = British Columbia.



(b)

Figure 3b. (Continued).



(c)

Figure 3c. (Continued).

dermatocystidia and hymenial cystidia; 4) basidia 55–70 × 8–12 µm, 4-sterigmate, clamped. The second specimen (F1075912) is similar to F075911, but includes a photo of fresh basidiomata showing slightly bluish tint.

Campanella inquilina presents a more complicated history. Kühner and Romagnesi (1953) included *Leptogloassum conchatum* Velenovsky [1925 Mykologia 2(3–4) 45–47] in their Flore Analytique, but Malençon and Bertault (1970): 419–422] were uncomfortable with this treatment. Romagnesi [1981 (1980)] published a detailed description of a fungus which he accepted as *Leptoglossum conchatum* Velenovsky and recombined the epithet into *Campanella*. Redhead (1984): 881] reported that Velenovsky's type specimen of *L. conchatum* was, in fact, *Arrhenia retiruga*, which left the non-typical sense of *L. conchata* without a name. Romagnesi (in Redhead 1984) supplied the binomial *Campanella inquilina* (Latin diagnosis only) to alleviate the situation.

Although ascribed to *Campanella conchata*, Romagnesi's [1981 (1980)] detailed description is the best available and constitutes a type specimen study. A diagnosis extracted from his description follows. 1) Basidiomata (his Figure 1) 5–12 mm broad, sessile, convex; 2) pileus dirty white with tints of very diluted brownish inward; 3) hymenophore (his Figure 1) composed of 2–3 lamelliform pleats, divergent from an eccentric or sublateral point, often forked, irregularly anastomosing from start to finish, with surface reticulate, whitish or pallid; 4) stipe or pseudostipe absent; 5) odour and taste not reported; 6) basidiospores (his Figure 2) 7–8 × 3.5–4 µm, amydgaliform, thin-walled, inamyloid; 7) cystidia (his Figure 4) hyphal, beset with diverticula in middle, with inflated terminus ("tetrapyrgoid"); marginal hairs (his Figure 3) elongate-claviform, 40–60+ × 5–6.5 µm; 8) basidia 25–35 × 10–10.5 µm, clavate, 4-spored; 9) cheilocystidia absent; 10) pileipellis not described; 11) fruiting on small stems of grasses. Romagnesi [1981 (1980)] compared his *C. inquilina* to the other species described in the same paper, *C. caesia*, which exhibited fewer regular lamellar folds, smaller spores, and different pileipellis structures. Romagnesi's [1981 (1980)] illustrations are clear and those by Malençon and Bertault (1970) are excellent. A colour photo appears in Moser and Peintner (2007), also *C. caesia*).

A specimen under the name *C. inquilina*, collected by A. Hausknecht in Austria, resides in the Field Museum (F1070576). By the time the specimen was cited by Singer and Hausknecht (1990) they had concluded that *C. inquilina* was conspecific to *C. caesia*. There is no evidence that Singer examined the material microscopically or that the name is correct, but in this study, the description of the specimen follows. 1) A single basidiome survives, conchate to roughly cupulate, attached by a central point of pileus reverse; 2) pileus matt, perhaps minutely pruinose, now "pale ochraceous salmon" 3A3, shallowly pulvinate (but not alveolate or pustulate); 3) hymenophore an intricate reticulum of meandering lamellar folds <0.5 mm broad, with no major radials, now "light ochraceous buff" 6A4; lamellar edges undulate (not even); context thin, gelatinised; 4) pseudostipe absent; 5) odour and taste not recorded; 6) basidiospores (Figure 1) (7.5–)9–10(10.5) × 4.5–5.5(–6) µm ($E = 1.50–2.11$; $E^m = 1.83$; $L^m = 9.2$ µm), ellipsoid to subovate, thin-walled, hyaline, inamyloid; 7) pleurocystidia absent; 8) basidioles clavate to subcapitulate (Figure S2A); basidia (Figure S2B–D) 30–42 × 10–12 µm, clavate, 4-sterigmate, easily disarticulated from sub-basidial hyphae; 9) cheilocystidia (Figure S3) 35–70 × 8–12 µm (at widest point), ten pin-shaped, usually with scattered setulae on the proximal portion, thick-walled (wall –1.0 µm thick over proximal portion), often branched with internal septa (not clamped), hyaline; 10) pileipellis composed of three elements: a) repent hyphae (Figure S4A,B) 3–4.5 µm diam., thin-walled, hyaline, conspicuously encrusted in annular patterns; b) a palisade of arboreal structures (Figures S4C–E; S5C,D); major axis 5–9 × 3–4.5 µm, thin-walled, often intricately roughened, branching into 2–3 major branches which rebranch once or twice to terminate in a cluster of nodulose ultimate termini; termini of slender processes 1.5–5 × 1–2 µm, hyphal or nodulose, refringent (PhC); refringent crystalline deposit frequent in pileipellis (Figure S5A,B); c) tetrapyrgoid dermatocystidia (Figures S4F,G) of complex diverticulate hyphae terminating in an ellipsoid or trichothecioid apex; 11) fruiting on dead root and stems of grass.

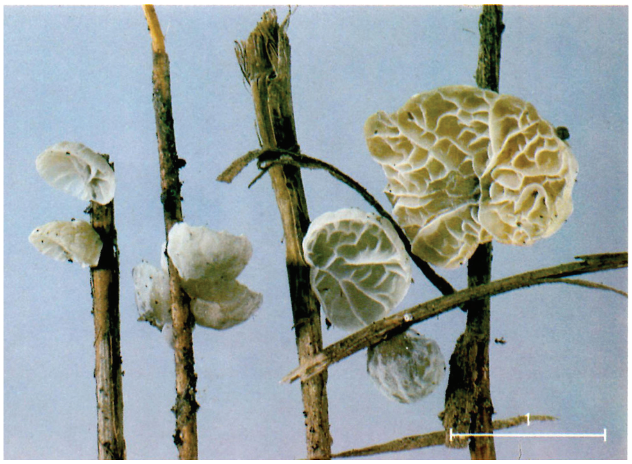


Figure 4. *Metacampanella caesia*. Photo by A. Hausknecht (as *C. inquilina*) in Moser & Peintner, Farb Atlas. Standard bar = 1 cm. Voucher: F1075911.

Commentary: Cheilocystidia of F1070576 is not unique in *Campanella*. Closest in morphology are those of *C. subdendrophora* (which also shares substratum dead grass culms), tetrapyrgoid dermatocystidia, and spore shape and size (Redhead 1981).

Although Index Fungorum indicates synonymy of *C. caesia* with *C. europaea* Singer ("ad inter."), several characters in Singer's description disagree with those in Romagnesi's description. Synonymy seems improbable, but the valid publication of *C. europaea* has not been consummated. Singer and Hausknecht (1990) considered *C. inquilina* Romagn. to be a taxonomic synonym under *C. caesia*.

Concerning *C. europaea*, published without a Latin diagnosis: this binomial is considered a nomen invalidum under Art. 39.1 (Melbourne) of the Code of Nomenclature. An extract of Singer's description follows. 1) Basidiomata up to 7 × 5 mm; 2) pileus pale yellowish brown, minutely pruinose, attached with a sublateral stipe or pseudostipe; 3) hymenophore lamellate and strongly anastomosing, 1–2 mm projecting, pale brownish; 4) basidiospores 6–8(–10) × 4–5(–6) µm, ellipsoid without bulges; 5) cystidia ("ten pin-shaped cystidia") on lamella edges and sides, 18–42 × 3–7 µm, thin- to firm-walled, mostly ampullaceous, some with short obtuse diverticula in the middle or below; the constricted portion 2.5–4 µm wide, the apical dilated portion 4.5–5.5 µm wide; 6) hyphae of the pileus- and hymenophoral tramae strongly gelatinised, 2–4 µm broad; 7) epicutis a *Rameales*-structure, occasionally almost asterostrommeloid; dermatocystidia ("tetrapyrgoid") versiform, often thick-walled, but mostly thin- to firm-walled, strongly diverticulated and sometimes branched, sometimes covered with a thin pale melleous resinous incrustation; 8) on *Agropyrum littorale* (grass) on young dunes, fruiting in fall.

There is no evidence that Singer saw or was informed about characters in fresh condition (*i.e.* colours, both in juvenile and mature basidiomata). The specimen may have been discovered in herbarium, with or without notes.

Singer also discussed separating characters of *C. europaea*. The species, for Singer, belonged to a taxonomic complex, basidiomata of which were similar to those of *C. tenuitunicata* in habitat, spores without abaxial bulges, and more strongly developed *Rameales*-structure with cystidioid terminations. It also differed from *C. austrochilensis* in regular ellipsoid spores and the yellowish-brown colour of the pileus and hymenophore. From the only other known extratropical [*i.e.* not neotropical and therefore not in the body of Singer's (Singer 1975b) monograph] species of *Campanella*, *C. subdendrophora*, *C. europaea* differed in bulgeless non-triangular spores and a much less developed stipe, but with which it shared a graminaceous host.

Two nrITS DNA sequences under the name *C. caesia* are listed in GenBank, KU168340. Italy, on grass and MW547409: voucher KUBOT-KRMK 2020-36 from India (99.1% sequence homology). Additional taxa that form a well-supported clade with *C. caesia* include Kenyan *Brachiaria* (grass) endophytes (KU680416, MW995635) and several cloned root endophytes from Prairie Dog dung (Herrera et al. 2011). It would appear that *C. caesia* has an environmental role as a grass endophyte.

Specimens examined: Austria, niederösterreich, Hollenstein, 47° 48′ 09.42″ N, 14° 46′ 22.08″ E, 25. X.1987, coll Hausknecht, s.n., F1075911 (barcode CO237478F); niederösterreich, Hollenstein, 25.X.1987, coll. A. Hauskncht, s.n., F1075912 (barcode CO237479F); Lower Austria, Galgenberg near Röschitz, 48° 39′ 57.36″ N, 15° 53′ 12.99″ E, 2.VII.1987. leg Hausknecht & Singer, Singer C 14017 (F1070576; WU 6606, under *C. inquilina*).

Metacampanella costaricensis R.H. Petersen, sp. nov. Figures 2, S6–S9, IF 901406

Holotype: Costa Rica, Prov. Puntarenas. Canton Coto Brus, Hacienda La Amistad, 8° 57′ 26.76″ N, 83° 04′ 27.71″ W, 4.VII.1998, coll RHP, TFB 9908 (TENN-F-056536).

Etymology: from Costa Rica.

Diagnosis: 1) basidiomata uniformly dull greyish green when fresh, not white or off-white; 2) attachment distinctly stipitate, with stipe remaining morphologically unchanged on drying; 3) hymenophore an intricate reticulum of meandering lamellar folds; 4) basidiospores broadly ellipsoid, sometimes exhibiting an abaxial bulge; 5) lack of metuloidal cystidia; 6) indistinguishable pleurocystidia. On standing dead limbs, abundant on leaf litter; Mixed tropical forest in subtropical Costa Rica.

Description [including two collections (see below)]: 1) Basidiomata (Figure 2a,b) 7–18 mm broad when mature, discoid, conspicuously stipitate, overlapping, broadly reniform or auriculoid; 2) pileus surface (fresh) "pale olive buff," 3B2 suffusing to "citrine drab" 4D5, brown-grey-greenish (~5D3); properly dried pileus "ochraceous tawny" 6C6 to "buckthorn brown" 5D6, ferruginous ("Mars yellow" 5C8), remaining subtly alveolate with white stipe; improperly dried (cooked) basidiomata deep chocolate brown, cartilaginous; 3) hymenophore (Figure 2b) of 3–5 radiating tortuous lamellar folds (<1 mm broad; often hardly distinguishable) with freely anastomosing, tortuous minor folds, narrower than major lamellar folds, when fresh "pale olive buff" 3B2 to "deep olive buff." 3C3, "mustard yellow" 4B5; poorly dried (dark, muddy opaque) lamellar folds instantly cinnabar orange to cinnabar brown in KOH; 4) stipe 1–4 × <1–1 mm, lateral and extending through a cleft in the pileus, equal, silky, on drying remaining off-white (pale greyish) with small white basal pad; stipe flesh bright cinnabar red in KOH; stipe base a small carbuncle of dark brown, sclerotic tissue; stipe medullary hyphae 3–7.5 µm diam., thin-walled, strictly parallel; stipe cortical hyphae (2–)3–4 µm diam., rather uniform, frequently branched; stipe vesture a complex thatch 10–25 µm thick; hyphae diverticulate to setuloid (a complex *Ramealis*-structure); stipe vesture hyphae of two types: a) coarsely dissected (frequently branched), the branches awl-shaped, 3–12 × 2–3 µm; and b) intricately dissected hyphal termini, appearing like broccoli spears; setulae 1–3(–4) × 1–1.5 µm, crowded; 5) odour and taste not recorded; 6) basidiospores (Figures 2c, S7E–H) 7.5–9(–10) × 6–7(–8) µm ($E = 1.06–1.54$; $E^m = 1.19$; $L^m = 8.35$ µm), ellipsoid, ovate to rounded triangular in profile, usually with abaxial bulge, hyaline, thin-walled, inamyloid; 7) pleurocystidia (i.e. "hymenial cystidia" of Singer) indistinguishable or absent; 8) basidioles clavate or urniform (Figures S6E, S7A); contents more or less homogeneous; basidia (Figures S6A–D, S7B–D) broadly clavate to urniform, 50–65 × 6–8 µm, 4-sterigmate; contents heterogeneous, especially in proximal portion but by maturity with several large, refringent bodies apical and passing through sterigmata to spores; 9) cheilocystidia (Figure S8) scattered, collybioid, composed of slender hyphae often branched and irregularly lobose; hyphae 2.5–3.5(–4) µm, conspicuously clamped, occasionally within individual cheilocystidia; 10) pileipellis (Figure S9) a thatch of diverticulate hyphal termini [more or less an "asterostromelloid" arrangement (of Singer)] with no detectible *Ramealis*-structure, similar to the arrangement in *M.dendrophora* f. *washingtonensis* and *M. subdendrophora*; hyphae 2–3.5 µm diam., thin- to firm-walled, frequently branched; branches 2–15 × 2–3 µm, awl-shaped; encrusted hyphae not observed; subpellis hyphae loosely interwoven, thin-walled, 2.5–6 µm diam., discrete in exuded hyaline gel; 11) fruiting on standing dead (dicot) limb (TFB 9908, TENN-F-056536), apparently also on dead *Chusquaea* (TFB 9648, TENN-F-056609); summer; presently known only from subtropical Costa Rica.

Commentary: *Meta campanella costaricensis* would seem to belong to sect. *Aeruginea* Sing., a section based largely on negative characters. As such, the two collections of *M. costaricensis* were found on very different substrates, doubtfully leading to *C. aberrans* Singer (1975: 855). From *C. aberrans*, *M. costaricensis* differs by its obvious and distinct stipe. In addition, *C. aberrans* is known only from its type specimen, collected in Bolivia.

Fortunately, cultures were established from TFB 9908 (TENN-F-056536; holotype) when originally collected. Dikaryon cultures on MEA were rapidly-growing, produced abundant aerial mycelium, and in age formed ill-defined submerged areas of mycelium "sayal brown" 6C5 to "clay colour" 5C6. Of aerial hyphae, hyphal "ropes" were common, usually associated with crystalline deposits; occasional capitulate hyphal termini reminiscent of pileal and hymenial "hairs" were observed.

Of the original SBIs, 18 were revived, from which 12 were selected for participation in a self-cross. In the self-cross, a tetrapolar mating system was revealed. Primary mating types (A^1B^1, A^2B^2) were distinct while subordinate mating types (A^1B^2, A^2B^1) displayed occasional unexplained compatible pairings. Clamp connections produced by compatible pairings were usually of the medallion type.

nr ITS and LSU sequences were obtained from a dikaryon culture of TFB 9908 (TENN-F-056536) and two monokaryon isolates (Single spore cultures 1 and 13). Interestingly, the dikaryon was heterozygous at 5 positions (0.7%) and the two single spore isolates differed from each other at these sites. The observed heterozygosity argues against a small genetically isolated population and for a larger genetically variable species. In a GenBank BLAST, no other taxon was within 95% match, and those at 94% were "uncultured Agaricales." Sequences from putative *C. subdendrophora* were clustered at approximately 93% nrITS match.

Specimens examined: Costa Rica, Prov. Alajuela, Reserva Terrestrial de Grecia, Bosque del Niña, 10° 08′ 30″ N, 84° 14′ 62″ W, 27.VI.1990, coll RHP, TFB 9648 (TENN-F-056609); Prov. Puntarenas. Canton

Coto Brus, Hacienda La Amistad, 8° 57′ 26.76″ N, 83° 04′ 27.71″ W, 4.VII.1998, coll RHP, TFB 9908 (TENN-F-056536).

Metacampanella dendrophora (Singer) R.H. Petersen, comb. nov. Figures 5, S10–S16, IF901404

Basionym: *Campanella dendrophora* Singer 1955 Mycologia 47(5): 763. IF 293994.

≡ *Pterospora dendrophora* (Singer.) Horak 1983b Sydowia 36: 13. IF 115309.

≡ *Tetrapyrgos dendrophora* (Singer) Horak 1986. Sydowia 39: 102. IF 131351.

Type specimen: Argentina, Prov. Neuquén, Puerto Manzano, 40° 48′ 17.91″ S, 71° 35′ 42.65″ W, 16.V. 1952, Singer M746 (LIL).

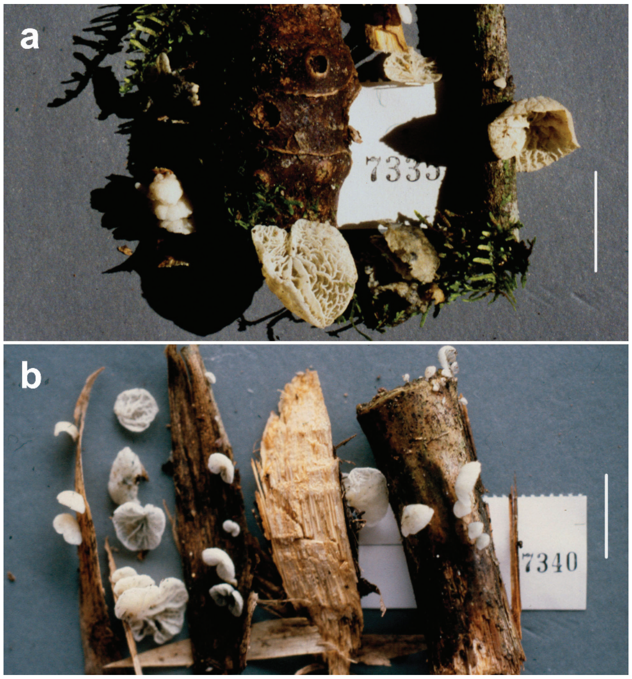


Figure 5. *Metacampanella dendrophora*. Basidiomata, habit. (a) TFB 7335 (TENN-F-054395). (b) TFB 7340 (TENN-F-054442). Standard bars = 10 mm.

1) Basidiomata (Figure 5) 1–5(–8) mm broad, broadly reniform to orbicular, distinctly laterally stipitate, conchate to *Favolaschia*-shaped, shallowly convex, cupulate to hemispherical, poorly dried basidiomata dark purplish-brown and cartilaginous; trama largely gelatinised, with gel appearing as pillow-like units not merging together (as though produced by individual hyphal cells); 2) pileus undulate to strongly pulvinate, puckered to subtly alveolate, matt, usually off-white to “tilleul buff” 7B2, with suffused patches of “pale olive buff” 3B2, slowly discolouring to “slate olive” 27E4, to “deep slate olive” 28E3, “tea green” 29C3, “Vetiver green” 29C4, “Andover green” 29D4 to 25E3-4, “dark ivy green” 29F4-5, or entirely without white; pileus necropigment “light ochraceous buff” 5A4, “cinnamon buff” 6B4; 3) hymenophore with 2–4 radial lamellar folds, with few (TFB 7357) to (usually) many meandering secondary rounded veins (not knife-edged) to appear merulioid or alveolate, <0.5 mm broad, when fresh white to “pale olive buff” 3B2; necropigment somewhat more orange than pileus to “light ochraceous buff” 5A4, “ochraceous buff” 5A5, “ochraceous tawny” 6C6; lamellar tramal hyphae similar to pileus trama, with gelatinised tissues appearing as scattered pockets; 4) stipe lateral, 0.5–1 × <0.5–0.5 mm, occasionally lacking, straight (when para- or negatively geotropic) to very strongly curved when geotropic, often slightly enlarged at base, vestured, white, inserted in substrate by a small basal pad concolorous with pileus; 5) odour and taste negligible; 6) basidiospores (Figure S10) (5.5–)8–10 × (4.5–)6.0–7.0(–8) µm (E = 1.13–1.90; E^m = 1.34; L^m = 8.25 µm), broadly ellipsoid to bulged abaxially to appear rounded-triangular to rounded-cuboid (derivative metrics of little value, depending on the view of individual spores), thin-walled, hyaline, smooth, inamyloid; hilar appendix narrow; contents minutely heterogeneous; 7) pleurocystidia (Figure S11) 30–35 × 8–10 µm, weakly fusiform, inconspicuously clamped; contents subtly heterogeneous; 8) basidioles (Figure S12A) broadly clavate, inconspicuously clamped; contents increasingly heterogeneous with age; basidia (Figure S13B–F) 30–38 (–42) × 10–14 µm, clavate, often suburniform or with slightly enlarged distal portion, 4-sterigmate (sterigmata stout, strong, slightly curved), inconspicuously clamped; contents heterogeneous; 9) cheilocystidia lacking or scattered in small clusters, of two types: a) tetrapyrgoid (Figure S13) (i.e. axial, often septate with median portion beset with numerous minute, branched ornamentation and usually with enlarged apical portion), 30–50 × 6–12 µm, hardly protruding beyond basidia/basidioles; b) metuloids (Figure S14) rare to common (apparently not in all basidiomata), apparently cheilocystidial in distribution, widely scattered, (28–)30–45 × 10–15 µm, fusiform with rounded apex, to ampulliform, thick-walled (wall <1.2 µm thick, smooth, hyaline), easily disarticulated from basal septum, probably clamped, often (but not more than 50%)

with apical crystalline deposit; apex difficult to observe; 10) pileipellis a tightly interwoven tissue of free (not gelatinized) ramified hyphae; superficial pileipellis composed as follows: a) thatch of arboreal hyphal termini; major axis 5–14 × 2.5–4.5 µm, often beset with numerous lateral outgrowths, from relatively simple (Figure S15C–F) to branching into 2–5 secondary branches, rebranching into crowded peg-like to awl-shaped termini 2–5(−15) × 1–1.5(−3) µm, (Figures S15A,B); this is not strictly a *Rameales*-structure; b) thin-walled repent hyphae (2.5–4.5 µm diam.) beset with densely scattered small side branches (especially on the outer surface) resembling a *Ramealis*-structure; c) inner pileipellis a repent layer of encrusted hypha 3–5.5 µm broad, with encrustation usually of annular thickenings (Figure S16A,B) with deeper hyphae becoming gelatinized with walls disappearing; clamp connections ubiquitous; 11) fruiting chiefly on *Chusquea* (TFB 7357= TENN-F-054439), but also occasionally on dead dicot bark (TFB 8328 = TENN-F-055002), on dead ?*Berberis* (TFB 7340 = TENN-F-054442); fruiting on both *Chusquea* and on *Nothofagus* twigs (TFB 7335 = TENN-F-054395); presently known from Argentine Andes and Isla de Chiloé; April, May. Stipe medullary hyphae free (not involved in slime or gelatinous matrix), more or less parallel, of two types: a) 2–5.5 µm diam., firm- to thick-walled (wall <0.5 µm thick); and b) 4–11 µm diam., firm- to thick-walled (wall −1 µm thick), appearing somewhat glassy in PhC. Stipe cortical hyphae variable, 3–8(−24) µm diam., thick-walled (wall −2.5 µm thick, not uniform), producing copious side branches. Stipitipellis structures of two types: a) weakly "asterostromelloid" (Singer 1975; diverticulate with diverticula awl-shaped), with hyphae rather uniform, 2.5–4 µm diam., thick-walled (wall <0.7 µm thick, hyaline); diverticula 3–8 × 2–3.5 µm; and b) tetrapyrgoid, axial with inflated apical lobe; axis 8–27(−35) × 2.5–5 µm, with copious short diverticula, often curved towards distal terminus but usually rebranched into clusters of minute diverticulate outgrowths; outgrowths 0.7–3.5 × 0.5–2 µm; inflated terminal lobe broadly ellipsoid to elongate-obovate, 4–9(−12) × 4–7 µm, thick-walled (wall <1.5 µm thick, hyaline, somewhat refringent).

Commentary: A rough and rearranged translation of Singer's (1955) Latin description of *C. dendrophora* follows, but it comprises two specimens and so is not a type specimen study. 1) Basidiomata (his Figure 1 "Ca") 10–16 mm broad, circular or conchate, attached directly posteriorly or pseudostipitate or affixed stipe; 2) pileus caeseous (bluish grey) or first white then caeseous, reticulate, transparent, rugulose, convex; 3) hymenophore sublamellate, anastomosed, projecting up to 1.5 mm, cristate; lamellae distant; 4) stipe concolorous, brief, lateral 2 × 1 mm; 5) odour and taste not recorded; 6) basidiospores (his Figure 1 "sp") 8.8–10.2 × 6.8–8.2 µm, hyaline, smooth, guttulate, generally triangular, rarely with dorsal, suprahilar or eccentric bulge, inamyloid; 7) pleurocystidia (his Figure 1 "Cy") ventricose or cylindrical, always capitate; capitulum 5.5–9 µm diam., centre portion 40–53 × 5.5–11 µm, collar part more slender, 4 µm broad, the walls of pseudophyses thinner, obscurely colouring in Phloxine, the basal part often diverticulate (his Figure 1 "DC") in individual cystidia, less cylindraceo-capitaulate; pseudophyses dendroid, epicuticular hyphal structure reminiscent of *Marasmiellus*, hyaline, branched, diverticulate-coralloid, sometimes humped, at least capitate; 8) basidia (his Figure 1 "B") 38–40 × 8.2–10.2 µm, clavate, 4–sterigmate; 9) thick-walled metuloids (his Figure 1 "M") 35–44 × 8.5–9.7 µm, like those of *Campanella simulans* present, opaque, hyaline, cylindrical or frequently fusoid-ventricose or fusoid-ampullaceous, with rounded apex, moderately numerous, with apical encrustation; 10) pileipellis an asterostromelloid structure, of simple or branched or totally composed of irregular hyphae (his Figure 1 "D"); fruiting on culms of *Chusquaea couleu* [sic]; eastern slope of Argentine Andes.

Having proposed *C. dendrophora* from temperate, montane Argentina (Singer 1955), the species was not included in the larger subsequent publication (Singer 1975b). Moreover, having compared the metuloids of *C. dendrophora* to those *of C. simulans*, the latter was also disregarded in his (Singer 1955) key, relegated to a description of extra-limital (Hawai'ian Islands) material. Instead, three metuloid-producing species appeared in both the key and descriptive text: *C. stipitata*, *C. diplocystis*, and *C. aequatorialis*.

Horak [(1983):130–131] used his collection (Horak 393 ZT) in the transfer of the species to *Tetrapyrgos*. Illustrations were as follows: basidiomata (his Figure 1D), basidiospores (his Figure 1E), basidia (his Figure 1F); metuloids (his Figure 1H); and pleurocystidia (his Figure 1G).

Based on Horak's [Horak 1983, Horak (1987(1986)] transfers, Honan et al. (2015) furnished a full holotype study supplemented by observations on a paratype and the Horak specimen (393 ZT), all from the general topotype area; Included were illustrations of microscopic structures. Two items were in doubt: 1) spores metrics were unavailable from the holotype but the Horak specimen [Horak 393 (ZT)] furnished the following: 8–10.5 × 5.1–7 µm (E = 1.3–1.9; $E^m = 1.5$; $L^m = 9.3$ µm); and 2) "There is some confusion concerning the presence or absence of apically incrusted metuloid hymenial cystidia reported in the protologue as they were not observed by Desjardin in any of the specimens cited … although Horak (1983 [from 393 ZT]) reported their presence." Singer (1955) also reported and illustrated them in the protologue.

Honan et al. (2015) examined and illustrated the holotype (LIL). A diagnosis extracted from their description follows: 1) seven basidiomes in fair condition; 2) pileus ovoid to circular in face view, glabrous, wrinkled-reticulate, now yellowish brown (no apparent blue or olive tones when dried); 3) lamellae remote, with many anastomosing cross-veins; 4) stipe 1 × 0.5 mm, lateral or as pseudostipe, cylindrical, pruinose, concolorous with pileus; 5) odour and taste not recorded; 6) basidiospores (their Figure 9a, b; not from type) not seen; 7) hymenial cystidia (their Figure 9c from type; d,e, not from type) subclavate to fusoid or tibiiform with broadly rounded, obtuse apices, entirely smooth, thin- to slightly thick-walled, refractive; 8) basidia 4-sterigmate; 9) metuloid cystidia or capitate-diverticulate cystidia not observed (by Desjardin). [Horak (Horak 1983) reported two types of hymenial cystidia, viz., metuloids and capitate-diverticulate cystidia]; 10) pileipellis a *Rameales*-structure of loosely interwoven, densely diverticulate hyphae; terminal cells coralloid, diverticulate; (capitate pileocystidia not observed); 11) habitat as above.

Of particular note is the distinctly slate green shades in fresh material, replaced by necropigment "cinnamon buff" 6B4 shades. The intricacy of hymenophore and dull greenish suffusion resemble traits of *M. dendrophora* f. *washingtonensis*, which lacks metuloids, forms pseudostipitate to sessile basidiomata, is widely geographically separate, and fruits almost exclusively on dicot wood.

Because Singer collected so many *Campanella* specimens along the Andes of South America, a comparison must be made between *C. dendrophora* and *C. aequatorialis*. Basidiomata of *C. aequatorialis* were not reported as suffusing in dull green shades (basically white) and were pseudostipitate. Conversely, both taxa are characterised as exhibiting a *Rameales*-structure pileipellis (although doubtfully so in *C. dendrophora*), ellipsoid, bulged spores, and some form of metuloidal cystidia. It would appear, in the absence of molecular evidence from *C. aequatorialis*, that the two taxa remain separable.

Singer (1975b) assigned a complex of metuloid-producing taxa to *Campanella*, with diagnostic characters including: 1) gelatinisation of pileus tramal hyphae; and 2) basidiospores with only a suggestion of tetrahedral shape (versus *Tetrapyrgos* in which spores are distinctly stellate-tetrahedral). Both of these diagnostic characters are present in TFB 8328 (TENN-F-055002), but the abundance of *Tetrapyrgos*-like cystidioid structures (as cheilo- and caulocystidia) raises questions about generic placement. If these characters are added to the fruiting habit on *Chusquea* (and occasionally on dicot bark) and the small size of basidiomata, TFB 8328 (TENN-F-055002) would seem to represent an undescribed taxon.

With a prominent, albeit small, stipe, TFB 8328 (TENN-F-055002) might also be sought under *C. stipitata* (basionym: *Campanella candida* var. *stipitata* Singer 1969). That taxon is characterised by: 1) basidiomata circular, about 10 mm broad; 2) pileus pure white with no indication of colour change; 3) hymenophore lamellate, with interveining, "dirty white" cross-veins, with evidence of browning on drying; 4) stipe greyish white, tomentose; 5) spores ellipsoid (no report of bulges); 6) metuloidal structures of two types: a) fusoid-ventricose-ampullaceous, with or without acute or obtuse tip and mellious crystalline deposit; b) ampullaceous; 7) on roots and branches, January to March, western Argentina.

In Singer's (1975b) key, the presence of metuloids is pivotal. Within this restriction, TFB 8328 (TENN-F-055002) is keyed near *C. diplocystis*. From *C. diplocystis* it differs in lacking two forms of metuloidal cystidia, basidiomata often (not exclusively) exhibiting a lateral to eccentric stipe and seemingly producing significantly smaller basidiomata.

In several mounts of one basidiome of TFB 7340 (TENN-F-054442) made to study hymenophoral structures, no metuloidal structures were seen, but mounts from a different basidiome of the same collection exhibited numerous metuloidal individuals. This phenomenon raises doubts about the primacy of this structure in the separation of taxa in Singer's (1975b).

Specimens examined: ARGENTINA, Prov. Chubut, Parque Nacional Los Alerces, 42° 51′ 31.84″ S, 71° 36′ 15.28″ W, 9.V.1996, coll M. Rajchenberg, TFB 8328 (TENN-F-055002); Chubut, Parque de los Alerces, between Lake Verde and Menendez, 6.V.1996, coll. D Sime, TFB 8505 (TENN-F-055076); Parque Nacional de Alerces, vic. Puerto Chucao, south shore of Lago Verde, 9.V.1996, coll D. Sime, TFB 8624 (TENN-F-054963); Prov. Rio Negro, Llao Llao, Parque Nacional de Nahuel Huapi, Puerto Blest, 40° 48′ 27.87″ S, 71° 44′ 56.69″ W, 2.IV.1995, coll RHP, TFB 7335 (TENN-F-054395); Llao Llao, Bahia Lopez Trail, 41° 03′ 12.71″ S, 71° 31′ 47.30″ W, coll RHP, 3.IV.1995, TFB 7340 (TENN-F-054442); same data TFB 7344 (TENN-F-054415). CHILÉ, Dpto. Osorno, Parque Nacional Payuhue, approx. 40° 40′ 14.52″ S, 72° 37′ 06.99″ W, 12.IV.1995, coll RHP, TFB 7373 (TENN-F-054410); Isla Grande de Chiloé, 20 km east of Aucud, 41° 52′ 37.37″ S, 73° 40′ 28.77″ W, 9.IV.1995, coll RHP, TFB 7357 (TENNF-054439).

Metacampanella dendrophora *f. washingtonensis* R. H. Petersen, forma nov. Figures 6, S17–S26. IF 901407

Type specimen: USA, Washington, King Co., (Walter P.) Magnuson Park, approx. 47° 40′ 59.09″ N, 122° 14′ 52.19″ W, 18.XII.2002, coll. M. Seidl (MTS 5001), WTU-F-121309.

Etymology: From USA, Washington State (Pacific Northwest).

Protologue description (not limited to type specimen study): 1) basidiomata (Figure 6) pseudostipitate, up to 25 mm diam., conchate when immature, expanding laterally through fan-shaped stages, becoming orbicular by maturity, usually with overlapping lobes surrounding point of attachment; substratum attachment with no differentiated stipe or pseudostipe rudimentary, <1 mm long; basidiomatal trama of hyphae loosely arranged; hyphae 2.5–3.5 μm diam., thin-walled, frequently branched, conspicuously clamped, often gelatinising and obliterating hyphal outlines; 2) pileus surface matt, pulvinate but not alveolate, often chafed, when fresh "dusky olive green" 30F8, "dusky yellowish olive" 28F6, "dark slate olive" 28E3, to glaucous grey-green, upon drying becoming "pale pinkish buff" 6A2, "light buff" 3A2, "light ochraceous buff" 5A4, "clay color" 5C6, "sayal brown" 6C5, "cinnamon buff" 6B4 to "pinkish buff" 6A3; context rubbery to firm-gelatinous when fresh, 1–2.5 mm thick, translucent, when dried becoming cartilaginous, appearing glassy; 3) hymenophore composed of 5–8 radiating lamellar folds, often with a single alternating row of lamellulae; neither lamellae nor lamellulae reaching pileus margin; anastomosing cross-veins abundant, distorting lamellar direction, appearing lacy, when fresh white with lamellar edges "deep bluish gray green" 25D6, to "dark bluish gray green" 25E5, upon drying and storage becoming "sayal brown" 6C5, "russet" 7D6 to "Mars brown" 8F7 where chafed, with lamellar edge paler, "ochraceous buff" 5A5, under high magnification (50–75×) appearing minutely roughened or barbed; 4) pseudostipe absent or rudimentary; superficial vesture furry, off-white; 5) odour and taste negligible; 6) basidiospores (Figures S17, S18D–F), 6.5–10 × 5.5–7 μm (E = 1.15–1.73; $E^m = 1.35$; $L^m = 7.2$ μm), broadly ovate to triangular but without abaxial bulges, smooth, thin-walled, hyaline, inamyloid; 7) pleurocystidia (Figure S19) arboreal, similar to dermatocystidial form; axis 3–8 × 3.5–4.5 μm, thin-walled, producing either *Rameales*-like setulae or ramifying into 2–4 major branches beset by diverticula; 8) basidioles (Figure S18A) broadly clavate, inconspicuously clamped;

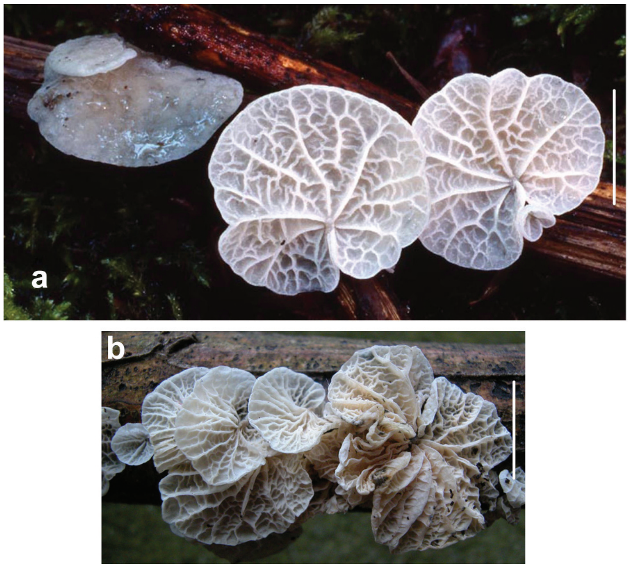


Figure 6. *Metacampanella dendrophora* f. *washingtonensis*. Basidiomata. (a) Dorsal view (left), ventral view (right). Photo courtesy of dr. Steve Trudell. (SAT 08-299-17), WTU-F-1388. (b) Ventral perspective. Standard bars = 10 mm. UBC T33841. Mushroom observer 65789 (courtesy O. Ceska).

basidia (Figure S18B) 47–57 × 7–8.5 µm, clavate, 4-sterigmate, often remaining as "husk" after expressing contents (Figure S18C), conspicuously clamped; contents heterogeneous, multigranular; 9) cheilocystidia of three types: a) ten pin-shaped cystidia (Figures S20, S21A–C, S22A) ampulliform, subrefringent (PhC), mostly near and at lamellar edge, axial with subventricose, thick-walled proximal portion 20–35 × 7–8.5 µm; proximal surface sometimes with scattered, short diverticula or setulae; distal shaft 10–25 × 4.5–6.5 µm, smooth; apical globose capitulum 7–9.5 µm diam., subrefringent (PhC); b) tetrapyrgoid cystidia (Figures S20D, S21B–E) similar to those of the pileipellis, axial with shaft beset by many short setulae; elongate-ellipsoid inflated apex often appearing thick-walled (wall −1 µm thick, hyaline); inflated apex 12–18 × 7–8 µm, ellipsoidal, smooth, often set off by a transverse septum; c) gymnopoid cystidia 12–30 µm long, with distal shaft and irregular inflated lobes; 10) outer pileipellis a complex tissue loosely arranged in a dry, non-gelatinised thatch (Figure S23A) of diverticulate hyphae (Figures S23B, S24A–D), a modified *Rameales*- or asterostromelloid structure; diverticulate hyphae 2.5–6 µm diam., thin- to firm-walled, conspicuously clamped, not gelatinising, producing numerous diverticula; diverticula 2–8 × 1.5–2.5 µm, awl-shaped, occasionally branched; inner pileipellis usually including a modified *Rameales*-structure in a thatch sometimes in a slime matrix; *Rameales*-structure of repent hyphae 2.5–4 µm diam., thin-walled, beset with peg-like or digitate setulae; setulae 1–3.5 × 1–1.5 µm; subpellis (Figure S19E,F) a layer of repent hyphae 2.5–7 µm diam., thin- to firm-walled, often encrusted with pigment scabs or occasionally annular patterns, conspicuously clamped, not gelatinised; dermatocystidia of two types: a) arboreal structures (Figure S25) with major axis 4–10 × 2.5–4 µm, thin-walled, conspicuously clamped, producing 0–3 major branches which ramify into terminal setulae; setulae 1–4 × 1–2 µm, widely scattered in pileipellis but becoming more numerous towards basidiome attachment; b) tetrapyrgoid structures (Figure S26) also most common near basidiome attachment, axial, usually unbranched; axis 7–35 × 2.5–4 µm, thin-walled, producing numerous diverticula; diverticula 1–3.5 × 1–1.5 µm, awl- to talon-shaped – curved, sharply tipped; inflated apical portion (usually not separated from the axis by a septum), obovate, firm-walled, 6–11 × 4–6.5 µm, subrefringent (PhC); 11) fruiting on dead, woody dicot stems, notably *Rubus spectabilis, Alnus rubra* and *Cytisus scoparius* in mixed forest with *Pseudotsuga menziesii*, *Arbutus menziesii*, *Quercus garryana*; southern British Columbia, western Washington, western Oregon, reportedly northern California; rainy season, Autumn – early winter.

Commentary: The most perplexing problem in proposing f. *washingtonensis* as a new taxon is countering molecular evidence: such an easily recognised morphotaxon assumedly ought not to produce ITS sequences highly matching those of a named (*M. subdendrophora*) and documented second taxon (*M. dendrophora*) as well as an unnamed collection from central Mexico [TFB 8451 (TENN-F-055280), see below]. An ITS-based sequence was assembled from DNA segments obtained from putative f. *washingtonensis*, UBC F33841, and was found to be congruent with several sequences of *M. subdendrophora* as were other collections of putative f. *washingtonensis*. Habit photos of UBC F33841 may be seen at Mushroom Observer no. 65789.

Honan et al. (2015) described basidiomata of *M.* (their *Tetrapyrgos*) *subdendrophora* as bruising or ageing to grey or beige shades, but no accommodation was made for a possible second taxon. Form *washingtonenis* differs from largely sympatric *M. subdendrophora* as follows: 1) basidiomata of *M. subdendrophora* distinctly, laterally stipitate; those of *M. washingtonensis* sessile or pseudostipitate with no or very rudimentary stipe; 2) hymenophore of f. *washingtonensis* much more intricate than that of *M. subdendrophora*; 3) basidiomata of f. *washingtonensis* suffused with grey-blue, blue-green to olive-green colours while in all authoritative reports those of *M. subdendrophora* white to pale pinkish off-white; 4) spores of f. *washingtonensis* are truly ellipsoid to rounded-triangular but are not bulged (see Figures S17, S18D–F) in addition to tetrapyrgoid-type hymenial cystidia present in both taxa, arboreal-diverticulate cystidia are present in f. *washingtonensis*, not reported for *M. subdendrophora;* 5) form *washingtonensis* basidiomata are produced on dead dicot woody stems and branches while those of *M. subdendrophora* are almost exclusively on dead grass stems.

The presence of f. *washingtonensis* in (northern) California is substantiated by a photo and description under the common name "*Campanella* 'veiny'" in a book on mushrooms of the redwood forests (Siegel and Schwarz 2016). Those authors also noted morphological differences between *C. subdendrophora* and the second species. Additional Mushroom Observer photos of putative f. *washingtonensis*: 396621 (Rockefeller, CA, USA); 268836 (Kalchmeri, CA, USA); 260888 (Ceska, BC); 257120 (Workman, Island Co., WA, USA).

When many spores are observed in mounts of hymenium of f. *washingtonensis*, numerous spores are often and consistently seen as germinated into short germ tubes. When such a germ tube is just emerging, it is easily mistaken for a "bulge" on the abaxial spore wall and maybe what has been termed "helmet-shaped." Moreover, metrics of basidiospores are misleading in f. *washingtonensis*. Above, length and width are merely the measurements of the longest and shortest sides. Spore profiles appear as broadly ovate or rounded-triangular to quadrilateral but artifactually appear bulged only in face view.

Very wide variation in cheilocystidial structures was observed, from tetrapyrgoid (diverticulate axis with inflated apices) through all intermediates to hardly roughened, thick-walled ten pin-shaped cystidia. All these variations are augmented with arboreal structures in which hyphal termini are distinctly *Rameales*-structure. True metuloids are lacking.

A distinction must be made concerning necropigments in *Campanella* generally. Basidiomata of *M. subdendrophora* change from white when fresh to yellow-brown after drying and storage (Redhead 1974), while those of f. *washingtonensis* change from grey-green to dark opaque dark red brick colours.

Specimens examined: CANADA, British Columbia, Vancouver Island, Saanich, Observatory Hill, west slope, 48° 31′ 13.04″ N, 123° 35′ 06.01″ W, 15.XII.2006, coll O. Ceska (as *C. inquilina*); UBC F32449; Saanich Peninsula, Observatory Hill, along paced road above the main gate, 48.520° N, 123.422° W, 7.XI.2007, coll. O. Ceska, F29477 (UBC) [Mushroom Observer 65,050 (see photo under this number)]; along paved road above the main gate, 48.520° N, 123.422° W, 7.XI.2007, coll. O. Ceska (as *T. subdendrophora*), F 29477 (UBC); ridge behind the small dome, 48.526° N, 123.422° W, 26.XI.2012, coll & det. O. Ceska (as *T. subdendrophora*), F25652 (UBC); Observatory Hill, 48.5262° N, 123.422° W, 28.IX.2010, coll O. Ceska, F24577 (UBC); Colwood, Mill Hill CRD Park, close to the parking lot, 48° 27′ 09.56″ N, 123° 28′ 55.50″ W, 20.X.2004, coll. O. Ceska (as *C. inquilina*), F31488 (UBC); off Williams Head Rd., approx. 48° 20′ 31.22″ N, 123° 32′ 30.46″ W, 4.I.2007, coll. O. Ceska (as *T. subdendrophora*), F29060 (UBC); Melchosin, Mary Hill, approx. 48° 20′ 55.26″ N, 123° 33′ 15.33″ W, 28.I.2003, coll O. Ceska (as *T. subdendrophora*), F33841 (UBC); Mushroom Observer 65,789; Melchosin, Mary Hill, approx. 49° 55.26″ N, 123° 33′ 15.33″ W, 28.I.2003, coll. O. Ceska (as *T. subdendrophora*), F 33841 (UBC) Mushroom Observer 65,789. UNITED STATES, Oregon, Lane Co., Florence, Oregon Dunes N.R.A., Sand Dunes Rd., approx. 43° 58′ 58.73″ N, 124° 06′ 02.46″ W, 19.XI.2010, coll. Noah Siegel, det. DE Desjardin, SFSU, s.n.; Tillamook Co., vic. Rockaway Beach, Camp Magruder, 45° 34′ 43.88″ N, 123° 56′ 59.46″ W, 25.X.2008, leg Steve Trudell (SAT 08-299-17), WTU-F-1388. Washington, King Co., Hazel Wolf Wetland, 4.X.2002, coll. B. Matheny & RHP, TFB 9877 (TENN-F-059502); location unknown, 13.II.2001, coll. Y. Edmundsen, s.n., det PB Matheny, WTU-F-12306; vic. Sammamich, Hazel Wolf Wetlands, 47° 35′ 56.73″ N, 122° 00′ 31.38″ W, coll & det PB Matheny (PBM 2011), MT Seidl, 22.X.2000, WTU-F-12308; Magnuson Park, 47.68056–122.25278, 18.XII.2002, coll M. Seidl (MTS 5001), WTU-F-121309 (holotype); [no locality given], date unknown, coll M. Seidl, det PB Matheny, WTU-F-12526.

"Mexicana"

A specimen from Mexico (TFB 8451: TENN-F-055280) was examined for this paper. Basidiomata exhibited green to olive green pigment when fresh, typical of f. *washingtonensis*, but presenting the same meandering gill folds and the same necropigments as *M. subdendrophora*. Encrusted metuloids were present, therefore qualifying the collection for inclusion in Singer's (1975b) *Campanella* sect. *Diplocystidiae*. Basidiomata in this collection exhibited spores from tetrahedral to hump-backed to ellipsoid, but its ITS sequence was a >99% match to Genbank ITS sequences of *M. subdendrophora*.

This is another case of molecular similarity, but morphological dissimilarity to specimens of *C. subdendrophora*.

Metacampanella olivaceonigra(E. Horak) R.H. Petersen, comb. nov. IF901408

Bas.: *Pterospora olivaeonigra* E. Horak 1983 Sydowia 36: 131. IF115313.

≡ *Tetrapyrgos olivaceonigra* (E. Horak) E. Horak 1986 Sydowia 39: 102. IF 412693.

≡ *Campanella olivaceonigra* (E. Horak) May and Wood 1995 Mycotaxon 54: 149. IF 131355.

Type specimen: New Zealand. Mid Canterbury: Craigieburn Range, Broken River, approx. 43° 08′ 51.11″ S, 171° 42′ 32.07″ E, *Dracophyllum* Flat, on stems of *Juncus* sp., 3.IV.1983, coll. E Horak, (PDD 27170 holotype; ZT 2131 isotype).

A diagnosis extracted from Horak's (Horak, E. 1983) German description follows: 1) basidiomata (his Figure 7A) <7 mm broad, circular, conchate to auriform, stipitate; 2) pileus convex, smooth, whitish to light grey with slight olive tint; 3) lamellae converging towards stipe, often anastomosed, concolorous with pileus; 4) stipe < 3 × <1 mm, cylindrical, equal, eccentric to lateral, dark olive overall, dry, solid; caulocystidia as cheilocystidia; 5) odour and taste none; 6) basidiospores (his Figure 7B) 8–10 × 5–6 µm, subtetrahedral, in lateral view often obscurely bulged, smooth, inamyloid; 7) pleurocystidia absent; 8) basidia (his Figure 7D) 25–35 × 7–8 µm, clavate, 4-spored; 9) cheilocystidia (his Figure 7C) 30–70 × 3–7 µm, swollen, capitulate (–8 µm diam.), with or without a few finger-shaped to conical processes, hyaline ("ten pin-shaped"); 10) pileipellis (his Figure 7E) with irregularly coralloid hyphal termini occasionally with a smooth-inflated apex; 11) fruiting on rotting stems of *Juncus novozelandicus* (Monocotyledon) in *Nothofagus* forest.

Commentary: Putative *C. olivaceonigra* was illustrated from Australian material by May (1989). May (1989): "The cap is connected to the apex of the short stem at one side and eventually points away from the substrate. The cap and stem are tinted bluish-green with finely pruinose surfaces. The gills are shallow and often forked and interconnected. The microscopic characters are equally bizarre, the spores being triangular, much like a pastie with a bulge on one side, and the cheilocystidia having medial finger-like protuberances and capitate apices."

May and Wood (1995): Based on Singer's (1986) arrangements and circumscriptions (pre-molecular taxonomy), *Tetrapyrgos olivaceonigra* was more comfortable in *Campanella* than in *Tetrapyrgos*, so the binomial was transferred.

Honan et al. (2015) examined both Australian and New Zealand (type) material, their summary of microscopic characters follows: "Basidiospores (their Figure 4a) 8–11 × 5.5–7 µm, triangular with a rounded lateral bulge, not distinctly tetrahedral, hyaline, inamyloid, thin-walled. Basidia (their Figure 4b) 32–38 × 8–9.5 µm, 4-sterigmate, clavate, clamped. Basidioles clavate. Pleurocystidia absent. Cheilocystidia (their Figure 4c) 40–55 × 3.8–6.5 µm, common, irregularly cylindrical with an apical capitulum 6.5–9.5 µm diam.; central axis with a few knobby diverticula (identical to those as drawn in the protologue), hyaline, thin-walled. Pileipellis a well-developed *Rameales*-structure of diverticulate hyphae; terminal cells entirely diverticulate or a few with a smooth apical capitulum like the cheilocystidia ['terrapyrgoid']. Pileus trama weakly gelatinised. Clamp connections present." " … the triangular spores with a broad lateral bulge (nearly tetrahedral), capitate cheilocystidia with central diverticula, weakly gelatinised tramal tissues, and well-developed stipe (albeit small and eccentric) indicate that it is best accepted in *Tetrapyrgos*." However, the ITS-based phylogeny by Honan et al. (2015) placed *T. olivaceonigra* (EF175541) in a small clade together with *T. subdendrophora* and sister to a clade including *Campanella* spp. and the *Marasmiellus candidus* complex. This study also confirmed placement

Figure 7. *Metacampanella subdendrophora*. Basidiomata on dead grass culms. Standard bar = 10 mm. TFB 5754 (TENN-F-052364).

near *M. subdendrophora* and within *Metacampanella* rather than in *Tetrapyrgos*.

According to Horak (1983), the basidiomata of *P. olivaceonigra* resemble those of Patagonian *P.* (*C.*) *dendrophora* (q.v). The South American basidiomata can be microscopically distinguished from the New Zealand taxon by thick-walled, encrusted metuloids and also ecologically. Likewise, *P. olivaceonigra* was reported as difficult to separate from *P* (*C.*) *subdendrophora* from Canada (q.v.).

Two GenBank sequences deposited as *C. olivaceonigra* (JX444167) and *C.* aff. *olivaceonigra* (JX444166), both from Australia, could not be placed within *Metacampanella* as described here and fall within *Campanella s.s.* They are not included in this study.

Metacampanella sinecystidia R.H. Petersen, sp. nov. Figures S27–S30. IF 901409

Etymology: Without characteristic cystidia.

Holotype: California, San Mateo Co., Junipero Serra Park, 37° 36′ 39.33″ N, 122° 25′ 23.28″ W, 5.III.2005, coll. AH Honan, AHH 120 (SFSU) GenBank EF175521, nrITS).

1) Basidiomata 2–8 mm broad, conchate to convex, laterally stipitate but stipe reduced; 2) pileus matt to minutely felted, here and there chafed to glabrous, when fresh probably white to pale cream to suffused with weak greyish tan, with necropigment dark olive; 3) hymenophore 3–5(–8) radial lamellar folds, often without anastomoses or with a single curved cross-vein; lamellar folds thick, rounded, at high magnification appearing rough (but not barbed); necropigment of lamellar faces and interlamellar areas opaque deep maroon; lamellar edges paler, near ochraceous buff; 4) stipe 0.7–2.5 × 0.4–0.7 mm, columnar, terete, matt, sometimes slightly narrowed below; stipe necropigment deep olive; 5) odour and taste unreported; 6) basidiospores (Figures S27D, S28E) 9–11 × 7.5–8.5 µm, triangular in profile (in adaxial face view appearing more or less quadrilateral); 7) tetrapyrgoid pleurocystidia (Figure S27A–C) locally common; axis 14–32 × 3–5.5 µm, setulae thickly scattered, 2–6.5 × 1–3 µm, often curved towards apex; apical inflation 6–13 × 5–8 µm, obovate to ellipsoid (not globose), smooth, thick-walled (wall –1.0 µm thick, hyaline, subrefringent, seldom with transverse septum between apex and axis); 8) basidia (Figure S28A–C) 4-spored; 9) cheilocystidia as pleurocystidia; ten pin-shaped cystidia lacking; 10) pileipellis a tight *Rameales*-structure; hyphae repent to interwoven, 3.5–5.5 µm diam., thin-walled, beset with thickly scattered diverticula; diverticula 1–5 × 1–2 µm, often bifurcate; tetrapyrgoid dermatocystidia common, similar to tetrapyrgoid pleurocystidia; 11) clamp connections ubiquitous; 12) on dead *Carex* debris; late Autumn-Winter; coastal central California. Subpileipellis and lamellar trama gelatinised. Stipitipellis with tetrapyrgoid cystidia, often lacking inflated apex (Figure S30). Habit: dead stems of *Carex* spp. Habitat and distribution: coastal central California.

Commentary: Morphologically indistinguishable from *M. subdendrophora* except 1) a host preference on dead sedge (*Carex*) debris; 2) ten pin-shaped cheilocystidia lacking; 3) weak pileus suffusion of greyish tan; 4) unique nrITS sequence; 5) known from three collections from western central California.

The holotype specimen was placed in a phylogeny of *Tetrapyrgos* by Honan et al. (2015). Although the specimen was labelled as *T. subdendrophora*, it was termed *Tetrapyrgos* sp. in the paper text. All three SFSU collections of *M. sinecystidia* fruited on sedge; basidiomata of its close phylogenetic relative, *M. subdendrophora*, were also found on this host as well as dead grass and rarely on dicot wood. A close nrITS match was obtained from a dune grass (*Elymus mollis*) endophyte, from the USA Pacific Northwest (David et al. 2016).

Specimens examined: California, Mendocino Co., Jackson State Forest, the road to Mendocino Woodlands off Hwy 408, 38° 34′ 34.63″ N, 123° 19′ 52.66″ W, 22.XI.2003, coll. & det. DE Desjardin (as *T. subdendrophora*), DED 7617 (SFSU); Napa Co., vic. Monticello Dam, along the banks of Putah Creek, 38° 30′ 49.06″ N, 122° 05′ 58.89″ W, 29.I.2005, coll. Fred Stevens, det. AH Honan, AHH 118 (SFSU); San Mateo Co., Junipero Serra Park, 37° 36′ 39.33″ N, 122° 25′ 23.28″ W, 5.III.2005, coll. AH Honan, AHH 120 (SFSU-F-s.n.).

Metacampanella subdendrophora (Redhead) R.H. Petersen, comb. nov. Figures 7, 8, S31–S36. IF 901410

Bas: *Campanella subdendrophora* Redhead 1974 Mycologia 66: 185. IF 310204.

≡ *Pterospora subdendrophora* (Redhead) E. Horak 1983 Sydowia 36: 137. IF 115319.

≡ *Tetrapyrgos subdendrophora* (Redhead) E. Horak 1986 Sydowia 39: 103. IF 131361.

Type specimen: Canada, British Columbia, Vancouver, University Endowed Lands, approx. 49° 16′ 29.73″ N, 123° 14′ 14.71″ W, 15.IX.1972, coll. SA Redhead, holotype, DAOM; Isotype, Field Museum, Chicago, F1017436, and USDA Mycology Herbarium in Beltsville, MD, No. 765673 (BPI). Ex*Typus* culture CCCM: UBC 5060).

There remains no direct evidence that Singer examined Redhead's isotype specimen (at F), although Redhead acknowledged so. My examination of the specimen (collection data above) can be considered a type study. The isotype specimen consists of grass-stem sections, 3–6.5 × 4–5 mm, glued to the interior of a herbarium box; 1) approx. 20 basidiomata (Figures 7 and 8a), not from type collection) attached to substratum; all but one basidiome immature, all laterally stipitate; 2) pileus lens- to spoon-shaped, matt (under 50×), now concolorous with stipe; margin minutely pruinose with cystidia; 3) hymenophore 1–4 radial lamellar folds, eventually with a few anastomosing cross-veins, now "ochraceous tawny" 6C6; 4) stipe < 1 × 0.3–0.7 mm, columnar with furry to pruinose vesture, now pallid tan; 5) odour and taste not recorded; 6) basidiospores (Figure 8b) 7–9 × (5.5–)6–7 µm (E = 1.14–1.64; E^m = 1.25; L^m = 8.2 µm), triangular to rounded-triangular in profile, often bulged to appear rounded-tetrahedral in frontal view, smooth, thin-walled; 7) pleurocystidia of two types: a) gymnopoid (Figure S31), 15–25 × 6–9 µm, axial to once-branched, lobate to roughly diverticulate, clamped; b) tetrapyrgoid pleurocystidia (Figure S32) scattered, 25–27 × 8–11 µm (at widest point), thin-walled throughout, beset with numerous scattered diverticula over proximal portion; apical swelling obovate, thin-walled (easily ruptured under pressure in squash mounts); 8) basidioles (Figure S33A) clavate, clamped; basidia (Figure S33B–E) 20–35 × 7–10 µm, clavate to subcapitulate, 4-sterigmate, obscurely clamped; contents heterogeneous, multigranular; 9) cheilocystidia of two types: a) ten pin-shaped (Figure S34) firm- to thick-walled throughout, usually with clusters of diverticula over proximal portion, with terminal, subglobose inflation 5–9 µm diam., subrefringent (PhC); b) rare ventricose-fusoid cystidial structures, 20–35 × 7–9 µm; contents similar to basidia; 10) superficial pileipellis (Figure S35A) a loose thatch of modified *Rameales*-structure, composed of two elements: a) arboreal diverticulate hyphae (Figure S35B–D) as hyphal termini; hyphae axial to branched, 2.5–3.5 µm diam.; diverticula scattered, hardly distinct from

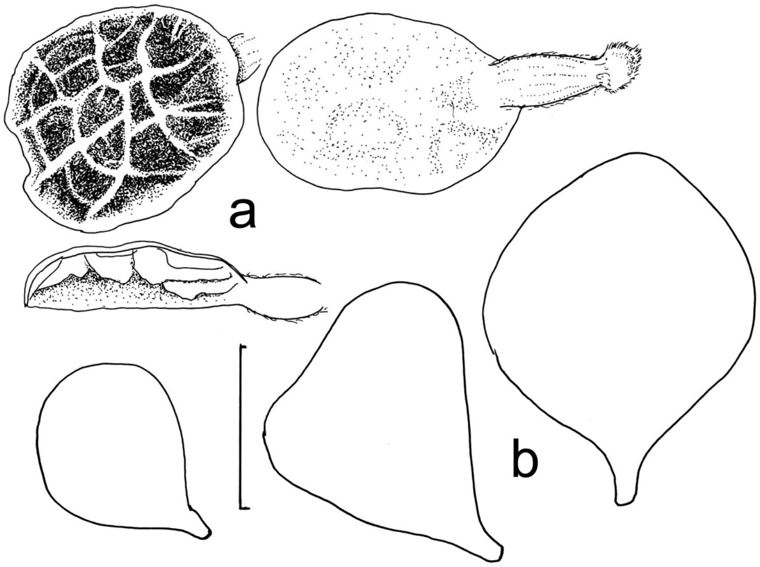


Figure 8. *Metacampanella subdendrophora*. (a) Basidiome from ventral, dorsal and lateral views. (b) Basidiospores. Basidiome is not to scale. Standard bar = 5 µm.

parent hypha, 2–6 × 1–2 µm, firm-walled, not refringent (PhC); b) tetrapyrgoid dermatocystidia (Figure S36), 15–40 × 7–9 µm, axial to once-branched, with thickly scattered diverticula and obovate inflated apex [apical swelling 5–8.5 × 4–7 µm, firm-walled, often subrefringent (PhC), perhaps very slightly pigmented, stramineous; inner pileipellis a loose thatch of rather uniform hyphae 2.5–3.5 µm diam., firm-walled, occasionally gelatinising; 11) fruiting on dead culms of grass (e.g. *Phalaris* sp.); Autumn, southern British Columbia, Canada. In addition: stipe vesture a thatch of two elements: a) axial to arboreal diverticulate hyphae 3–6 µm diam., thin-walled, clamped, hyaline; diverticula 1–8 × 1–2 µm, thickly scattered to erumpent in clusters, knobby to digitate; b) tetrapyrgoid caulocystidia (15–)20–55 × 9–14 µm at widest point, (thick-walled, refringent, often with fusoid proximal portion, clustered diverticula in median portion and obovate to ellipsoid distal portion.

Commentary: Redhead (1974, pp. 185–186) furnished both Latin and English diagnoses. A rearranged diagnosis from Redhead follows. 1) Basidiomata (his Figures 1 and 2) <11.5 mm broad, orbicular to auriform, laterally stipitate, convex, somewhat translucent; necropigment yellowish brown; 2) pileus smooth to minutely canescent, white, unchanging on bruising, dry; 3) hymenophore composed of 1–3 radiating "pseudolamellae" (up to 2 mm distant) with a few anastomosing cross-veins, white; 4) stipe lateral, minutely canescent, usually emerging from a cleft in the pileus, grey; 5) odour negligible; taste not recorded; 6) basidiospores (his Figure 3c) 8–10 × 6–7 µm, triangular, pyramidal or tetrahedron-like, hyaline, inamyloid, sometimes guttulate; 7) "tibiiform cystidia" (his Figure 3a) abundant on pseudolamellae and pileus margin; 8) basidia 28–35 × 7–8 µm, clavate, 4-sterigmate; 9) differentiated cheilocystidia not reported; 10) pileipellis with "dendrophysoid elements" ("tetrapyrgoid cystidia" sensu RHP, see above) (his Figure 3b) forming a "*Ramaeles*"-structure; 11) fruiting on dead culms of grass; Autumn through early Winter; [temperate west coast of North America from California to British Columbia, teste RHP; see also Redhead (1989)].

Redhead (1974) continued: "*Campanella subdendrophora* is distinguished from all other species of *Campanella* except *C. dendrophora* by the presence of dendrophysoid cystidia and angled spores measuring 8–10 × 6–7 µm. From *C. dendrophora* it is distinguished by the lack of metuloids and the whiter color of the pileus." This conclusion depends on a definition of "metuloid," and whether "tibiiform cystidia" qualify as such.

In dealing with the protologue of *C. subdendrophora* (Redhead 1974), it is necessary to note that its publication was preceded by a year Singer's (1975b) floristic monograph, in which "bulged" spores and metuloids were considered infrageneric diagnostic characters. The nomenclature of microscopic characters, therefore, is Redhead's, not Singer's.

Observing *Tetrapyrgos*-like micromorphology in *C. subdendrophora*, Horak first transferred the epithet to *Pterospora* Métrod; Horak (1983); see excellent illustrations), then for nomenclatural reasons, to *Tetrapyrgos* [Horak 1987(1986)], together with several other species that Singer considered under *Campanella*. No tetrahedral basidiospores were observed on the isotype, but spores were regularly rounded-triangular in profile and when frontally viewed appeared rounded-cuboidal. The illustration of spores by Horak (1983) shows a somewhat less pronounced tetrahedral shape than typical of *Tetrapyrgos*.

Cultures were established by Redhead from the type collection of *C. subdendrophora*. One culture was deposited at the University of British Columbia (CCCM: UBC 5060), a second at ATCC (ATCC 42449), and a third at DOAM. Vinnere et al. (2005) sequenced the ATCC culture (NR_171206; AY445121). The published ITS sequence for ATCC 42,449 (NR171206; AY445121) is atypical for *M. subdendrophora* in that it has a 74 bp deletion in the ITS2 region. The original culture from the University of British Columbia (CCCM: UBC 5060) does not have this deletion, nor do any other sequences of *M. subdendrophora*. We were unable to determine the reason for the apparent deletion and ATCC was unwilling to send a culture for re-sequencing to resolve the issue. At this time, CCCM: UBC 5060 should be considered representative of the type. These sequences are found as their small clade within the *C. subdendrophora* complex. nrITS and LSU sequences for CCCM: UBC 5060 have been deposited in GenBank (Table 1). ITS sequences of three California collections identified as

T. subdendrophora SFSU (DED7338; AHH 79, AHH 148), were found to be > 99% matches to CCCM: UBC 5060.

Cultures of a topotype collection of *C. subdendrophora* (TFB 5754, TENN-F-052364) were established at the time of collection, including single-basidiospore isolates. When 11 SBIs were paired in all combinations, a tetrapolar mating system was revealed. Tetrapolar mating systems have been found in other *Campanella* taxa and are to be expected in the future.

In a discussion regarding *C. fimbriata*, Dr. Jerry Cooper (Landcare Research, New Zealand) has written (Public note 35): "*Tetrapyrgos subdendroides* [sic] was described from North America but has been recorded from Australia (including as the synonym *Campanella subdendroides*) and one collection from New Zealand. Sequence data suggest two species with this name. I will stick with the name *Tetrapyrgos olivaceonigra* for New Zealand collections because they become glaucous with age, a feature not present for *T. subdendroides*." These sequences are found within the *Metacampanella* complex as *M. olivaceonigra* (Figure 3).

Illustrations and descriptions of *M. subdendrophora* can be found in Siegel & Schwarz (2016: 403) and Desjardin et al. (2015: 184–185); additional photos are available from MushroomObserver: 444572 (Rockefeller, CA, USA); 443698 (Rockefeller, CA, USA; GenBank MW433846).

Bullakh (2023) reported *M. subdendrophora* (as *Tetrapyrgos*) from the Russian Far East, based on morphological similarity.

A study of sequences (GU910532 and others) derived from herbivore (Prairie Dog) dung and deposited in GenBank as "uncultured Agaricales" were found to be close matches to members of the *M. subdendrophora* clade. The authors (Herrera et al. 2011) conjectured that Prairie dogs' diet may include grassroots and their endophytes. Fruiting of members of the *M. subdendrophora* complex fruiting on grass would make such conjecture justified.

Specimens examined: CANADA, British Columbia, Vancouver, University Endowed Lands, 49° 16′ 25.53″ N, 123° 14′ 56.13″ W, 6.X.1992, coll Paul Kroeger + RHP, TFB 5754 (TENN-F-052364); Vancouver, UBC Campus, 22.IX.1972, coll SA Redhead. F1017436 (F; isotype); Vancouver Island, Victoria, Saanich Peninsula, Observatory Hill, 48.5263° N, 123.422° W, 5.XI.2008, coll. O. Ceska & Ian Gibson, F29911 (UBC). Mushroom Observer 166516; same location, 20. X.2006, coll O. Ceska, F28919 (UBC); Queen Charlotte Islands, Kunga Island, Gwaii Haanas Nat. Park, 52° 46′ N, 131° 34′ W, 9.IX.2003, coll. P. Kroeger, Bryce Kendrick, Clint Kendrick, Judson Brown, det. P. Kroeger (PK2821), F18283 (UBC). MEXICO, Est. Mexico, Agua Bendita (Rte. 1), 19° 21′ 31.52″ N, 99° 18′ 30.19″ W, 14.VII.1996, coll RHP, TFB 8451 (TENN-F-055280). UNITED STATES, California, Mendocino Co., Jackson State Forest, jct of Hwy 408 & 409, 39° 22′ 18.42″ N, 123° 42′ 14.94″ W, 23.XI.2002, coll. F. Stevens & B.A. Perry, det. DE Desjardin (as *Tetrapyrgos subdendrophora*), DED 7493 (SFSU s.n.); Jackson State Forest, the road to Mendocino Woodland Camp off Hwy 408, approx. 39° 19′ 36.21″ N, 123° 44′ 15.86″ W, 19.XI.2005, coll. & det. AH Honan, AHH 149 (SFSU); San Mateo Co., Junipero Serra Park, 37° 36′ 39.33″ N, 122° 25′ 23.28″ W, 22.II.2005, coll. Fred Stevens, det. A.H. Honan, AHH 119 (SFSU); same data, AHH 79 (SFSU); Montara State Beach, NcNee Ranch, beginning of the trail to Montara Mountain, approx. 37° 33′ 14.33″ N, 122° 30′ 29.99″ W, 12.XI.2005, coll. & det. AH Honan, AHH 148 (SFSU); Sonoma Co., Salt Point State Park, Woodside Campground, 38° 34′ 34.63″ N, 123° 19′ 52.66″ W, 11. CI.2001, coll. & det. DE Desjardin, DED 7338 (SFSU); Oregon, Coos Co., Bullard's Beach, approx. 43° 07′ 32.15″ N, 124° 25′ 31.64″ W, 25.XI.2005, coll & det. AH. Honan, AHH 152 (SFSU). Citation of note: California, Humboldt Co., Prairie Creek Redwoods State Park, 41° 24′ 07.26″ N, 124° 02′ 32.83″ W, 26. XII.2020, A Rockefeller, MushroomObserver 433846; collection not preserved.

4. Discussion

Marasmiaceae, a family within the Agaricales comprises approximately 50 genera and close to 2,000 species (Kirk et al. 2008). Circumscription of genera and species within Marasmiaceae, however, is not always clear. Matheny et al. (2006) presented a multigene phylogeny including the Marasmiaceae that places *Campanella* sp. in the same clade as *Tetrapyrgos* (+ *Metacampanella* – this manuscript) *subdendrophora* and Kirk et al. (2008) considered *Tetrapyrgos* and *Campanella* to be synonymous. Honan et al. (2015) examined

Tetrapyrgos, recognising nine species in *Tetrapyrgos* based on molecular and morphological data and noting an additional seven species as belonging to *Campanella* with uncertain taxonomic placement. With the redescription and epitypification of the type species of *Tetrapyrgos* and *Campanella* (Desjardin et al. 2017), it became possible to more clearly evaluate species placed in either *Tetrapyrgos* or *Campanella*. In this report, we show that *Tetrapyrgos* and *Campanella* are phylogenetically distinct and separate from a group of taxa designated here as *Metacampanella*.

Acknowledgments

We extend thanks to Dr. Jerry Cooper (New Zealand) for furnishing his phylogenies of this fungal group and the use of his sequences of *M. olivaceonigra*. Thanks also to Dr. Dennis Desjardin for expediting the loan of SFSU specimens cited herein. Dr. Scott Redhead (DAOM) furnished data on type cultures of *M. subdendrophora*. We thank anonymous reviewers for their meticulous reviews.

Disclosure statement

No potential conflict of interest was reported by the author(s).

References

Bullakh EM. 2023. New records from the genera Campanella, Tetrapyrgos and marasmiellus from Russian Far East. Mykologie and Phytopathologie. 37:23–31.

Cubeta MA, Echandi E, Abernethy T, Vilgalys R. 1991. Characterization of anastomosis groups of binucleate *Rhizoctonia* species using restriction analysis of an amplified ribosomal RNA gene. Mol Plant Pathol. 81(11):1395–1400. doi: 10.1094/phyto-81-1395.

David AS, Seabloom EW, May G. 2016. Plant host species and geographic distance affect the structure of aboveground fungal symbiont communities, and environmental filtering affects belowground communities in a coastal dune ecosystem. Microb Ecol. 71(4):912–926. doi: 10.1007/s00248-015-0712-6.

Desjardin DE, Perry BA, Shay JE, Newman DS, Randrianjohany E. 2017. The type species of tetrapyrgos and *Campanella* (Basidiomycota, Agaricales) are redescribed and epitypified. Mycosphere. 8(8):977–985. doi: 10.5943/mycosphere/8/8/1.

Gardes M, Bruns TD. 1996. Community structure of ectomycorrhizal fungi in a *Pinus muricata* forest: Above- and below-ground views. Can J Bot. 74(10):1572–1583. doi: 10.1139/b96-190.

Geneious. 2017. Geneious version 11.0.3 created by Biomatters. Available from http://www.geneious.com/.

Herrera JP, Khidir R, Khidir HH. 2011. Molecular characterization of coprophilous fungal communities reveals sequences related to root-associated fungal endophytes. Microb Ecol. 61(2):239–244. doi: 10.1007/s00248-010-9744-0.

Honan AH, Desjardin DE, Perry BA, Baroni HE, Baroni TJ. 2015. Towards a better understanding of *Tetrapyrgos* (Basidiomycota, Agaricales): New species, type studies, and phylogenetic inferences. Phytotaxa. 231(2):101–132. doi: 10.11646/phytotaxa.231.2.1.

Horak E. 1983a. Mycogeography in the South Pacific region: Agaricales, Boletales. Aust J Bot. 10(10):1–42. doi: 10.1071/BT8310001.

Horak E. 1983b. Neufunde und Bemerkungen zu einem emendierten Gattungskonzept von Pterospora Métrod (Agaricales). Sydowia. 36:125–138.

Horak E. 1987 (1986). *Tetrapyrgos* Horak (nom. et gen. nov.) replacing *Pterospora* Métrod (1949; nom. preocc.). Sydowia. 39:101–103.

Huelsenbeck J, Ronquist F. 2001. MrBayes: Bayesian inference of phylogenetic trees. Bioinformatics. 17(8):754–755. doi: 10.1093/bioinformatics/17.8.754.

Hughes KW, Case A, Matheny PB, Kivlin S, Petersen RH, Miller AN, Iturriaga T. 2020. Secret lifestyles of pyrophilous fungi in the genus *Sphaerosporella*. Am J Bot. 107(6):876–885. doi: 10.1002/ajb2.1482.

Kerekes JF, Desjardin DE. 2009. A monograph of the genera *Crinipellis* and *Moniliophthora* from Southeast Asia including a molecular phylogeny of the nrITS region. Fungal Divers. 37:101–152.

Kirk PM, Cannon PF, Minter DW, Stalpers JA. 2008. Dictionary of the fungi. 19th. Wallingford, CABI. 10.1016/j.mycres.2009.07.003

Komura DL, Oliveira JJ, Moncalvo J, Margaritesco S, Zartman C. 2020. Six new species of *Tetrapyrgos* (Basidiomycota, Agaricales, Marasmiaceae) from the Brazilian Amazon. Phytotaxa. 440:193–214. doi: 10.11646/phytotaxa.440.3.2.

Kornerup A, Wanscher JH. 1967. Methuen handbook of colour. 2nd revised ed. London, UK: Methuen Co.

Kühner R, Romagnesi H. 1953. Flore analytique des champignons supérieurs. Paris, France: Masson et Cie.

Læssoe T, Petersen JH. 2019. Fungi of temperate Europe. Princeton, NJ, USA: Princeton University Press.

Malençon G, Bertault R. 1970. Flore des champignons superieurs du Maroc I. Travaux de l'Institut scientifique chérifien et de la Faculté des Sciences de Rabat. Ser Bot Biol Veg. 32:1–604.

Matheny PB, Curtis JM, Hofstetter V, Aime MC, Moncalvo JM, Ge ZW, Yang ZL, Slot JC, Ammirati JF, Baroni TJ, et al. 2006. Major clades of Agaricales: A multilocus phylogenetic overview. Mycologia. 98(6):982–995. doi:10.1080/15572536.2006.11832627.

May T. 1989. Report of F.N.C.V. Fungal Excursions 1986–1988. Vict Nat. 106:48–58.

May TW, Wood AE. 1995. Nomenclatural notes on Australian Macrofungi. Mycotaxon. 54:147–150.

Moncalvo JM, Lutzoni FM, Rehner SA, Johnson J, Vilgalys R. 2000. Phylogenetic relationships of agaric fungi based on nuclear large subunit ribosomal DNA sequences. Syst Biol. 49(2):278–305. doi: 10.1093/sysbio/49.2.278.

Moser M, Peintner U. 2007. Colour atlas of basidiomycetes. Vol. 24. Verlag, Germany: Lieferungen, Spectrum Acaden.

Nakasone KK, Hibbett DS, Goranova G. 2009. *Neocampanella*, a new corticioid fungal genus, and a note on *Dendrothele bispora*. Botany 87(9):875–882. doi: 10.1139/B09-046.

Nguyen LT, Schmidt HA, von Haeseler A, Minh BQ. 2014. IQ-TREE: A fast and effective stochastic algorithm for estimating Maximum-Likelihood Phylogenies. Mol Biol Evol. 32 (1):268–274. doi: 10.1093/molbev/msu300.

Nguyen LT, Schmidt HA, von Haeseler A, Minh BQ. 2015. IQ-TREE: a fast and effective stochastic algorithm for estimating maximum likelihood phylogenies. Mol Biol Evol. 32 (1):268–274. doi: 10.1093/molbev/msu300.

Oliveira JJS, Vargas-Isla R, Cabral TS, Rodrigues DP, Ishikawa NK. 2019. Progress on the phylogeny of the Omphalotaceae: *Gymnopus* s. str., *Marasmiellus* s. str., *Paragymnopus* gen. nov. and *Pusillomyces* gen. nov. Mycol Prog. 18(5):713–739. doi: 10.1007/s11557-019-01483-5.

Petersen RH, Hughes KW. 2021. *Collybiopsis* and its type species, *Co. ramealis*. Mycotaxon. 136(2):263–349. doi: 10.5248/136.263.

Petersen RH, Hughes KW, Redhead SA, Psurtseva N, Methven A. 1999. Mating systems in the Xerulaceae (Agaricales, Basidiomycotina, Flammulina). Mycoscience. 40(5):411–426. doi: 10.1007/BF02464396.

Redhead SA. 1974. A new species of *Campanella* from North America. Mycologia. 6(1):183–187. doi: 10.1080/00275514.1974.12019591.

Redhead SA. 1981. Agaricales on wetland monocotyledoneae in Canada. Can J Bot. 59(5):574–589. doi: 10.1139/b81-083.

Redhead SA. 1984. *Arrhenia* and *Rimbachia*, expanded generic concepts, and a reevaluation of *Leptoglossum* with emphasis on muscicolous north American Taxa. Can J Bot. 62 (5):865–892. doi: 10.1139/b84-126.

Redhead SA. 1989. A biogeographical overview of the Canadian mushroom flora. Can J Bot. 67(10):3003–3062. doi: 10.1139/b89-384.

Ridgway R. 1912. Color standards and color nomenclature. Washington, DC., USA: Public-Private.

Romagnesi H. 1981 (1980). Deux agarics pleurotelloides a hyménium plissé. Bull Trimest Soc Mycol Fr. 96:423–428.

Saitou N, Nei M. 1987. The neighbor-joining method: A new method for reconstructing phylogenetic trees. Mol Biol Evol. 4(4):406–425. doi: 10.1093/oxfordjournals.molbev.a040454.

Schoch CL, Seifert KA, Huhndorf S, Robert V, Spouge JL, Levesque CA, Chen W, Consortium FB, Voigt K, Crous PW. 2012. Nuclear ribosomal internal transcribed spacer (ITS) region as a universal DNA barcode marker for fungi. PNAS. 109(16):6241–6246. doi: 10.1073/pnas.1117018109.

Siegel N, Schwarz C. 2016. Mushrooms of the Redwood Coast: A comprehensive Guide to the fungi of Coastal Northern California. Emeryville, CA, USA: Ten Speed Press.

Singer R. 1955. New and interesting species of Basidiomycetes. IV. Mycologia. 47(5):763–777. doi: 10.1080/00275514.1955.12024492.

Singer R. 1975a. The agaricales in Modern Taxonomy. Chicago, J: Cramer.

Singer R. 1975b. The neotropical species of *Campanella* and *Aphyllotus* with notes on some species of *Marasmiellus*. Nova Hedwigia. 26L:847–895.

Singer R. 1986. The agaricales in Modern taxonomy. 4th ed. Koenigstein, Germany: Koeltz Scientific Books.

Singer R, Hausknecht A. 1990. Some interesting agarics from eastern Austria. Plant Syst Evol. 170(3–4):133–150. doi: 10.1007/BF00937699.

Trifinopoulos J, Nguyen LVH, Minh A, Minh BQ. 2016. W-IQ-TREE: A fast online phylogenetic tool for maximum likelihood analysis. Nucleic Acids Res. 44(W1):W232–W235. doi: 10.1093/nar/gkw256.

Vinnere O, Fatehi J, Sivasithamparam K, Gerhardson B. 2005. A new plant pathogenic sterile white Basidiomycete from Australia. Eur J Plant Pathol. 112 (1):63–77. doi: 10.1007/s10658-005-2191-y.

White TJ, Arnheim N, Erlich HA. 1989. The polymerase chain reaction. Trends Genet. 5:185–189. doi: 10.1016/0168-9525(89)90073-5.

Wilson AW, Desjardin DE. 2005. Phylogenetic relationships in the gymnopoid and marasmioid fungi (Basidiomycetes, euagarics clade). Mycologia. 97:667–679. doi: 10.1080/15572536.2006.11832797.